THE WILSON ORNITHOLOGICAL SOCIETY
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The Wilson Ornithological Society

Founded December 3, 1888

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President—Mary H. Clench, 1408 Oak Hollow Drive, Dickinson, Texas 77539.
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Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.
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The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for The Wilson Bulletin. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library’s holdings was printed in the September 1952 issue of The Wilson Bulletin and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

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THE PRESIDENT’S PAGE

When a society such as ours reaches its 100th year, it is inevitably a time of reflection—looking back at our history, anticipating our Centennial celebration in Philadelphia in June, and thinking about the future. Hence this resurrection of “The President’s Page,” an occasional feature of past issues of The Wilson Bulletin. In this instance I want to outline for our members the plans that are afoot for the next few months and to express some of our hopes for the future.

In 1988, the Wilson Ornithological Society will be chronicled by three past presidents, Jerry Jackson, George Hall, and Harold Mayfield, who are hard at work preparing a detailed history that we plan to distribute at the Centennial meeting as well as publish in The Wilson Bulletin for those who can’t make it to Philadelphia. These three gentlemen are digging deeply into our past, and their efforts should make fascinating reading. At the Utica meeting last spring we decided it would be as accurate and honest a history as they could make it, not just a eulogy of the society’s growth and triumphs over the years. Those, of course, will be included but the “warts” will be there, too.

The Centennial meeting will be held at Rosemont College in suburban Philadelphia. The officers and council wanted to have this historic meeting near Alexander Wilson’s “home town,” and Frank Gill was good enough to agree to host it. We appreciate Frank’s dedication to his field by running a second major meeting (he chaired the A.O.U. local committee in 1976). Most of us think that one per career is enough! The main meeting will be held on the Rosemont campus and should be affordable for most members. We particularly hope that we’ll have a fine turnout of students. We’re going to try to enhance the Wilson Prize—the award given for the best student paper at an annual meeting. And for the first time, the Society will subsidize banquet tickets for students competing for the prize—so the winner will be at the banquet to receive his or her congratulations (and check).

As planned by Jerry Jackson and the Centennial Committee, the Centennial meeting will be a day longer than past annual meetings, beginning on Wednesday night, June 8, and running through Sunday, June 12. Thursday and Saturday will be spent at Rosemont, for scientific paper sessions (arranged by Dick Banks and his committee), receptions, exhibits, morning field trips, banquet, etc., and on Sunday there will be day-long trips, still being planned at this writing. Friday, June 10, will be Centennial Day when the attendees will be taken by bus to the Academy of Natural Sciences of Philadelphia, for a day of celebration. Frank Gill and his
committee are organizing an international symposium on the Paridae (chickadees, titmice, and allies), a particularly interesting and world-wide group of birds that has been studied intensively on both sides of the Atlantic. Distinguished speakers will conduct the symposium and workshops, and we will have other Centennial activities as well—special exhibits relating to the Society’s history and Alexander Wilson (his collection of specimens is at the Academy) and trips to parts of historic Philadelphia. In the evening we will have a gala celebration and then return to Rosemont. It should be a memorable day.

Afterwards begin our second 100 years. The Society undoubtedly will see changes—improvements in our journal and the other things we do. My particular concerns in thinking about the years to come are two-fold. The first is membership, keeping our numbers growing in pace with the increasing numbers of people concerned with the natural world, particularly birds, their study, and their conservation. The second is the financial capability to carry out the traditional goals of the Society, publishing a quality journal, supporting field-based research (particularly by the generations of young ornithologists to come), and contributing to avian conservation efforts. All of this takes money. Each year when the officers and council meet, the Society’s finances are discussed, dissected, and squeezed, to try to make each dollar go as far toward our goals as possible. But there is never enough to do all we want. I hope that in the next few years we can build our endowment so that the annual budget planning will not be the somewhat painful process it is now. We want to do more. Wilson members have proved that they can be generous when asked. Response to the Centennial Fund has been gratifying, so with future gifts and bequests we can go toward our bicentennial a stronger society.

MARY H. CLENCH
Mourning Warbler (Oporornis philadelphia, top),
Common Yellowthroat (Geothlypis trichas, bottom),
and hybrid O. philadelphia X G. trichas (YPM 6958, middle).
All are males in first basic plumage. Watercolor and gouache by David A. Sibley.
A HYBRID *OPORORNIS PHILADELPHIA* × *GEOTHLYPIS TRICHAS*, WITH COMMENTS ON THE TAXONOMIC INTERPRETATION AND EVOLUTIONARY SIGNIFICANCE OF INTERGENERIC HYBRIDIZATION

ANTHONY H. BLEDSOE

Abstract. — A wood-warbler collected in 1955 near New Haven, Connecticut, originally identified as *Oporornis philadelphia*, proves to be a hybrid *O. philadelphia* × *Geothlypis trichas*. The hybrid indicates the existence of substantial genetic compatibility between the parental species. Two different classifications of *Oporornis* and *Geothlypis* are consistent with the genetic similarity implied by the hybrid, but in the absence of phylogenetic evidence, the provisional continued recognition of *Oporornis* and *Geothlypis* is suggested on phenetic and nomenclatural grounds. Although the number of intergeneric paruline hybrids (10) is greater than the number of intrageneric hybrids (4, other than between species-pairs), the inference that hybridization is more common between phylogenetically distant species than between closer relatives is not warranted because several of the genera involved in the hybridizations are probably paraphyletic. Received 17 Dec. 1984, accepted 19 Jan. 1987.

On 21 September 1955, the late David H. Parsons, formerly Chief Preparator at the Peabody Museum of Natural History, Yale University, collected an unusual wood-warbler in a scrubby clearing in deciduous woodland at West Rock, Hamden, Connecticut, 4 km NW of the New Haven Green, New Haven. The specimen was cataloged as a Mourning Warbler (*Oporornis philadelphia*) in the ornithological collection of the Peabody Museum (YPM 6958). David A. Sibley brought the specimen to my attention and suggested that it was not a Mourning Warbler but a hybrid between *Oporornis philadelphia* and the Common Yellowthroat

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(Geothlypis trichas). A detailed study of the specimen, presented here, confirms this diagnosis.

DESCRIPTIONS

I compared the specimen with series of fall adult male and first-year male specimens of O. philadelphia and G. trichas at the Peabody Museum of Natural History (Yale University), the American Museum of Natural History, and the University of Kansas Museum of Natural History. The specimen resembles a fall adult male Mourning Warbler, but its crown is brownish-olive instead of gray, its back brownish-olive instead of greenish, and its throat white instead of gray. The label indicates that the specimen is a male (testes not enlarged). The age of the specimen was not determined during its preparation, but it appears to be a first-year bird because remnants of natal down adhere to the tips of the rectrices. First-year males of O. philadelphia and G. trichas are variable, but differ from adults primarily in the colors of the head and breast. Typical first-year male O. philadelphia have a yellowish-white chin, limited black on the upper breast, no blackish neutral gray on the lores, a broken buffy orbital ring, and brownish-olive feathers on the crown and face. Some individuals lack black on the breast and have a yellow throat; others approach the fall adult male condition. First-year male G. trichas have traces of black in the malar and auricular regions, varying from a few feathers to a nearly complete “mask,” but usually have little (if any) black on the forehead or gray on the head. The orbital ring is buffy to white.

The hybrid and the first-year male fall plumages of O. philadelphia and G. trichas are described below. The color terminology is that of Smith (1975). Characters that do not differ among O. philadelphia, G. trichas, and the hybrid are omitted from the descriptions.

Forehead to nape. — philadelphia: olive-brown. trichas: forehead brownish-olive with a few (rarely many) jet black feathers with medium neutral gray tips, sometimes bordered caudally by a band of light neutral gray feathers (jet black basally) joining the superciliary line just above the eye. Top of head and hindneck brownish-olive concealing olive-gray midportions and dark neutral gray bases of feathers. Hybrid: brownish-olive (slightly grayer than in trichas) concealing medium neutral gray midportions and jet black bases of the forehead feathers and medium neutral gray midportions and bases of feathers of the rest of the crown and hindneck.


Rump and upper tail coverts. — philadelphia: auxiliary olive-green (color 47) but slightly greener than back. trichas: auxiliary olive-green (color 48), browner than in philadelphia and not perceptibly greener than back. Hybrid: greenish-olive with a brown tinge, slightly greener than back.

Face pattern. — philadelphia: face olive-brown (most individuals) to medium neutral gray (rarely). trichas: face brownish-olive (most individuals) to jet black (rarely), the feathers usually tipped with light neutral gray; superciliary line brownish-olive (in birds with brownish-olive faces) to jet black rostral of eye with light neutral gray caudal of eye and bordering car coverts (in birds with black faces). Hybrid: lores blackish neutral gray, cheek feathers and car coverts dark neutral gray, and feathers of malar stripe jet black tipped with (and partly concealed by) medium neutral gray, giving the appearance of a faint “mask”; superciliary line medium neutral gray; feathers surrounding orbit blackish neutral gray basally, faintly tipped with medium neutral gray.

Chin and throat. — philadelphia: pale yellowish-white to pale spectrum yellow, bases of feathers blackish neutral gray. trichas: spectrum yellow concealing whitish (rarely blackish
neutral gray) bases of feathers. **Hybrid:** white with a few flecks of blackish neutral gray; feathers at edge of throat tipped with very pale spectrum yellow; bases of lower throat feathers blackish neutral gray.

**Breast.** —**philadelphia:** feathers jet black with medium neutral gray and olive-brown tips; extent of tipping variable, but black usually fully concealed on upper breast, less concealed on lower breast. **trichas:** spectrum yellow, usually tinged with orange-yellow, occasionally with brownish-olive as well; bases of feathers blackish neutral gray. **Hybrid:** upper edge of breast white with blackish neutral gray flecks and very pale spectrum yellow tips (more extensive than in chin and throat); lower breast feathers jet black and variously tipped with white, light neutral gray, and pale sulphur yellow partly concealing black; edges of lower breast citrine slightly tinged with orange-yellow.

**Belly.** —**philadelphia:** spectrum yellow. **trichas:** variable, from white with a faint brown tinge (most individuals) to pale sulphur yellow (rarely). **Hybrid:** spectrum yellow, slightly paler than in **philadelphia.**

**Flanks.** —**philadelphia:** yellowish olive-green, limited in extent and not approaching midline. **trichas:** grayish-olive with a brown tinge, closely approaching midline. **Hybrid:** auxiliary olive-green (color 48), extent as in **trichas.**

**Undertail coverts.** —**philadelphia:** spectrum yellow, centers of feathers occasionally auxiliary olive-green (color 47). **trichas:** variable, from yellowish olive-green to spectrum yellow; centers of feathers occasionally yellowish olive-green, edges spectrum yellow. **Hybrid:** light spectrum yellow, centers of feathers auxiliary olive-green (color 47).

**Relative lengths of primaries.** —**philadelphia:** primary 6 usually shorter than primaries 7, 8, and 9 (outermost) but longer than primary 5; occasionally primary 6 nearly or quite as long as the longest of the three outer primaries. **trichas:** primary 6 longer than primaries 9 and 5, occasionally longer than primaries 7 and 8. **Hybrid:** primaries, in order of decreasing length: 6, 7 = 8, 9, 5.

**Tail shape.** —**Philadelphia:** slightly rounded, rectrices more or less evenly graduated in 1.0–1.5 mm increments but rectrices 3 and 2 nearly (or quite) equal. **trichas:** rounded, rectrix 6 (outermost) ca 3 mm shorter than rectrix 5, rectrices 5, 4, and 3 more or less evenly graduated in 0.5–1.0 mm increments, rectrix 2 usually less than 0.5 mm shorter than rectrix 1. **Hybrid:** distances between tips of rectrices are 2.2 mm (rectrices 6 and 5), 1.4 mm (5 and 4), 1.2 mm (4 and 3), 0.5 mm (3 and 2), and 0.2 mm (2 and 1).

**MEASUREMENTS**

The linear dimensions of the hybrid (in mm, measured with dividers and a dial caliper) are: flattened wing = 60.5, tail = 50.8, bill from rostral edge of nares to tip = 8.0, tarsus = 20.7. The linear dimensions (mm) of 15 specimens each of the parental species are (range, with mean in parentheses): **philadelphia.** —wing, 62.0–67.9 (64.0); tail, 49.0–56.5 (52.6); bill, 7.0–8.3 (7.8); tarsus, 19.3–22.2 (20.5); **trichas.** —wing, 53.5–60.0 (56.7); tail, 48.5–54.5 (51.5); bill, 7.4–8.2 (7.8); tarsus, 18.5–20.9 (19.6). Except for wing length, the linear dimensions of the parental species overlap, and the hybrid’s dimensions fall in the range of overlap. The wing length of the hybrid lies outside of, but between the ranges of, wing lengths of the parental species. The difference between the lengths of the wing and tail of the hybrid is 9.7 mm, falling outside of, but between the ranges of, wing-minus-tail values of **philadelphia** (Lanyon and Bull 1967) and of the 15 specimens of **G. trichas brachidactylus** measured in this study. The wing and tail measurements of **G. trichas campicola** (the other subspecies of Common Yellowthroat broadly sympatric with **philadelphia**) collected east of the Rocky Mountains are similar to those of **G. trichas brachidactylus** (Behle and Aldrich 1947).
DIAGNOSIS

The color pattern and the shapes of the bill, wing, and tail of the hybrid rule out as possible parental species all wood-warblers except *G. trichas* and the species of *Oporornis*. The colors of the head and breast rule out the Kentucky Warbler (*O. formosus*), and the black breast feathers argue against Connecticut Warbler (*O. agilis*) parentage. The pattern of black on the breast feathers argues against MacGillivray’s Warbler (*O. tolmiei*) parentage, as does to some degree the locality of collection.

The hybrid specimen is intermediate between *O. philadelphia* and *G. trichas* in the colors of the crown, back, and flanks, the patterns of the face and breast, the shape of the tail, and the wing-minus-tail value. A few parental characters (e.g., wing length and shape of *trichas*, continuous yellow on the belly of *philadelphia*) have been inherited nearly intact. The white chin and throat of the hybrid are abnormal for first-year males of either species; however, the parental throat colors are partially expressed, as the black flecks, occasional pale yellow tips, and blackish bases of the throat feathers of the hybrid indicate.

THE TAXONOMIC HISTORY OF *OPORORNIS* AND *GEOPTHLYPS*

In 1858, Baird classified the Mourning and MacGillivray’s warblers with the yellowthroats in *Geothlypis*. Baird (1858) nonetheless recognized the differences between the philadelphia-tolmiei and yellowthroat groups, which he divided into separate sections of *Geothlypis*. In the same volume Baird erected *Oporornis* for the Connecticut Warbler and the Kentucky Warbler.

Ridgway (1887) acknowledged the similarities between philadelphia, tolmiei, and agilis by placing them in *Oporornis* but at the same time reflected their similarities to the yellowthroats in maintaining *Oporornis* as a subgenus of *Geothlypis*. In 1902, Ridgway gave *Oporornis* full generic status, and since the third edition, the American Ornithologists’ Union’s “Check-list of North American Birds” (1910, 1931, 1957, 1983) has employed Ridgway’s arrangement (1902).

It is not clear whether Ridgway considered *Oporornis* and *Geothlypis* to be closely related (he placed four quite different genera between them), but other workers (Coues 1903, Griscom and Sprunt 1957, Mayr and Short 1970) clearly have. Lowery and Monroe (1968) merged *Oporornis* and *Geothlypis*.

The classifications of these workers were derived primarily from comparison of such phenotypic characters as the proportions of the wing, leg, tail, and undertail coverts (e.g., Baird 1858, Ridgway 1902:621, Griscom in Griscom and Sprunt 1957) and song patterns (e.g., Griscom in Griscom and Sprunt 1957). Such general similarities are shared among members of several paruline genera yet are variable within any particular genus, so that the variety of treatments of *Oporornis* and *Geothlypis* is not surprising. Macromolecular and cladistic morphological data have not been informative, largely because they either pertain to the higher relationships...
of the parulines (e.g., Bledsoe 1987) or are limited in extent (e.g., Raikow 1978, Avise et al. 1980). With respect to the latter studies, Raikow (1978) reported that *O. tolmiei* shares a derived condition of the *M. pronator profundus* with many paruline genera but not with *Geothlypis*, while Avise et al. (1980), using protein electrophoretic data, found that *O. formosus* and *G. trichas* (the only species of these genera studied) cluster tightly with one another.

**DISCUSSION**

The production of a hybrid between *O. philadelphia* and *G. trichas* provides strong evidence of substantial genetic compatibility between the parental species. The existence of genetic compatibility between these species and between the parental species of other paruline hybrids reviewed below indicates that parulines retain the ability to produce hybrids long after genetic isolation. These hybrids offer additional evidence that such compatibility is a general phenomenon among birds, as Prager and Wilson (1975) have suggested.

Recent classifications of *O. philadelphia* and *G. trichas* are consistent with the genetic similarity implied by the hybrid between them, either in merging *Oporornis* and *Geothlypis* (e.g., Lowery and Monroe 1968) or in listing them next to one another in linear sequence (e.g., Wolters 1982, A.O.U. 1983). Neither the evidence of hybridization nor other lines of evidence, however, resolves the phylogenetic relationships among these and other wood-warblers.

In the absence of phylogenetic information, the choice between classifications is left to rely on such provisional criteria as phenetic similarity and nomenclatural stability. In that *Oporornis* and *Geothlypis* (sensu A.O.U. 1983) are distinct from one another in their overall proportions and color patterns, and because maintenance of each genus conserves the scientific names now commonly in use, I suggest continued recognition of *Oporornis* and *Geothlypis* (sensu A.O.U. 1983).

The hybrid *O. philadelphia* × *G. trichas* is the tenth known intergeneric hybrid among wood-warblers. The others are: *Vermivora pinus* × *O. formosus* (two specimens, see Graves, in press), *Parula americana* × *Setophaga ruticilla* (Burleigh 1944), *P. americana* × *Dendroica dominica* (two specimens, see Sutton 1942), *D. fusca* × *Mniotilta varia* (Parkes 1983), *D. striata* (or possibly *D. tigrina*, Parkes 1978) × *Seiurus novaboracensis* (Short and Robbins 1967), *D. cerulea* × *M. varia* (Parkes 1978), and *Wilsonia canadensis* × *O. philadelphia* (United States National Museum, K. C. Parkes, pers. comm.). In addition, 4 intrageneric hybrid specimens (other than between primarily allopatrically distributed members of superspecies) are known: *V. ruficapilla* × *V. peregrina* (Carnegie

Parkes (1961, 1978) interpreted the relative numbers of inter- and intrageneric paruline hybrids to mean that hybridization between distantly related species is more common than between closely related species (other than members of superspecies). Banks and Johnson (1961) reached a similar conclusion for hummingbirds. These inferences rely on the assumption that all of the members of each genus involved share a more recent common ancestor with one another than with species in other genera; that is, the genera must be monophyletic (=holophyletic of Ashlock 1971).

Unfortunately, most avian systematists have constructed genera with an “evolutionary” approach (cf. Mayr 1981) based on perceived adaptive distinctiveness as well as on phylogenetic relationship. As a result, paraphyletic genera are likely to be common in current avian classifications. For instance, avian systematists have perceived the Black-and-white Warbler (*Mniotilta varia*) as adaptively distinctive and have thus placed it in a monotypic genus. However, its plumages, anatomy, and songs suggest that its sister group might lie among the living species of *Dendroica*. Few would suggest that it is the sister group of all living *Dendroica*. Unless it is, the possibility exists for the parental species of a *Mniotilta × Dendroica* hybrid to be closer phylogenetically than the parental species of a *Dendroica × Dendroica* hybrid. A similar situation probably exists among the warblers of the genera *Parula* and *Vermivora.*

We do not know for sure that *Dendroica* and *Vermivora* are paraphyletic, but neither do we know that these genera are monophyletic, as the interpretation of Parkes (1961, 1978) requires. Regardless, it simply is not possible at the present to derive empirically a relationship between frequency of hybridization and phylogenetic relationship because a well-corroborated phylogeny of the wood-warblers is not available.

The confusion of “evolutionary” genera with monophyletic groups provides one example of the problems associated with eclectic or “evolutionary” classifications. It is commonly assumed that the categories of such classifications convey phylogenetic information. Just how much they convey is always uncertain, however, because the phylogenetic information in eclectic classifications is necessarily implicit rather than explicit (Hull 1970). The implicit nature of such information is not a problem per se, as long as users of eclectic classifications recognize the phylogenetic limitations of such arrangements. However, because most workers look to a classification precisely for phylogenetic information, it seems more
sensible to make such information explicit through methods of phylogenetic classification (Hennig 1966, Wiley 1981) than to construct groups of ambiguous meaning.

ACKNOWLEDGMENTS

I am grateful to the late D. A. Parsons for his fine preparation of the hybrid, which allowed for its detailed study, and for sharing his unpublished information about the circumstances of its collection. I thank J. E. Ahlquist, F. H. Sheldon, C. G. Sibley, and F. C. Sibley for their comments on the manuscript. I also thank C. G. Sibley and E. H. Stickney (YPM), L. L. Short (AMNH), and R. M. Mengel (KUMNH) for permission to study specimens under their charge. I am especially grateful to D. A. Sibley for his suggestions and comments about the hybrid, and to K. C. Parkes for pointing out the existence of several additional hybrid combinations, for help in aging the hybrid specimen, and for his useful criticisms of this manuscript.

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COLOR PLATE

The Frontispiece painting by David A. Sibley has been made possible by an endowment established by George Miksch Sutton.
SONG-TYPE DISTRIBUTION IN A POPULATION OF KENTUCKY WARBLERS

NELLIE TSIPOURA AND EUGENE S. MORTON

ABSTRACT.—Male Kentucky Warblers (*Oporornis formosus*) have a single, individually distinctive song type. The songs of 29 males breeding at a single location were placed into 6 categories based upon similarity of song types. Based upon these categories, song types were randomly distributed in the breeding population; there was no tendency for neighboring males to have more similar songs than nonneighbors. Song types remained unchanged between years in three males that returned to breed. The songs in our single population were nearly as variable as a sample of songs derived from throughout the breeding range, indicating that Kentucky Warblers do not exhibit song dialects. Received 8 Jan. 1987, accepted 13 July 1987.

Like other *Oporornis* species, male Kentucky Warblers (*Oporornis formosus*) sing a single, relatively simple song type. The song consists of four to eight repetitions of identical syllables, each syllable containing several elements. Members of the genera *Seiurus*, *Geothlypis*, and *Basileuterus* also sing a single song type (Morton and Young 1986). Kentucky Warblers have the ability to change the energy distribution within their song and to raise or lower the frequencies encompassed by the song. The elements that comprise their song syllables, however, retain their shape and sequence. Thus, each male's song type, as defined spectrographically, remains the same but can be altered to match the energy distribution in songs of rivals (Morton and Young 1986). This ability may replace any advantage—as is common in species with multisong repertoires (Krebs and Kroodsma 1980)—for neighbors to copy each other's song types. With this in mind, we asked if neighboring males shared more similar song types than did nonneighbors. We also compared song-type variation in a single breeding population with a sample from throughout the breeding range. We asked if the song types that occurred in our study population represented a distinctive subset of the song types recorded from throughout the species' range. The results are discussed in relation to factors that may select for single song-type repertoires.

STUDY AREA AND METHODS

We studied warblers at the Conservation and Research Center of the National Zoological Park near Front Royal, Virginia, in 1985 and 1986. The area consists of mature and second-growth hardwoods dominated by tuliptree (*Liriodendron tulipifera*), oaks (*Quercus* spp.),

1 National Zoological Park, Smithsonian Institution, Washington, D.C. 20008.
and black locust (*Robinia pseudoacacia*). The breeding population at the Center consisted of 37 males in 1985 and 33 males in 1986. All males were color banded and their territories were mapped from late May through July of both years. A total sample of the songs of 29 males was tape recorded at intervals throughout the breeding seasons of the two years.

The songs of 19 additional Kentucky Warblers were obtained from the Library of Natural Sounds, Laboratory of Ornithology, Cornell University. The Cornell recordings were made in Georgia (4), Mississippi (1), Louisiana (2), Tennessee (2), West Virginia (3), Pennsylvania (1), Maryland (1), Ohio (1), and New York (2), and they encompass nearly the entire breeding range of the species.

Songs were analyzed with a Kay Elemetrics model 7800 Digital Sona-graph. Although each male's song was distinctive (see Morton and Young 1986), we could group songs into categories based upon the arrangement of elements within a song's single syllable (Table 1) (Fig. 1). This method is similar to that used by Marler and Pickert (1984) to categorize Swamp Sparrow (*Melospiza georgiana*) song syllables. Swamp Sparrow songs, like those of Kentucky Warblers, consist of the repetition of a single syllable. The criteria (Table 1) were chosen because the arrangement of elements within syllables is constant for an individual male Kentucky Warbler. Other possible components, such as the frequency range and energy distribution of an individual's song elements, were not used because they vary (see above).

We used seven categories to assess song similarity among neighboring males and to compare the Front Royal sample with songs from throughout the breeding range. For the neighbor comparison, we chose males with only a single neighbor or, where a series of territories occurred linearly along a stream valley, we compared each male with its closest neighbor. In this way, each individual was represented only once in the neighboring pair comparison.

We used a Kolmogorov-Smirnov one-sample test (Siegel 1956) to test the hypothesis that the song categories were nonrandomly distributed at the study site. Finally, the songs of three birds recorded both study years were examined for consistency between years.

### RESULTS

The song of the Kentucky Warbler consists of four to eight repetitions of identical syllables composed of several elements. Each individual sang one song which was distinctive for each bird and remained unchanged throughout the breeding season (Morton and Young 1986, pers. obs.). Although all songs differed at least slightly in frequency and temporal pattern, we recognized six categories of similarly structured songs in the Front Royal population (Fig. 1). The categories were labeled A to F in order of decreasing frequency of occurrence (Table 1). The most common song category, A, was used by 13 of the 29 individuals (45%).

We recorded 19 pairs of males whose territories abutted. Numbers of neighboring pairs having the possible song-category combinations, as well as the predicted numbers for each combination, assuming random distribution, are presented in Table 2. The songs of 25 individuals were used to estimate the expected song-category distribution among neighbors. The remaining 4 birds were on isolated territories and had no immediate neighbors. The Kolmogorov-Smirnov test shows that the distribution of songs does not differ significantly from random ($P > 0.05$). Fourteen of
Tsipoura and Morton • KENTUCKY WARBLER SONG TYPES

Table 1
Song Categories and Numbers of Songs in Each Category from the Front Royal Site and the Library of Natural Sounds

<table>
<thead>
<tr>
<th>Song category</th>
<th>No. of Front Royal birds in category (%)</th>
<th>No. of Library of Natural Sounds birds in category (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Initial low frequency chevron followed by two downslurs then a single higher upslur</td>
<td>13 (45)</td>
<td>8 (42)</td>
</tr>
<tr>
<td>B. Two cycles of connected upslurs and downslurs followed by a single higher element</td>
<td>6 (21)</td>
<td>3 (16)</td>
</tr>
<tr>
<td>C. Initial low frequency chevron followed by two cycles of connected upslurs and downslurs with a final low frequency upslur</td>
<td>4 (14)</td>
<td>5 (26)</td>
</tr>
<tr>
<td>D. Three cycles of connecting upslurs and downslurs with or without a final higher single element</td>
<td>3 (10)</td>
<td>1 (5)</td>
</tr>
<tr>
<td>E. Similar to A but with three downslurs instead of two</td>
<td>2 (7)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>F. Similar to B but with a separated downslur after the two cycles of connected upslurs and downslurs</td>
<td>1 (3)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>G. Two songs from the Library of Natural Sounds that did not fit into the song-type categories from Front Royal—both ended in high frequency connected up- and downslurs forming a “W” shape</td>
<td>0 (0)</td>
<td>2 (11)</td>
</tr>
</tbody>
</table>

the 19 neighboring pairs included one bird singing an A song (Table 2); however, only three pairs of neighboring males both used A songs. Furthermore, only 4 of the neighboring pairs of males used songs in the same category. We conclude that there is no clustering of more similar songs among neighboring males.

Songs of three individuals were recorded in both study years. All kept the same song type in both years even though they had new neighbors, with different songs, in the second year. They also occupied the same territories in both years.

Is the song-type variety in the Front Royal sample representative of Kentucky Warbler song in other areas of the breeding range? The 19 songs obtained from the Cornell Library of Natural Sounds (see methods for their geographical distribution) fit into 4 of the 6 song categories found at Front Royal (Table 1). Two songs, which did not “fit” into our Front Royal categories, were sufficiently similar to be placed into an additional category (G in Table 1 and Fig. 1). One G category song was obtained in Maryland and the other in Georgia. As at Front Royal, the A category was most common in the Cornell sample (8 songs, 42%). Therefore, it appears that the Kentucky Warbler songs in a single locality (e.g., Front
Fig. 1. Wide band spectrograms of individual syllables from Kentucky Warbler songs illustrating the 7 categories identified (see Table 1). A–F are from the Front Royal study site, G shows one from Maryland (right) and one from Georgia (left).
Table 2

<table>
<thead>
<tr>
<th>Song categories of neighboring pairs</th>
<th>No. in Front Royal population (%)</th>
<th>No. predicted (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A–A</td>
<td>3 (16)</td>
<td>3.5 (18)</td>
</tr>
<tr>
<td>A–B</td>
<td>5 (26)</td>
<td>4.2 (22)</td>
</tr>
<tr>
<td>A–C</td>
<td>2 (11)</td>
<td>2.1 (11)</td>
</tr>
<tr>
<td>A–D</td>
<td>1 (5)</td>
<td>1.3 (7)</td>
</tr>
<tr>
<td>A–E</td>
<td>3 (16)</td>
<td>2.1 (11)</td>
</tr>
<tr>
<td>B–B</td>
<td>1 (5)</td>
<td>1.1 (5)</td>
</tr>
<tr>
<td>B–D</td>
<td>1 (5)</td>
<td>0.8 (4)</td>
</tr>
<tr>
<td>B–E</td>
<td>1 (5)</td>
<td>1.1 (6)</td>
</tr>
<tr>
<td>C–D</td>
<td>1 (5)</td>
<td>0.4 (2)</td>
</tr>
<tr>
<td>C–E</td>
<td>1 (5)</td>
<td>0.6 (3)</td>
</tr>
</tbody>
</table>

a The songs of 25 individuals were used in estimating the expected frequency of songs among neighboring pairs.
b Song category pairs unrepresented at the Front Royal study site are not listed.

Royal) are as diverse as a sample from throughout the breeding range. We conclude that Kentucky Warblers differ from dialect species in that song-type similarity among neighboring males is low in any one locality and perhaps generally throughout the breeding range.

DISCUSSION

Kentucky Warbler song types among neighboring birds are diverse, given the restricted number of categories into which they can, apparently, be placed. Unlike other warblers with single song types (see Morton and Young 1986), the Kentucky has no “attenuated” songs given during territorial clashes. Lein’s (1981) description of the Ovenbird’s (*Seiurus aurocapillus*) song is similar to our finding for the Kentucky Warbler except that the Ovenbird uses attenuated songs in border clashes with intruders. As in the Kentucky Warbler, the Ovenbird has a single song type with great variation among the songs of neighboring males (Lein 1981). Whether Ovenbird songs can be placed into higher categories of song similarity as we have attempted to do for the Kentucky Warbler is unknown. In species with dialects, songs are copied from others. In contrast, the structural variation in songs of nondialect species such as the Kentucky Warbler and Ovenbird is apparently constrained by the limits of species specificity (Falls 1963; Lemon et al. 1983). Determining what these limits are, in nondialect species where selection does not favor song similarity among neighbors (selection might be favoring individuals with song *dissimilarity* to neighbors), needs further study as song function in nondialect, single
song species may generate unique questions. For example, they may have more innate control of song element ontogeny as suggested for the contrast between song acquisition in Swamp Sparrows and Song Sparrows (*Melospiza melodia*) (Marler and Pickert 1984).

The seven categories we determined may not be relevant biologically to a discussion of Kentucky Warbler songs. The number of categories we determined is not crucial for our conclusions. We should mention, however, that only the Front Royal songs were used to set up the six initial categories. Even then, the Cornell songs, obtained from throughout the species’ breeding range, fit into our categories relatively well. Moreover, if further research shows that Kentucky Warbler song variation is limited to seven biologically relevant categories, then perhaps this number represents the limit of song diversity needed to insure, on average, that an individual male will have a song dissimilar to those he may find as neighbors. This limit may reflect the balance between selection favoring both species specificity and individuality as found in the Kentucky Warbler.

We do not suggest that birds with dissimilar songs actively “choose” each other as neighbors, only that random choice may result in neighbors having dissimilar songs if the choice is from among seven categories.

The result of song dissimilarity on vocal interactions between males is also of interest. Individuals of several species have been shown to rely on memorized songs to estimate their distance from the singer (reviewed in Morton 1986; see also Margoliash 1986 for neurophysiological evidence). Distance is estimated by comparing degradation in the perceived song with the same song type in memory (termed “ranging,” Morton 1982). The species studied for their ranging ability, however, had repertoires of several to many song types with many held in common between territorial neighbors. In contrast, species such as the Kentucky Warbler, singing single, individually distinctive songs, should afford listeners inaccurate cues as to the singer’s distance from them. This is due to the presumed inability of birds to use degradation in songs for distance estimation unless they have the perceived song also stored in memory (Morton 1982, 1986). A song that is not in a neighbor’s memory might result in an incorrect estimation of the distance of a nonintruding rival and a response to the song as though the singer had intruded. For example, Carolina Wrens (*Thryothorus ludovicianus*) respond more vigorously to songs not in memory than to songs in memory when both are played back from outside of the males’ territorial boundaries (Shy and Morton 1986). Great Tits (*Parus major*) respond vigorously to degraded songs played back within their territories only if they are unfamiliar with them (McGregor and Krebs 1984). The experimental males respond as though their territories or mates are threatened even though they are not.
singing and foraging cannot occur at the same time (e.g., Lein 1981), valuable energy would be wasted through such responses. Thus any differences in territorial quality, particularly the food available on it over and above maintenance levels (e.g., providing energy during time used for singing and territorial defense), can be accentuated if territorial neighbors are forced to move in defense against a “sham” territorial intruder they detect through hearing song (Morton 1986).

Perhaps Kentucky Warblers, because they have but a single, distinctive song per male, have no song in memory that is precisely the same as that sung by any of their rivals. If so, following the logic of the ranging hypothesis (Morton 1986), this suggests that rivals are not able to base distance estimation on song degradation. Because of this, we predict that Kentucky Warbler songs should not be acoustically adapted to avoid degradation as, for example, was found in the Carolina Wren (Gish and Morton 1981). If degradation cannot be perceived, then singers need not develop songs resistant to degradation. On the other hand, Kentucky Warblers have the ability to modify the energy allocation and frequency in their song when responding to a particular individual rival (Morton and Young 1986). This suggests that Kentucky Warblers may have the benefit of a distinctive, unrangeable song, that disrupts listeners and provokes them into wasting energy. They may also benefit by the ability to modify the energy spectrum of their single song to match that of any rival’s song. Therefore, their single song can function in the same way that multiple song repertoires may function in other species by allowing for both song matching, for threatening, and song individuality, for disrupting, in intermale competition.

An alternative hypothesis, that individuality in songs of these species confers easy “neighbor recognition” (Weeden and Falls 1959, Lein 1981), might also contribute to the restriction of song repertoire size to one and to intramale variability in song type. Further study of the contribution of specific song structures shared between neighbors, in addition to categorizing them as simply “neighbor” or “stranger,” is needed (Shy and Morton 1986).

ACKNOWLEDGMENTS

Financial support was provided to Tsipoura through a student internship by Friends of the National Zoo. The staff of the Conservation and Research Center (National Zoological Park) provided facilities and consultation for Tsipoura, especially C. Wemmer and S. Derrickson. Sound analysis facilities were provided by a Scholarly Studies grant from the Smithsonian Institution to the National Zoological Park. We thank J. Gulledge and contributors to the Cornell Library of Natural Sounds for use of their recordings, and K. Bildstein, R. Lein, and K. Derrickson for reviewing the manuscript.
LITERATURE CITED


CENTENNIAL MEETING IN PHILADELPHIA, PENNSYLVANIA,
8-12 JUNE, 1988

The Wilson Ornithological Society will hold its Centennial Meeting at Rosemont College in suburban Philadelphia, Pennsylvania, from 8 to 12 June 1988. Frank B. Gill is chair of the Committee on Arrangements. Jerome A. Jackson chairs the Centennial Committee, and Richard C. Banks is the chair of the Scientific Program Committee. Highlights of Centennial Day, Friday, June 10, include festivities scheduled at the Academy of Natural Sciences of Philadelphia. Featured are a symposium on Paridae with presentations by international researchers, historical talks, an exhibit, and a gala reception. Wilson Society memorabilia assembled by the Centennial Committee will be on display at Rosemont College throughout the meetings. Registration forms for the meeting should be returned to the Academy of Natural Sciences of Philadelphia by 1 May 1988. Further information can be obtained by contacting Dawn F. Coughlan, Academy of Natural Sciences of Philadelphia, 19th Street and The Parkway, Philadelphia, PA 19103. Plan now to attend this historic event.
BREEDING SEASON HABITAT SELECTION BY THE HENSLOW'S SPARROW (AMMODRAMUS HENSLOWII) IN KANSAS

JOHN L. ZIMMERMAN

Abstract.—Spring burning preempts settling by Henslow's Sparrows (Ammodramus henslowii) on tallgrass prairie in the Flint Hills Upland of Kansas. Territories were mapped on four unburned watersheds totaling 211 ha on the Konza Prairie Research Natural Area during the breeding seasons of 1985 and 1986. Vegetation was compared for areas sequenced within territories and those excluded from territories. Males establish territories in patches with greater coverage by standing dead vegetation, lesser coverage by woody vegetation, and taller live grasses. It is hypothesized that the primary ultimate cause for this proximate selection is the depressing effect of standing dead vegetation on aboveground grass productivity which results in a more open substrate for this ground-dwelling species. Received 29 Apr. 1987, accepted 14 Sept. 1987.

The status of the Henslow's Sparrow (Ammodramus henslowii) in North America has recently been summarized by Knapton (1984:73), "The whys and wherefores of population fluctuations, or perhaps more accurately the long term gradual but consistent population decline in the Henslow's Sparrow throughout its range, are very poorly understood, and the species remains somewhat of an enigma." This comment reflects the impressions of ornithologists throughout the species' range, and certainly describes the basis for the species' evaluation in Kansas and other states as threatened or at least a species in need of conservation. The purpose of this study was to describe the habitat variables that are associated with its presence during the breeding season so that better decisions regarding its management might be made.

The Henslow's Sparrow arrives in Kansas in mid-April and departs to its wintering grounds along the coast of the Gulf of Mexico in October (Johnston 1965). In Kansas, breeding season records are distributed from along the western edge of the tallgrass prairie in the Flint Hills Uplands eastward through the forest-prairie mosaic (Marvin Schwilling, pers. comm.) into Missouri west and north of the Ozark Plateau (Clawson 1982). It maintains a monogamous mating system (Wiens 1969) with well-defined territories that are relatively stable throughout the nesting season (Wiens 1969, Robins 1971), but not necessarily contiguous with adjacent males even at high densities (Robins 1971). Loose colonies are

1 Division Biology, Kansas State Univ., Manhattan, Kansas 66506.
formed (Graber 1968, Wiens 1969), but isolated pairs also occur (Sutton 1959). The Henslow’s Sparrow breeds on the Konza Prairie Research Natural Area in Riley and Geary counties, Kansas, where it is an uncommon summer resident from mid-April until early September (Zimmerman 1985). Transect counts made during June on selected watershed-sized study sites from 1981 through 1986 (Table 1) reveal that it does not occur in grassland habitats burned in April, just prior to the birds’ arrival, but maintains a regular, low-density population in watersheds that have not been burned that year. These observations are in agreement with studies in Missouri (Skinner et al. 1984) where it occurs only on idle or lightly grazed, unburned prairie. During June and July of 1983 and 1984 an attempt was made to locate all singing males on Konza Prairie, mapping their presence on a 6.25 ha grid system established across the site. The plots of the 89 males in 1983 and 105 males in 1984 are mutually exclusive of the distribution of burned treatments in both years. Male Henslow’s Sparrows do not establish territories in burned prairie, although they occasionally invade prairie sites in late summer that had been burned that spring (Elmer Finck, pers. comm.; Skinner et al. 1984).

The most obvious difference between burned and unburned prairie is the almost complete absence of litter and standing dead vegetation in burned prairie, while these components can be substantial in unburned prairie, depending upon its previous fire history. Wiens (1969) demonstrated in Wisconsin that litter was significantly deeper and of greater coverage in Henslow’s Sparrow territories compared to other grassland birds and that the coverage by standing dead forbs was also greater. He made no mention of standing dead grasses. The study by Skinner et al. (1984) on the prairies of southwestern Missouri also made no mention of standing dead grasses, and unlike Wiens, they could find no significant relationship between the amounts of litter and the presence of Henslow’s Sparrows. Both Wiens (1969) and Skinner et al. (1984), however, demonstrated the species’ preference for tall and dense grass coverage. This measure may have included standing dead vegetation along with green grasses, but certainly also denotes selection for live grass.

If the distribution of males located during the preliminary studies of 1983 and 1984 is analyzed by geologic formation (Table 2), it is clear that males are significantly more abundant in unburned prairie on the Bar- neston (Florence limestone member) and Matfield formations (see Jewett 1941 for characterizations) than would be expected from the proportionate distribution of the different formations on Konza Prairie ($\chi^2 = 83.6, \text{df} = 3, P < 0.05$). The Matfield shale is overlain by a relatively deep, silty clay loam that has been shown to support a greater aboveground biomass of
Table 1  
Henslow’s Sparrows on June Transects at Konza Prairie

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</thead>
<tbody>
<tr>
<td>Watersheds not burned that spring</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total km</td>
<td>6.175</td>
<td>7.292</td>
<td>6.763</td>
<td>7.322</td>
<td>7.665</td>
<td>7.292</td>
</tr>
<tr>
<td>Total birds</td>
<td>16</td>
<td>18</td>
<td>22</td>
<td>33</td>
<td>25</td>
<td>45</td>
</tr>
<tr>
<td>Birds/km</td>
<td>2.6</td>
<td>2.5</td>
<td>3.2</td>
<td>4.5</td>
<td>3.3</td>
<td>6.2</td>
</tr>
<tr>
<td>Watersheds burned that spring</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total km</td>
<td>1.580</td>
<td>1.953</td>
<td>2.482</td>
<td>1.923</td>
<td>1.580</td>
<td>1.953</td>
</tr>
<tr>
<td>Total birds</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

* From Konza Prairie LTER data set CBP01.

Grasses than the shallower soils of other formations (Abrams et al. 1986). The amount of woody vegetation decreases as elevation increases from the Eskridge to the Barneston formation, with most of the woody vegetation present on limestone outcrops below the base of the Matfield. The distribution of males suggests a preference for denser grass and an avoidance of woody vegetation.

I hypothesized that in unburned watersheds, the habitat included within the territories would contain a greater height and coverage of standing dead vegetation compared to sites within unburned watersheds but outside the boundaries of the territories. Furthermore, I hypothesized that the coverage and height of live grasses would be greater within territories than outside of territories in these unburned watersheds and that coverage by woody vegetation would be less within territories than outside of territories.

METHODS

Prior to the arrival of the birds in the spring of 1985, transects for the sampling of the vegetation were established in three unburned watersheds of 36.1 ha, 39.0 ha, and 85.5 ha at the Konza Prairie Research Natural Area, southwest of Manhattan, Kansas. The beginning point on the perimeter of the watershed for each of four transects and its azimuth were chosen randomly. Sampling stations were then marked at random intervals along this transect in sequence until the boundary of the watershed was reached. In this way, about 150 sampling points used in both 1985 and 1986 were located.

After the birds arrived, the territories of individual males settling on these watersheds were mapped each year by plotting the positions of observations on large scale maps. The use of taped songs was very helpful in locating males, as the species is not a persistent singer and I have found that it often sings from perches within the canopy. The previously determined vegetation sampling points were then categorized as being within these territories or outside of these territories. As would be expected, few of these predetermined sampling points fell within Henslow’s Sparrow territories. To increase the sample size for the within-territory treatment, a randomly determined number of vegetation sampling points were
Table 2
Distribution of Males According to Geologic Formation

<table>
<thead>
<tr>
<th>Formation</th>
<th>% Surface exposure</th>
<th>% Total males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barneston (ca 425 m)</td>
<td>14</td>
<td>27</td>
</tr>
<tr>
<td>Matfield</td>
<td>25</td>
<td>55</td>
</tr>
<tr>
<td>Wreford to Blue Rapids</td>
<td>28</td>
<td>17</td>
</tr>
<tr>
<td>Crouse to Beattie</td>
<td>21</td>
<td>0</td>
</tr>
<tr>
<td>Eskridge (ca 350 m)</td>
<td>12</td>
<td>1</td>
</tr>
</tbody>
</table>

* See Jewett 1941.

located at random intervals on a transect oriented on the longest dimension of each Henslow's Sparrow territory in these watersheds. In 1985, territories were also mapped and vegetation analyzed in an adjacent watershed of 50.1 ha that was on an every two years burning schedule.

At each vegetation sampling point, those previously established as well as those positioned within known territories, ten subsamples were taken at randomly determined points around the sampling point. The presence or absence of contacts by standing dead vegetation at 5 cm intervals along a 1 mm in diameter vertical rod was recorded and the proportion of hits at each 5 cm interval for the ten subsamples gave the percentage of standing dead cover at each height interval. For each of the ten subsamples the life form of the tallest live plant (grass, forb, woody) and its height or absence of vegetation at that point were recorded. These data generated percentage cover and heights of live vegetation for each of the sampling points.

RESULTS

The vertical coverage of standing dead vegetation within territories compared to that outside of territories is presented in Fig. 1. Percentage data were converted by an arc-sine transformation for parametric statistical analysis. There were no differences between geologic formations in the amount of standing dead vegetation, which corroborates clipping data analyzed by Abrams et al. (1986). On the other hand, there was a significant difference between years in these data, and the results from each year were analyzed separately. The difference between years in standing dead vegetation is a reflection of the difference in the amount of precipitation during the previous years' growing seasons (Abrams et al. 1986). For both years, these data support the hypothesis that the amount of standing dead vegetation within the territories of male Henslow's Sparrows is greater than that in areas excluded from territories. Whether the males use this variable as a proximate cue for territory selection is not known, but it is clear that the resultant territories do contain a greater amount of standing dead vegetation. This difference is considerably more subtle than the difference manifest between burned and unburned prairie.

The hypothesis that the coverage by live grass would be different within
the territories of Henslow’s Sparrows compared to that outside of territories is not supported by the data, at least for one of the years (Table 3). The hypothesis that woody vegetation would be less within Henslow’s Sparrow territories, however, is supported for both years. The other consistent pattern is the lack of difference between the coverage by forbs in habitat included within territories and that excluded from territories. Even though the aboveground biomass of forbs in unburned prairie is significantly greater than that in burned prairie (Abrams et al. 1986), Henslow’s Sparrows apparently do not use coverage by forbs to discriminate during territory selection.

In the analysis of the heights of the live vegetation (Table 4), not only is there a difference between the two years, but there are differences between the geologic formations as well. The hypothesis that grass height would be greater within territories is supported in all comparisons within

---

**Fig. 1.** Vertical distribution of percent coverage by standing dead vegetation at 5 cm height intervals. Data for points outside of territories (open bars) are superimposed on data for points within territories (shaded). The differences are significant ($P < 0.05$), except at the 0–5 cm interval for both years, above 90 cm in 1985, and above 115 cm in 1986.
Table 3

Comparison of Percent Coverage of Live Vegetation between Points within Territories and Points Outside of Territories

<table>
<thead>
<tr>
<th></th>
<th>1985 Within (N = 204)</th>
<th>1985 Outside (N = 142)</th>
<th>1986 Within (N = 113)</th>
<th>1986 Outside (N = 149)</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass</td>
<td>83.3</td>
<td>70.0</td>
<td>78.6</td>
<td>79.2</td>
<td>ns</td>
</tr>
<tr>
<td>Forb</td>
<td>14.4</td>
<td>15.0</td>
<td>12.0</td>
<td>12.6</td>
<td>ns</td>
</tr>
<tr>
<td>Woody</td>
<td>0.7</td>
<td>1.8</td>
<td>0.8</td>
<td>2.7</td>
<td>2.43</td>
</tr>
<tr>
<td>Open</td>
<td>1.7</td>
<td>13.7</td>
<td>7.8</td>
<td>5.2</td>
<td>2.11</td>
</tr>
</tbody>
</table>

* Statistics are based on arc-sine transformed data with Student's \( t = 1.97 \) at \( P = 0.05 \).

the same formation except for the small sample sizes involved in the sub-Matfield strata measured in 1986. While forb height within territories is greater for the 1985 sampling period, this is not a valid conclusion for the 1986 data, and there are no significant patterns in the differences between the heights of the woody vegetation included or excluded from territories.

Discussion

These data demonstrate that Henslow's Sparrows establish their territories in habitat patches with significantly greater coverage of standing dead vegetation. I suggest that this association with higher densities of standing dead vegetation is related to the adverse effect of standing dead plant material and litter on the growth of new grass (Knapp and Seastedt 1986), thus providing a more open substrate for this largely ground-dwelling species. Although my data on coverage by live vegetation within and outside of territories on unburned watersheds do not reflect this difference, they were not collected at ground level. An alternate hypothesis would be that the increased cover afforded by standing dead vegetation and the significantly taller live grasses protect nests from more intense cowbird parasitism, predation, or microclimate extremes.

The implications of these conclusions for the management of the species are quite clear. Any practice that removes considerable standing dead vegetation will exclude the species. Obviously, spring burning preempts Henslow's Sparrows, but even without burning, moderate grazing during the previous growing season removes enough aboveground biomass so that there is insufficient standing dead vegetation the next year to meet the habitat requirements of this bird. The scarcity of sightings throughout the tallgrass prairie area of Kansas is perhaps related to the extensive use of fire in range management and stocking rates of at least moderate grazing intensities. But exemption from burning is also detrimental to the species'
Table 4
Comparisons of Height (cm) of Live Vegetation between Points within Territories and Points Outside of Territories

<table>
<thead>
<tr>
<th></th>
<th>Within</th>
<th>Outside</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1985</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florence</td>
<td>42.4 ± 0.9 (N = 61)</td>
<td>32.5 ± 1.1 (N = 25)</td>
</tr>
<tr>
<td>Break</td>
<td>47.0 ± 0.7 (N = 138)</td>
<td>33.2 ± 1.0 (N = 84)</td>
</tr>
<tr>
<td>Matfield</td>
<td>25.8 ± 0.7 (N = 20)</td>
<td></td>
</tr>
<tr>
<td>Sub-Matfield</td>
<td>32.5 ± 1.2 (N = 28)</td>
<td>33.2 ± 1.0 (N = 84)</td>
</tr>
<tr>
<td>1986</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florence</td>
<td>46.6 ± 0.7 (N = 45)</td>
<td>36.0 ± 0.9 (N = 87)</td>
</tr>
<tr>
<td>Break</td>
<td>45.5 ± 1.0 (N = 64)</td>
<td>31.6 ± 2.2 (N = 12)</td>
</tr>
<tr>
<td>Matfield</td>
<td>27.2 ± 3.0 (N = 15)</td>
<td></td>
</tr>
<tr>
<td>Sub-Matfield</td>
<td>32.9 ± 1.5 (N = 21)</td>
<td></td>
</tr>
<tr>
<td>Forb</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1985</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florence</td>
<td>43.7 ± 1.3 (N = 40)</td>
<td>31.2 ± 1.2 (N = 54)</td>
</tr>
<tr>
<td>Break</td>
<td>46.4 ± 1.0 (N = 102)</td>
<td>37.3 ± 6.1 (N = 9)</td>
</tr>
<tr>
<td>Matfield</td>
<td>27.2 ± 3.0 (N = 15)</td>
<td></td>
</tr>
<tr>
<td>Sub-Matfield</td>
<td>31.6 ± 2.2 (N = 12)</td>
<td></td>
</tr>
<tr>
<td>1986</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florence</td>
<td>39.6 ± 2.6 (N = 28)</td>
<td>38.8 ± 1.8 (N = 20)</td>
</tr>
<tr>
<td>Break</td>
<td>38.5 ± 2.4 (N = 40)</td>
<td>31.2 ± 1.2 (N = 54)</td>
</tr>
<tr>
<td>Matfield</td>
<td>23.7 ± 1.9 (N = 3)</td>
<td></td>
</tr>
<tr>
<td>Sub-Matfield</td>
<td>31.6 ± 2.2 (N = 12)</td>
<td></td>
</tr>
<tr>
<td>Woody</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1985</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florence</td>
<td>47.0 ± 9.0 (N = 2)</td>
<td>45.4 ± 3.2 (N = 9)</td>
</tr>
<tr>
<td>Break</td>
<td>55.7 ± 3.9 (N = 7)</td>
<td>47.8 ± 5.6 (N = 4)</td>
</tr>
<tr>
<td>Matfield</td>
<td>45.4 ± 3.2 (N = 9)</td>
<td></td>
</tr>
<tr>
<td>Sub-Matfield</td>
<td>47.8 ± 5.6 (N = 4)</td>
<td></td>
</tr>
<tr>
<td>1986</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florence</td>
<td>46.0 (N = 1)</td>
<td>50.7 ± 3.0 (N = 11)</td>
</tr>
<tr>
<td>Break</td>
<td>56.2 ± 9.0 (N = 5)</td>
<td>52.7 ± 5.7 (N = 3)</td>
</tr>
<tr>
<td>Matfield</td>
<td>73.3 ± 13.8 (N = 4)</td>
<td>50.7 ± 3.0 (N = 11)</td>
</tr>
<tr>
<td>Sub-Matfield</td>
<td>52.7 ± 5.7 (N = 3)</td>
<td></td>
</tr>
</tbody>
</table>

* Statistical comparisons are within each life form and within each year. Means (± SE) with the same superscript within each life form-year set are not significantly different (P > 0.05, using Student's t-test).

continued existence, as the species prefers sites with little woody vegetation. Perhaps more importantly, the stimulating effect of burning on aboveground productivity of grasses that then results in denser cover by standing dead vegetation in the subsequent year meets the species' needs.
The best management practice would be a rotational burning plan, perhaps on a three- or four-year cycle, involving three or four adjacent tracts of prairie. Incidental observations on the presence or absence of birds on unburned prairie suggest that each tract should be at least 30 ha in size. Under this protocol there would always be habitat with standing dead available, while at the same time periodic burning would remove woody vegetation and enhance aboveground biomass production for one year, augmenting the available standing dead vegetation the next year.

ACKNOWLEDGMENTS

E. Finck gathered the grassland bird transect data as part of his responsibilities as vertebrate ecologist in the LTER program. J. Briggs, LTER data manager, made these and other data available for my use. B. Willcutts assisted in the mapping of territories. J. D. Rising and R. W. Knapton provided valuable suggestions for the revision of the manuscript. But none of this would have been possible without the foresight of the late Professor L. C. Hulbert, whose dedication has made ecological research on the tallgrass prairie of Kansas possible. Funding for this work was received from the Nongame Wildlife Program of the Kansas Department of Wildlife and Parks, M. D. Schwilling, project leader.

LITERATURE CITED


BREEDING BIOLOGY OF WILSON'S PLOVERS

PETER W. BERGSTROM

ABSTRACT.—The breeding biology of Wilson’s Plovers (Charadrius wilsonia) was studied in Texas during 1979–81 and in Virginia in 1984. Nests were hundreds of meters apart on salt flats, roads, or unused runways. Ninety-eight percent of nests were within 30 cm of a clump of vegetation, but only 12% of the nests were near objects. Seven pairs renested after their first nest failed, and one pair laid a second clutch after its first brood was adopted. In Texas, egg laying occurred from mid-April to mid-June with two distinct peaks; in Virginia, egg laying was mainly in May. Clutches of 3 eggs were laid over 5–6 days, and about 8 days elapsed between the failure of a nest and a start of a renest. Mean egg size was 35.2 × 25.9 mm; length, breadth, and volume index (LB^2) varied significantly among females. Both sexes incubated; daylight attentiveness rose during the laying period; after clutch completion it averaged 77%. Parents were usually silent during nest relief. Eggs hatched over a span of 8–35 h after an incubation period of 25 days. Hatching success was low in Texas (12–54%), and it varied within and between years. Nest failure was associated with rain (usually flooding), mammalian predation, and cattle. The family moved to a wet area near the nest after hatching, and parents defended the chicks, but not a fixed territory. Chicks spent most of their time hidden in vegetation, attended by one parent at a time. Received 8 March 1987, accepted 21 August 1987.

Wilson’s Plovers (Charadrius wilsonia) breed on American seacoasts from Virginia south to Brazil and from Baja California south to Peru, and on the shores of the West Indies (Johnsgard 1981). Except for anecdotal information (e.g., Bent 1929), there is only one previous published report on their breeding biology (Tomkins 1944).

This report includes the first quantitative data published on many aspects of the breeding biology of this species, including nest sites, laying and hatching dates and intervals, egg sizes, renesting, and nesting success. Details of incubation behavior have been reported elsewhere (Bergstrom 1981, 1982, 1986). This report supplements recent reports on the breeding biology of other plovers (e.g., Graul 1975, Cairns 1982, Warriner et al. 1986).

STUDY AREAS AND METHODS

I studied Wilson’s Plovers in 1979 at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas (26°15'N, 97°15'W). Wilson’s Plovers nested on sparsely vegetated salt flats that are part of a former delta of the Rio Grande. These flats flooded during heavy rain. Bare soil with a salt crust was interspersed with clumps of halophytes, primarily saltwort (Batis maritima) and glasswort (Salicornia sp.). Fiddler crabs (including Uca subcyllindrica) were abundant on the flats.


25
In 1980 my study area was on Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas (28°15'N, 96°30'W). On the bay side of this sandy barrier island, Wilson's Plovers nested on salt flats similar in appearance and vegetation to those at Laguna Atascosa. Fiddler crabs were also abundant there, Wilson's Plovers also nested on the sandy beach on Matagorda, but I did not study them there.

I revisited Laguna Atascosa and Matagorda Island for 10 days in June 1981. In June 1984 I spent 7 days observing plovers on the beach at the north end of Metompkin Island, Accomack County, Virginia (37°45'N, 75°30'W). Observations refer to the Texas study sites unless otherwise stated.

Texas sites were hot and humid during the breeding season. Average daily temperatures in Brownsville, 45 km S of Laguna Atascosa, ranged from 24.5°C in April to 29.7°C in July, with maxima in July of 35°C, and 50% relative humidity. Normal rainfall is 6-10 cm/month in May and June, but rainfall was 4.9 cm below normal during this period in 1979, 10.7 cm above normal in May 1980, and 8.4 cm below normal (no rain) in June 1980 (NOAA 1979, 1980).

I found 29 nests each year in 1979 and 1980. I marked nest locations with wooden stakes (1979) or plastic flags on wire stakes (1980) 5-10 m from the nest. I observed behavior through 7 × 56 binoculars or a 55 × spotting scope from a truck parked about 50-75 m from the nest in 1979 and from a portable canvas blind 15-25 m from the nest in other years. In 1980 I recorded incubation behavior with time-lapse movie cameras photographing at 1-min intervals. I trapped at least one member of each pair on the nest with a funnel trap and banded birds with a unique combination of aluminum and plastic (from A. C. Hughes) color bands. When both parents were banded at a nest, I usually allowed several days between trappings to minimize the risk of desertion. Measurements are given as mean ± SE. Eggs were measured with vernier calipers.

RESULTS

Nest site.—Nests were on bare soil or pavement, usually near a clump of vegetation, but rarely near objects. Fifty-seven of 58 nests had plant stems within 0.5 m of the nest cup, although 4 nests had only small plants nearby (about 1 cm tall). As there were large bare areas present near most nests, nest placement appeared to be deliberate. None of 29 nests was within 30 cm of objects in 1979, when few objects were present. In 1980, more objects were present, and 7 of 29 nests were within 30 cm of objects at least as large as an egg: 5 were near cow manure, 1 was near a black pipe, and 1 was near a stone. Mean distance to an object for those nests was 12 ± 3.6 cm (range = 2–30).

At Laguna Atascosa, 22 of 29 nests were either in sparse vegetation in the center strip or at the edge of a road. The roads were 1–2 m above the salt flat and surfaced with crushed rock, shells, or gravel. For the seven remaining nests, mean distance to the nearest road was 9.1 ± 4.1 m (range = 2–33). I looked for nests from roads, but repeated attempts to find other nests away from roads were unsuccessful. Salt flats were flooded by heavy rains in early June, and plovers were rarely seen far from roads or water. Of the 22 road nests, 9 were on gravel and 13 on other substrates, even though there were relatively few gravel roads. Eggs on gravel appeared to be better camouflaged than eggs on other substrates.
On Matagorda Island, only 1 of 29 nests was along a road: 13 were on unused concrete or asphalt pavement (parts of a former airfield), and 15 were on soil. The 13 soil nests which I measured were a mean of 36.3 ± 8.9 m (range = 6-108) from the nearest road. Distances to water ranged from 50 m to 1.1 km.

I recorded the presence of vegetation near the nest in eight sectors surrounding each Matagorda nest and found a significantly nonrandom distribution (Cochran $Q = 17.3$, $P < 0.02$), with more nests having vegetation on the south and southwest sides. Prevailing winds were from the southwest at Matagorda (pers. obs.).

**Distances between nests.** — In almost all cases, nests were far enough apart for incubating birds to be out of sight of each other. The closest pairs of simultaneous nests were 35.5 m apart on a salt flat, separated by a slight rise, and 39.3 m apart on opposite sides of a raised road. Other pairs of nests, within sight of each other, were 57 m apart on a runway and 64 m apart along a road. All other active nests were at least 250 m apart. The closest three pairs of Wilson’s Plover nests in Virginia (out of 12 nests found) were 44, 45, and 52.5 m apart, and mean nearest neighbor distance for the 12 nests was 85 m (Bergstrom and Terwilliger 1987).

Wilson’s Plover nests were sometimes near those of other species in Texas. Several nests on Matagorda were near nests of Least Terns (*Sternula antillarum*) and Common Nighthawks (*Chordeiles minor*), and two nests at Laguna Atascosa were near Common Nighthawk or Snowy Plover (*Charadrius alexandrinus*) nests. One nest on Matagorda was 11 m from an active American Avocet (*Recurvirostra americana*) nest, and there was a Black-necked Stilt (*Himantopus mexicanus*) nest nearby. In Virginia Wilson’s Plover nests were always in the same area as Least Tern and Piping Plover (*C. melodus*) nests (Bergstrom and Terwilliger 1987).

**Renesting.** — The mean distance between first and second nests of 7 pairs whose first nest failed was 58.2 ± 17.6 m (range = 24-157). All of the second nests were on the same substrate as the first nest. Eggs in 2 of the 7 first nests had been eaten by coyotes, 4 were deserted, and in 1 nest the eggs disappeared for unknown reasons. One pair that hatched a second brood after its first nest hatched and its young were adopted (see below) moved 29 m for its second nest. Both parents were banded on the first nest in 5 of these 8 cases, and in all 5 cases the pairs remained together to renest. Birds sometimes changed nest substrates between years. Two pairs banded on Matagorda in 1980 were found nesting there in 1981; one was nesting 40.6 m from its previous nest on the same substrate, while the other had moved 303 m to nest on a different substrate.

**Nest starting dates.** — The first peak in nest starts came a week earlier in 1980 than in 1979 (Fig. 1). The earliest known nest each year was started on 15 April; however, as I found young chicks at Laguna Atascosa...
on 1 May 1979, egg laying there began by 1 April. There was a second peak of nest starts in both years during late May and early June (Fig. 1), which probably represents renesting. Egg laying ended in 1979 on 20 June and in 1980 on 7 June. The lack of rain in June 1980 (NOAA 1980) may have been a factor in the earlier ending that year.

Egg dates for Wilson’s Plovers in Texas were similar to those in Georgia (Tomkins 1944) and in Surinam (Renssen 1974). In Virginia, egg laying started later (early May, first chicks seen 8 June) and ended sooner (end of May, latest eggs 20 June; K. Terwilliger, pers. comm.), suggesting that renesting is less common there than in Texas.

Laying intervals. — Time required to lay a complete clutch was estimated for 6 nests. In one nest where I saw the laying of the first egg (at 11:36), the second egg was laid 54–68 h later, and the third egg 104–125 h after the first (about 5 days later). At another nest it took a minimum of 144–149 h to lay 3 eggs (about 6 days). Estimates at four other nests were 119, 120, 142, and 145 h to lay three eggs. At one nest where a minimum of 52.5 h elapsed between the laying of the second and third eggs, the time of laying of the third egg was determined from a film (16:26).

Mean time from nest failure to the start of a new clutch for 7 renests (after the first nest failed) was 7.6 ± 1.6 days (range = 5–13). One pair started a new nest 13 days after the hatching of its first nest, after its first brood was adopted (see below).

Egg size. — The 78 eggs measured were laid by 20 different females. All egg dimensions (Table 1) varied significantly among females (one-way ANOVA, $P < 0.001$ for length, breadth, and volume index [LB]). Eggs of the same female were not significantly smaller in second nests than in first nests (paired $t$-tests on clutch means, $P > 0.05$) (Table 1), as they often
Table 1

<table>
<thead>
<tr>
<th>Egg Measurements for Wilson’s Plovers in Texas</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
</tr>
<tr>
<td>All eggs</td>
</tr>
<tr>
<td>First nests</td>
</tr>
<tr>
<td>Second nests</td>
</tr>
</tbody>
</table>

^a All measurements are mean ± SE (N).

are in shorebirds (Miller 1979). There were no significant regressions of egg dimensions on female culmen length, although the two are often correlated positively in shorebirds (Miller 1979). Laying order within the clutch was recorded at 4 nests; there was no consistent trend in egg size with laying order in this small sample.

Clutch size. — Complete clutch size was four at 1 nest, three at 45 nests, and two at 5 nests (2.92 ± 0.047). Only one of the clutches of two eggs hatched, so some of the small clutches may have been deserted and incomplete. Modal clutch size in this species is also three in other areas (Bent 1929).

Incubation. — Regular incubation did not begin until the third egg was laid; however, the parents attended increasingly during clutch completion. Total daylight attentiveness (% of the daylight period that either parent was on the nest) was 16%, 13%, and 50% at one nest on days when there were 1, 1, and 2 eggs in it. At another nest, daylight attentiveness went from 53% to 80% and 84% after the third egg was laid. Most attentiveness during clutch completion was by the male, while after it, most was by the female (Bergstrom 1986). Mean daylight attentiveness (both sexes, 14 pairs) was 77% (range = 70–86%, Bergstrom 1986), but it was strongly affected by air temperature and nest substrate (Bergstrom 1982). Incubation behavior functioned both to warm and to cool the eggs (Bergstrom 1982).

Nest relief. — The noisy nest relief ceremony described for other plovers (Bunni 1959) was not observed in Wilson’s Plover. Often one parent left the nest a few minutes before its mate arrived. When the parents saw each other at the nest there was normally no call, but the departing bird (especially the male) occasionally tossed small objects over its shoulder. Occasionally the female gave Fweep calls (Bergstrom 1988) when she arrived at the nest. Nest relief changed shortly before hatching began, when the relieving bird usually came to the nest before the sitting bird left. There was also a reduction in incubation shift length at this time (Bergstrom 1986).
Incubation period.—At one nest, 25 days 3 h elapsed from the laying to the hatching of the third egg. Estimates of the incubation period at five other nests were 23–27 days. Bent (1929) reported an incubation period of 24–25 days for this species.

Hatching.—Hatch completions had two peaks per season, about 30 days after the peaks of nest starts (Fig. 1). These peaks were more distinct than those of nest starts, with no known nests hatching between 28 May and 25 June 1979, or between 22 May and 14 June 1980.

Parents removed eggshells within 30 min of hatching, usually flying off with them but sometimes running away with them. At a nest where I observed hatching on Metompkin Island, the shell was carried away 16 min after I first saw the chick’s head, during the parent’s second absence after hatching.

Hatching intervals.—At some nests, hatching took less than 24 h: three chicks hatched in a total of 8 h at one nest, and within 19 h at another nest, and two chicks hatched 4.5 h apart in a third nest (only two of the eggs hatched in that nest; the parents continued incubating for 24 h, and then deserted the third egg). In three other nests the hatching intervals were longer: three eggs hatched over a total of 34.5 h and 25–40 h, and two eggs in a third nest hatched 24–37 h apart. At Metompkin Island the first and last eggs in a nest hatched 23 h 56 min apart, but one egg or chick disappeared in the interim. Hatching intervals were usually unequal within a clutch, with one interval of about 24 h and one shorter, about 5–10 h, but which occurred first was not consistent.

Hatching success estimates.—The three estimates of hatching success I used (Table 2) are all biased to some degree. The first two estimates are probably too high because some nests that failed were not found (Mayfield 1961), but exposure estimates are probably too low, because the probability of failure within years was not constant (Green 1977). In 1980 clutch hatching success rose from 36% to 75% for nests found after 16 May (G = 4.14, P < 0.05). This date corresponds to the start of the second peak in nest starts (see above). In 1979, nests on gravel roads had significantly higher clutch hatching success than nests on other roads (57% vs 10%, G = 4.53, P < 0.05). Clutch hatching success was significantly higher on Matagorda Island in 1980 than at Laguna Atascosa in 1979 (G = 4.42, P < 0.05), and nest survival probability was also significantly higher in 1980 than in 1979 (G = 8.4, P < 0.01; Dow 1978).

Causes of nest failure.—The known causes of nest failure were mammalian predation, cattle, and flooding. Five failed nests (3 at Matagorda, 2 at Laguna Atascosa) had tracks or scats of coyotes near them. Tracks of a bobcat-sized cat and broken eggs were found near one failed nest at Laguna Atascosa. One 1979 nest, probably deserted after flooding, later
had eggshells that appeared to be punctured by a bird's beak. Cattle grazed on Matagorda (but not at Laguna Atascosa), and signs of cattle (crushed eggs and prints) were found near five failed nests and one nest that lost an egg there. Three failed nests at Laguna Atascosa were found under water. Small holes such as those made by rodents (Maxson and Oring 1978) were found in two previously deserted eggs in 1979.

At the other 15 nests that failed, there were no eggshells and no tracks. The parents might have removed eggshells after failure, or the eggs may have been eaten by a predator that left no tracks, such as a bird or a snake.

**Effect of rain.**—Nests tended to fail around the time of rain (2.5 mm/day or more) in both years, but not always from flooding. In 1979, 67% of 18 failures occurred on the 21 days with rain, significantly more than the 14% of failures expected if rain had no effect (14% of the days had rain; \( G = 26.1, P < 0.001 \)). In 1980, 33% of 12 failures occurred on the

---

### Table 2

<table>
<thead>
<tr>
<th>Wilson's Plover Hatching Success in Texas</th>
<th>Year</th>
<th>1979</th>
<th>1980</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nests</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number found</td>
<td>29</td>
<td>29</td>
<td></td>
</tr>
<tr>
<td>Deserted (after human disturbance)</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Outcome unknown</td>
<td>3</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Hatched one or more chicks</td>
<td>6</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Failed (no chicks hatched)</td>
<td>18</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Clutch hatching success*</td>
<td>0.25</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>Eggs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number laid</td>
<td>57</td>
<td>75</td>
<td></td>
</tr>
<tr>
<td>Number hatched</td>
<td>17</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>Left in nest after hatching</td>
<td>1</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Disappeared during incubation</td>
<td>0</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Egg hatching success</td>
<td>0.30</td>
<td>0.45</td>
<td></td>
</tr>
<tr>
<td>Exposure (Mayfield 1961, 1975)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nest-days (days all nests at risk)</td>
<td>230</td>
<td>404</td>
<td></td>
</tr>
<tr>
<td>Egg-days (days all eggs at risk)</td>
<td>---</td>
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<td></td>
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<tr>
<td>Nest survival probability</td>
<td>0.13</td>
<td>0.47</td>
<td></td>
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<tr>
<td>Egg survival probability</td>
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<tr>
<td>Hatching probability</td>
<td>0.94</td>
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<tr>
<td>Overall nesting success(^c)</td>
<td>0.12</td>
<td>0.34</td>
<td></td>
</tr>
</tbody>
</table>

* Equals no. of nests hatching 1 or more young/total no. of undisturbed nests with known outcome.

\(^a\) Not calculated as partial clutches were not lost in 1979.

\(^b\) Equals the product of the 3 probabilities preceding it.
9 days of rain, significantly more than the expected 9% ($G = 5.15, P < 0.05$). Most rains occurred early in the season (especially in 1980), and this probably accounts for the higher nesting success later in the season.

**Chicks.** — Mean weight at hatching of 18 chicks was $9.3 \pm 0.54$ g, with a mean culmen length of $6.0 \pm 0.13$ mm. The chicks stood up and started to walk within 1–2 h of hatching. I saw one family leave the nest: the third and last egg hatched at 06:45, and the family moved off together (after several false starts) at 08:56 the same day.

**Family movements.** — Most families moved after hatching to a low wet area where the chicks fed in halophytic vegetation, especially saltwort. In some cases there were suitable areas near the nest and the family did not move very far: one in 1979 moved 10–20 m with their chicks, and in 1980 one moved about 30 m with their chicks. Pairs nesting on roads generally moved farther: one male moved his family to a shallow pond about 100 m from the nest. In Virginia, families moved away from the beach to mud flats behind the dunes, about 100 m from their nest site (Bergstrom and Terwilliger 1987).

Parents appeared to defend an area around the chicks if there were other Wilson’s Plovers nearby. One male in 1979 did Parallel Run displays (Bergstrom 1988) with another male tending chicks nearby at the edge of the same pond. Another male in 1979, while he still had eggs, did Parallel Run displays with a male that had chicks nearby, and his mate sometimes did the display to the other male also (Bergstrom 1988).

During the day, one parent stayed near the chicks while the other parent was out of sight. The attentive parent did not follow, call to, or lead the chicks, but 50–80% of its time was spent alert, displaying or brooding (Bergstrom 1981). Both in Texas and Virginia, when not being brooded, chicks spent almost all of their time hidden in vegetation, presumably feeding. When the parents changed roles they often called to each other loudly with Tweet calls (Bergstrom 1988), in sharp contrast to the normally silent nest relief (see above). When the family moved from one area to another, often in the evening, I always saw both parents with the chicks.

I was unable to follow broods until fledging because of their mobility and cryptic behavior. There were indications of chick mortality (e.g., the only families seen with three chicks had young chicks), but it was not possible to estimate chick survival. Time to fledging is not known (the reference in Johnsgard 1981 to Tomkins 1944 on this subject is wrong: 21 days was only a minimum possible time given by Tomkins).

**Adoption.** — I saw one 1980 pair with three chicks the day after hatching, on 14 May. I banded two of the chicks, and then the parents led them down a road away from their nest. I next saw the parents on 19 May and they behaved as if they had no chicks. Their second nest was near their
first (see above) and was started about 26 May. I did not see the banded chicks again until 3 June, when one of them was being attended and brooded by an unbanded male. This male defended an area around the chick adjacent to the territory of its parents, using Parallel Run displays (Bergstrom 1988). The adoption probably occurred before 19 May, and it could have been caused in part by the banding of the chicks.

Adoption might result from the attraction to chicks of unrelated females, a phenomenon I saw in Texas and Virginia. On 2 occasions, after I had banded and released a chick, or visited a nest containing a chick, an unrelated female approached the chick and tried to brood it.

**DISCUSSION**

Two functions have been proposed for the tendency of plovers to nest near objects: nest concealment by disruption of its outline (Bunni 1959, Graul 1975), and use as a windbreak (Tomkins 1944). Vegetation near nests may have the same function in Texas, where objects are uncommon. At Mono Lake, Snowy Plovers nesting beside scarce objects had lower hatching success than pairs nesting elsewhere (Page et al. 1985). A windbreak would help keep eggs from rolling out of the nest in Texas, and the vegetation near nests tended to be in the direction of the prevailing winds. Most of the vegetation was not tall enough to function as a sunscreen.

Although Wilson’s Plovers nesting in Texas seem to have a breeding season long enough to allow double-brooding, no cases were found there. Double-brooded plovers usually have either single-parent incubation (as in Mountain Plovers [C. montanus], Graul 1973) or single-parent brood care (as in Snowy Plovers, Warriner et al. 1986). Both of these are rare in Wilson’s Plover (Bergstrom 1981).

Laying intervals in Wilson’s Plovers were similar to those in other plovers, except Killdeers (C. vociferus), which laid more rapidly (Bunni 1959, Cairns 1982, Graul 1975, Rittinghaus 1961, Warriner et al. 1986). This difference is not related to clutch size nor to the weight of the eggs or the clutch relative to female body weight (Graul 1973:88), as Killdeers are not distinct from this group in any of these variables.

The defense of the chicks, but not the nest site or a fixed feeding area, has also been reported in Snowy (Rittinghaus 1961, Boyd 1972) and Mountain plovers (Graul 1975). In plovers in which a relatively fixed feeding area is defended near water (Piping Plovers, [Cairns 1977], and Killdeers, [Lenington 1980]), the nesting territory is often used for brooding at night. However, as family movements within a species probably vary with the proximity of feeding areas to the nest site, it is not clear whether these are consistent species differences.
ACKNOWLEDGMENTS

I thank A. R. Kiester, K. Terwilliger, and the staffs of Laguna Atascosa National Wildlife Refuge and Aransas National Wildlife Refuge for help in the field. This research was supported in Texas by the Henry Hinds Fund, the Eli A. Nierman Foundation, the Frank M. Chapman Fund, the E. A. Bergstrom Fund, and the Alexander Bache Fund. Research in Virginia was supported by a Glenn Grant from Washington and Lee University, and the Nature Conservancy gave me permission to work on Metompkin Island. A. R. Kiester, G. W. Page, R. E. Phillips, T. Sordahl, E. H. Miller, and reviewers G. W. Page and J. R. Walters made helpful comments on earlier versions of the manuscript. I thank R. Floyd for computer assistance, and my wife, S. Still, for support and encouragement.

LITERATURE CITED


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BREEDING DISPLAYS AND VOCALIZATIONS OF WILSON’S PLOVERS

PETER W. BERGSTROM

ABSTRACT. — Breeding season displays and vocalizations are described for Wilson’s Plovers (Charadrius wilsonia) from Texas and Virginia. Aerial displays appeared to be absent, but horizontal and upright territorial displays and Parallel Runs (with horizontal posture) occurred. The female approached the side of the male in the Scraper-ceremony. Precopulatory postures include a posture (Forward-tilt) and a behavior during Marking time (tail flicking) not reported for other plovers. Mounting lasted 15–66 sec (N = 4), was confined to the nesting territory, and included the male grabbing the nape of the female and toppling by the pair. Alarm and distraction displays included Head-up, Squatting, Mock-brooding, Crouch-run, and Broken-wing displays. The Broken-wing display was rare before hatching in Texas, but not in Virginia. Ten vocalizations are described, including nine with sonagrams, several of which have never been described for this species. The displays and vocalizations of this species are compared to those of several other plovers. Received 8 Mar. 1987, accepted 24 Aug. 1987.

The lesser plovers (Charadrius) are a worldwide group of about 30 species, similar in anatomy, ecology, and behavior (Cramp and Simmons 1983). Relationships within the genus are unclear; similarities in displays (Phillips 1980) do not match similarities in plumage and anatomy (Bock 1958), although the displays are poorly known for many species. This paper describes a number of breeding displays and vocalizations of Wilson’s Plover (Charadrius wilsonia), few of which have been described previously (Bent 1929, Tomkins 1944). These descriptions, together with recent descriptions (Phillips 1980, Cairns 1982) and compilations (Johnsgard 1981, Cramp and Simmons 1983) of some of the displays and vocalizations of other lesser plovers, enable a more thorough comparative analysis than was possible previously.

STUDY AREAS AND METHODS

I studied Wilson’s Plovers in 1979 at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, and in 1980 at Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas. I made observations during April to July 1979, April to June 1980, and at both sites in June 1981. I also observed breeding Wilson’s Plovers at Metompkin Island, Accomack County, Virginia, in June 1984, but all the figures are from displays and calls of Texas birds. The study areas are described in greater detail elsewhere (Bergstrom 1988). I watched plovers from a truck or a blind with 7 × 56 binoculars or a 55 × spotting scope, and used the spotting scope as a 1000-mm telephoto lens for photography. I recorded vocalizations at a tape speed of 19 cm/sec with a Uher 4000 tape recorder, Uher microphone,

and Sony 48-cm parabola (1979), or with a Nagra E tape recorder and Sennheiser shotgun microphone (1980). I analyzed recordings with Kay Elemetrics 7029 or 7800 Sonagraphs on the 8 kHz scale with a wide band filter. All drawings of birds were made from photographs. Names of displays and vocalizations follow Cramp and Simmons (1983) where possible.

TERRITORIAL BEHAVIOR

Males were already establishing territories when I arrived in Texas on 11 April 1979 and 17 April 1980. Males chased males, and few females were seen. The following postures and displays were used in territorial contexts.

Standing. — In this posture, the back was held at an angle of about 30° above horizontal, and the bill was held just slightly below horizontal (about 5°, Fig. 1A). The neck was withdrawn and the breast band appeared narrow.

Horizontal-hunched. — This posture (Fig. 1B) was used during rushes toward or chases of other birds. The back was parallel to the ground, the neck shortened, and the tail was not fanned or lowered. Sometimes there was a hump created by back feathers (as in the upper male in Fig. 1F). Often a “Song-rattle” (see below) was given when the bird chased in this posture; at the same time the breast band bulged down, forming a variation, the Horizontal bulged-breast posture (Fig. 1C). This posture had a hump in the back, as if the feathers were compressed laterally, and it was held only briefly by the chasing bird. During rapid chases on the ground I saw a third form of this display, the Horizontal spread run (Fig. 1D), in which the breast feathers were spread out past the wings with neither the back nor the breast band feathers bulged.

Upright-hunched. — This stationary posture was used by males as a threat either before or after a run using the Horizontal-hunched or Horizontal spread run posture. The back was more vertical than in the Standing posture (70° above horizontal), the neck and breast band were expanded, and the white breast feathers were fluffed out and spread over the forward edges of the folded wings. Chasing males often gave this posture both before and after a chase, but the chased male used only the Horizontal-hunched posture. Fig. 1E shows the same pair of males as Fig. 1D, when the chasing male had paused in the Upright-hunched posture, and the chasing male had paused looking back at him.

Parallel Run. — In territorial encounters, two males (or in one case a defending female and an intruding male) sometimes ran parallel to each other, both using the Horizontal-hunched posture, occasionally with bulged breast (2 cases) but not a spread run. The two usually followed a straight line that appeared to mark a territory boundary, then each would turn outward 180°, and repeat the run along the same line in the opposite
direction. This display was seen during territory establishment (two males on 17 and 18 April 1980 at Matagorda), when a pair with chicks was near a pair with eggs (14 June 1979 at Laguna Atascosa, with the female with eggs involved as well), and between two males tending chicks near a puddle
(19 July 1979 at Laguna Atascosa). The latter pair are shown in Fig. 1F; the males were actually farther apart than shown. It was also seen on 13 May 1980 at Matagorda between a nesting male on his territory and another male that had adopted one of his chicks, which was being tended nearby (Bergstrom 1988). No vocalizations were heard during this display.

**COURTSHIP AND COPULATION**

I arrived in Texas too late to see pair formation. I also did not see the aerial displays used by other male plovers (Cramp and Simmons 1983), but I suspect that Wilson’s Plovers lack this display (at least in Texas and Georgia), as it continues during scraping (Cramp and Simmons 1983), and Tomkins (1944) did not see it either. The first time I saw pairs together was at scraping (see below). I saw precopulatory displays (only up to marking time) 10 times, and complete copulation 6 times. These sequences always took place in the territory near a scrape, never after clutch completion, and usually (but not always) immediately after a Scrape-ceremony. All complete copulations seen followed a Scrape-ceremony. I saw the following displays and behavior by pairs.

**Scraping.** — The male made several scrapes in his territory. Males did most of the scraping, but females sometimes scraped in a depression started by their mate. Both sexes engaged in ground-pecks and then side-throws (Cramp and Simmons 1983), when they tossed bits of stone or twigs back toward the scrape as they left it. Then, while they were on the scrape, these bits were arranged in a circle around the nest cup, or occasionally as a crude lining. The nest cup was made by kicking back with the breast down and tail up, rotating the body to make a round depression. I could not see the details of the foot movements. The cup was about 8 cm across. Similar scraping occurred on concrete or asphalt pavement, but it only cleared a bare spot.

**Scrape-ceremony.** — If a female came near a scraping male, he would step sideways out of the scrape away from the female, with his side toward her. If she approached, he pointed in the direction of the scrape with his bill (“bow,” Phillips 1980), lowered his wing near the scrape and raised his wing away from the scrape, and fanned his tail down. Once a faint “Mooing” call was heard, presumably by the male (see below). The female then entered the scrape, passing the male’s head (Fig. 2A). I saw this ceremony five times, as early as 20 April (1980) and as late as 2 June (1981). Once it included only the male stepping out of the scrape sideways, just before the female laid the first egg in the nest.

**Horizontal bulged-breast.** — This was used only by males in approaches to females prior to and after scraping. A similar posture was used in territorial chases (Fig. 1C), but during courtship it was held for longer periods, was silent, and was used with an exaggerated “prancing” gait.
Forward-tilt. — This precopulatory display often followed the Horizontal bulged-breast. The male lowered his head but kept his bill almost horizontal, with his back about 45° above the horizontal (Fig. 2B and 2C). Males also “pranced” after females in this posture.

Upright-hunched. — If the female stood still in the posture shown in Fig. 2C and 2D, the male switched to the Upright-hunched posture directly behind her, as shown in Fig. 2D. The female posture was tipped forward slightly from Standing. The male’s Upright-hunched posture was less extreme than the version used in chases, with less puffing of the breast feathers.

Marking time. — If the female continued to stand in front of him, the male (while in the Upright-hunched posture) began kicking his feet up (approx. 2 kicks/sec) until they almost touched his breast, as shown in Fig. 2D with the male on the left. He flicked his tail from side to side with each kick, and often continued kicking and tail flicking for 30 sec or more. The 10 incomplete sequences I saw (including the one shown in Fig. 2) usually ended at this point, when the female walked away while the male was Marking time.

Mounting and copulation. — I saw plovers copulate 6 times, always in the pair’s territory. The male hopped on the female’s back and continued the foot movements in a reduced form, but with no tail flicking, for timed intervals of 15, 25, 44, and 66 sec (called “trampling” by Tomkins 1944). In 1 instance mounting was not preceded by Marking time. In all cases the male then grabbed the back of her neck with his beak, thrust his pelvis down, passed his tail around hers, and maintained cloacal contact for only a few seconds. The pair then fell back together in 5 of the 6 cases. Both birds preened after copulation; no vocalizations were heard before, during, or after it.

ALARM AND DISTRACTION DISPLAYS

The displays described below were given in response to my presence (usually outside the truck or blind, but see below) unless otherwise noted.

Head-up. — In alarm, Wilson’s Plovers raised their heads, extended their necks, and tilted their bodies back to about 60° above horizontal (Fig. 3A). Birds also used this posture when they occasionally approached me in the truck or blind and stood about 3 m away giving Tweet calls (see below). Less extreme, silent versions (with less neck extension) were given by groups by adult plovers to a dog that came near a pond where they were drinking and bathing, to a thirteen-lined ground squirrel (Citellus tridecemlineatus) near nests in 1979 at Laguna Atascosa, to a western diamondback rattlesnake (Crotalus atrox) near nests in 1980 at Mata-
Fig. 2. Courtship postures of Wilson's Plovers: (A) male on left bowing as female on right enters scrape, (B) two different males doing Forward-tilt, (C) male on right doing Forward-tilt toward female on left, before Marking time, (D) same pair as in C, male on left in Upright-hunched posture and Marking time, female on right.
gorda, and in 1980 at Matagorda by a single male in response to a coyote (Canis latrans) and a perched Great Horned Owl (Bubo virginianus) near its nest.

*Squatting.*—Squatting appeared to be a more extreme alarm display (Fig. 3B). In addition to responding to me in this manner, I also saw Wilson's Plovers use this in response to Willets (Catoptrophorus semipalmatus) that were walking near their nest. It differed from Mock-brooding (see below) in that the head was low and the body was flattened during Squatting.

*Mock-brooding.*—Plovers often responded with Mock-brooding when I approached their nests during incubation. Groups of 10–20 plovers would gather near me, giving Tweet and Peet calls (see below), standing in Head-up postures. Birds at the edge of the group, usually females, would run silently 10 m or more from me in a Horizontal-hunched posture. They then settled behind a clump of vegetation or in a hollow for 6–17 sec (N = 3), as if settling on a nest, and then jumped up to repeat the display elsewhere.

*Distraction-lures.*—The “Crouch-run” had the tail fanned down and wing tips held out and quivering (Fig. 3C). No call was heard, and the wing movements were minor, so it was probably not a true rodent-run display (Cramp and Simmons 1983). Although less common than either of the following, it often occurred along with them. The “Broken-wing” display, which occurred in both stationary and moving birds, was accompanied by a buzzy “Distraction” call (see below). The stationary display (Fig. 3D) included birds beating their wings up and down together (Cramp and Simmons 1983:160) with the wingtips moving in a circle, and the tail fanned down. In some instances (Fig. 3E), birds drooped one wing toward me, reminiscent of the Scrape-ceremony. This display was often given next to an object, such as the cow manure in Fig. 3E. Sometimes both wings were held in the air briefly (Fig. 3F). Stationary Broken-wing displays were also given to Willets, once to a Willet near a plover nest and once to a Willet trying unsuccessfully to steal a fiddler crab (Uca sp.) from a plover. Mobile Broken-wing displays were performed farther from me; the bird dragged its wings on the ground while moving away from me. The mobile form was more common, unless chicks were visible nearby, in which case the stationary display was more common.

Broken-wing displays were normally performed 10 m or more away from me. Wilson's Plover parents came no closer than 5 to 8 m while I was banding their 1- to 3-day-old chicks, and most often gave Head-up postures and Tweet calls (see below) during the banding rather than distraction displays. Broken-wing displays were rare in Texas unless chicks
were present (usually after mid-May). During incubation, a Head-up posture with Tweet calls (see below) and Mock-brooding were the most common responses to me. In contrast, Wilson’s Plovers in Virginia used the Broken-wing display frequently in response to humans both during incubation and the chick period (K. Terwilliger, pers. comm.).
VOCALIZATIONS

Tweet call.—This was the most common call given to me when I was near the nest, and seemed to be mainly an alarm call. It was a clear whistle slurred up, ranging in frequency from 1.5–5 kHz (Fig. 4A). It was usually given by a bird in the Head-up posture, and birds always bobbed their bodies slightly as they gave the call; it seemed to be used most often by males. It was always separated from other calls, and was always given singly. I heard it less often in other contexts: territorial fights between males, and when one parent tending chicks was replaced by the other parent (see Bergstrom 1988).

Peet call.—This short whistle occurred singly or, more commonly, in pairs or triplets, often following a Tweet call (Fig. 4B). Peet calls were more common when I was moving, while Tweet calls were more common when I stood still. When I moved near a group of birds that were using Mock-brooding, they often gave a chorus of Peet calls (Fig. 4C), which varied in frequency. A sound spectrogram I made from a record of Wilson's Plover calls from Puerto Rico or the Virgin Islands (Reynard 1969) is virtually identical to the Tweet and triplet Peet calls shown here.

Pip call.—This sounded like and looks like a low-intensity Peet call. It was given when one bird left the nest, but never at nest relief. Pip calls given by a female leaving the nest are shown in Fig. 4D. Pip calls were heard at 9% of 81 male departures from the nest at six nests watched from a blind in 1980 for 108 h. Females gave Pip calls during 9% of 102 departures from the same nests; one female gave the call twice just before her mate went to the nest (not at nest relief). Both sexes of three pairs used the calls, only the male in one pair, and neither sex in two pairs. As it was usually given when the mate was not present, and not at nest relief, its function is unclear; it could have been in response to me in the blind.

Fweep call.—This call was louder than the Pip call, and it was used mainly by the arriving bird during nest relief. It was often given in series (Fig. 4E). It was used most often when the sitting bird was slow to leave the nest, and it was followed by nest relief. I heard this call during 32% of 38 nest reliefs seen in the same 6 pairs in 1980; 67% of the 12 birds giving those calls were females. The structure of this call is similar to parts of the “Song-rattle” (see below) but the Fweep call was lower in volume and much shorter.

“Song-rattle.”—This was given by both sexes during territorial displays and by males during chases, both on the ground and in the air (Fig. 4F and G, by the same male). It appeared to be given by chasing birds only. It was sometimes given to me by birds giving alarm displays. It often was accompanied by puffing out the neck band.
"Brood" call. — A call was used by parents to lead or brood their chicks; in both Texas and Virginia I could see the parent’s throat move (about once per second) and the chicks following or brooding, but I could not hear the call. A probable variant of the “Song-rattle,” the Chup call (Fig. 4H), was given by a male leading his chicks along a road near my truck at Laguna Atascosa in 1979. Although this was the only call I heard given
by parents to chicks, its similarity to the “Song-rattle” and the bird’s proximity to my truck make me suspect that the call was given in response to me, and it was probably not the normal call to the chicks.

**Peep call.**—This was a soft call made by a young chick while I was holding it, and it resembled the *Pip* call of adults (Fig. 4I).

**Cheep call.**—This was a louder, higher-pitched distress call given by the chick mentioned above while I was banding it (Fig. 4J). This usually caused the parent(s) to come closer to me and give *Tweet* calls.

**“Distraction” call.**—This was a buzzy call given only during Broken-wing displays. It was given in series, and usually descended in pitch (Fig. 4K). This female gave three bursts of 4, 3, and 7 calls each, with a mean pause between bursts of 1.0 sec and within bursts of 0.63 sec.

**“Mooing” call.**—I heard this call during the Scrape-ceremony, but did not record it. It sounded like the distant mooing of a cow.

**DISCUSSION**

The displays and vocalizations of Wilson’s Plovers in Texas and Virginia were similar to those described by Tomkins (1944) for the same species in Georgia (Table 1), with a few exceptions. The only territorial posture he mentioned was squatting, which I saw in alarm contexts only (see above). Tomkins (1944) saw Broken-wing displays during incubation, when they also occurred in Virginia but not in Texas (see above). Copulation in Texas appeared to be more limited to the nesting territory than it was in Georgia (Tomkins 1944:262). I did not see or hear a male display and call given from the scrape preceding the Scrape-ceremony, with bill and tail up (Tomkins 1944:265).

An increase in the intensity of distraction displays during the breeding cycle, similar to that in Wilson’s Plovers in Texas, also occurs in other shorebirds, including several plovers (Gochfeld 1984, Bomford 1986). Geographic variation in the timing and occurrence of distraction displays (such as that found in the use of the Broken-wing display) is less common, but also occurs in several other shorebirds (Gochfeld 1984:336).

Many behavioral patterns of Wilson’s Plovers resemble those of other plovers. Similarities with the behavioral patterns of three other plovers, Snowy Plovers (*Charadrius alexandrinus*), Mountain Plovers (*C. montanus*), and Double-banded Dotterels (*C. bicinctus*) were determined subjectively, based on similarity of structure and context with published descriptions and sonagrams (Table 1). Alarm and distraction displays are not listed because they are quite similar in many plover species (Cramp and Simmons 1983). The name used by other authors for a similar behavior or “same” (if they used the same name) is listed.
Bergstrom • BREEDING BEHAVIOR OF WILSON’S PLOVERS 47

Table 1
SIMILAR DISPLAYS AND VOCALIZATIONS IN OTHER PLOVERS

<table>
<thead>
<tr>
<th></th>
<th>Wilson’s Plover*</th>
<th>Snowy Plover*</th>
<th>Mountain Plover*</th>
<th>Double-banded Dotterel*</th>
</tr>
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<tbody>
<tr>
<td>Territorial displays</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Horizontal-hunched</td>
<td>Same</td>
<td>Head-down threat</td>
<td>Same</td>
<td>Same</td>
</tr>
<tr>
<td>Horizontal bulged-breast</td>
<td></td>
<td>Horizontal threat</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Horizontal spread run</td>
<td>Horizontal threat</td>
<td></td>
<td>Horizontal spread</td>
<td></td>
</tr>
<tr>
<td>Upright-hunched</td>
<td>Same</td>
<td>Upright threat</td>
<td></td>
<td>Erect puff breast</td>
</tr>
<tr>
<td>Parallel Run</td>
<td>Same</td>
<td>Same</td>
<td></td>
<td>Same</td>
</tr>
<tr>
<td>Courtship displays</td>
<td></td>
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<tr>
<td>Scrape-ceremony</td>
<td>Nest-location</td>
<td>Scrape exchange</td>
<td>Scrape exchange</td>
<td></td>
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<tr>
<td>Horizontal bulged-breast</td>
<td>Running crouch?</td>
<td>Horizontal dance*</td>
<td>Head-low</td>
<td></td>
</tr>
<tr>
<td>Upright-hunched</td>
<td>Stands erect?</td>
<td>Same</td>
<td>Upright precopulatory posture</td>
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</tr>
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<td>Marking time</td>
<td>Same</td>
<td>Same</td>
<td>Upright posture</td>
<td>Parade march</td>
</tr>
<tr>
<td>Vocationalizations</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Tweet</td>
<td>Peet</td>
<td>Same</td>
<td>Tu-lup</td>
<td>Same</td>
</tr>
<tr>
<td>Peet</td>
<td>Tut-tut</td>
<td>Same</td>
<td>Prrr</td>
<td>Same</td>
</tr>
<tr>
<td>Fweep</td>
<td>“Song-rattle”</td>
<td>Same</td>
<td></td>
<td>“Cheedle”</td>
</tr>
<tr>
<td>“Distraction” call</td>
<td>Harsh guttural</td>
<td>Same</td>
<td></td>
<td></td>
</tr>
<tr>
<td>“Mooing”</td>
<td>Dove note</td>
<td>Same</td>
<td>Same</td>
<td>Same</td>
</tr>
</tbody>
</table>

* C. wilsonia, Tomkins (1944), except Bent (1929) for Tut-tut.
* C. alexandrinus, Cramp and Simmons (1983).
* C. montanus, Graul (1973a) for displays, Graul (1974) for calls.
* Boyd (1972); similar context, but posture lacks bulged breast.

The plovers listed all use a horizontal posture in the Parallel Run, but some other plovers (e.g., Killdeers [C. vociferus], Phillips 1972, and Piping Plovers [C. melodus], Cairns 1982) use an upright posture in a similar display. Tail flicking during Marking time has not been reported in other plovers. The only posture in other plovers resembling the Forward-tilt of Wilson’s Plovers is the Forward-oblique display of Ringed Plovers ([C. hiatricula], Cramp and Simmons 1983:135, fig. A right), which is used by females but not males before copulation. Many of the other postures of
Table 2

CHARADRIUS PLOVERS WITH PLUMAGE OR DISPLAYS SIMILAR TO WILSON'S PLOVER

<table>
<thead>
<tr>
<th>Plumage group (Graul 1973b)</th>
<th>Display group (Phillips 1980)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilson's Plover</td>
<td>Wilson's Plover</td>
</tr>
<tr>
<td>Collared Plover (C. collaris)</td>
<td>Collared Plover</td>
</tr>
<tr>
<td>Madagascan Sandplover (C. thoracicus)</td>
<td>Madagascan Sandplover</td>
</tr>
<tr>
<td>Ringed Plover</td>
<td>Snowy Plover</td>
</tr>
<tr>
<td>Little Ringed Plover (C. dubius)</td>
<td>Three-banded Plover (C. falklandicus)</td>
</tr>
<tr>
<td>Semipalmated Plover (C. semipalmatus)</td>
<td>Kittlitz Sandplover (C. pecuarius)</td>
</tr>
<tr>
<td>Long-billed Plover (C. placidus)</td>
<td>Malaysian Sandplover (C. peronii)</td>
</tr>
<tr>
<td></td>
<td>Chestnut-banded Sandplover (C. pallidus = venustus)</td>
</tr>
</tbody>
</table>

Ringed Plovers are different from those of Wilson’s Plovers. The greatest number of similarities in the table occur with Snowy Plovers; they lack only the bulged breast in the horizontal posture in territorial and courtship contexts.

The Scrape-ceremony and copulation behavior of Wilson’s Plovers resemble those of seven other Charadrius in which the female also approaches the side of the male, the male grabs the nape of the female during Mounting, and the pair topples (Phillips 1980) (Table 2). Mountain Plovers lack the nape-grabbing, and Double-banded Dotterels have a choking display not found in Wilson’s Plover (Phillips 1980). This display group has some anatomical similarities (Phillips 1980) but it has a variety of plumage patterns, while six other Charadrius with head plumage patterns similar to those of Wilson’s Plover (Graul 1973b) (Table 2) have a variety of Scrape-ceremonies and copulation behaviors (Phillips 1980, Cramp and Simmons 1983).

Bock (1958) grouped Wilson’s Plover with the ringed plovers, similar to the plumage group in Table 2. In basing his groupings within this genus mainly on plumage, he assumed that plumage was a primitive characteristic. However, plumage could be subjected to considerable selection pressure (Graul 1973b), so similarities in plumage could be derived, just as similarities in behavior could be either primitive or derived. In the absence of firm knowledge about either set of characteristics, it is useful to use both in a taxonomic analysis (Bock 1958:71). Further analysis, possibly using different characteristics, is needed to determine the phylogenetic relationships within this genus.

ACKNOWLEDGMENTS

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Research in Virginia was supported by a Glenn Grant from Washington and Lee University. I thank A. R. Kiester, K. Terwilliger, and the staffs of Laguna Atascosa National Wildlife Refuge and Aransas National Wildlife Refuge for assistance in the field; the Nature Conservancy for permission to work on Metompkin Island; L. Bergstrom for drawing the figures; S. J. Arnold and S. A. Altman for the use of their sound recording equipment; and C. S. Adkisson and J. Mehner for letting me use their sonographs. I thank W. Graul, A. R. Kiester, E. H. Miller, G. W. Page, R. E. Phillips, T. Sordahl, and reviewers G. W. Page and J. R. Walters for helpful comments on earlier versions of the manuscript, and I thank my wife, S. Still, for support and encouragement.

**LITERATURE CITED**


Voucher photographs (accession nos. V06/3/001–V06/3/010) illustrating postures and displays described in the above article have been deposited with VIREO, Academy of Natural Sciences, 19th and The Parkway, Philadelphia, PA 19103.
WADING BIRD COLONY FORMATION AND TURNOVER RELATIVE TO RAINFALL IN THE CORKSCREW SWAMP AREA OF FLORIDA DURING 1982 THROUGH 1985

G. Thomas Bancroft, John C. Ogden, and Barbara W. Patty

Abstract.—Thirty-seven colony sites were used by nine species of nesting wading birds (Ciconiiformes) in the Corkscrew Swamp area (2320 km²) of southwestern Florida during a four-year census. Yearly turnover in colony site use averaged 30–40% with a maximum of 25 active colonies in any one year. The number of species nesting in a colony was correlated with the year-to-year stability of the colony. Fewer colonies formed during drought years. Colony formation occurred later in a season that followed 18 months of below-normal rainfall. Received 12 Feb. 1987, accepted 20 July 1987.

The location and timing of nesting by colonial wading birds (Ciconiiformes) are correlated with surface water conditions and feeding opportunities (Kahl 1964, Kushlan et al. 1975, Kushlan 1976, Ogden et al. 1980). This study was designed to document the species abundance in an area around Corkscrew Swamp Sanctuary of the National Audubon Society in southwestern Florida, and to examine the relationship between rainfall, nesting, and colony locations. The goal of this study was to show responses by nesting wading birds to annual rainfall patterns on a regional rather than individual colony basis.

METHODS

The study site was within a 32-km radius (3217 km²) of the observation tower at Corkscrew Swamp Sanctuary in northern Collier County, Florida. Of this area, 27% was in the Gulf of Mexico and not suitable for wading birds. The four major natural habitats in the area were coastal lagoons with mangrove swamps, freshwater marshes, cypress swamps, and pine-live oak uplands. Much of the upland vegetation had been cleared for farming, ranching, and housing.

We conducted aerial censuses from fixed-wing, single engine aircraft flying at either 200 or 600 m above ground level along 10 transect lines spaced 6.4 km apart in the study area. We flew censuses monthly from March through August, 1982–1985, and during September 1982. To maximize our chances of locating all active colonies, the compass direction of the transects and the altitude flown was alternated between censuses. A constant altitude was maintained throughout a census until a colony was found. Colonies were circled at 200 m to determine activity. We estimated the total number of pairs present regardless of species. Numbers of Wood Storks (Mycteria americana) and Great Egrets (Casmerodius albus) could

1 Ornithological Research Unit, National Audubon Society, 115 Indian Mound Trail, Tavernier, Florida 33070.
be separated from the total count. We did not attempt to count small dark herons. Snowy Egrets (*Egretta thula*) were not abundant in the area (pers. obs.), and we considered all small white herons to be Cattle Egrets (*Bubulcus ibis*). We classified colony sites into saltwater and freshwater habitats. The freshwater sites were further classified based on vegetation that supported the nests: tall-woody vegetation (>10 m), low-woody vegetation (<10 m), and mixture of tall- and low-woody vegetation.

We summed the maximum count of the number of pairs at each colony to determine the total number of breeding pairs in the study area. This procedure provides a minimum estimate of pairs because it does not account for failures before the peak count, or for birds that settle to nest after the count.

We calculated colony site turnover rates using the following formula (Erwin et al. 1981, McCrimmon and Parnell 1983):

$$T_n = \left( \frac{S_1}{N_1} + \frac{S_2}{N_2} \right)$$

where $T_n$ is the turnover between two years; $S_1 =$ number of sites occupied only at first census; $N_1 =$ total number of sites, first census; $S_2 =$ number of sites occupied only at second census; $N_2 =$ total number of sites, second census. $T$ can be converted to a percentage ($T_{max} = 1$). When more than one year exists between surveys, annual turnover rates can be calculated as $T/\text{number of years}$.

**RESULTS**

During the four-year study, 37 different colony sites were used by nesting wading birds (Table 1) (Fig. 1). In 1982 and 1984, 20 sites were active; in 1983, 25 were active; and in 1985, 14 sites were active. Of the 37 total colony sites, 6 were used in all 4 years, 7 were used in 3 years, 10 were used twice, and 14 were used once. The 6 sites active in all 4 years were in large relatively permanent wetlands. Two of these were found on islands in coastal lagoons, three were found in large natural marshes and swamps, and one site was located in a manmade water impoundment. Of the 6 sites used in all years, one coastal colony and two inland colonies moved short distances (<0.5 km) between years.

Colony turnover (see McCrimmon and Parnell 1983) was 32% between 1982–1983, 35% between 1983–1984, and 39% between 1984–1985. Comparing colony use in 1982 to 1984 showed a turnover rate of 55%. Between 1982 and 1985 the turnover rate was 51%. Three colony sites used in 1982 were abandoned during 1983 or 1984, but reused in 1984 or 1985 (Table 1). Of the 37 sites used during this study, ten were known to have been used previously. Two additional sites (Ft. Myers Airport, 1976; Big Hammock, 1980) were active in one of the previous six years but were not active during this study, although several hundred birds settled in Big Hammock during one month of 1985, but did not nest.

Nine species were found nesting in the area during the study (Table 2). White Ibis (*Eudocimus albus*) and Glossy Ibis (*Plegadis falcinellus*) nested
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<tbody>
<tr>
<td>Baucom Cypress</td>
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<td>+</td>
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<tr>
<td>Biggar</td>
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<td>+</td>
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<td>Camp Keais</td>
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<td>Sunniland South</td>
<td>+</td>
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<tr>
<td>12-mile Slough</td>
<td>-</td>
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<td>+</td>
<td>+</td>
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<tr>
<td>West of 12-mile Slough</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tbody>
</table>

*A + indicates the site was active that year, a – indicates no activity.*
Fig. 1. Wading bird colony sites active during 1982-1985 in the Corkscrew Swamp area of southwest Florida. Sites are numbered as in Table 1 (closed circle = active 4 times, open circle = active 3 times, square = active twice, triangle = active once).

only in 1983. Wood Storks nested each year in Corkscrew Swamp Sanctuary, and in 1983 at Sadie Cypress Swamp. Cattle Egrets were found at the greatest number of colony sites each year (Table 2).

The number of species nesting at a site appeared to be related to the yearly use of the site ($\chi^2 = 20.6, P < 0.06$). Fewer than 3 species nested at all 14 sites used only once, compared with 3 or more species nesting at 83% of the 23 sites used more than once. More species tended to nest at sites that were active more often. Of the 14 sites used only once, 9 contained only one species, 4 contained 2 species, and the species present in one were not recorded (probably only Cattle Egrets). Cattle Egrets nested in at least eight of the 14 sites used only once. The one site used in all
Table 2
Number of Active Wading Bird Colonies and Number of Pairs Nesting in a 32-km Radius around Corkscrew Swamp Sanctuary

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<tr>
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<tr>
<td></td>
<td>Wood Stork</td>
<td>1</td>
<td>18</td>
<td>2</td>
<td>2200</td>
<td>1</td>
<td>990</td>
<td>1010</td>
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<tr>
<td></td>
<td>Great Egret</td>
<td>12</td>
<td>650</td>
<td>14</td>
<td>400</td>
<td>12</td>
<td>350</td>
<td>8</td>
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<td></td>
<td>Cattle Egret</td>
<td>13</td>
<td>8500</td>
<td>20</td>
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<td>10,000</td>
<td>9</td>
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<td>Little Blue Heron</td>
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<td>13</td>
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<td>7</td>
<td>+</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Tricolored Heron</td>
<td>2</td>
<td>+</td>
<td>7</td>
<td>+</td>
<td>7</td>
<td>+</td>
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<tr>
<td></td>
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<td>3</td>
<td>+</td>
<td>3</td>
<td>+</td>
<td>6</td>
<td>+</td>
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</tr>
<tr>
<td></td>
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<td>6</td>
<td>15</td>
<td>12</td>
<td>15</td>
<td>4</td>
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</tr>
<tr>
<td></td>
<td>White Ibis</td>
<td>0</td>
<td>1</td>
<td>+</td>
<td>0</td>
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<tr>
<td></td>
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<td>0</td>
<td>1</td>
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<td>&gt;9183</td>
<td>25</td>
<td>&gt;9115</td>
<td>20</td>
<td>&gt;11,346</td>
<td>14</td>
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<tr>
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<td>colonies and pairs</td>
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</table>

*a Number of active colonies with that species nesting.
*b Estimated number of pairs nesting in study area, + indicates species present, but no total count made.

four years that contained only two species was Corkscrew Cypress, which had Wood Storks and Great Egrets.

The three coastal sites (<0.5 km from the coast), which had mangroves as the dominant vegetation, were active in 11 of the 12 colony years. Of the inland sites, five sites had only tall-woody vegetation (>10 m), six had a mixture of tall- and low-woody vegetation, and 23 sites had only low-woody plants (<10 m). For inland sites, the proportion of times a site was active varied significantly with the vegetation type ($\chi^2 = 15.8$, df = 2, $P < 0.001$). Pair-wise comparisons at the 0.01 level for significance showed that sites with a mixture of tall- and low-woody vegetation were active a significantly greater proportion of the time (83% of 24 colony-year records) than those with only low-woody vegetation (39%). Sites with only tall vegetation (60%) did not differ significantly from either low or mixed vegetation types in the proportion of times they were active. Cypress (Taxodium spp.) were the dominant plants at all but one of the colony sites that had tall-woody vegetation. Willows (Salix spp.) were the dominant plants at all except one of the sites with low-woody vegetation.

Nesting populations of wading birds fluctuated greatly among the four years (Table 2). About 9000 pairs nested in 1982 and 1983, 11,000 pairs nested in 1984, and 3300 pairs nested in 1985. Much of the total and annual variation was due to changes in the numbers of nesting pairs of Cattle Egrets (Table 2).
In 1982 the number of colonies active each month peaked between July and September (Fig. 2). In 1983 the peak was in June, in 1984 it was in June–July, and in 1985 a much lower peak occurred in May. In 1982, numerous colonies were still active in September, whereas the number of active colonies had decreased substantially by August in the other 3 years. Fewer than 500 pairs were recorded nesting during March through June of 1982, whereas over 4000 pairs had begun nesting by May of 1983. Although colonies began to form in 1985, as they had in 1983 and 1984, the number of pairs nesting in 1985 was substantially lower than the number of birds that first appeared in colony sites. In addition, in 1985, birds briefly occupied four additional sites, but abandoned each before they began to nest (counts not included in totals for 1985).

Variation in the timing and intensity of nesting seems to be related to the annual pattern and variation in rainfall (Fig. 2). Southwest Florida is characterized by a dry winter–spring and a wet summer (Thomas 1974). In southwest Florida, monthly rainfall averages 40–60 mm from November through April and increases to 180–210 mm from June through September (Thomas 1974, N.O.A.A. 1981–1985). The calendar years of 1981 and 1985 were dry with less than 1000 mm of rainfall at Immokalee Airport (N.O.A.A. 1981, 1985) (Fig. 2). Total annual rainfall ranged from 1450 to 1700 mm in 1982–1984 (N.O.A.A. 1982, 1983, 1984) (Fig. 2).

The delay in the onset of nesting exhibited in 1982 compared with
1983–1984 appears related to the dry year in 1981 and dry winter–spring of 1982 (Fig. 2). Only 225 mm of rain fell from January 1982 to 21 May 1982 (compared to 560 mm in 1983 and 354 mm in 1984 during the same period). When more typical rains began in early summer 1982, wading birds that had not nested earlier began to do so. Presumably the rains triggered nesting activity by reflooding nesting habitats (waders in south Florida rarely nest over dry habitats) and by increasing feeding habitats. That nesting wading birds failed to increase to the levels of the previous three summers in 1985 was almost certainly caused by the relatively small amounts and the lateness of the summer rains (Fig. 2). During 1985 at Immokalee Airport, only 9 mm fell in May and 107 mm in June, which was substantially less than the rainfall in May and June of 1982 (617 mm), 1983 (221 mm), or 1984 (338 mm). In 1985, colonies formed initially but most were abandoned by the end of June when many of the sites were dry. The dryness probably resulted in a lack of suitable nest sites. Through mid-July, most of the study area was quite dry with no water under many of the willow “heads” used for nesting and the marshes were dry. Few feeding herons and egrets were observed throughout the circle. Although marshes finally became wet in late July and August 1985, nesting did not resume.

**DISCUSSION**

Only 16% of the colonies in our census area were active in all four years. For colonies throughout peninsular Florida that were censused at least five times between 1976 and 1982, we found that of 46 coastal sites (estuarine and marine), 80% were active in at least five years, whereas only 39% of the 79 inland sites (freshwater) were active that often (Nesbitt et al. 1982; National Audubon Society, unpubl. data). Black et al. (1984) using data from Nesbitt et al. (1982) found that 83% of the 52 colony sites in southwestern Florida used in 1976 were also used in 1977 and 1978. For coastal colonies along the Atlantic Coast from Florida to Maine, Custer et al. (1980) found that 91% of the 186 active colonies in 1975 were also active in 1976. Similarly, other studies have found lower turnover rates for wading bird colonies in coastal North Carolina and coastal Massachusetts (Erwin 1978, McCrimmon and Parnell 1983).

Two factors contribute to making our turnover estimates higher than others. First, because we ran transects across our study area, we were confident that we found all active colonies in each year. For other studies done over larger areas the researchers were less certain that all active colonies were located annually, and therefore, they looked at turnover by considering only those colonies that had been censused in all years. This would make their turnover estimates lower than they actually may have
been (e.g., Black et al. 1984). The second explanation for our higher turnover estimates is that coastal colonies have a much higher probability of being active each year than do inland colonies (National Audubon Society, unpubl. data). Coastal colonies are in habitats in which the total area of inundated wetlands surrounding each colony is more consistent among years than is the case for many inland freshwater sites. Some of the inland colony sites we observed were used in years when they were flooded and not when they were dry.

The timing of the maximum number of active colonies varied among years. Ogden (1978), using data collected by R. P. Allen, reported that the historical pattern for southern Florida was for colonies to form in the spring, with peak number of colonies active during May and June. During the mid-1970s, more colonies were active later in the summer with peak numbers of active colonies occurring in June and July (Kushlan and White 1977, Ogden 1978). Our data show both patterns. Following the extremely dry 1981 summer and dry winter-spring of 1981-1982, we found a higher frequency of summer nesting after the initiation of rains during May–June 1982. During the relatively normal rainy seasons (see Thomas 1974) of fall 1982 through fall 1984, we found nesting starting earlier than in 1982 (Fig. 2). During the extremely dry year of 1985, little nesting occurred, and much of that was not successful. Because many birds abandoned colonies before they would have completed nesting in 1985, peak nesting occurred in May.

The quantity and timing of rainfall affects the chances of successful nesting by wading birds by determining the availability of suitable colony sites and by influenceing the availability of food. Nests were placed in trees over water in all freshwater sites except one island site in a borrow pit. When these sites were not flooded, the birds did not nest in them (pers. obs.). Secondly, rainfall influences the amount of food in the environment and the food’s availability to the birds. Average or above average rainfall during the preceding summer probably allows fish populations to increase to high levels (Kahl 1964, Kushlan et al. 1975). A dry period results in the concentration of fish into pools where herons, egrets, and storks feed on them. This seasonal dry period appears to be critical for successful nesting by wading birds in southwest Florida (Kahl 1964, Kushlan et al. 1975, Kushlan 1976, Browder 1984). Although Cattle Egrets are terrestrial feeders, rainfall may trigger nesting not only by increasing the availability of suitable nesting sites, but also by increasing the abundance of their primary prey, orthopterans (Lowe-McConnell 1967, Fogarty and Hetrick 1973, Siegfried 1978). Thus, the high summer peaks in nesting were largely caused by heavy Cattle Egret nesting during “normal” summer rainfall years.
ACKNOWLEDGMENTS

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LITERATURE CITED


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THE FREQUENCY OF CUCKOLDRY IN THE EUROPEAN STARLING (STURNUS VULGARIS)

ANN S. HOFFENBERG, HARRY W. POWER, LINDA C. ROMAGNANO, MICHAEL P. LOMBARDO, AND TERRY R. McGUIRE

Abstract.—Cuckoldry was studied in a New Jersey population of European Starlings (Sturnus vulgaris). Biopsy of both blood and pectoral muscle was done on 550 wild birds, including both adults and all chicks at 95 nests between 1983–1985. Vertical thin-layer polyacrylamide gel electrophoresis (PAGE) was employed rather than starch gel electrophoresis because we found through using both that PAGE has greater resolution for the enzymes we examined. Thirty-three loci were screened, but only three were both resolvable and found to have bona fide polymorphism. Two unambiguous cases of cuckoldry were discovered, each involving two chicks. Another six cases may have been either cuckoldry or intraspecific brood parasitism; they involved only one chick each. If only the two unambiguous cases are counted, the frequency of cuckoldry was 2.1%. If the six ambiguous cases are included, the frequency was 8.4%. Low measured frequencies do not necessarily imply a low risk of cuckoldry because they may reflect the conservatism of electrophoresis and the effectiveness of anticuckoldry behaviors. Cuckoldry may be a serious, but contained, risk in our population. Received 18 Mar. 1987, accepted 15 June 1987.

Cuckoldry is defined as “a male’s involuntary rearing of another male’s offspring as a result of the latter male (the “cuckolder”) having inseminated the mate of the former male (the “cuckold”)” (Power et al. 1981). This can occur as a result of extrapair copulation(s) by a female when she is unguarded by her mate, with or without her cooperation. Although there has been some disagreement regarding its usage (Gowaty 1982, 1984; Power 1984), the term “cuckoldry” seems to be the best term to describe the above defined phenomenon. Cuckoldry specifically refers to the situation in which males are the victims of an act of mate infidelity, and distinguishes between that phenomenon and brood parasitism. In this paper we use the term “cuckoldry” as it is this specific phenomenon that we wish to address.

Cuckoldry is significant from an evolutionary standpoint, because it negatively affects the reproductive success of the cuckold. Thus, males should evolve anticuckoldry behavior, and this behavior should evolve in tandem with the evolution of male parental investment. Without cuckoldry avoidance behavior, cuckoldry should impede the evolution of male parental investment, because males who do not provide parental investment will be rewarded genetically while males who do provide it will be

Because birds comprise a group of animals in which male parental care is prevalent and highly developed, we expected to find behavior associated with cuckoldry in European Starlings (Sturnus vulgaris). In fact, many observations suggesting that cuckoldry is indeed a serious threat to the male who makes a substantial parental investment have been made in recent years in various avian species. For example:

(1) Mate guarding, the close association between males and their mates occurs with the highest frequency during the fertilizable period (Birkhead 1979, Power et al. 1981, Lumpkin et al. 1982).

(2) Extrapair copulations (EPCs) have also been observed in many apparently monogamous species of birds (McKinney et al. 1984), indicating the widespread existence (or at least possibility) of cuckoldry.

(3) EPCs have elicited various responses from males towards their mates. In some species, particularly ducks, EPCs are sometimes accomplished by force (McKinney et al. 1984), and in some of these the female’s mate has been observed to copulate with her immediately afterward, apparently in response to the forced copulation of the intruder male(s). This response is consistent with the threat of cuckoldry as well as the notion of sperm competition and the “last male advantage.” Female birds of some species are known to be able to store sperm for substantial periods of time (McKinney et al. 1984) with the most recently introduced sperm being the most likely to fertilize the eggs, both because of viability due to the age of sperm and their location in the female reproductive tract.

(4) In Ring Doves (Streptopelia risoria), males were found to reject females forcibly as prospective mates when these females had actually or apparently already been inseminated by other males (Erickson and Zenone 1976, Zenone et al. 1979).

Because the European Starling is an apparently monogamous species in which the male provides a good deal of parental care (Kessel 1957, Feare 1984), we looked for cuckoldry and associated behavior in this species. Certain apparently anticuckoldry behavioral patterns have, in fact, been documented in our Piscataway, New Jersey, population of starlings suggesting that cuckoldry is a threat to the male birds in this population. Male starlings have been found to monitor carefully the movements of their mates during the egg-laying period and to delay the onset of their own incubation duties, apparently so that they may continue to monitor their mates closely until the end of this vulnerable period (Power et al. 1981).

Until recently the existence of cuckoldry and the actual frequency with which extrapair copulations resulted in fertilization of eggs could only be
estimated crudely. Here we used electrophoresis to provide unequivocal evidence of genealogical relationships.

Evans (1980) had already used these methods to examine genetic variation in the European Starling in Britain in relation to its population biology. Other investigators have applied these methods to other species and have shown the existence of multiple parentage (Eastern Bluebirds \textit{[Sialia sialis]}, Gowaty and Karlin 1984; Bobolinks \textit{[Dolichonyx oryzivorus]}, Gavin and Bollinger 1985; Acorn Woodpeckers \textit{[Melanerpes formicivorus]}, Joste et al. 1985; Mumme et al. 1985).

**MATERIALS AND METHODS**

We studied starlings on the Kilmer Campus of Rutgers—The State University of New Jersey, in Piscataway, Middlesex County, New Jersey. The campus supports a population of starlings that has been monitored since 1975 (Power et al. 1981). Starlings nest in wooden nestboxes that are mounted on telephone poles along roadways. The area delineated by the roadways included some scattered buildings, fields in various stages of succession, and some large areas of mowed lawn.

Censuses were made regularly and were begun a few days before the date on which we expected laying to begin. In 1983 and 1984, nests were visited twice daily during the laying period, once in the morning and once again in the afternoon. In 1985, nests were visited three times daily during the laying period. Censuses began at 07:00, 11:00, and 16:00 EST.

Eggs were numbered in sequential order with a waterproof marking pen. Censusing ceased at any particular nest when no additional eggs were laid for three consecutive days. In order to identify hatchlings as to egg number, we modified a technique developed by Rotterman and Monnett (1984) that enabled us to dye the embryos before hatching. The dyes used were Durkee and McCormick brand food colors in red, blue, green, and yellow.

Embryos were colored by injecting dye into the air chamber of the egg when pipping was observed. Subsequently, the egg number of each hatchling was preserved by clipping its toenails according to a scheme in which each toe represented a number (Romagnano 1987). The clipped toe remained discernible for some time, enabling us to band and identify each chick in a nest by its egg number at the time of biopsy.

Because the use of electrophoresis required that we obtain tissue samples, we captured all adults and young. Upon capture, all birds were given numbered aluminum U.S. Fish and Wildlife Service bands. In addition, adults were given sex-specific color bands. Sex was determined according to the color of the iris and the base of the bill (Kessel 1951, Evans 1980, Feare 1984).

Adult females were captured at night when they brooded chicks, the sixth day after hatching of the last chick. Adult males were captured by means of a radio-control trap (modified from a design used by Lombardo and Kemly [1983]) the following morning when they went to feed chicks.

Our biopsy procedure was modified from Baker (1981) and Seidensticker (1970) (Romagnano 1987). A small portion of pectoral muscle was removed and placed in a tube with homogenizing solution. This preparation was then placed on ice. Next, blood was drawn from the bird's brachial vein. Heparinized microhematocrit tubes were filled with blood
and then emptied into a plastic tube. The tube was immediately placed on ice. Only one of the 365 chicks biopsied died as a result of this procedure (Stangel 1986, Westneat et al. 1986).

Upon returning to the lab, muscle tissue was immediately frozen at -80°C. Blood was refrigerated at 4°C and spun for 10 min in a 13,750-rpm centrifuge (within 48 h of collection). After separation, the plasma was decanted and frozen at -80°C. The cellular fraction remaining in the tube was reserved and frozen. Plasma was then ready for use and could be thawed and loaded into a gel. Previously frozen pectoral muscle, however, had to be thawed and ground manually in the homogenizing fluid already present in the tube. The sample was centrifuged, and the supernatant decanted to separate it from cellular material. The supernatant was refrozen at -80°C until needed.

Electromorphs were determined for each bird at the three loci found to be resolvable and genetically polymorphic among the 33 that were screened. The three genetically polymorphic loci were amylase in plasma, and esterase zones 1 (more anodal) and 2 (less anodal) in pectoral muscle. An electromorph, for purposes of parental exclusion, was presumed to represent a genotype. A male was considered to have been cuckolded if his electromorph was not consistent with that of all of his putative chicks, provided there was no evidence of brood parasitism. If there was evidence of the latter, a judgement as to whether a male was cuckolded or the victim of brood parasitism was made based on field observations (see below).

A total of 550 birds were captured and biopsied at 178 nests, including both adults and all chicks at 95 nests in 1983–1985. Vertical thin-layer polyacrylamide gel electrophoresis (PAGE) was employed rather than starch because it has greater resolving power for the enzymes we examined. The procedures used for PAGE are described by Taggart et al. (1978). Recipes for stains were taken from Steiner and Joslyn (1979). Separation (pH 8.8), stacking (pH 6.8), and electrode buffer (pH 8.3) solutions were made in accordance with recipes for System A in Taggart et al. (1978). The gels themselves were mixed to obtain a 7% separation gel and a 5% stacking gel (Taggart et al. 1978).

Upon completion, gels were scored and photographed for our permanent records using black-and-white film. Scoring was according to Brewer (1970).

RESULTS

Each of the three electrophoretically resolvable polymorphic loci used was found to conform to Hardy-Weinberg equilibrium (Romagnano 1987). The adult allelic frequencies for amylase were 0.42 for the allele we designated F and 0.58 for S. The allelic frequencies for esterase 1 were 0.04 for F, 0.92 for S, and 0.04 for D. Those for esterase 2 were 0.94 for A and 0.06 for B.

Table 1 lists the genetic mismatches that were detected by electrophoresis in 1984 and 1985. The final assignment of any particular mismatch to one of three categories (cuckoldry, parasitism, or unassigned) depended ultimately on a careful review of the field notes.

Cuckoldry could be detected only electrophoretically, but a mismatch between the male resident at a nest box and his putative chicks could not be taken by itself as sufficient evidence of cuckoldry, as mismatch could arise if intraspecific brood parasitism had occurred. Field evidence of intraspecific brood parasitism included (1) the discovery of two new eggs
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<th>Parasitem</th>
<th>Unassigned</th>
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<td>Chick 2 = FS</td>
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<td>Male = FF</td>
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<td>Female = FS; AA</td>
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<td>Chick 1 = FF; AB</td>
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| (5) Clutch size = 7 (1985) |
| System = Esterase 1 |
| Female = SS |
| Male = FS |
| Chick 3 = SD |

| (6) Clutch size = 4 (1985) |
| System = Esterase 1 |
| Female = SS |
| Male = SS |
| Chick 4 = FS |

* Year.
in a nest in one 20-h interval, (2) removal of previously marked eggs, and (3) the discovery of unmarked eggs at the base of a nestbox pole. Points (2) and (3) were considered evidence of brood parasitism because egg removal and dumping are tactics of brood parasites (Lombardo, unpubl. data). Because eggs are more or less female specific (Feare 1984), egg color, size, and shape were also noted in field notes as possible indicators of parasitism. Consequently, field notes were reviewed carefully for all nests at which mismatches were detected before a final determination was made. Cuckoldry was considered to have occurred if a mismatch with the male was detected and none of the above signs of parasitism had been observed. (For a detailed account of determinations, see Hoffenberg [1986] and Romagnano [1987].)

Cuckoldry was clearly detected at two nests in 1985 in second broods (Table 1). Five of the genetic mismatches were attributable to brood parasitism. The remaining mismatches were unassigned due to ambiguous evidence. They can be regarded as potential additional cases of cuckoldry. If only the two unambiguous cases are considered, then the frequency of cuckoldry was 2.1% (2/95 complete families). If the six ambiguous cases are added, the frequency of cuckoldry was 8.4% (8/95 complete families).

In order to detect cuckoldry through electrophoresis, the cuckold must have a genotype that differs from that of the putative father. Otherwise cuckoldry will go undetected. For two of our enzyme systems (esterases 1 and 2), the allelic frequencies indicated that the birds were nearly monomorphic (i.e., the most common alleles at each locus were 0.92 and 0.94, respectively), making it highly probable that a cuckold and a cuckolder would have the same genotype. Therefore the cuckoldry frequencies detected by this study yield conservative estimates of the actual frequency of cuckoldry.

**DISCUSSION**

It is noteworthy that each of the two unambiguous cases of cuckoldry occurred in second broods (all other genetic mismatches occurred in first or replacement broods). Second broods were not as closely attended by males as first broods (pers. obs.) and we believe that females were likewise not as carefully guarded.

Each of the two unambiguous cases involved two chicks, suggesting that cuckoldry may frequently involve more than one egg per nest. In contrast, usually only single parasite eggs are found in nests (Power, unpubl. data; Romagnano 1987). This difference probably reflects the different logistics of cuckoldry and brood parasitism. Cuckoldry is logistically simple because a single insemination can potentially fertilize several eggs, given that starlings can store sperm. Bullough (1942) described uterovaginal folds similar to those later found to be sperm storage organs in other
species (Compton et al. 1978, McKinney et al. 1984). Brood parasitism, however, is logistically more difficult because (1) a female starling can lay only one egg in a day (Romagnano 1987) and (2) parasites must get past host defenses each time they try to dump an egg. This makes the occurrence of more than one parasite egg/nest uncommon.

The detection of cuckoldry in our population supports our interpretation that the close guarding of females by males during the fertilizable period functions to protect males against cuckoldry. The range of frequencies (2.1–8.4%) that we measured is lower than we had expected based on our observations of cuckoldry avoidance behaviors, but this does not necessarily imply a low risk of cuckoldry as it might simply reflect the conservatism of electrophoresis, or the effectiveness of anti-cuckoldry behavior. Thus while the behavior of males suggests that cuckoldry is a serious risk in our population, it may be a contained one.

The low frequency of cuckoldry that we detected is consistent with similarly low frequencies of multiple paternity detected by electrophoresis in other species (Gowaty and Karlin 1984, Gavin and Bollinger 1985, Joste et al. 1985, Mumme et al. 1985). However, we do not know whether these low frequencies imply that cuckoldry (or multiple paternity) actually occurs at low levels, or whether this finding is only an artifact of electrophoresis and its associated techniques. The various difficulties we encountered (low variability in enzyme systems, nongenetic patterns of polymorphism) call into question whether electrophoresis is actually a good technique for this kind of study. Mumme et al. (1985) were quite explicit about the problems they encountered, and emphasized the low return that is obtained in relation to the great effort expended in such a study.

Other techniques must be explored for detecting cuckoldry in birds. Some possibilities that may be worth exploring are radiotracers (Scott and Tan 1985) and DNA marker analysis (Burke and Bruford 1987, Quinn et al. 1987, Wetton et al. 1987). We agree with Mumme et al. (1985) that electrophoresis, in its current state, is simply too time-consuming and expensive, considering the data it yields.

ACKNOWLEDGMENTS

We would like to thank K. Cybulski, H. Heintz, T. Vail, and P. C. Stouffer for their assistance in the lab and field, as well as the students in Animal Social Behavior Lab 444 at Rutgers University for their time and effort in the field. This study was supported by NSF grant BSR 8316361 to H. W. Power and T. R. McGuire, and two Busch Memorial Grants from Rutgers University to H. W. Power.

LITERATURE CITED


TECHNICAL PAPERS SOUGHT BY THE NORTH AMERICAN BLUEBIRD SOCIETY

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SUCCESSFUL INCUBATION OF EXPERIMENTALLY ENLARGED CLUTCHES BY HOUSE WRENS

MICHAEL E. BALTZ AND CHARLES F. THOMPSON

Abstract.—We tested the hypothesis that clutch size is limited by the inability of female House Wrens (*Troglodytes aedon*) to incubate more eggs than they typically lay in a clutch. We studied wrens that were breeding in nestboxes placed in a forest in central Illinois. We added two eggs to clutches of seven eggs early in the breeding season and two eggs to clutches of six eggs late in the breeding season in 1986. Incubation success was measured by counting the number of chicks present in the nest four days after the first egg of the clutch had hatched. In both early- and late-season nests, incubation success of experimentally enlarged clutches was significantly higher than that of control clutches. We conclude that clutch size of House Wrens is not likely limited by the female’s inability to incubate additional eggs. Received 29 Apr. 1987, accepted 19 Aug. 1987.

Clutch size is an important component of reproductive effort in birds, and many hypotheses have been proposed to explain how it is limited in nidicolous species (see reviews by Lack 1968, Klomp 1970, von Haartman 1971, Winkler 1985). The focus of most research has been on the nestling-fledgling stages of the breeding cycle (Lack 1947, 1954, 1968). Considerably less attention has been given to the possibilities that in nidicolous species: (1) energy or nutrient availability during egg synthesis may limit production of eggs by females, or (2) the ability to incubate the eggs may constrain clutch size.

Because previous work on our study area showed that House Wrens (*Troglodytes aedon*) were able to rear experimentally enlarged broods without apparent ill effect on the chicks or on the female within a breeding season (Finke et al. 1987), we experimentally enlarged clutches to test the hypothesis that the natural clutch size of House Wrens corresponds to the maximum number of eggs that females can incubate successfully.

MATERIALS AND METHODS

The experiment was conducted in 1986 on a 108-ha forested study area 18.5 km north and 8.5 km east of the McLean County Courthouse, Bloomington, Illinois (Section 4, T 25N, R 3E, Gridley quadrangle, McLean County), where House Wrens have been studied since 1980, when nestboxes were first placed in the forest. In 1986, wrens built 554 nests (first and second broods, as well as renests) in the 585 identical, evenly dispersed nestboxes on the study tract. The 8.4 cm × 9.0 cm floor of each nestbox was 14.6 cm below the center of the entrance hole. Additional information about the study area and nestboxes is presented in Drilling and Thompson (1984) and Finke et al. (1987).
Nestboxes were checked twice weekly after wrens began breeding in May. The day on which the first egg was laid in a nest is referred to as the egg-1 day of the nest. Clutch size typically ranged from 3 to 8 eggs, with a modal clutch size of 7 eggs early in the season and 6 eggs late in the season (Finke et al. 1987). Only the female incubated the eggs (Kendeigh 1952, Thompson, pers. obs.). For most enlargements, we added two eggs to modal-size clutches. Thus, early in the season most enlarged clutches had 9 eggs (original clutch size = 7 eggs) and late in the season most had 8 eggs (original clutch size = 6 eggs). Unmanipulated early-season clutches of 7 eggs and late-season clutches of 6 eggs served as controls. Additional controls in which eggs were switched among clutches, but clutch size remained the same, were not employed because earlier experiments had shown that House Wrens did not reject conspecific eggs added to their nests during egg laying (D. Price, pers. comm.). A few clutches that we increased to sizes other than 8 or 9 eggs were analyzed separately.

The age, incubation history, and size of the donor clutch relative to that of the recipient clutch could influence the outcome of the experiment, and we attempted to match recipients and donors as closely as possible. Eggs were added on or before the day after egg laying ended in 25 of 28 (89%) early-season nests and 14 of 22 (64%) late-season nests; the age and incubation status were matched as closely as possible in the remaining nests. Some of the eggs used to create enlarged clutches came from females induced by daily egg removal to lay additional eggs beyond the normal clutch size (see Kendeigh et al. 1956); eggs used from these nests came from the first eight eggs to be laid. Nine of 22 (41%) early-season nests from which eggs were taken for addition to the experimentally enlarged clutches had clutches of 7 eggs, and 17 of 22 (77%) late-season donor nests had clutches of 6 eggs (Table 1).

Nests were checked daily as the estimated date of hatching approached, which allowed determination of the number of eggs surviving the incubation period and of the day on which the first chick hatched (brood-day 0). We used the number of chicks (brood size) present on brood-day 4 as the measure of the females' ability to incubate clutches of different sizes. This measure of incubation success combines losses from two distinct, but potentially related, sources. The first is loss caused by the failure of eggs to hatch and the second is loss caused by the death of chicks shortly after they emerge from the egg. We cannot distinguish between these sources of mortality, because parents remove dead chicks (usually) and unhatched eggs (occasionally) between our visits to the nest (Thompson, pers. obs.). Assuming that one egg is laid each day, the incubation period was estimated as the interval from the day that the last egg of the clutch was laid (calculated as egg-1 day + clutch size) to brood-day 0. Data on unmanipulated clutches from the 1984 and 1985 breeding seasons were included for some comparisons.

Statistical tests were performed using subprograms of the Statistical Analysis System (SAS 1985).

### Table 1

<table>
<thead>
<tr>
<th>Season</th>
<th>Un-known&lt;sup&gt;a&lt;/sup&gt;</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>No. of clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>4.5</td>
<td>31.8</td>
<td>40.9</td>
<td>9.1</td>
<td>4.5</td>
<td>4.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>22</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late</td>
<td>13.6</td>
<td>77.3</td>
<td>9.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>22</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Nest abandoned before clutch was completed.

<sup>b</sup> Nests in which the female was induced to lay additional eggs by removing eggs on successive days; see text.
RESULTS

Nest survival.—Of 28 early-season 7-egg clutches to which two eggs were added, 24 (85.7%) survived the incubation period and had at least one chick successfully hatch from the eggs of the clutch. Of these 24 enlarged clutches, 23 (95.8%) still had chicks on brood-day 4. In 7-egg controls, 98 of 113 clutches (86.7%) survived to hatching, with 92 of these 98 clutches (93.9%) surviving with chicks to brood-day 4. There is no significant difference in the proportion of control and enlarged clutches surviving incubation \( (\chi^2 = 0.02, \text{df} = 1, P > 0.05) \) or in the proportion of those hatching that survived to brood-day 4 \( (\chi^2 = 0.14, \text{df} = 1, P > 0.05) \).

Similarly, of 22 late-season 6-egg clutches to which two eggs were added, 19 (86.3%) survived the incubation period to hatch at least one chick. Of these 19 clutches, 17 (89.4%) had chicks present on brood-day 4. In 6-egg controls, 57 of 66 clutches (86.4%) survived to hatching, with 50 of these 57 clutches (87.7%) surviving with chicks to brood-day 4. Again, there is no significant difference in the proportion of control and enlarged clutches surviving incubation \( (\chi^2 < 0.01, \text{df} = 1, P > 0.05) \) or of those surviving from hatching to brood-day 4 \( (\chi^2 = 0.15, \text{df} = 1, P > 0.05) \).

Early- and late-season enlarged clutches that failed before brood-day 4 and control clutches that failed were equally likely to have been abandoned as to have failed from other causes (Early, \( \chi^2 = 0.34, \text{df} = 1, P > 0.05 \); Late, \( \chi^2 = 0.40, \text{df} = 1, P > 0.05 \) (Table 2).

Incubation success in unmanipulated clutches.—The number of chicks present on brood-day 4 (incubation success) in unmanipulated early- and late-season nests in 1984–1986 generally increased as clutch size increased (Fig. 1), and there was not a marked decrease in the proportion of eggs
Fig. 1. Number of chicks present on brood-day 4 (incubation success) of unmanipulated clutches in 1984, 1985, and 1986, in relation to clutch size. Horizontal bar is the mean; filled rectangle is ±2 SE. Sample size for each clutch size is given above the rectangle.
that hatched or neonates that died between hatching and brood-day 4 over the range of natural variation in clutch sizes.

To determine if incubation success varied seasonally among years, the effects of clutch size, year, and their interaction on brood size were investigated using a 2-way analysis of variance. For both early- and late-season nests, there is a significant effect on brood size of clutch size (early: $F_{6,493} = 23.0, P < 0.001$; late: $F_{6,494} = 54.7, P < 0.001$), but not of year (early: $F_{2,493} = 2.1, P > 0.05$; late: $F_{2,494} = 1.9, P > 0.05$) (Type III sum of squares) (SAS 1985). Neither interaction is significant ($P > 0.05$). Thus, incubation success of unmanipulated clutches did not vary significantly among the 1984-1986 breeding seasons. Another comparison among these three breeding seasons was made by considering the incubation success of unmanipulated early-season, 7-egg clutches and late-season, 6-egg clutches. Incubation success is not significantly different among years in early-season, 7-egg clutches (Kruskal-Wallis test, $\chi^2 = 2.88, P > 0.05$), but it is significantly different in late-season, 6-egg clutches (K-W test, $\chi^2 = 6.08, P < 0.05$). Incubation success of late-season unmanipulated clutches was lower in 1986 ($\bar{x} = 5.1$ chicks) than it was in 1984 ($\bar{x} = 5.4$ chicks) and in 1985 ($\bar{x} = 5.5$ chicks).

**Incubation success in enlarged clutches.**—In both early- and late-season nests, enlarged clutches produced significantly more chicks on brood-day 4 than did control clutches (Fig. 2). In early-season clutches, the median brood size produced by enlarged clutches was 8 chicks ($\bar{x} = 7.5$) and by control clutches it was 7 chicks ($\bar{x} = 6.2$) (Wilcoxon 2-sample test, $Z = 4.22, P < 0.0001$) (Fig. 2A, B); in late-season clutches, the median brood size produced by enlarged clutches was 7 chicks ($\bar{x} = 6.9$) and by control clutches it was 5 chicks ($\bar{x} = 5.1$) ($Z = 4.61, P < 0.0001$) (Fig. 2C, D).

Four early-season clutches of 7 eggs and five early-season clutches of 8 eggs were increased to 10 eggs (Table 3). In five of these nine clutches, the number of chicks present on brood-day 4 was greater than the original clutch size laid by the female. One early-season clutch of 9 eggs was increased to 11 eggs, producing 10 chicks on brood-day 4.

**Incubation period.**—Incubation periods of enlarged early-season clutches ($\bar{x} = 12.3$ days $\pm 0.19$ [SE]) were significantly longer than those of controls ($\bar{x} = 11.7$ $\pm 0.08$ days) ($t = 3.54, df = 120, P < 0.001$). For late-season clutches, the incubation periods are not significantly different: enlarged clutches, $\bar{x} = 11.2$ $\pm 0.14$ days; control clutches, $\bar{x} = 11.4$ $\pm 0.11$ days ($t = 0.92, df = 74, P > 0.05$).

**DISCUSSION**

The addition of two eggs to nests containing the most common clutch size in both early and late seasons resulted in significantly more chicks
Fig. 2. The distribution of number of chicks present on brood-day 4 (incubation success) for enlarged and control early-season nests with an original clutch size of 7 eggs (A and B, respectively) and for enlarged and control late-season nests with an original clutch size of 6 eggs (C and D, respectively).

hatching and surviving to brood-day 4. Thus, House Wrens laying modal-size clutches were able to incubate more eggs than they laid, suggesting that clutch size was not limited by incubation ability. Two problems, however, need to be considered when interpreting our results. The first is the use of artificial nest sites, and the second is the lower hatching success of late-season control clutches in 1986 compared with that of unmanipulated clutches in earlier years.

The use of nestboxes rather than natural cavities may have influenced the outcome of the experiment, as our nestboxes are probably larger than most natural cavities (pers. obs.). The effect, if any, of this difference is unknown, but clutch sizes in our nestboxes are similar to those reported from nests in natural cavities (e.g., Sage et al. 1913, Trautman 1940). Nonetheless, the effect of the use of artificial nest sites on incubation success cannot be directly assessed and must await studies of House Wrens nesting in natural cavities.

The lower incubation success of late-season controls in 1986 compared
Table 3

<table>
<thead>
<tr>
<th>No. eggs laid in enlarged clutches</th>
<th>No. eggs added</th>
<th>No. chicks on brood-day 4</th>
<th>No. clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>8</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>

* Clutch depredated by raccoon (Procyon lotor) during incubation.

with that in late-season unmanipulated clutches in 1984 and 1985 raises the question of the generality of conclusions based on results from 1986. The difference, however, occurred during the latter half of the breeding season only and is not great (≤0.4 chicks). Furthermore, whatever was responsible for the decrease in the incubation success of late-season controls in 1986 may well have decreased concomitantly the incubation success of enlarged clutches. If conditions in late 1986 were unfavorable, they should have affected enlarged clutches more severely than controls. That this did not happen suggests that the significant differences between enlarged and control clutches in late 1986 are not a product of unusual conditions at that time.

Kloomp (1970) summarized results of early studies on the ability of females to incubate additional eggs, and Winkler and Walters (1983) discussed the evidence for incubation-limitation in precocial species. In general, many species seem to be able to incubate enlarged clutches successfully. For example, both American Avocets (Recurvirostra americana) (Shipley 1984) and Fieldfares (Turdus pilaris) (Slagsvold 1982) incubate enlarged clutches successfully. In contrast, inability to incubate additional eggs has not been frequently reported, although Andersson (1976) and Tarburton (1987) demonstrated that parents given enlarged clutches failed to produce as many hatchlings as parents incubating unmanipulated clutches in Long-tailed Jaegers (Stercorarius longicaudus) and in White-rumped Swiftlets (Aerodramus spodiopygius), respectively.

The possibility that clutch size may be limited ultimately by an inability to incubate additional eggs has been considered unlikely because (1) hatching success typically does not decrease proportionately with increasing clutch size over the natural range of clutch sizes and (2) clutch size, which has been determined by other selective forces, and the ability to incubate a specific number of eggs have evolved in parallel (Kloomp 1970:37). The first is inapplicable if each female's clutch size is adjusted to her incubation...
ability, resulting in either no correlation or in a positive correlation between clutch size and hatching success; there is no reason to expect a negative correlation. Perrins (1965) and Nur (1984, 1986) have emphasized this with regard to individual variation in ability to rear additional chicks during the nestling stage, and the same argument applies for ability to incubate additional eggs. As House Wrens were clearly able to incubate additional eggs successfully, clutch size was not individually adjusted to the maximum number of eggs that a female could incubate. The second point needs to be considered further only if it can be demonstrated that females are not able to incubate successfully clutches larger than those they initially attempt. This is clearly not the case in the House Wren under the conditions of our experiment.

The possibility remains that although females can incubate additional eggs, females doing so would experience reduced survival or reduced future reproductive success, or both (i.e., they would incur a cost of reproduction). Although there is no general agreement as to the energetic demands of incubation, it is unlikely to be so great as that of other stages of the breeding cycle (see summary by Walsberg 1983). Haftorn and Reinertsen (1985) concluded that, even at the northern limit of the Blue Tit's (Parus caeruleus) breeding range, females in nestboxes are easily able to maintain egg temperatures well above the temperature below which no embryonic development occurs. House Wrens incubate their eggs in well-insulated cavities, and there is little reason to suspect that incubation is so energetically demanding for House Wrens that it is necessary for them to decrease their clutch size to save energy or to maintain egg temperature. Costs, however, may be exacted in other ways.

One possible cost incurred by females incubating enlarged clutches was the extension of incubation by half a day early in the season. Length of the House Wren's incubation period is directly related to ambient temperature, which exerts its influence by affecting female attentiveness (Kendeigh 1952). At low ambient temperatures unattended eggs cool rapidly, and Kendeigh (1963) showed that heat energy applied to eggs by incubating females decreases as air temperature decreases. Furthermore, the amount of heat applied to the eggs is a function of the number of eggs in the clutch (Kendeigh 1963). In our study, early-season ambient temperatures averaged about 7.5°C lower than they were later when incubation periods of controls and enlarged clutches were not significantly different. A prolonged incubation period in enlarged clutches early in the breeding season suggests that females with enlarged clutches were unable to maintain egg temperatures as high as those maintained by females with smaller control clutches. The importance of a half-day's delay in hatching is unknown; however, this effect in 1986, a year in which May temperatures
were 1.3°C above the long-term average, raises the possibility that in unusually cold springs, females laying clutches much larger than the modal size may experience some difficulty during incubation.

In conclusion, House Wrens were able to incubate enlarged clutches in our nestboxes in 1986, and it is unlikely that inability to incubate additional eggs has been an important selective force limiting clutch size in this species.

ACKNOWLEDGMENTS

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LITERATURE CITED


MEETING OF THE ASSOCIATION OF FIELD ORNITHOLOGISTS

The Association of Field Ornithologists (formerly NEBBA) will hold its annual meeting 13–15 May 1988 at the Vermont Institute of Natural Sciences, Woodstock, Vermont. Housing and the Saturday evening banquet will be at the nearby Kedron Valley Inn. The meeting will include invited and contributed papers, workshops and field trips. For information about the meeting, contact: SARAH B. LOUGHLIN, AFO Local Committee Chair, Vermont Institute of Natural Science, Woodstock, VT 05091 (802/457-2779). For information about the scientific program, contact: PETER F. CANNELL, Program Committee Chair, Division of Birds, NHB 116, Smithsonian Institution, Washington, DC 20560 (202/357-2334).
CONSPECIFIC BROOD PARASITISM IN THE
HOUSE SPARROW

PAUL E. KENDRA,*1-2 ROLAND R. ROTH1-3 AND DOUGLAS W. TALLAMY3

ABSTRACT.—We studied 94 clutches of the House Sparrow (Passer domesticus) in Newark, Delaware, to determine: (1) the frequency of apparent conspecific brood parasitism (CBP); (2) if the laying of eggs in a conspecific's nest is truly a parasitic interaction with the recipient; and (3) that indeterminate laying can predispose a species to CBP. Eight clutches yielded evidence of CBP; electrophoresis of egg albumin detected a genetically odd egg in 4 of 42 clutches, while 4 other clutches provided indirect evidence of CBP—visibly odd eggs in other than the ultimate position and two eggs laid in one day. An egg-removal experiment suggested that House Sparrows are indeterminate layers before the third egg is laid; thus a female can increase her fecundity by laying one or more parasitic eggs before completing her own clutch of normal size. A complementary egg-addition experiment showed that a recipient female may reduce her contribution to her own clutch by one egg if an egg is inserted before she lays her third one. Insertion after the third egg can result in an enlarged clutch to the potential detriment of both host and parasite. Received 19 May 1987, accepted 10 Sept. 1987.

Females of over 50 species of birds are known to lay eggs in the nests of conspecifics (Yom-Tov 1980a, Andersson 1984). This behavior, variously termed intraspecific (or conspecific) nest (or brood) parasitism (e.g., Yom-Tov 1980a, Andersson 1984, Emlen and Wrege 1986), has been recognized since about 1900 (Weller 1959, Yom-Tov 1980a), but until recently it was treated largely as incidental, aberrant behavior. Its brief treatment under “dump nesting” and its exclusion from “brood parasitism” by Terres (1980) and Campbell and Lack (1985) are evidence of past perspectives. Our terminology throughout will refer to parasitism, even though the purist would object that we have not demonstrated cost and benefit of the behavior to the recipient and donor, respectively.

Several recent authors have hypothesized which individuals should be parasitic and under what circumstances (Yom-Tov 1980a, Andersson and Eriksson 1982, Andersson 1984, Emlen and Wrege 1986, Gibbons 1986). We summarize these as the: (1) “last resort hypothesis”—a female lays parasitically because, as a result of inexperience, social status, or accident, she lacks a nest of her own; (2) “enhancement hypothesis”—a female lays a clutch in her own nest and increases her fecundity by laying one or more eggs in other nests; (3) “pure parasite hypothesis”—a female lays all her

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eggs in other conspecifics' nests; and (4) "the accident hypothesis"—a female mistakenly lays in a nest not her own (Hamilton and Orians 1965, referring to interspecific parasitism). Scant testing of these hypotheses exists. Emlen and Wrege (1986) provide limited experimental support for the "last resort hypothesis" in the White-fronted Bee-eater (*Merops bullockoides*). Petrie (1986) and Gibbons (1986) report nonexperimental data supporting the enhancement hypothesis for the Common Moorhen (*Gallinula chloropus*). Their findings are exceptions in a literature that has asked and tested few selection-based questions about egg dumpers. Most efforts instead have focused on effects of conspecific brood parasitism (CBP) on egg recipients (hosts).

Most verified conspecific parasites are precocial species (Yom-Tov 1980a). Among the small number of altricials are the European Starling (*Sturnus vulgaris*) (Yom-Tov et al. 1974, Power et al. 1981, and others summarized by Andersson 1984); Cliff Swallow (*Hirundo pyrrhonota*) (Brown 1984); Eastern Bluebird (*Sialia sialis*) (Gowaty and Karlin 1984); White-fronted Bee-eater (Emlen and Wrege 1986); Fairy Martin (*Petrochelidon ariel*) (Manwell and Baker 1975); and several passerids (Yom-Tov 1980a, Dhindsa 1981), including the House Sparrow (*Passer domesticus*) implicated in an aside to a genetics study (Manwell and Baker 1975).

House Sparrows exhibit the following qualities of potential hosts (H) and parasities (P) proposed by Hamilton and Orians (1965) as conducive to the development of interspecific parasitism: (1) hole nesting (H) (Bent 1958, Summers-Smith 1963:52); (2) colonial nesting (H) (Summers-Smith 1963:102, McGillivray 1980); (3) indeterminate laying (H, P) (Witschi 1935, Klomp 1970, this study, but see Brackbill 1960); and (4) limited or no nest-building role for female (P) (Summers-Smith 1963:55). One should expect CBP in a species with those features because conditions conducive to parasitism exist in each female as both host and parasite.

Anecdotal evidence suggests that parasitic laying occurs among House Sparrows. First, reports of enlarged clutches, possibly "dump nests" or joint efforts, exist (Bent 1958, Summers-Smith 1963:75–76, Fleischer 1982). Second, single clutches usually contain one or two eggs differing in color and spotting pattern from the rest of the clutch (Bent 1958, Brackbill 1960, Dawson 1964, Murphy 1978, Lowther, 1988). Most authors state or assume that these are the ultimate and penultimate eggs in a clutch. However, Seel (1968:270) refers to the "most recently laid" egg as being paler and brighter, a condition that "generally lasted less than 24 hours." Lowther (1988) invokes an effect of fortuitous hormonal shifts at the end of laying in speculating on the proximate cause of the
oddness. Electrophoretic evidence shows that odd-appearing eggs in at least some clutches, however, are from females other than the nest owners (Manwell and Baker 1975, this study). Thus, two kinds of oddness may be involved.

In this paper we report initial tests of the hypothesis that laying in a conspecific's nest increases the fitness of an egg donor at a reproductive cost to the egg recipient. We confirm the occurrence of CBP in the House Sparrow, examine indeterminate egg production as a catalyst for CBP, and provide preliminary evidence that CBP can reduce fitness in host females.

METHODS

The study nests were at two sites 300 m apart on the University of Delaware Farm in Newark, Delaware. Nests were in farm sheds at one site and in several nest boxes (erected in March, 1983) and an adjacent row of bushes (Cupressos cyparis leylandi) at the other. We checked the contents of the nests daily (mid- to late-afternoon) on 29 April–11 June 1983 and 30 May–10 July 1984. All of the 1983 nests were in the sheds. Completed clutches were collected, photographed, and refrigerated for later electrophoresis. In 1983 we delayed collection of some clutches until embryonic development had started. By comparatively aging the embryos in such clutches, we determined the position of the odd-appearing egg in the laying sequence. We examined electrophoretically only those clutches lacking macroscopically visible embryonic development to insure that only maternal proteins were sampled.

Albumin is entirely of maternal origin and therefore reflects the female genotype (Brush 1968). Electrophoresis of albumin resolves the House Sparrow genotype into a distinct banding pattern of four proteins, of which one, transferrin (conalbumin), is polymorphic, consisting of three patterns (Manwell and Baker 1975). Though like patterns cannot distinguish parentage, the occurrence of an odd transferrin pattern within a single clutch indicates an egg of different maternal origin (Fleischer 1985). Thus, electrophoresis does not reveal all cases of House Sparrow dumping, but it is a useful index of occurrence and minimum relative frequency. Gowaty and Karlin (1984) list additional reasons why the frequencies would be underestimates.

Our electrophoretic technique was a nondenaturing, polyacrylamide gel system: 12% separatory gel and 4.5% stacking gel with a pH 9.0 Tris/boric acid buffer (modified from Allen 1974). Gels were run overnight at constant current (10 ma). Proteins were stained and fixed in the gels with 0.1% Coomassie brilliant blue in 50% TCA. Entire clutches were run on single gels to allow direct comparison of eggs for protein polymorphism.

Two manipulative experiments were conducted in 1984. An egg-removal experiment used six active nests in boxes to determine if House Sparrows are indeterminate layers. From three nests, we removed one egg/day (always the oldest one) beginning after the laying of the second egg, leaving one egg in the nest. Eggs were removed from the remaining three nests after a third egg had been laid, leaving two eggs in the nest.

To determine the effect of a nonhost's egg on host clutch size, we added one egg to each of 17 clutches. The time of addition varied, being after the first, second, third, or fourth egg was laid. The inserted eggs came from other partial, unincubated clutches, including ones abandoned in the egg-removal experiment. The eggs were stored at 4°C until needed and warmed to ambient temperature before being put in a nest. Fifteen unmanipulated nests served as controls. During the daily nest checks, newly laid eggs were numbered to facilitate
identification and to determine the laying sequence and the number of eggs laid in the host nest. Electrophoresis was used to check for natural egg dumping events in all clutches.

RESULTS

Evidence of parasitic laying.—In 1983, 17 of the 54 complete clutches collected were suitable for electrophoresis. Four of those (24%) contained one egg genetically different from its clutch-mates. The genetically unique eggs differed in color and spotting pattern from their clutch-mates in 3 of the 4 cases, but no record was made of their position in the laying order. All were laid during the hosts’ laying periods. The first laying dates and final sizes of the clutches in which each appeared were 2 May (4), 30 May (5), 2 June (6), 5 June (7), and 10 June (4). In 1984, 1 of 25 clutches (4%) that were electrophoretically examined contained one egg that was both genetically and morphologically unique. (See item 5 in the next paragraph for peculiar details of that clutch.)

Circumstantial evidence of parasitic laying came from several observations made during daily nest checks. Although not definitive, five results are consistent with such behavior. Two involved genetically odd eggs. (1) An exceptional clutch of 7 eggs was laid 5–11 June 1983. Mean size of 14 other complete clutches begun on 5 June ± 7 days was 4.43 ± 0.25 SE. One of the 7 eggs was genetically, but not visibly, odd. (2) Two eggs appeared on the same day in one nest, an unlikely possibility for a single female (but see Nolan 1978:189). The two differed in appearance; one resembled the first egg of the clutch, and the other had a lighter background and fewer spots than the rest of the clutch. Damage of the eggs in storage prevented electrophoretic analyses. (3) In 1983, 41 of the 54 clutches held at least one visibly odd egg as did 11 of 15 control clutches in 1984 (see below). Over the two years, 75% (N = 69) of the clutches held a visibly odd egg. Four clutches in 1983 and one in 1984 held two eggs that differed visibly from the rest of the clutch. In four of those, the two eggs were of similar, lighter background and had fewer, bolder spots than their clutch-mates. In the fifth, the two odd eggs differed from one another as well. This last case, if none other, indicates laying by at least two different females in the nest. (4) A visually odd egg appeared in the penultimate position in one clutch each year and as the second of four eggs in a nest in late April, 1983. This latter result is evidence of parasitic laying even if females typically lay an odd egg last and sometimes next to last. (See the egg-removal experiment below for another case of this type.) (5) One nest received a clutch of three eggs on 27–29 April 1984 and then apparently was abandoned by the owner. The clutch remained unchanged until 5 May, when an egg was missing. On 6 May a new egg visibly different
from the original eggs appeared. No additional laying or incubation occurred. Electrophoresis confirmed the egg to be of different genetic composition. This case may not represent CBP (see Discussion).

Egg-removal experiment. — When egg removal occurred in the interval between the second and third eggs, two females continued to lay for extended periods (Table 1). One female laid 11 eggs in three pulses over 17 days. The second female laid 14 eggs over a period of 22 days in 3 laying pulses. The latter presumably also had laid five eggs on 4–9 June that were collected from the same box on 9 June in the egg-addition experiment (see below). The first female did not stop to incubate when the last three eggs of the second cycle were not removed, but initiated another cycle and added three more eggs to the clutch. She incubated those six eggs, of which five hatched, and the nestlings fledged. The third female abandoned her nest after laying her fourth egg, which appeared two days after the third was laid and the first removed. A one-day skip followed the third egg.

Two females did not extend laying to replace lost eggs when removal of single eggs occurred after the nest held three eggs, i.e., leaving two eggs in the nest (Table 1). The females incubated the two eggs that remained in the nest after laying stopped. The third female abandoned her nest after her third laying day when we removed her first egg.

The second egg in the second pulse (fifth one laid) of the first extended layer was visually odd, as was the egg laid at the end of each pulse by the second extended layer (Table 1). No odd eggs appeared in the clutches of the nonextended layers. No electrophoretic differences were found among the eggs collected.

Egg-addition experiment. — We combined the data for different laying
intervals to create two groups: insertions before and insertions after egg 3 had been laid. We term the eggs not inserted by us the “host clutch.” They, plus the inserted egg, equal the “final clutch size.” We assume any actual parasites had equal access to experimental and control nests.

The host clutch in the “pre-3” nest was smaller than in the “post-3” and control nests (Table 2). “Post-3” clutches were more similar to controls than to pre-3 ones. ANOVA indicated significant differences among the groups ($P = 0.01$), but a Least Significant Difference test failed to group the post-3 nests solely with controls (Table 2). The small N for the post-3’s may have been a factor in that failure. The final clutch size of the pre-3 group equaled the controls while that of the “post-egg 3” group was 0.7 egg larger.

In addition to the premature termination of host laying, the dumping experiment revealed three behavioral responses to egg addition. (1) One host female removed from her nest three different eggs that we had inserted singly after she had laid her first, second, and third eggs. The marked eggs were found on the ground not far from the host nest on the day following addition. (2) At 3 of the 17 manipulated nests, the host female failed to add an egg to the clutch on the day following egg addition. These occurrences were clearly skips in the middle of the normal laying cycle. One control clutch with five eggs had a one-day skip after egg 2. (3) Two of the 17 manipulated nests were abandoned after we added an egg, but none of the 15 control nests was abandoned.

DISCUSSION

Our electrophoretic analyses confirmed the occurrence of parasitic laying in the House Sparrow and corroborated at least one observation, an over-sized clutch, as such. A second case (laying in an apparently abandoned clutch) may have been erroneous parasitic laying. It also could have been an aborted change of ownership (P. Lowther, pers. comm.).

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**Table 2**

HOST CLUTCH SIZE IN EXPERIMENTAL AND CONTROL NESTS OF HOUSE SPARROWS

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Clutch size minus inserted egg</th>
<th>Mean</th>
<th>SE</th>
<th>N</th>
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<tr>
<td>Unmanipulated (control)</td>
<td>5.13a</td>
<td>0.09</td>
<td>15</td>
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</tr>
<tr>
<td>Egg added before egg 3</td>
<td>4.17b</td>
<td>0.32</td>
<td>12</td>
<td></td>
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<tr>
<td>Egg added after egg 3</td>
<td>4.80a,b</td>
<td>0.37</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

*Values with same superscript not significantly different (ANOVA, Duncan’s Multiple Range Test, $F_{2,19} = 4.99, P = 0.014$).*
We will not consider it to be CBP hereafter. Manwell and Baker (1975) reported 2 of 32 clutches (6%) contained electrophoretically mismatched eggs. Wetton et al. (1987) found that 8% of nestlings in a population in England were genetically mismatched with their presumed parents. We found 24% and 0% to be genetically odd in the two years, respectively. These values are conservative, because House Sparrows exhibit polymorphism at only one albumin locus. Detection of genetic differences is limited by the degree of protein polymorphism within a species and because different females may possess the same alleles (Gowaty and Karlin 1984). Fleischer's (1985) technique, which we could not attempt, would have permitted estimating the probability that eggs of the same electromorph were from different birds.

Eight of the 94 clutches examined in the study showed evidence of CBP. The evidence included: (1) four clutches with electrophoretic confirmation of parasitic laying; (2) fourth, but not fifth, egg of a five-egg clutch visibly odd; (3) second of four eggs visibly odd in one clutch; (4) two eggs laid in a nest in same 24 h period; and (5) fourth and fifth eggs in a five-egg clutch visibly different from each other and the rest of the clutch. The 8.5% parasitism rate is a crude estimate, because not all nests were tested electrophoretically nor treated equally by virtue of the experiments in 1984. The value is slightly less than estimates for other altricial species: 12–46%, European Starlings (references in Andersson 1984); 10–27%, White-fronted Bee-eaters (Emlen and Wrege 1986); and 0–24%, Cliff Swallows (Brown 1984). Gibbons (1986) found 18% parasitism in Common Moorhens and that 20% of the laying females were parasites.

The visibly odd eggs common to Passer clutches (Bent 1958, Yom-Tov 1980b, Lowther 1988) remain enigmatic. Virtually every writer commenting on the oddness of the last-laid egg has used a qualifier of “usually,” “normally,” etc. (e.g., Bent 1958, Dawson 1964, Murphy 1978). We found mismatched eggs usually, but not always, to be the last egg in the clutch, as did Lowther (1988). Four of five eggs in our study and 2 of 2 in Manwell and Baker's (1975) data that were genetically odd were also odd-appearing. These results beg a closer look at the origin of the last egg in House Sparrow nests, especially in light of reports that European Starling and White-fronted Bee-eater parasites tend to lay near the end of the host's laying period. One possibility is that the last odd egg is indeed from the resident female and that only the odd eggs detected in other positions are parasitic ones. We failed to distinguish systematically among types of oddity, e.g., darkness, lightness, etc., in relation to clutch-mates and cannot test that point.

Egg-removal experiments indicated that the female House Sparrow is an indeterminate layer up to a clutch size of 3 eggs. After three eggs appear
in a nest, total egg production appears to be determined at 4–6 eggs. These data suggest that a House Sparrow could increase her fecundity through parasitic laying before she has laid three eggs in her own nest. If parasitic eggs achieve reproductive maturity with any regularity, selection should favor the tactic described by the enhancement hypothesis.

Results of the egg-addition experiments indicate indeterminate laying can be a favorable trait for a parasite but a reproductive liability for a host. The host’s cost may be reduced fecundity and diluted resources for her own young. If an egg is inserted before the host has laid her third egg, the parasitic egg may stop egg production, prematurely reducing the host’s fecundity by one. This consequence has been recognized in the Redhead (*Aythya americana*) (Weller 1959) and the Common Goldeneye (*Bucephala clangula*) (Andersson and Eriksson 1982). If insertion occurs after a House Sparrow lays her third egg, the host can be left with an oversized clutch. The parasite shares this problem, but its young is a “bonus” and a smaller portion of its fecundity than are the host’s young of its fecundity. Oversized clutches can result in decreased food delivery per young, lower weights, and decreased survival of nestlings and fledglings (Klomp 1970, Askemo 1977, Schifferli 1978). Notably, we found only one clutch larger than six.

The logical existence of antiparasite defenses has been anticipated (e.g., Lanier 1982, Andersson 1984, Emlen and Wrege 1986, Gibbons 1986). We saw limited evidence of the typical defensive responses to parasitic eggs—nest abandonment and egg-removal. Egg-removal has been observed in another passerid, the Village Weaver (*Ploceus cucullatus*) (Victoria 1972), and in White-fronted Bee-eaters (Emlen and Wrege 1986).

Another behavior seen during the egg-addition experiment suggests another type of defense. To avoid an oversized clutch, a host could lay one of her own eggs elsewhere. In three cases in our egg-addition experiment, host females failed to lay an egg in their nests on the day immediately following an egg addition. If eggs are produced consecutively at a rate of one per day, such skips may indicate instances in which the host laid elsewhere. An initial case of parasitic laying could result in a “domino effect,” perpetuating the behavior among several females. If this pattern prevailed, most females would end up with a “normal” clutch to raise and would have laid their usual number as well. The advantage would go ultimately to females that were successful at parasitism but that also had defenses against foreign eggs, thereby keeping their own clutches pure and at a lower number.

We did not try to determine the status of the parasites. Possibilities include secondary females of polygamous matings, females disrupted at laying time, mated females contesting the same nest, unmated females
laying in their parents’ nests, cooperative breeders, inexperienced females, and any or all females (Summers-Smith 1963:48, Sappington 1977, Yom-Tov 1980a, Andersson 1984, Emlen and Wrege 1986, Gibbons 1986). Our results do not permit us to reject any of the possibilities. Likewise, we cannot reject any of the four hypotheses of CBP enumerated in the introduction.

This study confirms the occurrence of CBP in the House Sparrow, provides insight to specifics of reproductive biology of the species which predispose it to such behavior, and supports the hypothesis that the donor-recipient interaction is parasitic in nature. Nevertheless, CBP remains poorly understood both in House Sparrows and as a general phenomenon. A more thorough assessment of the behavior and its costs and benefits for both donor and recipient House Sparrows is in progress. Similar studies of other species are required before the behavior can be accepted or rejected with confidence as parasitism and as a regular adaptive phenomenon.

ACKNOWLEDGMENTS

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LITERATURE CITED


**NORTHEAST RAPTOR MANAGEMENT SYMPOSIUM AND WORKSHOP**

The Northeast Raptor Management Symposium and Workshop, hosted by the National Wildlife Federation’s Institute for Wildlife Research, will be held 16–18 May 1988 at the Hotels at Syracuse Square, Syracuse, New York. The Symposium will feature technical papers on the status and management of northeastern raptors and land use issues which impact raptor populations. Interactive workshops will encourage participants to discuss raptor management issues in the region and develop management recommendations. For more information, contact the National Wildlife Federation, 1412 Sixteenth St., N.W., Washington, D.C. 20036-2266 or call (703) 790-4264.
HISTORICAL STATUS OF THE AMERICAN KESTREL (FALCO SPARVERIUS PAULUS) IN FLORIDA

MARK L. HOFFMAN AND MICHAEL W. COLLOPY

Abstract.—We investigated the magnitude and cause of the decline in numbers of Florida's resident population of American Kestrels (Falco sparverius paulus) by contrasting the records of early oologists and present-day observations. Historical information was available for three different region-habitat type combinations. In areas formerly dominated by longleaf pine (Pinus palustris) flatwoods in north-central Florida (Alachua and Levy counties), kestrels have declined an estimated 82% since the early 1940s; nest-site availability has decreased significantly due to the clearing of isolated longleaf pine trees from agricultural fields. Along the central Florida ridge in Lake, Orange, and Seminole counties, kestrels declined with the conversion of the original longleaf pine-turkey oak (Quercus laevis) vegetation to citrus groves. Recent observations indicate a very small population now exists in this area. In Dade County, the kestrel apparently disappeared as a breeding species from the pine forests of the Miami Rocklands between 1935 and 1950. The cause of the kestrel's extirpation in this region is unclear. Received 18 Mar. 1987, accepted 31 July 1987.

Although the American Kestrel (Falco sparverius) is one of the most common and widely distributed raptors of the Western Hemisphere (Cade 1982), field ornithologists in Florida have noted a decline in the abundance of the state's resident population (F. s. paulus) (Kale 1971, 1980; Ogden 1971, 1972; MacFarlane 1973; Wiley 1978). In 1977, F. s. paulus was formally listed as “threatened” in Florida (Kale 1978); the magnitude and cause of the decline in numbers were unknown, but they were thought to be associated with nest-site destruction (Wiley 1978).

Historical records are necessary to assess changes in the status of F. s. paulus in Florida; however, published information concerning the kestrel's former distribution and abundance has been of a general nature, preventing the determination of population trends. For example, Howell (1932) and Sprunt (1954) simply considered F. s. paulus to be “locally common” in Florida, north of the Everglades; other early avifauna lists of specific locations (as reviewed in Howell 1932) are similarly vague. Two important factors contributed to this lack of information in the literature: (1) most early ornithological work in the state was conducted during winter and early spring (Howell 1932) and (2) F. s. sparverius is a common winter resident and migrant throughout the state, which tends to mask the true status of F. s. paulus (Bent 1938).

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In contrast, substantial unpublished information, which refers specifically to breeding *F. s. paulus*, exists in the records and specimens of oologists active in Florida during the first half of the 1900s. Elsewhere, this type of oological data has proven useful in understanding the population changes of several raptor species (Ratcliffe 1980, Bechard 1981). Our review of specimen material in American museums indicated there existed three substantial series of American Kestrel egg sets from restricted geographical regions of Florida, which we used to assess the population’s former abundance and habitat preferences in detail. Additionally, by examining the kestrel’s current population status in these same areas, our objective was to determine the magnitude and cause of the kestrel’s decline, and the extent to which decreased availability of nest sites and foraging habitat contributed to the decline.

**STUDY AREAS AND METHODS**

*Doe’s oological records.*—Specimens and field notebooks of Charles E. Doe archived at the Florida State Museum provided records of 307 clutches of kestrel eggs from Alachua and Levy counties between 1935 and 1942. For each clutch collected or described, we recorded date, location, incubation stage, clutch number (first, second, or third clutch of pair that year), characteristics of nest tree, and surrounding land use or vegetation. We determined clutch number based on Doe’s comments, date of collection, the kestrel’s ability to renest (Bird and Lague 1982), and stage of incubation.

We identified 6 specific and 5 general collecting locations, in which to conduct surveys for nesting kestrels, by comparing road numbers and landmarks used by Doe with present-day analogs (Fig. 1). Specific collecting locations were areas where exact fields or farms could be identified as the collecting site. General collecting locations refer to areas adjacent to roads where Doe collected kestrel egg sets, but for which the specific location of collection is unknown. The precise location of historical sites and the recent surveys is described by Hoffman (1983).

Four major plant communities occurred along Doe’s travel routes: (1) slash pine (*Pinus elliottii*) flatwoods, (2) longleaf pine (*Pinus palustris*) flatwoods, (3) longleaf pine-turkey oak (*Quercus laevis*) sandhills, and (4) hardwood hammocks. These communities are described in detail by Laessle (1942), Monk (1968), and Veno (1976). None of the collecting locations was dominated by slash pine flatwoods, and sandhill vegetation was limited to a portion of the Bronson Road area. Throughout the study area the original associations have been altered extensively for agriculture and commercial slash pine plantations.

Our survey methods were designed to be analogous to Doe’s methods. We searched intensively each specific collecting location on foot, scanning likely perches for kestrels. General collecting locations were searched by driving slowly (17–40 km/h) along roadside survey routes. When kestrels were found, Doe would attempt to flush incubating females from nearby snags; we spent additional time monitoring dead trees and other potential nest sites. Observations were focused on all areas within 0.4 km of the roadside survey routes, the normal distance to the next parallel field edge or hedgerow from the survey route. This distance was selected because Doe’s notes indicated he invariably collected in fields adjacent to roads and rarely searched less accessible areas. We surveyed each area four times between 1 May and 30 June (see results for years of survey). Because of the conspicuous nature of
Fig. 1. Approximate location of collecting areas of C. Doe in north-central Florida. Letters indicate specific collecting locations: (A) Parker Church Road, (B) East of Archer, (C) Booth Farm, (D) East of Chiefland, (E) Turpentine Still, (F) Behind Church. Numbers indicate general collecting locations: (1) Bronson Road, (2) Trenton Cross-roads, (3) Southwest of Chiefland, (4) Newberry Road, and (5) High Springs Road. Broken lines adjacent to numbers signify outer boundaries of general collecting locations.

most kestrel nest sites in these areas (dead pines in fields), we felt 4 surveys were sufficient to locate any kestrel nests that would have been found by Doe.

We determined the minimum number of kestrel pairs in each collecting location, which could have produced the egg sets collected or observed by Doe. Because of large annual variation in Doe's efforts, we used his data from 1938-1940, the years of most consistent coverage, to represent the population size in each area during his era. The medians of these values were compared to the maximum number of pairs found in the recent surveys using the sign test (Siegel 1956).

To assess changes in vegetation and land use between Doe's era and the present we quantified, for each collecting location, the number of standing longleaf pines in agricultural fields and the percent composition of 6 cover types: hardwood hammocks, longleaf pine forests, slash pine plantations, agricultural fields (including pastures), farm sites, and urban areas. For specific collecting locations, the entire area was quantified. Habitat analyses of general collecting locations were based on a random sample of 25% of the 16-ha plots within 0.4 km of the roadside survey routes. This analysis was not performed for the general collecting location on Bronson Road because Doe only collected in two fields, neither of which we located. The time periods compared for changes in land use and vegetation were based on USDA aerial photographs and varied due to their availability (see results for years).

For purposes of comparison between the two time periods, we assumed that nest-site
availability was proportional to the number of standing live longleaf pine trees in agricultural fields. Doe's notes indicated that kestrels were found nesting in dead pine trees in cultivated or fallow fields and pastures. Because these dead trees are not readily discernible on aerial photographs, we used the number of live pines as an index of the number of dead pines in a particular field. Because dead pines originate as live pines, there should exist a correlation between these counts. It is assumed that the proportion of live to dead pines is similar between time periods. If snag removal has increased in recent years, then our estimate of habitat (snag) loss is conservative. We recorded counts of dead pines in the plots sampled for cover type analysis to assess the magnitude of the association and found an average of 4.8 live pines per dead pine (N = 97 live pines).

We considered kestrel foraging habitat to be agricultural fields, which includes pasture, cultivated fields, and fallow fields (Cade 1982, Bohall-Wood and Collopy 1987). Although not all cultivated fields are used by kestrels for foraging, distinction between potential foraging and nonforaging areas was not possible from the aerial photos. We used Wilcoxon's matched-pairs signed-ranks test (Siegel 1956) to compare the number of pines and area of each cover type per sample plot between the two time periods for the general collecting locations.

Nicholson's and Bailey's oological records. — In 1983, we solicited copies of the data slips associated with kestrel egg sets collected in Florida from museums with over 1000 total egg sets or having Florida as an area of special representation (Kiff 1979). This survey and examination of field notebooks revealed 57 F. s. paulus clutches were collected in south-central Florida between 1909 and 1959 by Donald J. Nicholson and his co-workers; from these data we summarized information on nest-site characteristics. Copies of Donald and Wray Nicholson's field notes were made available for reference through the Western Foundation of Vertebrate Zoology. No attempt was made to assess current kestrel population levels in areas covered (primarily Lake, Orange, Osceola, and Seminole counties) by the Nicholsons through field work. We did, however, collect and summarize recent (post-1960) records of F. s. paulus from these counties, published in American Birds (formerly Audubon Field Notes) and solicit reports from field observers.

Data on 34 kestrel egg sets collected in Dade County by H. H. Bailey and his relatives (H. B. and M. P. Bailey) between 1922 and 1932 were found during the survey of museums. Additional information on the kestrel's historical status in Dade County came from published works by Bailey (1924, 1925, 1927) and others (Howell 1921, Holt and Sutton 1926). The present status of the F. s. paulus in south Florida was assessed using the literature (Robertson 1955, Robertson and Kushlan 1974) and contact with local ornithologists.

RESULTS

Doe's oological records. — The number of kestrel pairs in Doe's collecting locations declined significantly (P < 0.01) between 1938–1940 and 1981–1983 (Table 1). The estimated population size for all collecting locations combined was similar each year (1938, 45 pairs; 1939, 45; 1940, 46) during Doe's era. A maximum of 8 pairs was recorded in the recent surveys, a decrease of 82% from the 1938–1940 median.

Comparing vegetation and land-use characteristics between Doe's era and 1982 for the specific collecting locations reveals that nest-site availability (number of standing longleaf pine trees) decreased in each area (Table 2). Parker Church Road was the only specific collecting location that still had a living longleaf pine in 1982; it also was the only specific
collecting location with nesting kestrels. Kestrel foraging habitat was greatly reduced or eliminated in the Booth Farm and Turpentine Still areas, due to the conversion of agricultural fields to pine plantations (Table 2). In the other specific collecting locations, foraging habitat had not decreased to less than 75%.

In all of the general collecting locations, the density of pines decreased significantly between Doe’s era and 1982 (Table 3). A greater than 95% decline in pine tree densities was recorded in each location, except the Newberry Road area, where the decrease was of smaller magnitude. Analysis of cover type composition indicated that despite significant increases in hardwood hammocks, pine plantations, and urbanization in some areas, over 50% of each area remains in agriculture (Fig. 2). No changes in the amount of agricultural land was found in the Trenton Cross-roads and Southwest of Chiefland areas and the declines in the Newberry Road and High Springs Road areas were 24–28%.

Examination of aerial photographs for a portion of the Southwest of Chiefland area illustrates the changes in vegetation and land-use that have occurred between Doe’s era and 1974 (Fig. 3). In the 1940 photo, agricultural fields dotted with longleaf pine trees are located throughout, with concentrations in blocks 1, 8, 9, 11, 15, and 16 (see figure legend for block

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**Table 1**

**Estimated Number of American Kestrel Pairs Occurring in Doe’s Collecting Locations in 1935–1942 and in 1981–1983**

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<td>Southwest of Chiefland</td>
<td>0</td>
<td>5</td>
<td>8</td>
<td>7</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Newberry Road</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>11</td>
<td>0</td>
<td>9</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>High Springs Road</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

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*See Fig. 1 for reference to collecting locations.
*Median of kestrel numbers during 1938–1940.
*Area not surveyed.
Table 2
NUMBER OF STANDING LONGLEAF PINES AND % COVER-TYPE COMPOSITION FOR SPECIFIC COLLECTING LOCATIONS DURING Doe'S ERA AND 1982

<table>
<thead>
<tr>
<th>Collecting location*</th>
<th>Size of area (ha)</th>
<th>Number standing longleaf pines</th>
<th>Hardwood hammocks</th>
<th>Longleaf pine forest</th>
<th>Pine plantation</th>
<th>Agriculture</th>
<th>Farm sites</th>
<th>Urban</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parker</td>
<td>48.6</td>
<td>1937 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Church Road</td>
<td>1982 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>East of Archer</td>
<td>22.7 3</td>
<td>1937 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1982 0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Booth Farm</td>
<td>97.1 170</td>
<td>1940 100.0</td>
<td>18.7</td>
<td>98.2 1.8</td>
<td>80.0 1.2</td>
<td>33.8 1.6</td>
<td>18.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1982 0</td>
<td>0</td>
<td>7.9</td>
<td>98.4 1.6</td>
<td>78.4 1.6</td>
<td>18.6 0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>East of Chiefland</td>
<td>48.6 52</td>
<td>1940 98.4</td>
<td>1.6</td>
<td>99.6 0.4</td>
<td>96.7 3.3</td>
<td>96.7 3.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turpentine Still</td>
<td>109.3 24</td>
<td>1949 96.7</td>
<td>100.0</td>
<td>96.7 3.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1982 0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* See Fig. 1 for reference to collecting locations.

numbering scheme). In the 1974 photo, isolated pines are generally confined to the western portion of block 16 and block 8. The latter block accounted for 55% of the pines found in the Southwest of Chiefland vegetation sampling; most fields are totally devoid of isolated pines. Areas of former native pasture with an abundance of longleaf pines in blocks 2, 3, and 13 have been cleared or converted to pine plantations (block 3).

In the Trenton Cross-roads area, where sample size was the largest, kestrels nested in 3 different 16-ha plots adjacent to the survey route during 1982 and 1983. A comparison of the density of longleaf pines and major cover types in this survey area (Table 4) showed that the plots with nests were similar to the random sample from 1940 in having high average values for number of standing longleaf pines and longleaf pine forest cover and low values for pine plantation, as opposed to recent averages.

Doe characterized the vegetation surrounding nest sites as: field (N = 56); old field (13); plowed field (12); brush field (6); not cultivated (5); watermelon or corn field (3); cultivated field (3); in woods (2); and field of stubs (2). He also described 8 nests as “pine stubs” and listed 104 additional nest trees simply as “stubs”; we suggest these trees also were pines.
It is apparent that the agricultural fields during Doe’s era had many standing pine trees, whereas today trees are nearly absent from these same fields. Foraging area also has been reduced in some locations due to the conversion of farmland to pine plantations, but not in a magnitude that could account for the kestrel’s decline.

Nicholson’s oological records.—All specimen data (N = 57 egg sets) collected in south-central Florida by D. Nicholson and his associates (C. E. Carter, J. C. Howell, W. H. Nicholson, F. W. Walker) indicated that kestrels formerly nested in the sandhill areas of Lake, Orange, and Seminole counties and in the vicinity of scrub and pine flatwoods in Osceola County. Unknown annual variation in collecting efforts and locations visited, combined with the lack of nesting habitat descriptions (except for those sets collected by D. Nicholson), limited analyses.

D. Nicholson described in detail the vegetation surrounding 11 kestrel breeding sites found between 1917 and 1923 in Orange and Seminole counties; all were in the longleaf pine-turkey oak sandhills (see Hoffman 1983 for complete descriptions). Between 1937 and 1959, he described 6 breeding locations in Lake, Orange, and Seminole counties; these also were in sandhill areas. These latter sites differed from those of the earlier period because the sandhill areas were being converted to citrus groves. For example, Nicholson wrote “the nest-site was but a few acres left of cut-over timber land—oak and pine—among many newly planted citrus groves” (Flat Lake, Lake County, 26 April 1954, notebook). The four

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**Table 3**  
**STANDING LONGLEAF PINE DENSITY (MEAN NUMBER/16-ha PLOTS) FOR GENERAL COLLECTING LOCATIONS DURING DOE’S ERA AND 1982**

<table>
<thead>
<tr>
<th>Collecting location</th>
<th>Size of area (km²)</th>
<th>Nc</th>
<th>Year</th>
<th>Mean (SE)</th>
<th>% change</th>
<th>p*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trenton Cross-roads</td>
<td>75.6</td>
<td>97</td>
<td>1940</td>
<td>7.42 (1.15)</td>
<td>95 &lt;0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1982</td>
<td>0.39 (0.22)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Southwest of Chiefland</td>
<td>61.5</td>
<td>92</td>
<td>1940</td>
<td>14.22 (3.13)</td>
<td>98 &lt;0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1982</td>
<td>0.22 (0.13)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Newberry Road</td>
<td>11.0</td>
<td>34</td>
<td>1949</td>
<td>1.55 (0.65)</td>
<td>43 &lt;0.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1982</td>
<td>0.88 (0.72)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High Springs Road</td>
<td>13.0</td>
<td>40</td>
<td>1949</td>
<td>5.15 (1.20)</td>
<td>96 &lt;0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1982</td>
<td>0.20 (0.11)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* See Fig. 1 for reference to collecting locations.  
* Area within 0.4 km of roadside survey route.  
* Number of 16-ha plots sampled for vegetation characterization.  
* Wilcoxon’s matched-pairs signed-ranks test.
nesting locations in Osceola County described during this time period were pine flatwoods or scrub areas.

D. Nicholson attributed the cause of the decline of *F. s. paulus* in sandhill areas of south-central Florida to the clearing of land for citrus groves and, in general, the cutting of timber. He wrote (Dec. 1956, notebook): “between 1900 and 1920 this little hawk was very numerous in all of south central Florida, particularly in Orange, Lake, and Polk counties. . . . Since 1940 the Little Sparrow Hawk has become extremely rare in all of this region due to the cutting of timber and land cleared for [orange] groves.” Details on the kestrel’s status in Osceola County were less clear; however, he suggested that the increased cutting of dead trees for firewood eliminated potential breeding sites.

Between 1960 and 1969, no breeding American Kestrels were reported
Table 4

<table>
<thead>
<tr>
<th>Sample</th>
<th>Number standing longleaf pines/16 ha</th>
<th>% cover type</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Longleaf pine forest</td>
</tr>
<tr>
<td>1940</td>
<td>97</td>
<td>7.4</td>
</tr>
<tr>
<td>1982</td>
<td>97</td>
<td>0.4</td>
</tr>
<tr>
<td>Plots with nests</td>
<td>3</td>
<td>4.7</td>
</tr>
</tbody>
</table>

* Number of 16-ha plots sampled.

b Cover types not listed (hardwood hammocks, farm sites, and urban) represent 2% or less cover in each sample.

in Audubon Field Notes from Lake, Orange, Osceola, and Seminole counties. Beginning in 1970, the “Florida Region” editors began emphasizing that F. s. paullus was apparently declining, and they solicited observations. Subsequent reports were limited to one observation in Osceola County (Kale 1980) and two in Lake County (Paul 1982); none were reported from Orange or Seminole counties, where the Nicholsons had found kestrels nesting in longleaf pine-turkey oak areas. Additionally, no independent reports were received for these counties; however, given the large size of the area and general scarcity of observers, the potential for a small kestrel population in these counties certainly exists, particularly in northern Lake County. Kestrels are fairly common in portions of the Ocala National Forest in Marion County (Hoffman 1983), and similar habitats extend into Lake County.

There continue to be scattered summertime observations of kestrels in Polk County (Kale 1970, Paul 1982, J. N. Layne, pers. comm.). Although not part of the regular collecting areas of Nicholson, this county includes a large portion of the central Florida ridge, which, as in Orange and Seminole counties, was formerly dominated by the longleaf pine-turkey oak association and has been largely converted to citrus production.

Bailey’s oological records.—The museum survey revealed the Baileys collected 34 kestrel egg sets in Dade County between 1922 and 1932. Location data indicate sites scattered within the Miami Rockland pine forests (Loope et al. 1979) and include Coral Gables (N = 8), Princeton (5), Cutler (4), Goulds (3), Homestead (3), and Florida City (2).

Bailey (1925) refers to the nesting areas as the “pine timber,” with each pair of birds having a “separate piece of woods.” The egg set data include 14 sets with descriptions of kestrel nesting habitat: open pine woods (N =
Sixteen of the egg-set data slips specifically mention evidence of fire on the nest tree or in the nest area. Twenty-nine (85%) of the egg sets were identified as coming from pine trees, with 4 sets collected from coconut palms (*Cocos nucifera*) in Coral Gables. Bailey (1927) describes kestrels nesting in human habitations in Dade County, although none of his egg sets came from these situations.

Other early ornithologists working in south Florida also found the kestrel to be closely associated with slash pine (*P. elliottii* var. *densa*) forests. Flowed (1921) refers to *F. s. paulus* as being “not uncommon in pineland and between Florida City and the [Royal Palm] Hammock.” Holt and Sutton (1926:429) wrote that *F. s. paulus* was “abundant in certain parts of the pine-lands as far west as Long Pine Key, but never seen anywhere but in the pines.” They also state “it was so common in some areas that every separate clump of trees was certain to have its pair of birds” (Holt and Sutton 1926:429).

Robertson (1955) considered *F. s. paulus* to be a “species formerly occurring in the pine forests” of south Florida. Robertson and Kushlan (1974) believed breeding kestrels were gone from southeast Florida ca 1940. At present, the kestrel is still absent as a breeding species in Dade County (W. B. Robertson, Jr., pers. comm.).

**DISCUSSION**

From comparison of the records of Doe, Nicholson, and Bailey to present-day observations, it is apparent that *F. s. paulus* has declined greatly in the specific regions and habitat types of Florida where these ornithologists located nesting kestrels. Except for the records of T. G. Pearson (see Hoffman and Collopy 1987), ornithological data from other areas or habitats of the state are limited to scattered egg sets and is not amenable to a comparable analysis. We suggest the areas considered here represented a significant portion of the kestrel’s historic range in Florida and greatly contributed to the historic belief that the kestrel was “locally common” in “open pine woods” (Howell 1932). Additionally, the magnitude, timing, and cause of the declines have varied in each region.

**Doe’s ornithological records.**—Charles Doe found *F. s. paulus* to be relatively common during the late 1930s and early 1940s in the agricultural areas of western Alachua and northern Levy counties. Surveys in these same areas during 1981–1983 demonstrated that a significant decline in the kestrel population had occurred. We consider 82% (from 45 to 8 pairs) a conservative estimate of the decline, because the areas covered in the recent surveys near Chiefland (Trenton Cross-roads, Southwest of Chiefland) were likely larger than those visited by Doe. The areas sampled in
the other collecting locations, however, are thought to be the same as those visited by Doe.

Analysis of changes in vegetation and land use suggest the decline in the kestrel population has been due to a decrease in nest-site availability. Doe found kestrels nesting principally in pine trees standing in agricultural fields. Although most stands of old-growth longleaf pine had been cleared by Doe’s era for pastures and cultivation, many isolated trees were left standing by farmers. In the early 1900s, farmers left these pine trees standing because mechanized farm equipment was not widely available and plowing and clearing of land was done with mules. The increased use of tractors after World War II (Black 1980, Chew 1983), however, provided the means to clear pines from the fields, thus eliminating the existing and potential nest sites of the kestrel.

Although the total area of agricultural land has not changed substantially, the quality of this land-use category for kestrel foraging may have declined with more intensive agricultural practices in recent years. Bohall-Wood and Collopy (1987) found that kestrels nesting in agricultural areas of western Alachua County captured more insect and less reptilian prey, than did birds nesting in sandhill habitats of Levy County, and that male kestrels captured more than twice as much biomass per unit time in the latter habitat type. Given the crucial role of the male kestrel as a food provider during the breeding cycle (Cade 1982), the kestrel’s ability to reproduce successfully in agricultural locations may be affected negatively by prey availability. Agricultural areas in Florida lack the small mammal populations typical of most farmland in North America. Although the scattered longleaf pine forests present during Doe’s era could have provided a refugia for reptilian prey, the magnitude of the change in nest-site availability has been so great that we consider it the primary factor in reducing and now limiting kestrel populations.

The extent to which kestrels were able to use the original old-growth longleaf pine forests of this region is unknown. Evidence indicates kestrels at least nested in “deadenings,” a term used to describe a large area of dead trees within the old-growth forest (Hoffman and Collopy 1987). If kestrels were originally confined to these locations, the clearing of the land for agriculture may have resulted in an increase in the kestrel population. Any increase in abundance was shortlived, however, as demonstrated by the changes in kestrel numbers between Doe’s era and the early 1980s.

The same factors that caused the decline of F. s. paulus in northern Levy and western Alachua counties, no doubt influenced kestrel populations throughout much of north Florida. Longleaf pine declined from 45% to 8% of Florida’s forests between 1936 and 1980 (Bechtold and
Parts of Gilchrist, Suwannee, and Lafayette counties are very similar in vegetation and settlement history to the former collecting locations of Doe. The comments of Stockard (1905) suggest the high density of nesting kestrels in cutover pinelands as observed by Doe may have been a widespread occurrence following the removal of the old-growth longleaf pine forest in the Southeast. He described a situation in Mississippi that must have been very similar to the areas visited by Doe: “I found them ... nesting in a manner almost social or colonial. In a newly cleared field there were many old stumps of deadened trees ... and many pairs of this little hawk were nesting in these stumps” (Stockard 1905:153).

Nicholson’s oological records.—The records of Donald Nicholson suggest the decline of *F. s. paulus* numbers in the longleaf pine-turkey oak sandhills of Lake, Orange, Polk, and Seminole counties was due largely to the conversion of this native vegetation to citrus groves. Populations were reduced much earlier than in north Florida; Nicholson commented on fewer kestrels in his 1922 notes and made other references to a decreased population as of 1920.

Several important factors contributed to the development of the citrus industry in the sandhill areas of south-central Florida and tend to support Nicholson’s statements regarding the timing of the kestrel’s disappearance. The severe freezes of 1894-1895 and 1899 resulted in a movement of the industry southward (Camp 1954). Prior to these winters, citrus was grown throughout the state, with areas of peak production surrounding Orange Lake in Alachua County, and along the northern portion of the St. John’s River (Scott 1931). By 1928, however, Lake, Orange, and Polk counties dominated the citrus industry in Florida (Scott 1931).

The introduction of “rough lemon rootstock” for orange horticulture also facilitated the conversion of the sandhills to citrus groves. This rootstock came into extensive use sometime between 1905 and 1910 (Camp 1954), because it was found to grow well on the higher sandhill ridges. As Camp (1954:8) stated: “in a sense the industry’s size today is based mainly on the discovery of rough lime (lemon) stock because it made possible the use of lands not formerly suited to citrus production.” Also, it was soon realized that the high sand ridges provided additional protection against severe freezes and the development of sandhill areas along the central ridge of Florida proceeded at a rapid pace.

Studies of kestrels in north-central Florida sandhill areas demonstrate that high density kestrel populations can be supported in these areas (Hoffman 1983, Bohall-Wood and Collopy 1986); however, the scarcity of observations of breeding kestrels in south-central Florida suggests the population is small in this region. The replacement of native sandhill
vegetation with citrus groves has been on a massive scale, involving almost
all the original sandhills in Orange and Polk counties and most sites in
Lake and Seminole counties (Bechtold and Knight 1982). Remaining
sandhill areas are small, isolated, and depauperate of the original fauna
(Humphrey et al. 1985). Unlike the situation in the former collecting areas
of Doe, however, both foraging and nesting habitat have been eliminated.
Consequently, the potential for natural kestrel reestablishment is low.

_Bailey's oological records._—H. H. Bailey and other field observers found
*F. s. paulus* to be relatively common during the 1920s in the slash pine
flatwoods extending from Miami to Long Pine Key. Robertson’s (1955)
extensive field work in the same area during the early 1950s failed to
locate any breeding kestrels, and the subspecies is still absent from this
area. Thus it appears kestrels disappeared from this area between the mid-
1930s and late 1940s.

Robertson and Kushlan (1974) reviewed changes in the south Florida
avifauna in historic times and considered the kestrel a species whose
disappearance was “probably not primarily in response to man’s impact
on the environment.” They considered habitat destruction (i.e., lumbering
of the pine forests) inadequate to account for the extirpation of the kestrel
and several other pine forest species. Robertson (1955) summarized the
history of the cutting of the pine forests in south Florida and noted that
the virgin slash pine had been cut by the time of his field work in the
early 1950s. Lumbering began in the early 1900s and continued unabated,
with many areas being cut several times (Robertson 1955). The virgin
slash pine forests of Long Pine Key were cut in the late 1930s and 1940s
(Olmsted et al. 1983), corresponding to the time of the kestrel’s disap¬
pearance. The references of Bailey (1925) and Holt and Sutton (1926)
that each pair of kestrels had its “own woods” is interpreted to mean that
pairs were found in stands of old-growth pines surrounded by cut-over
forests and agriculture. The kestrel, however, is not solely dependent upon
old-growth forests; the records of Bailey include nesting in cut-over pine
forests.

Because the kestrel requires an open understory in which to maneuver
and visually locate prey, a decrease in the frequency of ground fires in the
pine forests and the resultant effects on the understory (Loope and Du-
nevitz 1981, Taylor and Herndon 1981) could negatively impact habitat
quality. There is no evidence, however, that fires decreased significantly
between the 1920s and the 1950s (Robertson 1955, Taylor 1981). It also
is possible that the thick understory created by pine regeneration in cut
forests adversely influenced kestrel populations, acting in a manner similar
to fire exclusion; with the widespread cutting of the old-growth slash pine,
large areas may have been rendered unsuitable for kestrel occupancy.
Robertson and Kushlan (1974) suggest that the extirpation of the kestrel from southern Florida is part of a larger trend caused by the warming of the postglacial climate and the concomitant northward retreat of the continental fauna. The records of Doe and Nicholson, however, indicate the kestrel’s recent scarcity in two significant habitats of north-central and south-central Florida is due to man-induced changes. Although it is not possible to identify a particular cause for the kestrel’s disappearance in Dade County, we believe the most significant influences include the cutting of the virgin slash pine forest and changes in the understory of the pine forest in response to clearing and fire. Given the conversion of pine forests to agricultural land and housing developments, there is little likelihood of the kestrel becoming reestablished in extreme southern Florida; both foraging and nesting habitat largely have been eliminated.

ACKNOWLEDGMENTS

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Financial support was provided by the School of Forest Resources and Conservation, Institute of Food and Agricultural Sciences, University of Florida, and McIntire-Stennis Project No. 1774. The staff of the Florida State Museum, J. W. Hardy, T. Webber, and J. Cox, were most helpful in providing access to the Doe collection. L. F. Kiff of the Western Foundation of Vertebrate Zoology made available copies of the Nicholson field notes for the FSM archives. We also thank J. N. Layne and W. B. Robertson, Jr., for providing unpublished information on the kestrel’s distribution and K. L. Bildstein, J. N. Layne, and J. Smallwood for their helpful comments. This paper is contribution No. 8331 of the Journal Series, Florida Agricultural Experimental Station, Gainesville.

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Hoffman and Colloly • KESTRELS IN FLORIDA


INTERNATIONAL 100TH ANNUAL MEETING OF DEUTSCHE ORNITHOLOGEN-GESELLSCHAFT

The Deutsche Ornithologen-Gesellschaft will hold its 100th annual meeting as the “International 100th Annual Meeting” Sept. 24 through Oct. 1, 1988, at the Museum Alexander Koenig in Bonn, West Germany. The two key themes will be “Zoogeography and Systematics,” and “Behavioral Ecology.” All interested in participating should contact:

Dr. K. -L. Schuchmann
Museum Alexander Koenig
Adenauerallee 150-164
D-5300 Bonn
Federal Republic of Germany
MERLIN PREDATION ON WINTERING DUNLINS: HUNTING SUCCESS AND DUNLIN ESCAPE TACTICS

JOSEPH B. BUCHANAN,1 CHARLES T. SCHICK,2 LEONARD A. BRENNAN,3 AND STEVEN G. HERMAN4

ABSTRACT.—Interactions between Merlins (Falco columbarius) and Dunlins (Calidris alpina) were studied at estuarine areas in western Washington during winter, 1979 to 1985. Twenty-five of 111 hunting flights by Merlins were successful (22.5%). Five of seven capture attempt techniques were used successfully with a success rate of 4.9%. The most common capture techniques were the stoop at a flock and the chase of an individual isolated from the flock. Most hunting flights (54%) lasted less than 1 min, but hunts of over 5 min were observed (10%). Hunting success rates varied little with the duration of the hunting flight or the size of the Dunlin flock initially targeted. Success rates for hunting flights by Merlins were much higher in Washington (22.5%) than reported from California (12.5%); these higher rates may be the result of a functional response by Merlins in Washington. Dunlins exhibited three distinct types of synchronized predator evasion flights. Dunlins isolated from flocks were often pursued and captured. The most common evasive measure used by isolated birds was a lateral dodge executed while in linear flight away from the flock. Received 5 June 1987, accepted 15 Oct. 1987.

The Dunlin (Calidris alpina) is the most abundant Calidridine sandpiper wintering at estuaries along the Pacific coast of North America (e.g., Page et al. 1979). Throughout much of this range, the Merlin (Falco columbarius) may be its most common diurnal predator (see Page and Whitacre 1975). Shorebirds are an important source of prey for Merlins (Cade 1982). Previous studies of predation by Merlins have concentrated on hunting success rates and mortality of prey species (Rudebeck 1951, Page and Whitacre 1975, Kus et al. 1984). Only Kus (1985) has given more than cursory attention to behavioral interactions between predator and prey. Published descriptions of the flocking behavior of Dunlins (Major and Dill 1978, Davis 1980, Potts 1984) also lack quantitative accounts of behavioral interactions between predator and prey. Because of this, we examined the behavioral relationship between Merlins and Dunlins during winter. Our objectives were: (1) to describe and quantify hunting and capture techniques used by Merlins in pursuit of Dunlins, and (2) to describe techniques used by flocks and individual Dunlins to evade Merlins.

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STUDY AREA AND METHODS

The data were collected at sites in four estuaries in western Washington. Three study sites, Samish Bay, Nisqually River delta, and Kennedy Creek delta are located in Puget Sound. Bowerman Basin is located in Grays Harbor on the outer Pacific coast. Site descriptions are provided in Brennan et al. (1985). Additional observations were also made at Eld Inlet, in southern Puget Sound, and at North Bay and Ocosta in Grays Harbor (Herman and Bulger 1981).

Field work began at Bowerman Basin and Samish Bay during winter 1979. Between December 1980 and March 1981 all four sites (Samish, Nisqually, Kennedy, Bowerman) were visited weekly. Subsequent visits were made to Bowerman Basin through 1982 and Kennedy Creek delta through 1985.

During each visit to a site, we observed movement patterns of foraging flocks of Dunlins throughout the tidal cycle. Direct counts or estimates of shorebird numbers were made as the birds foraged on exposed tidal flats. During hunting flights by Merlins, we recorded the method of attack used, the locations of hunts, predator avoidance behavior exhibited by Dunlins, and, if possible, the size of the flock being attacked. Hunting flight duration was usually determined using a watch, but it occasionally was estimated if several hunts occurred in succession. In some cases an exact determination of duration was impossible, because a hunt was in-progress when first observed. In these cases, we recorded duration from the time the Merlin was first observed hunting. All observations were made during winter (November–March), using binoculars and spotting scopes.

Because more than one Merlin hunted at several of the sites, and because individual Merlins often could not be distinguished, our results represent a composite sample rather than information about the hunting of specific individuals.

Definitions of hunting behavior. — In this paper we discriminate between two different types of hunting behavior: the hunting flight and the capture attempt. We define a hunting flight as a single flight involving any number of capture attempts at suitable prey in any number of different flocks. A capture attempt is an attempt to seize or knock down a specific prey individual during a hunting flight; this seems to correspond with the term attack used by Kus (1985). We used this modified definition of the hunting flight for two reasons: First, Merlins occasionally followed moving Dunlin flocks for great distances (up to 1000 m) and attacked the flock at widely separated locations without perching in the interim. These hunts were directed at the same prey, although at different locations after several minutes had elapsed. Second, hunting flights involving multiple capture attempts often occurred when Dunlin flocks were either splitting into smaller units or in the process of rejoining other flocks, thus causing confusion as to whether the focus of attack had changed to such an extent that classification as an additional hunt was warranted. This apparently was the intent of Page and Whitacre’s definition (G. Page, pers. comm.), and our definition is identical to it.

Chi-square analysis was used to test for differences in behavior described here. Because some data on hunting flight duration were inexact, hunting flights were grouped into interval classes of one minute for purposes of analysis (e.g., <1 min, 1–2 min). We used Yates’ correction for continuity (Zar 1984) to improve the approximation of the chi-square distribution in all tests with df = 1.

RESULTS

Populations of Dunlins and Merlins. — Winter numbers of Dunlins ranged from ca 700 at Eld Inlet to ca 13,000 at Bowerman Basin (Table 1) (see
Table 1

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Maximum Dunlin count</th>
<th>Number of known individual Merlins</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979-80</td>
<td>Samish</td>
<td>7,000</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Bowerman</td>
<td>15,000</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>North Bay</td>
<td>1,000</td>
<td>1</td>
</tr>
<tr>
<td>1980-81</td>
<td>Samish</td>
<td>10,500</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Nisqually</td>
<td>2,300</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Kennedy</td>
<td>2,400</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Bowerman</td>
<td>15,000</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>North Bay</td>
<td>4,000</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Ocosta</td>
<td>3,000</td>
<td>2</td>
</tr>
<tr>
<td>1981-82</td>
<td>Eld</td>
<td>700</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Kennedy</td>
<td>4,100</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Bowerman</td>
<td>11,500</td>
<td>2</td>
</tr>
<tr>
<td>1982-83</td>
<td>Kennedy</td>
<td>2,450</td>
<td>3</td>
</tr>
<tr>
<td>1983-84</td>
<td>Kennedy</td>
<td>2,030</td>
<td>1</td>
</tr>
<tr>
<td>1984-85</td>
<td>Kennedy</td>
<td>4,400</td>
<td>2</td>
</tr>
</tbody>
</table>

* Based on individual plumage characteristics.

Brennan et al. [1985] for census details for winter 1980–1981 at the four primary sites). We believe that at least 12 different Merlins were observed during this study (Table 1). We identified individuals of the subspecies *columbarius* and *suckleyi* (Brown and Amadon 1968).

*Descriptions of hunting activities.*—We observed seven distinguishable methods used by Merlins to capture Dunlins: (1) nearly vertical stoops at or into flying flocks, originating at heights 10–30 m above water; (2) stoops directed at single Dunlins, originating at heights 5–15 m; (3) a low-angle glide-stoop, directed at flocks or individuals, and initiated from a brief burst of powerful flapping while in descent flight; (4) a low stealth attack, by which the Merlin would approach a flock, either on the ground or in flight, using a low and rapid flight in which surprise seemed important; (5) the flock chase, a horizontal pass through a flying flock, invariably initiated after the failure of other techniques; (6) the low chase attack of a single Dunlin isolated from a flock; and (7) ringing, which occurred when the Merlin attempted to seize the Dunlin from below or above as a solitary Dunlin circled upward in an attempt to remain above the Merlin.

An additional behavior exhibited by Merlins, the feint stoop, merits description here. The feint stoop is a shallow, incomplete stoop which
terminates above the in-flight flock of Dunlins. It is not a capture attempt technique as defined here, and it is not considered such in this discussion. The feint stoop may be a method used by Merlins to test cohesiveness in a Dunlin flock. An alternative hypothesis, however, is that the Merlin merely miscalculated its stoop and terminated descent to prepare for another stoop.

**Predator evasion flocking behavior.**—Dunlins exhibit three distinct types of predator evasion flocking behavior in response to hunting Merlins. In *flashing* flight, Dunlins gather in dense, cohesive spherical or elliptical aerial flocks. Their highly synchronized movement results in “flashing,” when the birds’ dark-colored dorsal and light-colored ventral surfaces are alternately exposed. Flashing appears to result from one of two different movements: (1) a very rapid change in flight direction which appears synchronous among flock members, although the maneuver seems to be initiated by a single bird (Potts 1984) or (2) a tilt in body position relative to the bird’s longitudinal axis. Dunlins regularly exhibited *flashing* behavior when foraging during rising tides, as well as in response to the presence of hunting raptors. We discuss *flashing* only in terms of its effectiveness as a predator evasion mechanism.

The second flocking behavior, *rippling* flight, resembles *flashing* but does not involve a change in flight direction by the flock. A seemingly localized synchronous movement, caused by a delayed timing of flock members as they shift body axis position, passes through the flock in one or more waves, producing a rippling effect. These waves of movement always start at one side of the flock and sweep completely through the flock, either horizontally or vertically.

In the third type of flocking, *columnar* flight, Dunlins coalesce into a towering tornado-like vertical column which often undulates throughout its length. Rippling and flashing movements commonly occur in *columnar* flocks. Intergradation between *flashing* and *rippling* flocks is common.

**Success rates.**—We observed 111 Merlin hunting flights with known outcomes. Twenty-five were successful, for a success rate of 22.5%. The success for hunting flights did not vary significantly among the four primary study sites (Samish 16.7%, N = 30; Nisqually 14.3%, N = 7; Kennedy 18.4%, N = 49; and Bowerman 25.0%, N = 16; $\chi^2 = 0.48$, df = 3, $P > 0.75$). During the 1980-81 winter, when all four primary sites were visited with nearly equal frequency, we did not detect monthly differences in success rates when all sites were combined (December 20%, N = 5; January 25%, N = 8; February 21%, N = 14; and March 24%, N = 17; $\chi^2 = 0.06$, df = 3, $P > 0.99$).

Nine hunting flights were successful on the initial capture attempt; this represented 8% of all hunts with known outcomes and 36% of successful
Table 2

Frequencies of Capture Attempt Techniques Used by Merlins in Western Washington

<table>
<thead>
<tr>
<th>Capture attempt technique</th>
<th>Number of attempts</th>
<th>Success rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stoop at flock</td>
<td>151</td>
<td>5.3</td>
</tr>
<tr>
<td>Stoop at single Dunlin</td>
<td>50</td>
<td>2.0</td>
</tr>
<tr>
<td>Low chase of single Dunlin</td>
<td>149</td>
<td>5.4</td>
</tr>
<tr>
<td>Flock chase</td>
<td>32</td>
<td>0.0</td>
</tr>
<tr>
<td>Ringing flight</td>
<td>16</td>
<td>6.2</td>
</tr>
<tr>
<td>Low stealth attack</td>
<td>48</td>
<td>8.3</td>
</tr>
<tr>
<td>Low-angle glide-stoop</td>
<td>2</td>
<td>0.0</td>
</tr>
<tr>
<td>Totals</td>
<td>448</td>
<td>4.9</td>
</tr>
</tbody>
</table>

flights. Of these nine hunts, six utilized the stoop at the flock and three were by the low stealth attack (see below).

The success rate for all capture attempts was 4.9% and ranged from 2.0 to 8.3% for the five successful techniques (Table 2). The flock chase and the low-angle glide-stoop were never successful. Success rates were not significantly different ($\chi^2 = 1.89, df = 4, P > 0.75$) among successful capture attempt techniques. There were, however, significant differences in the frequency of occurrence of those five techniques ($\chi^2 = 190.5, df = 4, P < 0.001$).

**General hunting behavior.**—The most frequent initial capture attempt technique was the stoop, usually preceded by a conspicuous high elevation approach flight (53% of observed initial capture attempts). A low stealth attack was used 47% of the time. Of the unsuccessful hunting flights which initially used the low stealth attack and later incorporated stoops, 9 were successful (20%). A stoop through the flock was included in 59% of the flights ($N = 65$). Feint stoops were noted in 20% of the hunting flights. Merlins often made several feint stoops before stooping down through a flock. Feints, however, did not improve the success rate for hunting flights (9%), suggesting that this activity was not an adaptation to improve hunting efficiency.

Merlins isolated Dunlins from flocks by using stoops, horizontal pursuits, or feint stoops (93% of instances with known cause of isolated bird; $N = 26$). Of the flights which included any kind of stoop (including feint stoop), 27% ($N = 18$) succeeded in splitting the flock into at least two subflocks. Split flocks were the most common source of isolated birds (43%), followed by stoops which failed to split the flock (25%), horizontal pursuit (21%), lack of flock synchronization (7%), and feint stoop (4%).
Prey was captured in flight during all but two successful hunting flights. The two exceptions occurred when Dunlins were knocked into or landed in water and were retrieved by the Merlin.

The size of Dunlin flocks initially targeted by Merlins was quite variable (Fig. 1), ranging from 50 to 10,000. Flocks tended to separate into smaller groups when pursued, although flocks smaller than 50 birds were rarely seen. Because flocks often split or rejoined during hunts, we were occasionally unable to monitor the size of flocks being targeted. Success rates of hunting flights in relation to flock size during the initial attack are presented in Fig. 1.

Most hunting flights by Merlins lasted less than 6 min (Fig. 2). Hunts lasting longer than one minute (46% of all hunts) typically involved combinations of stoops, feint stoops, flock splitting, or chases of individual Dunlins. We found no difference in success rates per hunt between hunts which lasted less than 1 min and all other hunt durations up to 6 min ($\chi^2 = 0.96, df = 5, P > 0.95$), although hunts which lasted less than 1 min were significantly more common than those lasting 2 min ($\chi^2 = 21.6, df = 1, P < 0.001$).

**Evasive responses.** — Dunlins exhibited flashing or rippling flocking be-
behavior in 76 of 83 (92%) hunting flights (Table 3). Dunlin flocking behavior was difficult to monitor because flocks usually separated into smaller units which may have exhibited different evasive tactics. For this reason, we combined flashing and rippling for this analysis, although flashing was clearly more common. Columnar flocking was observed only seven times during hunting flights by Merlins.

There was a tendency for evasion flights to move away from salt marsh, often several hundred m from exposed mud flats or salt marshes. Significantly more flocking took place over water than over mud flats immediately prior to chases of isolated birds ($\chi^2 = 5.8$, df = 1, $P < 0.025$). Consequently, more chases of isolated birds occurred over water than over any other substrate (e.g., mud flats, salt marsh) ($\chi^2 = 12.6$, df = 1, $P < 0.001$).

When separated from a flock, Dunlins flew out over open water in zigzagging flight, rarely more than 0.3 m above the water. Isolated birds moved linearly away from the flock when pursued by a Merlin. The most frequent evasion technique used was a quick lateral dodge ($N = 44$) executed at the last possible moment to evade a Merlin approaching from behind. Other evasion techniques were landing on water ($N = 7$), ringing flight ($N = 6$), and landing on mud or salt marsh ($N = 2$). The lateral dodge technique was significantly more common than any other ($\chi^2 = 78.3$, df = 3, $P < 0.001$).
Table 3
Dunlin Flocking Types in Response to Hunting Flights by Merlins

<table>
<thead>
<tr>
<th>Flock type</th>
<th>Number of flights</th>
<th>Dunlin evasion success</th>
<th>Merlin attack success</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flashing</td>
<td>53</td>
<td>85%</td>
<td>15%</td>
</tr>
<tr>
<td>Flashing, rippling</td>
<td>23</td>
<td>91%</td>
<td>9%</td>
</tr>
<tr>
<td>Flashing, rippling, columnar</td>
<td>7</td>
<td>71%</td>
<td>29%</td>
</tr>
</tbody>
</table>

Landing in water seemed to be used as a last resort, after repeated lateral dodges failed to discourage the attacking Merlin. Dunlins using this method resumed flight after the Merlin passed overhead. Twice Dunlins were knocked into the water by Merlins. On one occasion the Merlin returned quickly and captured the Dunlin before it regained flight.

Discussion

Hunting by Merlins.—Our observed success rate for hunting flights of 22.5% was significantly higher than the 5% success rate reported by Rudebeck (1951) or the 12.8% reported by Page and Whitacre (1975) ($\chi^2 = 14.0, \text{df} = 1, P < 0.001$, and $\chi^2 = 4.38, \text{df} = 1, 0.025 < P < 0.05$, respectively). Also, Kus (1985) reported a success rate of 10.0% in a three-year study in California, but she used a different definition of the hunting flight, making it difficult to compare the two studies. Toland (1986) reported a success rate of 25% from 8 hunting flights in Missouri. The low success rate noted for migratory Merlins by Rudebeck (1951) involved hunts directed at passerines. Highest success rates for Merlins (Page and Whitacre 1975, Kus 1985, Toland 1986, this study) were recorded at wintering sites where falcons hunted on a regular basis for several months. Familiarity of territory and resident prey species during extended wintering periods may enhance success.

We do not know why hunting success rates are higher in Washington than in California. Perhaps these success rates reflect different energetic demands experienced by Merlins and Dunlins in these two regions, although this seems unlikely. Our study area is over 1000 km north of Bolinas Lagoon, California, where Page and Whitacre (1975) made their observations, and lies within 250 km of the northern extent of the common winter range of the Dunlin. The winter shorebird guild in Washington exhibits less diversity than in California (Pitelka 1979), and the Dunlin is by far the most abundant shorebird in this region. The Merlin’s greater reliance on this species is likely a functional response, and this may explain the higher success rate for hunting flights (Murdoch and Oaten 1975).
The Merlin observed by Page and Whitacre (1975) directed 81% of its hunts at sandpipers on the ground, and it failed in all 82 flights or stoops at flying sandpipers. Kus (1985) found that 55% of the hunts were directed at birds on the ground. In Washington, however, the stoop at flying flocks was the most frequent capture attempt technique observed (34%); low stealth flights were common (11%) but never resulted in the capture of prey on the ground.

Page and Whitacre (1975:82) found that, as the shorebirds decreased in number, success rate also decreased. In Washington, we did not observe this decline in hunting efficiency. Populations of Dunlins at the four primary study sites remained fairly stable throughout the 1980–81 winter (see Brennan et al. 1985), and during this period hunting success rates for Merlins changed very little (see Results).

Kus (1985) found that Merlins in California directed most hunts at solitary birds or large flocks even though the success rate of attacks (=capture attempts) and hunts declined with increasing flock size. This is slightly different from the findings of Page and Whitacre (1975) whose success rates were high for hunts directed at single birds (25.6%) and large flocks (21.4%) but low for smaller flocks (6.9–8.3%). In arriving at these figures, they considered only those hunts directed at birds on the ground. Of the ground-oriented attacks, less than half were directed at flocks larger than 50 birds. Our data are not comparable since less than 4% of the hunts in Washington were initially directed at flocks smaller than 50 birds. Although our data on the frequency of hunting flights directed at various flock sizes are otherwise inconclusive, the success rates of hunts did not decline with increasing initial flock size (Fig. 1). This was probably a result of the high proportion (24%) of hunting flights (N = 6) which were successful on the initial stoop into a flock.

Evasive responses.—Once a flock of Dunlins is in flight, the primary defense mechanism appears to be flock cohesion. This is common to all three flocking types. An additional mechanism in flashing flight is the highly synchronous nature of flock movements. In rippling and columnar flights, the occurrence of ripple movements might be more confusing to the falcon than simple flashing because some of the flock would be made up of birds whose bodies are tilted in one of two extreme positions. There would also be birds in various positions between these extremes, including birds in the level flight position. A Dunlin positioned with the wings held vertically may represent a more elusive target for a Merlin attacking from above than one in the normal horizontal flight position, because the upper wing may serve to impede contact by the falcon (see Webb 1986). Of the captures we saw clearly, Dunlins appeared to be captured while in a fairly
level flight position. Rippling flight may thus serve as a means of evasion for a constantly changing subgroup of the flock.

In columnar flight, flock surface area necessarily increases to produce the vertical column. The surface areas of the flock which expand, however, are the sides, which are less susceptible to attack. The surface exposed to attack, the top, is reduced in size. The top surface of a columnar flock actually tracks a Merlin circling above, and this creates much of the undulation effect. Flashing, rippling, increased column height, decreased area of frequent attack, and irregular undulations make this the most complex flocking behavior and potentially the most confusing to a predator.

All three types of defensive flocking behavior may be used during one Merlin hunt, suggesting that these tactics are used in response to a changing set of stimuli. The decreasing frequency of occurrence of the three flocking types (flashing, rippling, columnar) seems puzzling; however, if the probability of flock asynchronization is higher during columnar flight (because it is more complex), this could explain the rarity of this behavior.

In contrast to Boyce's findings in California (1985), we did not observe that flocks retrieve isolated birds. When a Dunlin becomes isolated the Merlin appears to force it farther away from the flock. Such behavior by the Merlin probably reduces the likelihood of the Dunlin's quickly rejoining the flock, thereby increasing the Merlin's potential for success.

ACKNOWLEDGMENTS

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LITERATURE CITED


SHORT COMMUNICATIONS

Distribution and population status of Harlequin Ducks (*Histrionicus histrionicus*) wintering in eastern North America.—In the western Atlantic, Harlequin Ducks (*Histrionicus histrionicus*) winter primarily on saltwater off outer islands, and along exposed ledges, and headlands (Bent 1925, Godfrey 1986) from southern Labrador and Newfoundland to Massachusetts, and, in diminishing numbers, south to Virginia (Armistead 1981, 1982, 1985). The species also occurs in very small numbers in North Carolina and, as vagrants, south to Florida, Texas, and points inland (A.O.U. 1983). Bent (1925) and Kortright (1943) both considered the species rare in the east and Palmer (1976:335) stated that “the total numbers of Harlequins cannot be large; the number that travels s. to Nfld., the Maritimes, and farther southward probably is in the hundreds, certainly not now in thousands.” Since the 19th century, concentrations of Harlequin Ducks have recurred at particular sites every winter (Palmer 1949; Griscom and Snyder 1955; Tufts 1986; R. R. Veit, unpubl. data). Here I summarize the current knowledge of winter distribution and population size of Harlequin Ducks in eastern North America and include data on recent Harlequin Duck censuses around Isle au Haut and surrounding islands in Penobscot Bay, Maine.

Methods.—I examined all Christmas Bird Count (CBC) data collected from 1979-80 to 1984-85, from Atlantic Canada, New England, and the Mid-Atlantic region (Am. Birds) and reviewed literature on the winter distribution of Harlequin Ducks. Since 1976, I have been an observer on seven boat trips that have attempted to circumnavigate Isle au Haut; rough sea conditions prevented full coverage on four of these trips. During earlier trips, the islands adjacent to Isle au Haut were not censused (Table 1). In 1983, I conducted an aerial survey of the waters surrounding Isle au Haut, adjacent islands, and all outer islands from the Kennebec River to eastern Penobscot Bay. Harlequin Ducks are small and dark (Vickery 1983) and are often difficult to detect and identify from the air. The single engine Cessna 152 was flown at 25 to 75 m above sea level at a speed of 60-80 knots and facilitated close approach and permitted ready identification of this species. The plane passed along the perimeter and in each cove of each island.

Atlantic Canada.—The literature regarding the Harlequin Duck’s historical status in Atlantic Canada has been unclear (Taverner 1937, Todd 1963, Godfrey 1986) though Phillips (1925:381) reported a “marked reduction” in the Atlantic Maritimes in the late 19th-early 20th century. Between 1979-80 and 1984-85, CBCs have been conducted in as many as 42 areas along the Atlantic Canada coast (Fig. 1). Only two CBCs in Atlantic Canada have recorded more than 5 Harlequin Ducks (Table 2). The largest and most consistent concentration, present annually at Cape St. Mary’s, Newfoundland, recorded a high count of 145 individuals in 1980-81. Historically, Harlequin Ducks seem to have been absent or unrecorded from the St. Lawrence River in Quebec (Wintle 1896), though Ouellet (1974) considered the species occasional. Several additional winter sightings have been noted in recent years (H. R. Ouellet, pers. comm.). Harlequin Ducks may have been more numerous off Anticosti Island, Quebec, in the 19th century (Brewster 1884), though Ouellet (1969) believes that the species has been rare in winter throughout this century.

CBCs in Atlantic Canada do not extend along the north shore of the St. Lawrence beyond Baie-Comeau, Quebec, and Harlequin Ducks could occur in this remote part of the Gulf. However, a recent 3-year winter survey of sea ducks (1974-1976) in the northern part of the Gulf of St. Lawrence, including the Gaspé Peninsula, Anticosti Island, and the north shore to Blanc Sablon, Quebec, conducted by the Canadian Wildlife Service found only three individuals (Reed and Bourget 1977). Atlantic Canada CBCs from the Gaspé Peninsula, Prince Edward Island, New Brunswick, and Nova Scotia, further indicate that Harlequin Ducks...
Ducks are absent, or rare, in the Gulf of St. Lawrence in winter. Peters and Burleigh (1951) considered Harlequin Ducks uncommon winter residents in Newfoundland; Tuck (1948) reported the species as rare in winter near Argentia-Dunville. Tuck and Borotra (1972) considered them uncommon in winter on St. Pierre-Miquelon, and CBCs have not recorded them on these French islands.

Canadian Wildlife Service waterfowl biologist Ian Goudie (pers. comm.) suggests that wintering Harlequin Ducks around Newfoundland may have numbered in the low thousands prior to 1940 and that heavy hunting pressure may have reduced their populations since then. In the absence of specific data, Goudie cites anecdotal evidence from local hunters and the colloquial references in place names, e.g., Lord and Lady Cove, to support this contention. In addition to the Cape St. Mary's concentration, he also reports 20-30 individuals from the Ramea archipelago on the southwest coast and believes that <200 additional Harlequin Ducks probably winter in Newfoundland.

CBC data have recorded fewer than 20 Harlequin Ducks for Nova Scotia and New Brunswick combined. In Nova Scotia, Tufts (1986) noted several localities where, although uncommon, small numbers occurred with some regularity. Squires (1952) believed that Harlequin Ducks rarely wintered in New Brunswick. He stated that 10 specimens were collected near The Wolves (small islands near Grand Manan Island) and that several individuals recurred at Pt. Lepreau, both localities in the Bay of Fundy. During Canadian Wildlife Service winter sea duck aerial surveys, P. Hicklin (pers. comm.) has observed small numbers of Harlequin Ducks near The Wolves; a boat census of 87 individuals, 14 April 1986, may reflect a spring migratory concentration, but Hicklin believes >50 may winter regularly at this locality. In addition, in recent years N. Famous (pers. comm.) has observed up to 22 Harlequin Ducks off East Quoddy Head, Campobello Island, New Brunswick.

Maine and New Hampshire.—Norton (1896) reported that Harlequin Ducks were common only in the eastern part of Maine. Knight (1908) believed that fewer than 200 individuals wintered along the coast at the turn of the century but stated, without providing evidence, that they had been more numerous previously. Palmer (1949) specifically reported Isle au Haut and its surrounding islands as an area where Harlequin Ducks have wintered regularly for at least 60 years.

CBC data and Isle au Haut surveys indicate that Harlequin Ducks (>5 individuals) are presently known to winter along the Maine coast at only six locations (Table 3). The estimated total of 300 individuals wintering in Maine in recent years may reflect a population increase from Knight's report (1908), but the difference could also be due to improved censusing.
Fig. 1. Distribution of recurring Harlequin Duck concentrations along the Atlantic coast of eastern North America.
Table 2

NUMBER OF HARLEQUIN DUCKS SEEN ON COASTAL ATLANTIC CANADA CHRISTMAS BIRD COUNTS, 1979–1984

<table>
<thead>
<tr>
<th>Year</th>
<th>No. counts</th>
<th>Total No. Harlequins</th>
<th>Cape St. Mary's, Newfoundland</th>
<th>Port Hebert, Nova Scotia</th>
<th>Others</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979–80</td>
<td>31</td>
<td>89</td>
<td>80</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>1980–81</td>
<td>35</td>
<td>145</td>
<td>143</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>1981–82</td>
<td>39</td>
<td>108</td>
<td>101</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>1982–83</td>
<td>42</td>
<td>91</td>
<td>71</td>
<td>13</td>
<td>7</td>
</tr>
<tr>
<td>1983–84</td>
<td>41</td>
<td>71</td>
<td>56</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td>1984–85</td>
<td>39</td>
<td>101</td>
<td>90</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Mean</td>
<td>37.8 ± 1.7</td>
<td>100.8 ± 10.2</td>
<td>90.2 ± 2.3</td>
<td>6.0 ± 2.2</td>
<td>4.7 ± 0.8</td>
</tr>
</tbody>
</table>

Harlequin Ducks occur irregularly and only in small numbers along the New Hampshire coast (D. J. Abbott, pers. comm.).

Massachusetts south to Virginia. —Griscom and Snyder (1955) believed Harlequin Ducks had declined and were extremely rare in Massachusetts at the turn of the 19th century, although they noted the species had increased since that time. They reported as many as 35 individuals wintering regularly off Squibnocket, Martha’s Vineyard. Since 1979, 10 or more Harlequin Ducks have been found annually in Rhode Island (D. L. Emerson, pers. comm.). In February 1981, 18 individuals were observed at Sachuest Pt. (Vickery 1981), where similar numbers have returned each winter. Twenty-two occurred there in 1984–85 (Heil 1985). It seems that Sachuest Pt. (Newport County), Rhode Island, and Martha’s Vineyard, Massachusetts (=60 km apart), may share a common population; in the past three years, increases at one locality were matched by equivalent decreases at the other locality (Table 4). A small concentration of 2–7 Harlequin Ducks off Montauk, Long Island, New York has persisted for many years (Bull 1964). The species was basically unknown in southern New Jersey (Stone 1937), or Virginia (Bailey 1913) at the turn of the century.

Coastal CBCs for Massachusetts, Rhode Island, Connecticut, New York, New Jersey, and Maryland form a near continuous series of winter censuses with a high level of coverage.

Table 3

LOCALITIES IN COASTAL MAINE RECORDING HARLEQUIN DUCKS (>5 INDIVIDUALS)

<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Isle au Haut</td>
<td>149</td>
<td></td>
<td></td>
<td>240</td>
<td>210</td>
<td></td>
</tr>
<tr>
<td>York County</td>
<td>10</td>
<td>14</td>
<td>22</td>
<td>35</td>
<td>23</td>
<td>17</td>
</tr>
<tr>
<td>Scarborough</td>
<td>12</td>
<td>5</td>
<td>9</td>
<td>6</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Jonesport</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Biddeford Pool</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Georgetown</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>285</td>
<td>271</td>
</tr>
</tbody>
</table>

* Difficulty of access has prevented annual census of this concentration.
Table 4

Christmas Bird Counts from Massachusetts to Maryland in Which Harlequins Ducks Were Recorded, 1979–1984

<table>
<thead>
<tr>
<th></th>
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<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Massachusetts</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cape Ann</td>
<td>2</td>
<td>cw(^a)</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>2.0 ± 0.5</td>
</tr>
<tr>
<td>Cape Cod</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>6</td>
<td>2.3 ± 0.6</td>
</tr>
<tr>
<td>Martha’s Vineyard</td>
<td>0</td>
<td>3</td>
<td>6</td>
<td>10</td>
<td>20</td>
<td>5</td>
<td>7.3 ± 2.9</td>
</tr>
<tr>
<td>All others</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>1.5 ± 0.4</td>
</tr>
<tr>
<td>Rhode Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Newport-Westport</td>
<td>8</td>
<td>3</td>
<td>6</td>
<td>17</td>
<td>7</td>
<td>22</td>
<td>10.5 ± 3.0</td>
</tr>
<tr>
<td>South Kingston</td>
<td>0</td>
<td>1</td>
<td>6</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1.8 ± 0.9</td>
</tr>
<tr>
<td>New York</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Montauk, Long Island</td>
<td>2</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>2.3 ± 0.7</td>
</tr>
<tr>
<td>All others</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4(^b)</td>
<td>0.7 ± 0.7</td>
</tr>
<tr>
<td>New Jersey</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cape May</td>
<td>5</td>
<td>3</td>
<td>4</td>
<td>8</td>
<td>cw(^c)</td>
<td>0</td>
<td>3.5 ± 1.2</td>
</tr>
<tr>
<td>All others</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>5(^c)</td>
<td>1.3 ± 0.8</td>
</tr>
<tr>
<td>Maryland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ocean City</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>7</td>
<td>2.3 ± 1.5</td>
</tr>
<tr>
<td>Total No. Harlequin Ducks seen</td>
<td>19</td>
<td>15</td>
<td>33</td>
<td>44</td>
<td>47</td>
<td>56</td>
<td>35.7 ± 6.6</td>
</tr>
</tbody>
</table>

\(^a\) cw = Harlequin Duck seen during count week, calculated as 1 individual.
\(^b\) All on South Nassau County, Long Island CBC.
\(^c\) All on Barnaget CBC.

The number of wintering Harlequin Ducks clearly diminishes southward (Table 4). An additional 2–4 individuals regularly winter at the Chesapeake Bay-Bridge Tunnel, Virginia, not included in any CBC (Armistead 1981, 1982, 1985); a high count of 15 individuals was noted there 5 March 1978 (Virginia Checklist Comm. 1979). Other recent maxima include 6 at Virginia Beach, Virginia, in 1981 (Armistead 1981), and 5 at Rodanthe, North Carolina Jan. 1984 (LeGrand 1984). Almost all Harlequin Ducks from New Jersey south are found at stone jetties or bridge abutments, all recent man-made constructions.

CBC data from Massachusetts south, 1979–1985, indicate that Harlequin Ducks have increased significantly at the southern limit of their range during this period (r, = 0.943, P < 0.01) (Fig. 2).

Discussion.—Two natural influences probably contribute to the Harlequin Duck’s distribution in eastern North America. First, Harlequin Ducks appear to require rocky ledges or exposed headlands and outcroppings as winter habitat, possibly for the high energy food sources available at such sites (Goudie and Ankney 1986). Most of the coastline south of Maine is sand. The species’ only regular wintering locality on the sandy terminal moraine of Cape Cod is an area of scattered rocks at East Orleans (R. R. Veit, unpubl. data). The expansion in winter range to southern New Jersey, Maryland, and Virginia may be linked to the relatively modern construction of bridge abutments and stone jetties, which mimic rocky shoreline.
Second, it appears that Harlequin Ducks are faithful to specific wintering localities; 90% of the individuals observed on CBCs and at Isle au Haut, Maine, 1979–1985, were recorded annually at the same localities. Site fidelity requires predictably tolerable wintering conditions at these sites. The consistently ice-free conditions along the Maine coastline, Bay of Fundy, and the southeast coast of Newfoundland may help explain the comparatively large numbers found there. Conversely, the Gulf of St. Lawrence, especially the north shore to Blanc Sablon, is characterized by frequent, extensive ice build-ups (Reed and Bourget 1977; M. Gosselin, pers. comm.).

Ice-free rocky shoreline is available along much of the southern and eastern coasts of Newfoundland, and Harlequin Ducks may occur there in greater numbers than those registered on the Cape St. Mary’s, Newfoundland, CBCs. To date the rest of this coastline has not been censused adequately. Although additional concentrations may exist, the absence of literature references from Newfoundland or St. Pierre-Miquelon (Tuck 1948, Peters and Burleigh 1951, Tuck and Borotra 1972), suggests that it is unlikely that the species was obviously widespread or abundant in this region.

The two limiting habitat factors—rocky shoreline and predictable ice-free conditions—not withstanding, the western Atlantic Harlequin population appears to be well below its wintering carrying capacity, occupying only a small fraction of the seemingly suitable sites available.

Approximately 650–700 Harlequin Ducks are presently known to winter in eastern North America, supporting Palmer’s (1976) contention. An additional 200–300 individuals may occur along the coasts of Newfoundland and Nova Scotia, but such numbers have yet to
be documented. Although the species is presently increasing at the southern limit of its range, it seems likely that Harlequin Ducks in eastern North America are now and have historically been quite rare and of local distribution.

Acknowledgments.—I thank H. Kimball, whose competence as a pilot made the aerial survey possible. The Penobscot Valley Chapter of the Maine Audubon Society scheduled the boat trips around Isle au Haut. A. J. Erskine, N. Famous, R. I. Goudie, P. Hicklin, and H. R. Ouellet generously made available previously unpublished data. M. Gosselin was especially helpful with useful information and insights. R. Banks, K. Bildstein, R. A. Lautenschlager, H. Ouellet, B. Vickery, and an anonymous referee reviewed this manuscript several times, providing many useful ideas and considerably improving the original text. In addition, P. Brown, W. Halteman, M. Hunter, W. Glanz, and W. Krohn supplied valuable suggestions. The Maine Chapter of The Nature Conservancy supplied facilities and support for which the author is grateful. This is contribution No. 1208 of The Maine Agricultural Experimental Station.

LITERATURE CITED


KNIGHT, O. W. 1908. The birds of Maine. Published by the author. Bangor, Maine.


Evidence of intraspecific brood parasitism in the Tree Swallow. — Intraspecific brood parasitism is of interest because it selects against the evolutionary maintenance of parental care and genetically rewards individuals who do not provide care (i.e., parasites) and genetically punishes those who do (i.e., hosts). In the best known examples (e.g., Evans 1980, Power et al. 1981, Brown 1984, Gowaty and Karlin 1984, Emlen and Wrege 1986) brood parasitism appears to be related to competition for access to a limited number of nest sites (see Yom-Tov 1980). Here I present evidence of intraspecific brood parasitism in a nest-site limited...
species, the Tree Swallow (Tachycineta bicolor). Tree Swallows are nonexcavating cavity nesters.

From 1980 to 1983 I monitored 120 Tree Swallow nests at a nest-box trail on the salt marshes of the J. F. Kennedy Memorial Wildlife Refuge at Tobay Beach on the south shore of Long Island, New York (see Schaeffer 1972 for a description of the study site). Each nest was visited once each morning from the day the first egg was discovered until no new eggs had been laid for two days. Nests were usually visited after the normal laying period for the day. Each egg was numbered in sequence with an indelible marker.

At seven of 120 (5.8%) nests, two eggs appeared in less than 24 h. Kuerzi (1941) also reported two eggs appearing in less than 24 h at three of 68 (4.4%) Tree Swallow nests. The frequency I found, however, is likely an underestimate because parasitic eggs that were laid the day before host clutch initiation or the day after clutch completion were undetectable by my methods (cf. Frederick and Shields 1986a). Using Frederick and Shields (1986a) method of correcting for this underestimation produces a corrected estimate that 11 of 120 (9.2%) nests were parasitized. This frequency is similar to the frequencies of parasitized nests estimated for other passerines (e.g., Cliff Swallow [Hirundo pyrrhonota], 0-25% depending on colony size, Brown 1984; Eastern Bluebird [Sialia sialis], 15%, Gowaty and Karlin 1984; European Starling [Sturnus vulgaris], 11-37%, Evans 1980, Power et al., unpubl. data; White-fronted Bee-eater [Merops bullockoides], 10-27% depending on colony, Emlen and Wrege 1986), but greater than the frequency of 1.5% estimated by Frederick and Shields (1986b) for the White Ibis (Eudocimus albus). However, it is much lower than the frequencies reported for some species of duck (Anatidae) (e.g., Weller 1959, Morse and Wright 1969, Clawson et al. 1979, McCamant and Bolen 1979) where one-half to two thirds of nests are sometimes parasitized.

At another eight of 120 (6.7%) nests, eggs disappeared from clutches during egg laying. None of these eggs appeared damaged before they disappeared. (Tree Swallows often remove damaged eggs from their nests [pers. obs.]) Egg removal may be evidence of intraspecific brood parasitism because egg removal appears to be an important tactic in the brood parasitism strategies of other species (e.g., Brown 1984; Emlen and Wrege 1986; Lombardo et al., unpubl. ms.). More study is needed, however, to determine whether Tree Swallow brood parasites remove host eggs before replacing them with their own.

Acknowledgments.—I thank J. R. Crook, P. C. Frederick, H. W. Power, and L. C. Romagnano for their comments on the manuscript. The Town of Oyster Bay, New York, kindly allowed me to use the Kennedy Refuge as a study site. Financial support was provided by a BRSG Grant to H. W. Power from Rutgers University and from grants from the F. M. Chapman Fund, the Northeastern Bird Banding Association, Sigma Xi, the J. Leatham Fund of the Zoology Department, and the Ecology Graduate Program of Rutgers University.

LITERATURE CITED


Nest-construction tactics in the Cedar Waxwing. — Nest construction involves a large expenditure of time and energy (Collias and Collias 1984). Putnam (1949) estimated that building a nest would require a pair of Cedar Waxwings (Bombycilla cedrorum) to make over 2500 trips. In addition to the cost of transporting material to the nest site, observations of the struggles of birds to break off twigs or pull fibers loose, and the frequent failures involved, suggest that nest building is an energetically expensive activity. Nonetheless, it seems that little attention has been paid to the tactics that birds might use to reduce the costs associated with nest construction. Collias and Collias (1984) suggested that energy costs may be reduced considerably if good sources of nest materials are located close to the nest site. Skutch (1976) suggested that birds may save labor by removing material from other nests, either deserted or occupied, and gives examples of such behavior in several tropical and colonially nesting species.

During a study of the breeding biology of the Cedar Waxwing at the Prince Edward Point National Wildlife Area, near Picton, Ontario, we made a number of observations of waxwings engaging in activities that could substantially reduce the large expenditure of time and energy required for nest building. These involved taking material from either old nests or active nests of other birds, and reusing abandoned nests of conspecifics.

On several occasions we observed waxwings taking material from old nests of Cedar Waxwings and other species. The main drawback to gathering material from old nests is likely to be the possibility of acquiring ectoparasites from the material. Putnam (1949) reported two cases of Cedar Waxwings deserting nests infested with mites, and in both
instances the birds had taken nesting material from old nests of Common Grackles \( (\text{Quiscalus quiscula}) \). This possibility may be reduced when birds take material from active nests under construction. Tyler (1950) commented on Cedar Waxwings stealing material from active nests of other birds, and he mentioned the Eastern Kingbird \( (\text{Tyrannus tyrannus}) \) and Yellow-throated Vireo \( (\text{Vireo flavifrons}) \) as species that have been recorded as victims of this behavior. At Prince Edward Point, we have seen waxwings taking material from active nests of Eastern Kingbirds, Northern Orioles \( (\text{Icterus galbula}) \), and American Robins \( (\text{Turdus migratorius}) \). Waxwings have also been observed on a number of occasions removing substantial quantities of material from active nests of Yellow Warblers \( (\text{Dendroica petechia}) \) near Elgin, Ontario (M. Studd, pers. comm.). This tactic suffers somewhat from the relative scarcity of nests that are under construction, as well as the owners’ defense of their nest when the waxwings are observed carrying off material.

In addition to taking material from old nests, we observed 3 cases in which a pair of waxwings apparently took over and renovated an abandoned Cedar Waxwing nest. One nest was found by us on 11 June 1984 with the female sitting on the nest. The pair deserted the nest, however, probably in response to our disturbance. By 15 June the nest had deteriorated noticeably. Waxwings were noticed visiting this nest again on 15 and 17 July, and on 23 July a female was sitting on the nest. Four young were eventually fledged from this second nesting attempt. In 1985 two similar occurrences were recorded. We discovered one of the nests while it was still under construction on 17 June. We assumed that eggs were laid and incubation had begun because the female was sitting on the nest as late as 28 June. The nest was abandoned for unknown reasons, possibly due to predation (it was empty on 12 July). On 18 July, however, a female was sitting on the nest, and this nesting attempt produced 5 young which fledged around 13 or 14 August. The other nest was found on 28 June while it was under construction. It was active until at least 5 July, but was later abandoned for unknown reasons. On 20 and 22 July, however, 2 waxwings were carrying material to the nest and apparently rebuilding it. This pair eventually produced young, but the nest was depredated between 12 and 15 August. On closer examination we found that in this case the birds had not renovated the old nest but had built a separate structure on top of the old cup. In all 3 cases, the birds involved in the first attempt were not marked, so it is not certain if the same pair returned to their old nest or a new pair occupied it. It seems unlikely, however, that a pair would return to a nest they had already abandoned.

In instances of nest reuse where the birds do not build a new nest cup they may realize a significant energy savings. It is possible though that this behavior may have drawbacks. In addition to the problem of ectoparasites, an old nest might be contaminated by fecal material if it has been occupied by nestlings. It seems likely that only unsuccessful nests will be suitable for reuse, as nests that have housed a brood of large nestlings tend to become expanded and flattened by the activity of the young. If the location of the nest site is associated with the probability of fledging young, for example by being in an area regularly visited by a predator, then reuse of unsuccessful nests may decrease the chance of successfully raising young (Blancher and Robertson 1985).

Most species of birds build their own nest, and typically build a new nest for each brood. The use of a nest built by other individuals of the same species seems to be uncommon, perhaps because such a nest is likely to be defended by the original owners if it is still suitable, and conspecifics are apt to be relatively equally matched competitors. Nonetheless, in species that are site limited or which build complex nests, the same nest may be used repeatedly. However, nest reuse seems to have been rarely reported among the very large number of passerine species which build open cup nests. Nest reuse has been reported in the American Robin (Tyler 1949) and in the Eastern Kingbird (Blancher and Robertson 1985). In robins at least, though, the nest was believed to be reused by the same pair. Nolan
(1978) noted one case where a female Prairie Warbler (*Dendroica discolor*), after having its own nest destroyed by the investigator, apparently used a nest that had been abandoned by another female.

Reuse of nests abandoned by conspecifics may be more likely to occur in Cedar Waxwings than in other passerines because of two factors. First, the absence of territorial behavior may allow other pairs access to old nests, and secondly, the propensity of this species to desert its nest (Tyler 1950) may increase the probability of a pair finding a complete nest. The tactics described here for Cedar Waxwings could result in a significant reduction in the costs associated with nest construction. More work is needed to ascertain how these benefits might be offset by drawbacks such as a potential reduction in nest success. Researchers studying the breeding biology of other open-nesting passerines should consider the possibility that other species may use similar tactics, as further information could provide useful insights into the selective pressures operating on nest-building behavior.

**Acknowledgments.** — We are grateful to H. Levesque and the Canadian Wildlife Service for allowing us to work at Prince Edward Point and providing accommodations. Stephen Maxwell assisted us in the field. We thank R. D. Montgomerie, P. T. Boag, D. R. Petit, and an anonymous referee for comments on earlier drafts. This study was supported by an NSERC grant to RJR.

**LITERATURE CITED**


Sightings of Golden-cheeked Warblers (*Dendroica chrysoparia*) in northeastern Mexico.— Relatively little is known about the Golden-cheeked Warbler (*Dendroica chrysoparia*) outside of its breeding range in the Edwards Plateau of Texas. Although it has been reported that the species winters in southern Mexico (Miller et al. 1957, Alvarez del Toro 1980, Braun et al. 1986) and Central America (Pulich 1976), observations of this species during migration are rare. Pulich (1976) summarized spring migration records outside the United States and noted only a single record other than in the northern regions of the Sierra Madre Oriental...
in Mexico. The observations reported here were made in northeastern Mexico at Rancho del Cielo, a biological station operated by Texas Southmost College. Rancho del Cielo is on the eastern slope of the Sierra de Guatemala about 40 km north of Cuidad Mante, Tamaulipas, in Mexico’s northernmost cloud forest. The forest, at an elevation of about 1100 m, is a dense oak-sweet gum complex (Webster 1974).

On 18 March 1987, approximately one h after sunrise, we observed 5-7 male Golden-cheeked Warblers foraging near the crown of a large oak (Quercus sartorii). Observations through a telescope clearly revealed the combination of black back, throat, and dark line through the eye that separates the Golden-cheeked from other yellow-faced warblers. The warblers were part of a loose assemblage of 35-50 birds including Solitary Vireos (Vireo solitarius), Black-throated Green Warblers (Dendroica virens), Wilson’s Warblers (Wilsonia pusilla), and Blue-gray Gnatcatchers (Polioptila caerulea). The progress of the flock was followed through several trees, most or all of which were flowering. An additional sighting of an individual was made later the same morning.

LITERATURE CITED


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Site 1 was in an area of sandy soil; Site 2 was in an area of firmly packed gravel. The numbers of surface nests and burrows in use at each site were counted during five visits in winter (June-August) and summer (February).

African Penguins nested on the surface at sandy Site 1 more frequently in winter (19 surface nests, 111 burrows) than in summer (3 surface nests, 60 burrows) ($\chi^2 = 4.08, \text{df} = 1, P < 0.05$). Season had no effect on the number of surface nests at Site 2 ($\chi^2 = 0.025, \text{df} = 1, P < 0.01$) (winter: 3 surface nests, 97 burrows; summer: 3 surface nests, 85 burrows), which is not susceptible to burrow-flooding and collapse. In winter a significantly greater proportion of penguins nested on the surface at Site 1 (the sandy site), which was susceptible to burrow-flooding and collapse than at Site 2 ($\chi^2 = 8.81, P < 0.01, \text{df} = 1$). In summer there was no significant difference in the proportion of surface nesters between the two sites ($\chi^2 = 0.176, P > 0.05, \text{df} = 1$).

The results indicate that, for African Penguins, ambient temperature and insolation affect the proportion of the population that occupies surface nests. Scolaro (1984) found that Magellanic Penguins ($S. \text{magellanicus}$) show a tendency to nest in soils of high clay content compared to soils of low clay content. The results of this study confirm the tendency of penguins preferentially to burrow in suitable substrata and suggest that the quality of the burrowing substratum is important for spheniscid penguins.

Acknowledgments. —I thank the Sea Fisheries Research Institute for transport to and accommodation on Dassen Island, and D. C. Duffy and S. Hunter for commenting on the manuscript. This work forms part of the Benguela Ecology Programme, sponsored by the South African National Committee for Oceanographic Research.

LITERATURE CITED


Wilson Bull., 100(1), 1988, pp. 132-134

A case of polygyny in the Black-throated Blue Warbler. —Polygyny has been reported for only 12 of the some four dozen species of North American Parulinae (for a review, see Ford, Current Ornithol. 1:329-356, 1983). Here, we document the first reported case of polygyny in the Black-throated Blue Warbler ($D. \text{caeruleascens}$).
Observations were made in spring and summer 1986 in the northern hardwoods forest of the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. The study area and habitat at this site have been described by Holmes and Sturges (J. Anim. Ecol. 44: 175–200, 1975). Adult Black-throated Blue Warblers were captured in mist nets and banded with U.S. Fish and Wildlife Service aluminum bands, and with unique combinations of colored plastic leg bands.

The polygynous male's first nest (A) was initiated on 13 or 14 May, 1986, with the female (F1) completing a four-egg clutch by 24 May. Three eggs hatched on 5 June, and three young fledged on 15 June (the fourth egg was infertile). The male fed nestlings regularly at nest A. During this period, the male displayed what appeared to be normal territorial behavior, engaging in frequent countersinging and territorial fights with males on three adjacent territories.

On 27 May, we observed the male following a nest-building female (F2) approximately 300 m from nest A (where F1 was incubating). The male exhibited behavior indicative of courtship, including "soft singing" (singing in a distinctly lower volume than regular song), close surveillance of the female as she foraged and gathered nesting materials, and frequent chases through the forest shrub layer. F2 completed a five-egg clutch in this nest (B) on 7 June. No other Black-throated Blue Warbler territories intersected the area between nests A and B, even though the habitat in this area was continuous and presumably suitable. Thus, the male was able to travel between the two nest sites without interference from other males.

The male spent a far greater proportion of time near nest A than in the vicinity of nest B. The close proximity of three neighboring males to nest A, and the lack of males near nest B, may have necessitated greater territorial vigilance by the male at nest A. During the laying and incubation phase at nest B the male made only sporadic visits there. These visits usually lasted no longer than 5 min and were characterized by bouts of intensive singing near the nest followed by long flights back towards nest A. Twice during the polygynous male's absences, we observed two other male Black-throated Blue Warblers in the vicinity of nest B (extraterritorial intrusions; Ford 1983). Both intruding males sang within 10 m of the nest and one banded male, known to have an active nest approximately 350 m away, was seen to chase F2 as she returned to her nest after foraging. The second male, which was unbanded and probably not mated, was not seen again.

Following fledging of young at nest A, the male continued to feed one color-banded fledgling while maintaining territory A. He continued to feed the fledgling until at least 7 July.

On 19 June, all five nestlings hatched in nest B. We observed attentiveness of both adults from a blind 12 m from the nest, for almost 27 h during the first eight days. Observations were made primarily during morning and early afternoon, with most sessions lasting 2.5–3.5 h (range = 1–6 h). F2 made 2.5 times more feeding trips than did the male (294 vs 115). In monogamous Black-throated Blue Warblers, feeding duties are shared approximately equally by the sexes (C. P. Black, Ph.D. diss., Dartmouth College, Hanover, New Hampshire, 1975; pers. obs.). Here, the disparity in parental care may have resulted from the male's preoccupation with the fledgling from nest A and with the continued maintenance of territory A.

On days 7–9 the young in nest B appeared extremely hungry. On at least six occasions, F2's attempts to settle on the nest to brood were obstructed by the vigorous gapes of the nestlings, which forced her to back away from the nest. After each unsuccessful brooding attempt, F2 departed the nest to continue foraging. Feather development was clearly retarded in these young relative to nestlings of identical age. On day 8, weights of these nestlings were considerably lower than those of similar-aged nestlings of monogamous pairs (K. E. Petit and R. T. Holmes, unpubl. data).
On day 9, we observed a red squirrel (Tamiasciurus hudsonicus) prey upon the nestlings in nest B. In most Black-throated Blue Warbler nests, nestlings fledge prematurely if disturbed after day 7. The fact that the nestlings could not escape the squirrel’s attack indicates their retarded state of growth.

A second clutch (nest C) was initiated by FI and the polygynous male on 29 June. Four eggs in this third nest hatched on 14 July and feeding duties appeared to be shared equally by the male and female. The four young in nest C fledged on 24 July. Thus, this male was presumably responsible for fertilizing 13 eggs, 12 of which hatched, and seven of which resulted in fledged young.

Of 20 Black-throated Blue Warbler pairs closely monitored at Hubbard Brook in 1986, this was the only case of polygyny we found. Monogamy is thought to occur in birds when parental care is needed to successfully raise the young (Lack, Ecological Adaptations for Breeding in Birds, Methuen, New York, New York, 1968). Our observations of the failure of nest B support this contention. Additional work is required to explain the proximate causes of this reproductive strategy.

Acknowledgments. —This study was supported by a grant from the National Science Foundation to Dartmouth College. We acknowledge the Northeast Forest Experimental Station, U.S. Forest Service for allowing us to work at Hubbard Brook, and K. L. Bildstein, P. A. Gowaty, D. R. Petit, L. J. Petit, N. L. Rodenhouse, T. W. Sherry, K. G. Smith, and an anonymous reviewer for their comments on an earlier version of the manuscript. — KENNETH E. PETIT, Dept. Biological Sciences, Kent State Univ., Kent, Ohio 44240; MARK D. DIXON, Dept. Animal Ecology, Iowa State Univ., Ames, Iowa 50011; and RICHARD T. HOLMES, Dept. Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755. (Present address KEP: 348 Church St., Doylestown, Ohio 44230.) Received 20 Apr. 1987, accepted 11 Sept. 1987.


Two nests of the Azure-hooded Jay with notes on nest attendance. —The Azure-hooded Jay (Cyanolyca cucullata) inhabits humid montane forests and forest edges from south-central Mexico to western Panama (Carriker 1910, Miller et al. 1957, Slud 1964, A.O.U. 1983). In Costa Rica the species occurs mainly on the Caribbean slope of the central highlands, but it is also common at Monteverde, on the Pacific slope of the Cordillera de Talaman (Slud 1964), where we discovered two active Azure-hooded Jay nests. This report is apparently the first published nesting record for the species.

We discovered the first nest on 14 April 1983 when one adult came to feed a small, naked nesting that was barely able to lift its head. The nest was 7 m high in a tree (Saurauia veraguensis; approximately 8 cm dbh) overhanging the bank of a dirt road that bisects the Monteverde Cloud Forest Reserve, Puntarenas Province, Costa Rica (1510 m elevation; Lower Montane Rain Forest life zone [Holdridge 1967]). On 2 and 3 May, we saw two adults bring katydids (Orthoptera: Tettigoniidae) to at least two nestlings, now with well-feathered heads. The young fledged between 3 and 7 May, and thus spent at least 20 days in the nest. On 7 May an adult visited the nest several times without food, and the young had left.

On 15 May, we found two adults and two fledglings calling near the nest, and KGM easily captured a fledgling by hand. The color pattern of the plumage was similar to the adults’ except that the hood was duller blue and the back feathers were a duller, less shiny black. Both the bill and the body were noticeably smaller than those of the adults. The fledgling “squawked” repeatedly for 4 min while held, eliciting alarm calls from the other fledgling and the two adults.
On 22 July 1983, we collected the nest (Florida State Museum No. UF 13159). The foundation is coarsely constructed of 2–3 mm diameter twigs. The inside diameter of the nest cup is 11 cm, and the outside diameter varies from 19–33 cm due to the various lengths of the outer twigs. The inside cup is 5 cm deep and woven of thin fibrils and twigs (averaging about 0.5–1.0 mm in diameter) but contains no feathers or other soft material. It was lodged over side branches next to the main trunk of the tree which was 3 cm in diameter at this height. Although the nest was partly obscured (in the tree) by bamboo, it was easily visible from the road below; the nest material contained very little moss or other concealing material. In general, the construction and materials are similar to those of other jay nests (Goodwin 1976).

On 4 June 1987, we found a second nest of similar construction in almost exactly the same location as the first. The second nest was 5 m high in the crown of a small tree (*Oreopanax xalapensis*, approximately 8 cm dbh) that also overhung the road in the Monteverde Cloud Forest Reserve. We observed two adults regurgitate food to chicks at the nest between 10 and 27 June; on 2 July the nest was empty. During 7 h of observations on 23, 25, and 27 June, we saw only 8 feeding trips by the adults; intervals between feedings were long (20, 37, ≥ 78, and ≥ 87 mins). The adults typically foraged together and were observed frequently by KGM, who was conducting other studies in the area every morning and never saw more than two at one time.

Jays of the genus *Cyanolyca* are secretive dwellers of humid montane forest throughout Central and South America; the nesting habits of most species are virtually unknown (Hardy 1964, Goodwin 1976). The Central American species of *Cyanolyca*, at least, appear to be relatively nonsocial (Hardy 1964). Our limited observations suggest that only two adults attended the Azure-hooded Jay nests at Monteverde.

Acknowledgments.—These observations were made incidental to other research supported by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, Sigma Xi Grants-in-Aid, the Organization for Tropical Studies, the University of Florida, Hope College, and the Towsley Fund. We thank the Tropical Science Center, San Jose, Costa Rica, for facilitating our work in the Monteverde Reserve, T. James Lewis for sharing his observations on these nests with us, and J. A. Cox, J. W. Hardy, M. F. Lawton, and T. A. Webber for their comments on the manuscript.

LITERATURE CITED


Apparent sibling cannibalism by a nestling Pigeon Guillemot.—During a study of nestling growth of Pigeon Guillemots (Cepphus columba) on Protection Island, Jefferson Co., Washington (48°08'N, 122°55'W; 1.6 km²; 1.5 km from mainland) from June to August 1982, I recorded an incident of apparent sibling cannibalism in this species. Pigeon Guillemots on Protection Island commonly nest under driftlogs (Banks, M.S. thesis, Andrews Univ., Berrien Springs, Michigan, 1981); the nest in which the incident occurred was beneath a driftlog approximately 5 m long, about 1.3 m from one end. Two eggs laid in this nest hatched on 4 July 1982. On 5 July the chicks were leg banded; Chick A weighed 35 g, and Chick B 50 g. On 16 July Chick A weighed 185 g, and Chick B weighed 125 g; both appeared healthy. On 19 July (16 days of age) Chick A was dead, and its head was missing, although the tongue and trachea were still attached, along with bits of tissue, to the neck. The body had not noticeably decomposed. Chick B was apparently healthy and had semi dry blood on the beak, gape, and left alula. The body of Chick A was removed on this date, and Chick B continued growing normally.

Circumstantial evidence suggests that Chick A was partially eaten (or at least pecked at) by Chick B: 1) Chick B had blood on its gape and bill but lacked injuries; 2) the nest entrance was too small to admit avian predators, and no mammalian or reptilian predators occur on the island except shrews (Sorex spp.) (Banks 1981), which seem unlikely to have removed the head of a 185 g nestling; 3) Chick A had not been moved from the nest; and 4) ants were not found on the body. In seven other cases in this study, one chick died in the nest and was not removed or mutilated by the other chick, the parents, or other organisms.

Cannibalism by siblings and adults is common in owls and Falconiformes, and adult gulls of several species commonly cannibalize chicks (Terres, p. 82, The Audubon Society Encyclopedia of North American Birds, 1980). Cannibalism of siblings usually occurs incidentally in species that practice brood reduction (Terres 1980). Sibling cannibalism has not previously been reported in the Alcidae, probably in large part because most species lay only a single egg (for a review of clutch size and nesting biology in alcids see Sealy, Ornis Scandinavica 4:113–121, 1973). In those aled genera in which clutches of two or more eggs are usual (Cepphus and Synthliboramphus [including Endomychura]), there are no published records of sibling cannibalism. Synthliboramphus murrelets leave for sea at about two days of age, when they feed themselves, so brood reduction is probably not practiced in these species, and sibling cannibalism would not likely be witnessed if it occurs at all. Young of Cepphus species, however, remain in the nest for over 30 days, so opportunities for sibling cannibalism would seem greater, but this behavior is unreported in the genus. In the Spectacled (Sooty) Guillemot (C. carbo), only one chick normally survives to fledging. The second may be found dead in the nest, severely pecked on the head (Thoresen, Western Birds 15: 145–160, 1984).

Seasonal predation of large prey by Merlins.—The diet of the Merlin (*Falco columbarius*) has been summarized as 80% birds, 15% insects, and 5% mammals (Brown and Amadon 1968). However, the type of prey can vary seasonally and with age and/or sex of the Merlin. For example, a preponderance of insects is common in the diet of immature birds in summer and fall (Jewett 1939, Lawrence 1949, Oliphant 1974, Dickson 1983), and many Merlins depend on insects during fall migration (Allen and Peterson 1936, Bond 1951, Johnson and Cole 1967). Among raptors, differences in diet between male and female are linked to sexual dimorphism (Snyder and Wiley 1976, Newton 1979). The size of Merlin prey can vary widely, but males tend to take smaller prey than females (Newton et al. 1984). In general, the primary prey of all Merlins is the most locally abundant bird species of less than 50 g (Cade 1982), and very few birds taken by Merlins are larger than 180 g. The Rock Dove (*Columba livia*) belongs in this group of larger prey, weighing between 180 and 370 g (Cramp and Simmons 1985), and has been recorded in field studies of Merlin food habits on only a few occasions (Fisher 1893, Dement’ev and Gladkov 1966, Newton et al. 1978, 1984, Lange 1985). This note describes observations of Richardson’s Merlins (*F. c. richardsonii*) feeding on Rock Doves during a study of breeding and wintering Merlins in Saskatoon, Saskatchewan, Canada.

Prior to 1984, Oliphant observed Merlins on five occasions chasing Rock Doves in Saskatoon, all in late fall or early spring. Three of these Merlins were females, one a male, and the fifth of unknown sex. In early March of 1984, Warkentin observed two radio-tagged female Merlins (2- and 4-year-old birds) eating from dove carcasses. One of the Rock Doves was a road-kill, the other was frozen to a roof top and may not have been killed by the falcon. On 23 February 1986, Warkentin saw a first-year female Merlin eating a Rock Dove on the ground next to a building on the University of Saskatchewan campus in Saskatoon. Except for a 10-min period after she was inadvertently flushed from the carcass, the Merlin continued to eat, even when two Black-billed Magpies (*Pica pica*) approached within 30 cm and sat and called for several min. After nearly 2 h, the Merlin hopped off the carcass, seized it with her left foot and twice attempted to fly. She was unsuccessful in flying with the carcass, dropped it, and flew to a tree 10 m away where she preened for several minutes before moving to a perch several hundred m away. Examination of the carcass suggested no obvious cause of death aside from Merlin predation. The Rock Dove had a full crop of grain, and the remaining carcass weighed 300 g.

An immature male caught near Saskatoon on 12 November 1986 in a coop for homing pigeons had killed 12 birds inside the chamber over a 4-day period. On examination he was found to have a healed puncture wound just ventral to his right wing that appeared to impede his flying ability. A female Merlin of unknown age was observed eating a Rock Dove in Regina, Saskatchewan on 2 December 1985, and another first-year female was seen feeding on a recently killed dove in Saskatoon on 8 January 1987. It is not known if either of these females actually killed the doves or were simply scavenging them. Lange (1985) observed Merlin attempts on Rock Doves in fall and winter and a kill in December 1982, and Dement’ev and Gladkov (1966) described Rock Doves as Merlin prey during passage and winter. Also, Newton et al. (1978) discovered Rock Dove remains near nest sites in early spring.

Merlins associated with freshly killed Rock Doves (as opposed to the apparent scavenging by second- and fourth-year females reported here) tend to be first-year birds. We believe that, due to their lack of hunting experience and the greater likelihood of being unable to
meet energetic demands, first-year Merlins may be more likely to chase, and occasionally kill, larger prey. These results, combined with the absence of reports of Rock Dove predation by Merlins during the breeding season, suggest that such predation is more likely to occur outside the breeding season. We propose four possible explanations for this apparent tendency: (1) Merlins probably gain their experience with large prey during their first winter when they are relatively inexperienced, less effective hunters, and more likely to attack inappropriate prey. (2) Predation on Rock Doves is unlikely to occur during incubation and the early nestling stage because male Merlins who do most, if not all, of the hunting during this period are probably too small to kill Rock Doves under normal circumstances and certainly cannot carry them. (3) There appears to be little point in a female’s killing a Rock Dove during the late nestling/postfledging period to feed her young. As demonstrated in the observations above, she would have difficulty carrying the carcass back to the nest due to its weight, and dismemberment of prey before transport to the nest has not been reported for Merlins. (4) Only when energetic demands are increased and other prey are less plentiful or more difficult to capture, and the potential benefits of such predation outweigh the costs due to the greater risk of injury involved in attempting to kill prey of equal or greater body size, is such predation likely to occur (i.e., during the winter period).

Mueller and Berger (1970) showed that adult Sharp-shinned Hawks (Accipiter striatus) were less likely to attack inappropriately large prey than juveniles during migration. They credit this ability to distinguish appropriate prey to experience, which fits the criteria we have outlined above. It would be interesting to see if this concept of the seasonality of larger prey, particularly among inexperienced birds, can be applied to raptors in general.

Acknowledgments.—We thank E. Haug and K. Wood for their reports of Merlins feeding on Rock Doves. P. C. James, J. C. Bednarz, and J. B. Buchanan reviewed earlier versions of this manuscript. The study was funded by the Natural Sciences and Engineering Research Council of Canada, Canadian Wildlife Service University Research Support Fund, Frank M. Chapman Fund, and Canadian Plains Research Centre. This paper was written while the senior author held a University of Saskatchewan graduate scholarship.

LITERATURE CITED

Opportunistic foraging of Ruddy Turnstone on mowed lawn.—At 10:20 h on 12 January 1986 at Hog Island, Mount Pleasant, Charleston County, South Carolina, I watched a Ruddy Turnstone (Arenaria interpres) forage on a mowed lawn that adjoins the shoulder of a paved service road. The site is about 70 m from a salt marsh, but separated from it by a 50-m-wide strip of coastal scrub (maximum height, 10 m), that forms an abrupt edge at the lawn. The nearest beach or mudflat habitat is about 150 m away. The sky was clear, the wind was less than 10 km/h, and the temperature was 53°F. The lawn (grass depth, 2–3 cm) had been mowed recently, and the mowing machine had ejected the cut grass in congealed tufts. These had dried intact to form dried clumps of hay. During the 5-min period that I watched the bird, it turned four of these clumps. The bird turned them by inserting its beak and then entire head under the clump, then running forward until the clump had flipped over. The bird then directed its attention to the newly exposed area. I turned five clumps and looked under them, but found no arthropods. The turnstone had probably engaged in this foraging activity for some time, as I found 43 freshly turned clumps in a 6 × 15-m area surrounding the site where I first saw the bird. The average depth of ten clumps was 6.2 ± 1.7 [SD] cm; length, 22.8 ± 12.0 cm; width, 16.9 ± 5.5 cm. The average weight of four clumps was 39.3 g (range = 20–57 g).

Thirteen Killdeers (Charadrius vociferus), the closest of which was about 15 m from the turnstone, also foraged on the lawn. When the Killdeers gave alarm calls, the turnstone stopped feeding and assumed an alert posture. At that time a Sharp-shinned Hawk (Accipiter striatus) flew from the scrub edge, about 12 m from the turnstone, and pursued it. The turnstone joined the Killdeers in the air, and flew away from the hawk.

Although Ruddy Turnstones have been reported using unusual foraging sites, including boats, roofs of shacks, and mangrove roots (Stout, The Shorebirds of North America, Viking Press, New York, 1967), I know of no instances where they have been seen turning clumps of grass on mowed lawns.—W. Post, The Charleston Museum, 360 Meeting Street, Charleston, South Carolina 29403. Received 18 Feb. 1987, accepted 22 Sept. 1987.
Island Scrub Jay predation on cliff nests of House Finches.—The Island Scrub Jay (*Aphe-locoma coerulescens insularis*) is found only on Santa Cruz Island, 30 km from the coast of southern California (34°00'N, 119°42'W). Not as well studied as the jays of the adjacent mainland, many aspects of its biology remain unknown. In this note, I document predation by Island Scrub Jays on the nests of House Finches (*Carpodacus mexicanus*). Although such predation is well known among other Corvids, no specific reports of it have been published before for the Island Scrub Jay.

On the morning of 7 July 1984, I was hiking up Cascada Canyon in the Central Valley of Santa Cruz Island. On the right side of the canyon was a high cliff, pocketed with many small holes. As I looked up at the cliff, I saw two Island Scrub Jays hopping across its nearly sheer, vertical face, one approximately 25 m above the other. As I focused my binoculars on a jay, it entered a small hole in the cliff. A second later, it emerged and entered a nearby hole. After inspecting it quickly, the jay moved to still another hole, apparently looking for something. Two adult House Finches appeared and began diving at the jay. The finches apparently had a nest in the area and were trying to drive the jay away from it. Undaunted by their actions, the jay inspected a few more holes until it found a nest in one of them. Disappearing completely from view as it entered the House Finch nest hole, the jay re-emerged a few seconds later holding a light-colored egg in its beak. It then flew to a point on the cliff 30 m away and ate the egg. A few minutes later, the jay returned to the House Finch nest and took another egg, despite more threatening aerial dives by the parent finches. After removing the second egg to a safe distance, the jay ate it. I watched the jay for a few more minutes while it foraged among other holes in the cliff, and I saw it steal yet another egg from a different House Finch nest. As I turned my attention to the second jay, I saw it being mobbed by another pair of House Finches farther up the cliff. This jay, like the first, was not intimidated by the finches, and hopped into their nest hole and disappeared from view. A few seconds later, it reappeared carrying an egg in its beak, and flew to the other side of the canyon. A few minutes later, a jay returned to the same nest and took another egg exactly as before. In all instances, the defensive behavior of the finches seemed to have no effect on the jays. Each jay foraged alone and did not depend on the other for assistance. The entire episode lasted approximately 0.5 h.

Acknowledgments.—My research on Santa Cruz Island was made possible by the kindness of Carey Stanton, Lyndal Laughrin, Shirley Clarke, The Santa Cruz Island Company, The Marine Science Institute of the University of California—Santa Barbara, and the U.S. Navy. — PAUL D. HAEMIG, Lewis and Clark's Rangers, 3724 Boca Chica Blvd., Suite C-200, Brownsville, Texas 78521. Received 5 June 1987, accepted 28 Sept. 1987.

Wing-spreading in Chilean Blue-eyed Shags (*Phalacrocorax atriceps*).—During a field study of Patagonian cormorants, we observed wing-spreading in Blue-eyed Shags (*Phalacrocorax atriceps*) in Llanquihue and Chiloé provinces, Región X, south-central Chile. We report on our observations to clarify the function of wing-spreading, a behavior previously thought not to occur in blue-eyed shags (van Tets pers. comm, in Bernstein and Maxson 1982a; Bernstein and Maxson 1982a, 1982b; Robertson and van Tets 1982; Siegel-Causey 1986). The plumage of cormorants seems to be more wettable than in most water birds
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(McAtee and Stoddard 1945; Rijke 1968, 1987; Bernstein and Maxson 1982a; but see Elowson 1984, 1987; Mahoney 1980, 1984), and the wing-spreading posture characteristic of some species may help dry the feathers (Owre 1967, Clark 1969, Francis 1981, Bernstein and Maxson 1982a, Hennemann 1984). Feather drying is apparently the main function of wing-spreading in Double-crested and Flightless cormorants (P. auritus and P. harrisi; Hennemann 1984); in other species wing-spreading may allow heat gain or loss (Clark 1969, Curry-Lindahl 1970, Kahl 1971). Jones (1978) hypothesized that in Reed Cormorants (P. africanaus) wing-spreading may be an intraspecific signal of fishing success.

On 18 and 19 January 1987, Rasmussen saw wing-spreading by 4 of about 75 total individuals observed from 09:30-14:00 h (18 January) and by one between 08:30-12:30 h (19 January) in part of a cliff-nesting colony of Blue-eyed Shags at Punta Guapacho (41°45'S, 73°53'W), Península Lacuy, Chiloé Island, Chile. On 29 January 1987, both authors observed wing-spreading by several individuals we watched for about 10 min (starting at 0930) in a loafing flock of 8 adults and 4 juveniles on a gravel bar at Isla Elvecia (41°45'S, 73°09'W), near Calbuco, Llanquihue Province, Chile. Observations were made using 8 x 56 binoculars. All three days were sunny; on 18 January there was a light wind, and the approximate temperature was 21-28°C; on 19 January there was a strong wind, and the temperature was about 15-20°C; 29 January was calm with temperatures estimated at 21-28°C (all weather data estimated informally by Rasmussen). Adult Blue-eyed Shags were distinguished from juveniles by the characters given in Rasmussen (1986); subadults were distinguished by the presence of numerous pale juvenal feathers mixed with black basic feathers of the dorsum.

Shags were considered to be wing-spreading when the wings were held extended with remiges more or less parallel to the axis of the body (Fig. 1A), or with wings somewhat less outstretched than shown in the figure. Shags performed two types of wing-extended behavior that we did not consider to be wing-spreading: juveniles near fledging often flapped their wings vigorously, and juveniles (and occasionally adults) often extended their wings nearly parallel to the ground when walking on uneven rocky areas (probably for balance, as described for pelicans, Pelecanus spp., and anhingas, Anhinga spp.; van Tets 1965). During wing-spreading, shags preened the breast, abdomen, and flanks (with one exception), and they sometimes flapped and shook their wings. Bouts of wing-spreading lasted from 2-77 sec (N = 28 instances involving 18 individuals). Fourteen instances of wing-spreading lasted less than 10 sec, and 14 instances lasted over 10 sec. One shag held out each wing in turn for 2-3 sec, and another shag wing-spread three consecutive times for 3-5 sec, with pauses of about 1 sec each with the wings folded, then it wing-spread 7 consecutive times for 20-60 sec with pauses of about 1 sec each. At Calbuco, we observed five instances of individual wing-spreading shags walking through the resting flock, holding their wings fully extended and slightly raised, moving them as necessary to avoid bumping into the others. Most, if not all, wing-spreading shags had just returned from foraging and had wet plumage. We did not see shags returning to the water after wing-spreading. Wing-spreading shags did not appear to elicit reactions from other shags nor incite foraging trip departures by neighboring shags.

Our observations of wing-spreading in Chilean Blue-eyed Shags and its absence in Antarctic Blue-eyed Shags (P. atriceps bransfieldensis) support Bernstein and Maxson's (1982b) hypothesis that, in the Antarctic, climatic factors outweigh the putative advantages of wing-spreading. In the temperate Chiloé area, heat loss due to wing-spreading would be less than in Antarctica, and the fact that we saw wing-spreading several times during warm weather and only once in cool windy weather suggests it is used when heat conservation is not essential.

We observed several cases of wing-spreading in calm weather, but only once during strong winds on 19 January in 4 h of observation at Punta Guapacho. Windy weather may serve
Fig. 1. (A) Typical wing-spreadng posture and (B) wing-drooping and gular fluttering in Blue-eyed Shags.

to dry the feathers without wing-spreadng. In addition, wing-spreadng birds could easily be blown off their perches on days such as 19 January, when many birds could not even land at their nests without multiple attempts.

Wing-spreadng has been observed in birds of several orders (e.g., Pelecaniformes, Falconiformes, Ciconiiformes) when ambient temperatures required heat loss or gain (see Hauser 1957, Schreiber 1977). We observed other postures of probable thermoregulatory function in Chilean Blue-eyed Shags during the cooler and warmer parts of the day. In cool morning weather, birds usually assumed a hunched, closed-wing posture. During the warmer parts of our observation periods, many birds let their wings droop slightly at the carpal joint (Fig. 1B), and most birds gular-fluttered continuously. We often saw shags wing-drooping at nests as well as on loafing areas (as in Flightless Cormorants, Hennemann 1984). Shags that were wing-drooping did not wing-spread during the same general time periods (although the two behaviors are associated in the Great Frigatebird, *Fregata minor*, Mahoney et al. 1985). Because we usually saw wing-spreadng performed during warm weather, and because we did not observe it in conjunction with other thermoregulatory behavior (e.g., wing-drooping and gular-fluttering), we do not think that wing-spreadng primarily serves a thermoregulatory function in Chilean Blue-eyed Shags.

Jones (1978) found that Reed Cormorants that had just successfully foraged wing-spread more often than did unsuccessful birds, and he postulated that the birds signaled foraging success by wing-spreadng. This hypothesis is not supported by the behavior of Chilean Blue-eyed Shags, because wing-spreadng shags did not appear to incite foraging by nearby shags. A simpler explanation for the disparity in performance of wing-spreadng by Reed Cormorants is that unsuccessful birds do not “dry” their wings because they must return to the water to forage sooner than successful birds.

Wing-spreadng in Chilean Blue-eyed Shags appears to be used less frequently and to be less prolonged than in most species of cormorants (e.g., van Tets 1965, Owre 1967, Berry 1976, Jones 1978, Hennemann 1984, Brothers 1985); however, the frequent association of wing-spreadng with flapping, shaking, opening and closing of the wings, and walking probably speeds feather drying (Francis 1981, Bernstein and Maxson 1982a, Hennemann 1984).
The hypothesis that wing-spreading in the Chilean Blue-eyed Shag serves primarily to dry feathers is supported by our observations that wing-spreading was often associated with preening, most wing-spreading birds had wet plumage, and shags did not return to the water immediately after wing-spreading.

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LITERATURE CITED


Male initiation of pair formation in Red Phalaropes.—The mating system of phalaropes has been labeled “female access polyandry” because females compete for and defend males (Emlen and Oring 1977). Males are smaller than females, more cryptically colored, and assume all incubation and brood-rearing duties. All previous studies of phalarope pair bond formation have described females pursuing and courting males (Hohn 1967, 1971; Bengtson 1974; Howd 1975a, b; Kistchinski 1975). In each of these studies, except Gillandt (1974), the sex ratio was one-to-one or female-dominated. In this paper, we present observations on pair formation in the Red Phalarope (Phalaropus fulicaria) during a period when extra males occurred in the study population.

We made behavioral observations on Red Phalaropes at Barrow, Alaska, (71° 17' N, 156° 47' W) from 7 June through 7 July 1975 as part of a study of the mating system and breeding behavior of these birds (Schamel and Tracy 1977 and unpubl.). The main study area (0.67 km²) was a flat, wet sedge marsh with numerous small ponds. Phalaropes were color banded for individual recognition. Behavioral interactions were recorded on tape recorders. We determined the sex ratio in the local population by census counts and by monitoring the sex composition of birds in aerial chases. These two techniques provided independent estimates of the local sex ratio. We found that a male bias in census counts was complemented by a male bias in aerial chases and vice versa (Schamel and Tracy 1977). Although the other studies listed above did not rely upon census data to estimate the sex ratio, data presented in those studies show more than one female approaching and pursuing males and an apparent predominance of females in the local population. Further details of our study area and methods are found in Schamel and Tracy (1977). We observed three pairs during the initial stages (first 24 h) of pair bond formation. In two instances, the female was known to be forming a pair bond with a second male shortly before (one instance) or shortly after (one instance) completing a clutch of eggs for her first mate. All three pair bonds formed during a brief period (10–17 June, see Schamel and Tracy 1977) when males outnumbered females in the study area. All three pairs produced clutches.
We observed a reversal of the courtship roles previously reported for phalaropes. Males aggressively competed for access to females. This was most clearly seen as we observed a female in transition between successive mates. While this female was associating with her first mate, other males approached the pair but were repelled by aggressive acts by the paired male or dissuaded by “pushing” (Bengtson 1968), a nonaggressive behavior displayed only between paired birds. The pushing display identifies birds who are unavailable for pairing and reduces aggression between paired birds and mate-seeking conspecifics. All encounters between the pair and other males were brief (less than a minute). Subsequently, this female’s mate went to the nest (three of the final four eggs were present), where he remained most of the day, incubating the eggs. Within 15 min of his departure, the female was approached by several lone males. She was continuously involved in aerial chases with one to three males for the next 17 min, when the group was lost from view. As the males walked towards her, she flew, closely followed by the males. When she landed, the males landed near her and overt attacks (Howe 1975b) occurred between the males. The female would fly again within a few seconds of landing, pursued by the males. When we relocated this female 5 h later, she was in the early stages of pair formation (as described later) with a new male, with whom she paired and later produced a clutch.

The status of the pursuing males was not known, but we believe they were chiefly unpaired males. Two banded males were known to be unpaired. A census of the study area the day before this interaction indicated 22 pairs, 15 lone, nonincubating males, one lone, incubating male (incubating males are easily distinguishable by their feeding behavior [unpubl. pers. obs., Ridley 1980]), and two lone females. Aerial chases involving one female and two or more males occurred frequently during, and only during, the time when lone, nonincubating males were observed during the census counts (Schamel and Tracy 1977). In addition, harassment of pairs by conspecifics was chiefly by males at this time and almost entirely by females later in the season, when the operational sex ratio was skewed towards females (Tracy and Schamel, unpubl. data). Some males in aerial chases could have been paired or incubating males seeking copulations with females other than their mates. Our observations of paired birds did show that males occasionally left their mates briefly to join aerial chases or to attempt copulations with other females (Tracy and Schamel, unpubl. data). However, paired and early-incubating males were still numerous after lone, nonincubating males were no longer observed in the census counts, but no aerial chases involving extra males or fights between males associated with these chases were observed. Thus, we believe most of the males observed competing for females were unpaired males seeking mates.

During the early stages of pair formation, the male followed the female closely in all three pairs observed, while the female was more independent in her movements. Females often responded aggressively towards their new mates, exhibiting 28 head forward threats (Howe 1975b), two flying threats (Howe 1975b), and five overt attacks towards new mates during 465 min of observations. Most aggressive interactions (33 of 35 aggressive acts) occurred when the new mate (male) approached to within 0.5 m of the female. When another male approached a pair, the new mate always (N = 25) moved closer to the female, which sometimes (8 of 25) resulted in an aggressive response to the new mate. The new mate (male) usually (28 of 35 aggressive acts) responded to aggression from the females by moving a short distance away and sometimes (5 of 35 aggressive acts) showed apparent appeasement behavior (crouching, fluffing feathers, and peeping rapidly). This same vocalization was given by both members of a pair during pushing. In contrast to the relatively high level of female aggression, males of the forming pairs were aggressive towards the female on only one occasion (in retaliation to an overt attack by the female).

Most aggression by new pairs towards other conspecifics was directed by the paired males towards intruding males (seven head forward threats and five flying threats). Other aggressive
interactions were rare: one flying threat by a newly paired male towards another female, one head forward threat by a newly paired female towards another male, and no aggression by the newly paired females towards other females.

These observations show that the sex roles in phalarope pair formation are flexible and may be dependent upon the sex ratio of birds available for pairing. Pair formation is characterized by: (1) aerial chases, with several birds of the same sex initiating the pairbond chasing a single potential mate (Höhn 1967, Bengtson 1968, Gillandt 1974, Howe 1975b, Kistchinski 1975); (2) the initiating bird attempting to remain close to and persistently following the potential mate (Höhn 1967, Gillandt 1974, Howe 1975b); (3) the initiating bird attempting to drive away conspecifics of the same sex (Höhn 1967, 1971; Bengtson 1968; Howe 1975b; Kistchinski 1975); (4) some aggression between the potential pair members, usually by the potential mate towards the initiating bird when the latter approaches too closely (<0.5 m) (Höhn 1967; Howe 1975a, b; Kistchinski 1975); and (5) a gradual acceptance of the initiating bird by the potential mate (Höhn 1967, Gillandt 1974, Howe 1975a).

In all literature cited above, the female was the “initiating” sex during pair formation, and, except for Gillandt (1974), the sex ratio was equal or female-dominated. Our observations show that all of the above roles of sexes in pair formation can be reversed when males outnumber females in the local population, making males the “limited” sex and females the “limiting” sex (Emlen and Oring 1977). These observations demonstrate the extreme behavioral plasticity of individuals, leading to great flexibility in the mating system (Schamel and Tracy 1977).

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LITERATURE CITED


Notes on the foraging behavior of the Zigzag Heron.—The only recent field observations reported for the poorly known Zigzag Heron (Zebrilus undulatus) (Hancock and Kushlan, Herons Handbook, Croom Helm, London, 1984) are those of Davis et al. (Condor 82:460-461, 1981). Here we report on a bird watched intermittently by NJCM for about 13 h between 8 and 30 August 1985 at an oxbow lake with open swamp forest in the Tambopata Nature Reserve (12°49'S, 69°18'W) near Puerto Maldonado, Madre de Dios Department, Peru. Its primaries were slatey-black as described by Blake (Manual of Neotropical Birds, University of Chicago Press, Chicago, 1977) and not noticeably blue as shown in Haverschmidt (Birds of Surinam, Oliver & Boyd, Edinburgh, 1968). Its posture resembled that shown by Haverschmidt (1968) and Davis et al. (1981) more accurately than that illustrated by Hancock and Kushlan (1984).

Principal periods of activity during the 14 days on which the heron was observed were before 11:00 and between 15:30 and 17:30. On three occasions, the bird was found around midday quietly perched 5-10 m up in a forest tree some 30 m from the water. The bird foraged from branches overhanging the water, from the emergent roots of swamp trees, and while in the water. It hopped along low branches of swamp trees or partly submerged logs moving its tail, apparently for balance. Tail-flicking described by Davis et al. (1981) was frequently seen during feeding bouts but not in their context of nervous preening. During preening bouts, the heron scratched its head directly with its left foot, and flicked its tail a few times.

When the heron saw possible prey it appeared tense and started to flick its tail from side to side. If the prey moved away, the bird relaxed and ceased tail movements. If the prey did not move away, the usual consequence was the adoption of a more horizontal stance on the branch. The neck was gradually extended as the bird leaned forward on its perch preparatory to a diving strike. If the prey was immediately below the bird and the bird was perched more than 0.5 m above the water, the elongated bird would reach a position of hanging head downwards. The tail was then depressed to "clasp" the perch. Thereafter the bird dove at its prey, partially immersing itself in the water. When perched at water level or just above it, the vertical hanging was omitted and the tail was not used as a "clasp."

On one occasion, the heron stood in a tangle of branches in the bittern-posture and caught flying insects, probably dragonflies (Odonata). Once the bird struck at prey while it was standing in water up to its abdomen. In addition, small prey items were seized by pecking into the water while wading slowly or standing still. During unsuccessful strikes at prey, the bill often impaled dead leaves floating in the water. These were removed by vigorously beating the bill against branches.

Of 15 strikes at aquatic prey, four (26%) were successful. The prey were fish ca 5 cm long (the length of the bill). After capturing a fish, the heron carried it to a perch, manipulated
it and swallowed it head-first. An armoured catfish (Callichthyidae) was found with typical heron-inflicted injuries.

On one occasion, the heron was surprised in a thicket. It rapidly hopped away through the tangle, giving an alarm call: a high pitched *kreeik* which soon degenerated to *krik*.

**Acknowledgments.** — We thank Max Guenther of Peruvian Safaris who enabled NJCM to stay at the Explorers Inn for the duration of the study. We thank the editor and his referees for their courteous and helpful comments which have made this contribution shorter and clearer. — NIGEL J. C. MATHews, 61 Albion Rd., Rondebosch, 7700 South Africa, and Richard K. Brooke, FitzPatrick Institute, Univ. Cape Town, 7700 South Africa. Received 15 April 1986, accepted 21 Oct. 1987.

During the last 25 years, the expansion of the biological sciences has led to the division of a previously coherent discipline into distinct fields with increasingly different languages and goals. More than ever, workers who specialize on a particular taxonomic group find themselves at risk of losing touch with developments outside their own areas of study. The need for communication among the divergent biological sciences may help explain the continuing success of the “Current Ornithology” series in the face of stiff competition in a market full of compendia and review volumes. Editor Richard Johnston deserves much of the credit for this success, because he has consistently selected topics of interest to avian biologists and chosen authors who not only can discuss the results of avian studies in a general context, but who incorporate important developments in other fields as well. Volume 4 is no exception to this.

In “Evolutionary Processes and Patterns of Geographic Variation in Birds,” Robert Zink and J. V. Remsen provide a much-needed critical review of previous studies of geographic variation in birds in light of current evolutionary theory. They also discuss the role of studies of geographic variation in research on speciation. I was surprised that Zink and Remsen did not review the problem-ridden reinforcement model of speciation in this section or the studies on geographic variation and reproductive interactions in the *Icterus galbula* and *Vermivora chrysoptera-pinus* complexes, for which pertinent genetic and behavioral data exist. Otherwise, the section on geographic variation and speciation is thorough, and the article as a whole is quite thought-provoking.

“The Heritability Concept Applied to Wild Birds,” by Jack Hailman, works especially well with Zink and Remsen’s article, because Hailman provides a general model of the interactions between genetic and environmental components of the expression of traits, such as the geographically varying characters discussed by Zink and Remsen. Hailman’s perspective is refreshing; as an ethologist, he is keenly aware of the role of environmental (especially social) effects on the expression of traits during development and maturation, unlike many quantitative geneticists. Most readers will not be surprised to learn that studies of heritability in natural populations are rife with difficulties, which Hailman documents fully.

Three chapters reveal the ecological side of the series in addressing the regulation of avian populations. “Clutch Size in Nidicolous Birds,” by Edward Murphy and Erkki Haukioja, extensively reviews the literature on why the clutch size that produces the largest number of fledglings is often smaller than the modal clutch size, contrary to the ideas of Lack. Murphy and Haukioja illustrate the limitations of adaptationist paradigms in studies of clutch size but argue convincingly that dismissals of Lack’s hypothesis have been premature.

“Competition in Breeding Birds: On the Importance of Considering Processes at the Level of the Individual,” by Thomas Martin, aims to demonstrate the utility of the individual-level perspective in studies of interspecific competition. Martin pleads for a less all-or-nothing view of competition and calls into question dismissals of its importance.

“Distribution and Abundance of the Dickcissel,” by Stephen Fretwell, reviews the life-history of *Spiza americana* and offers a model of its population regulation with a striking implication, the imminent extinction of the Dickcissel. The evidence is circumstantial, yet the reasoning of his argument makes sense, even if it is hard to follow and accepts certain data (e.g., Breeding Bird Surveys) too uncritically. Some unusual characteristics of the life-
The remaining chapters stand somewhat apart from the other articles. The title of Pat Rich and Robert Baird's "History of the Australian Avifauna" is somewhat misleading because the article pertains mainly to the geographic, geologic, and taphonomic characteristics of fossil sites in Australia and New Guinea. Rich and Baird discuss the biases of the Australian fossil record critically and in detail, and thus provide a commendable addition to a generally uncritical literature on avian paleontology. However, they do not address the biases of fossil identification. A list of genera would have added to the utility of the tabulations of taxa per family at each site.

In scanning the contents of the volume, I was initially pleased to see the last article, "A Bibliography of Ornithological Translations," by Douglas Siegel-Causey and Janet Hinshaw, which lists the readily available English translations of research articles in other languages. Unfortunately, in my first attempt to use the subject indices, which classify the numbered articles by subject inferred from their titles, I discovered so many errors that I was forced to inspect all 1030 citations to insure that I had found the pertinent references. For example, the chaffinches (Fringilla) are indexed inconsistently under Emberizidae and Fringillidae. The former includes a reference to two species of wheatears (Oenanthe) and the latter a reference to an article on the Chiffchaff (Phylloscopus collybita). Even worse, nearly all references to rails, coots and gallinules (Rallidae), and one to the Pin-tail Snipe (Gallinago stenura), are indexed under Anseriformes. It appears that roughly 15% of the articles are indexed incorrectly in one way or another. If this level of error is characteristic of the citations themselves, then I dread the effects of the article's use, given the regularity with which preparers of reviews inappropriately cite publications without seeing the original sources.

This volume might euphemistically be termed "Currently Ornithology," because some of the conclusions reached may prove much broader (or in a few instances narrower) than the title of the volume would suggest. For instance, Zink and Remsen's analysis of the degree to which North American birds conform to Bergmann's rule (poorly) and Gloger's rule (very well) has implications outside of avian biology per se. So do Hailman's model of the interplay of genetic and environmental factors in the expression of traits and Rich and Baird's analysis of the biases of fossil sites in Australia. In contrast, I found Martin's argument for the importance of an individual-level perspective on competition uncompelling, in light of the need for measures of relative fitness of those individuals, which requires population-level studies. Regardless, all of the articles make substantial contributions and should appeal to specialists and general readers alike.

The problems with the bibliography of Siegel-Causey and Hinshaw, the ten or so typographical errors I noticed, and the apparent inconsistency in the level and type of editing suggest that the bugs characteristic of the earlier volumes of the series linger on. However, they do not detract seriously from the utility and value of this volume as a whole. I strongly recommend it for university libraries, museums and any active ornithologist or evolutionary biologist. —Anthony H. Bledsoe.
The first point to note about this "revision" is that it isn't. Most of the material is held over from Edition 4, Edition 3 . . . . This is not necessarily bad, however, in that the old material was pretty useful for an undergraduate class. Still, I am somewhat disappointed that there is not a single ornithology text on the market that meets the needs of today's students; perhaps that is not possible. It appears that most of the new material was written by "guest authors," noted experts in their respective areas (see below).

As in other editions, the "laboratory" chapters (including Topography, Feathers and Feather Tracts, Anatomy and Physiology, External Structural Characters, Laboratory Identification, and Plumages and Plumage Coloration) are quite useful for that portion of the course. Students are still required to "color in" topographic areas of a "typical" bird, which can be instructive but wipes out students buying used books. Some students have complained that "coloring" went out in the primary grades. One might wonder why skeletal drawings of the wing and leg and their concomitant descriptions are in the Topography chapter and not in the Anatomy and Physiology chapter beginning on p. 53, especially since the information in Figure 4, p. 14, is repeated in Figure 26, p. 57. In the latter chapter, mention should be made of the varying quality of the figures. Most are quite adequate, in fact well done. Berger's line drawings of the muscles are excellent (as in past editions) as are Gaunt's sketches of an "idealized" syrinx (Fig. 33). However, some of the figures photocopied from other sources are suspect. The quadrotional (Fig. 28) is missing in my book (the label arrow points to air), the lungs and air sac system (Fig. 32) are difficult to understand, and the circulatory system drawing (Fig. 35) has no practical application to a student working on a double-injected pigeon. Some of the feather pictures (e.g., Fig. 23, p. 46) and the internal anatomy figures (Fig. 34, p. 78, and Fig. 36, p. 81) are poor quality, black-and-white photocopies of colored pictures in earlier editions.

Fig. 11 (p. 28) from the new and interesting, yet surprisingly superficial, chapter on flight should be removed. The idea is sound but the Belted Kingfisher artwork is questionable. What is that bird doing?

The External Structural Characters chapter is satisfactory, but additional drawings are needed for such bill features as: chisel-like, serrate vs lamellate, angulated commissure, operculum vs cere, and linear vs ovate vs circular nostrils; tail characters such as emarginate vs forked; and feet characters such as zygodactyl vs heterodactyl and semipalmate vs total-palmate vs palmate. The revised sections on Order and Family synopses and the new key to Order and Families are excellent, owing to the hard work of Ken Parkes and Jay Loughlin at the Carnegie Museum.

The real issue concerning the "lab" chapters is one of "to include or not to include." One must decide if it is advisable to have so much laboratory material, some of marginal quality (especially sample data sheets and questionable figures) in a handsomely bound Academic Press style book of nontrivial expense, or should this material be combined with a solid lab anatomy text (loosely bound, inexpensive, rugged) leaving the needed textual material in an expanded, up-to-date format hard-copy book. I would opt for the latter approach, especially since it just does not seem right to bring such a nice textbook into the lab where it may be exposed to formalin, visceral fluids, feces, and semisadistic zoology students.

The chapter on distribution is repeated, almost intact, from previous editions, including the rather unfortunate table on Birds of the Coniferous Forest (p. 184) and figure on Altitudinal Succession (p. 191). Most of the information in this chapter is available in a good field guide. Other unrevised chapters were reviewed for previous editions and need not be repeated here.

The strengths of this edition lie in the newly written chapters, those done by guest authors. Much of this information is current and timely. Of special note are the chapters on Behavior by J. P. Hailman and Migration by S.A. Gauthreaux. Hailman is quite successful at reducing
the voluminous information on bird behavior to only 30 pages, including a pretty good list of references. Most major aspects of the field are outlined, and a section of field studies is an added touch. The migration chapter is completely reorganized from previous editions. Gone are pages of wasted space including sample data sheets, being replaced with useful illustrations such as the Lowery "moon watching technique" and radar tracking photographs. For some reason the famous "kite study" is not reported here. The section on Theoretical Origins is a little brief but does not overly detract from the value of the chapter. It is a good coverage of an important topic.

In summary, the book could have been a major help to a university level ornithology class and many parts are useful. I admire anyone who attempts to cover such a widely based, important subject in a single book, a task which is probably not possible. As it stands now, I will make this book available to the students as a reference text, along with the others currently available, and go back to photocopied reprints and a good field guide for the bulk of the course material. — ROBERT C. WHITMORE.

DUCKS OF NORTH AMERICA AND THE NORTHERN HEMISPHERE. By John Gooders and Trevor Boyer. Facts on File Publications, New York, New York and Oxford, England, 1986: 176 pp., 29 full page color plates, numerous other paintings, black-and-white drawings, charts, and range maps. $24.95.—As the title suggests, the 52 species of ducks that occur in the Northern Hemisphere are the subjects of this book, which provides paintings and flight profiles of each, along with a short discussion of subjects such as plumages, life histories, and conservation. As a supplement to the field guides, the book illustrates a number of helpful hints not widely available elsewhere. The layout is attractive, and the illustrations are sharp and clear. Small maps indicate the primary breeding and winter ranges of each species. A small chart at the top of each account provides data on wing length and weight for both sexes, egg color, clutch size, incubation, and fledging periods. Much of the data in these charts is repeated in the text, although frequently the information in the chart and that given in the text don’t agree; or in the chart the authors may imply that data are unavailable (e.g., the incubation period for the Cinnamon Teal [Anas cyanoptera]) and then proceed to provide this information in the text. Undoubtedly, the primary reason for this publication is to showcase Boyer’s paintings. These are, as a lot, attractive and technically well-executed, yet to this reviewer’s eye many fail to convincingly portray their subjects; a few are nearly decoy-like, lacking the realistic appearance of feathers.

Ducks of North America and the Northern Hemisphere is, essentially, a British book (a European edition was published at Oxford, with apparently little but the title differing from the American version). British spelling and usage aside, the North American edition might have benefited from editing by someone more thoroughly familiar with waterfowl throughout this continent. Even a quick editing, for example, might have changed the statement that Long-tailed Ducks (Oldsquaw) (Clangula hyemalis) come inland only as a result of storms or oiling (which may be more or less true in Europe), and we may not have been told that migrating Ruddy Ducks (Oxyura jamaicensis) "... avoid the Appalachians." This book will appeal to many bird watchers with a general interest in the ducks of the Holarctic region, primarily for its color plates. Few serious students of North American waterfowl will be tempted to discard their copies of Kortright or Palmer in favor of this volume; still, the reasonable price, along with its good color reproduction, make the book worth consideration. — ROBERT C. LEBERMAN.

WILLIAM L. FINLEY/PIONEER WILDLIFE PHOTOGRAPHER. By William Mathewson. Foreword by Roger Tory Peterson. Oregon State University, Corvallis, Oregon, 1986:197 pp.,
over 200 photographs. $29.95.—Bowdoin College, which I attended in the late 1920s, had an endowed lectureship earmarked for bringing to the campus each year an illustrated program about birds. As a cub reporter for the college newspaper, one of my assignments was to interview William L. Finley from Oregon, attend his film program, Camera Hunting in the Northland, and later report on it. Finley filled the local theater to capacity, his reputation as one of the leading wildlife lecturers of the day having preceded him. Prepared as I was for excellent motion pictures of birds and mammals, I never expected to be enchanted by Finley's presentation, his precise timing of words to action on the screen, his lively sense of humor, and his flair for the dramatic as he built up his audience to climactic scenes. I was impressed, deeply so. Never again did I attend a lecture on wildlife that impressed me more.

William L. Finley was born in Santa Clara, California, on August 9, 1876. The next year the Finley family moved to Portland, Oregon, and from then on William Finley's name would always be associated with Oregon. Young Finley soon made friends with the boy next door, Herman Bohlman. Together they formed a team, taking photographs of birds for a decade, between 1899 and 1908. According to Mathewson, "it can be argued that these years of association with Bohlman were the highlight of Finley's long career."

In 1906 Finley married Nellie Irene Barnhart, while in that same year Bohlman went into business with his father and gave up photography. Irene made up for the loss of Bohlman with her interest in birds and talent as a writer. She assisted her husband in his first book, American Birds (1907), and with her husband published two other books, Little Bird Blue (1915) and Wild Animal Pets (1928). During the 1920s and 1930s William Finley gained national recognition for his personally narrated wildlife movies sponsored by the American Nature Association. To obtain the necessary footage, the Finleys traveled widely in Wyoming, Washington State, western Canada, and Alaska.

William Finley died in 1953. Famed as he had been in his lifetime as a photographer, writer, and lecturer, an often overlooked accomplishment was his becoming an ardent conservationist and more instrumental than any other person in Oregon for making "the eastern establishment" in the United States aware of his state's vast wildlife resources and the need for creating national refuges in his state for their protection.

The first 18 pages of this book are biographical, based on Mathewson's diligent research on the story of William Finley's career, including his many friendships as well as his "differences" with friends. The bulk of the book, pp. 19-193, is essentially a splendid album of photographs (usually one to a page) by Finley, Bohlman, and many others. Assembling the photographs represented a commendable task. The superb quality of the selected wildlife photographs is remarkable, especially when one considers the conditions in the field with which the photographers coped—the awkward, bulky cameras as well as the heavy, glass-plate negatives and the vials of chemicals for their development.—Olin Sewall Pettigill, Jr.

Forest Bird Communities of the Hawaiian Islands: Their Dynamics, Ecology, and Conservation. By J. Michael Scott, Stephen Mountainspring, Fred L. Ramsey, and Cameron B. Kepler; illus. by H. Douglas Pratt. Studies in Avian Biology, No. 9, Cooper Ornithological Society, 1986:341 figs., 75 tables. $26.50.—This is a magnificent work. I believe it to be one of a kind. I believe, further, that anyone who has done field studies in mountain rain forests with an annual rainfall of 300 inches or more, and typically with a very rough and treacherous lava substrate, will agree.

More endemic bird species have become extinct in Hawaii than in any other part of the world. After their studies of fossil material, Storrs Olson and Helen James concluded that more than 40 species of endemic birds became extinct between the arrival of the early
Polynesians and the rediscovery of the islands by James Cook in 1778. Since that date, another 20 species or subspecies have become extinct, and at least 31 taxa are now classified as threatened or endangered.

Except for the theses on the endemic Hawaiian honeycreepers by Dean Amadon (1950) and Paul Baldwin (1953), there seem to have been no field studies on the Hawaiian forest birds between the early 1900s and 1964. The first member of the U.S. Fish and Wildlife Service was assigned to work in Hawaii in 1965. "Eugene Kridler, John L. Sincock, and J. Michael Scott conceived the idea of a state-wide forest bird survey in 1975, because such an approach was needed to identify areas requiring protection, research priorities, and management strategies."

Detailed surveys were made in all native forests above 1000 m elevation on the islands of Hawaii, Maui, Molokai, and Lanai, as well as "the known distributional area for endangered forest birds on Kauai." John L. Sincock had spent several years in the cold, rain-drenched Kauai forests, hence had a great deal of base-line data for the survey.

"The principal objectives of the Hawaiian Forest Bird Survey were to determine for each bird species in the forests we studied: (1) distribution; (2) population size; (3) density (birds/km²) by vegetation type and elevation; (4) habitat response; and (5) geographical areas where more detailed studies were needed to clarify distributional anomalies and to identify limiting factors of various species."

The authors have done an outstanding job in presenting the results of their thorough surveys, as suggested by the 341 figures, 75 tables, and many maps. We now have excellent data on the distribution and status of the endemic Hawaiian forest birds, as well as on the many introduced bird species, a number of which have invaded the mountain forests. We may hope that this excellent report will stimulate the State of Hawaii finally to take a much greater interest in protecting the few remaining native forests and their unique bird life. It may be noted here that no survey was made on the island of Oahu "because of the low density of native birds," which is only a suggestion of the dire straits of most of the unique Hawaiian birds.

This book should be in the library of every field ornithologist, ecologist, and anyone with an interest in endangered birds.

The dedication to Eugene Kridler and John L. Sincock, two dedicated and effective field biologists with many years of experience in Hawaii, is most appropriate. —Andrew J. Berger.

The Birds of Burma. 3rd ed. By B. E. Smythies, illus. by CDR A. M. Hughes, R. N. Silvio Mattacchione & Co., Pickering, Ontario, 1986:432 pp., 32 color plates with caption pages, 1 map, 18 text figs., 19 black-and-white photographs. ISBN 0-9692640-0-3. $95.00 (special deluxe edition, $475.00). —Long out of print (2nd edition published in 1953) and difficult to obtain, this new edition is welcome. The species accounts make up the bulk of the book and vary in length, depending on what is known about the bird in Burma. Subheadings in the accounts are: (1) Local name; (2) Identification; (3) Voice; (4) Habits and food; (5) Nest and eggs; (6) Status and distribution. Accounts range from 5 lines to 1½ pages. There are 32 pages of introductory material, a 9-page bibliography, and an index. The useful distribution table was not included in the new edition.

The species accounts summarize all that is known about the birds of Burma, including much natural history data, which often makes interesting reading. These accounts virtually are the same as the 1953 edition, except for the addition of a few new distributional records. The identification sections are useful but often have been superseded by more modern texts, especially for the difficult species and groups. Generally the natural history data (when given) and the Status and Distribution section are the more useful parts of the accounts, as they
are complete for Burma. Better identification materials may be found elsewhere. Unrecorded species likely to be found in Burma are listed.

Burma is a large country with an extensive avifauna of 967 known species. It encompasses tropical rain forest, wet temperate forest, mixed deciduous forest, savannah, thorn scrub, and paddy lands, as well as marshes, swamps, etc. Besides all these habitats, Burma extends from about 10°N-29°N, a range that brings it into contact with the Himalayas, Indian Subcontinent, SW China, Indo-Malayan area, and Malaysia. The introduction gives more details of the biogeography and habitats. Unfortunately, for over 25 years, the maximum visit by foreigners has been limited to one week. Since there are no Burmese ornithologists, this time restriction has virtually halted scientific ornithology. The 1953 edition bibliography included references up to 1950, and only 20 new entries are to be found in the 1986 edition. Only three of those papers concern new distribution records for Burma; the rest are more general works that affect Burma. Nearly all of the new distributional records for Burma in that 36-year period have come from bird-watching tours. The impact on knowledge of bird distribution in the tropics from tours should not be underestimated. The leaders are often experienced field observers who can make a significant contribution.

The second edition was a thick, heavy book at 4 pounds, but the new edition is a whopping 6 pounds of coffee table size, 13½" × 8¾" × 1¾". The second edition was not a book you could carry in the field, but you could take it along on a trip and leave it in your hotel room for reference. I expect most will prefer to leave the new monster edition at home.

The 32 color plates by CDR Hughes are well done, and the individual birds, all recognizable, range from good to excellent. They illustrate 290 of the commoner species of Burma. The 18 line drawings are mostly old-to-ancient cuts, several of species that do not occur in Burma! To me, they are neither pleasing to the eye nor particularly accurate, and they add nothing to the book, except as coffee table book embellishments to fill blank space. The 19 black-and-white photos are interesting, but of little variety. Six of them are of working elephants and another six are of high altitude winter scenes in northern Burma, leaving only seven for the rest of Burma. The front cover birds are identified as Greater Necklaced Laughingthrushes (Garrulax pectoralis), but they are White-crested Laughingthrushes (Gar- rulax leucolophus). I found several typos, but mostly the resetting was done well. The type is large and easily read and all the same size, except keys which are done in smaller type. I found several typos, but mostly the resetting was done well. The type is large and easily read and all the same size, except keys which are done in smaller type.

This is an expensive book, but for those interested in the birds of Burma, it is the only summary of what is known and thus indispensable. — Ben King.

WADERS: THEIR BREEDING, HAUNTS, AND WATCHERS. By Desmond and Maimie Nethersole-Thompson. Buteo Books, Vermillion, South Dakota, 1986:400 pp., 32 black-and-white photos, numerous line drawings, 8 text figs., 5 tables, appendices. $45.00.—The name Nethersole-Thompson on a bird book brings to mind the five monographs that Desmond has written (the most recent one, Greenshanks in 1979, was also co-authored with his wife, Maimie). While Desmond was studying Common Greenshanks (Tringa nebularia) and Eurasian Dotterels (Charadrius [Eudromias] morinellus), treated in a 1973 monograph, he encountered all of the other 16 species of commonly nesting British shorebirds. This book reports their observations on all 18 species in the same enthusiastic style as their earlier books. Desmond found nests of all but one of these species. Their own observations on the breeding biology of these birds are supplemented by a review of the literature, and 16 rare or possible breeding species (for Great Britain) are described more briefly.

The value of this book depends on whether one considers it a work of descriptive natural history, to be read from cover to cover, or a technical reference for shorebird biologists. I think it tries to be a bit of both, but it fulfills neither aim completely.
As a work of natural history, it is less satisfying to read than their earlier works, because the encounters with the birds here are shorter, and the observations are less detailed. The sections on Greenshanks, Dotterels, and Eurasian Woodcocks (Scolopax rusticola) are exceptions to this rule. However, there is more variety here than in the earlier books, and there are also descriptions of British shorebird habitats and shorebird watchers. Desmond describes how he found the nests of many species, and his enjoyment of nest-hunting is obvious.

As a technical handbook it suffers by comparison to Birds of the Western Palearctic (Vol. III, 1983) edited by S. Cramp and K. E. L. Simmons. The latter volume has far more detail and more references (many of them more recent) on all 18 species. The Nethersole-Thompson's present some of their own data, but the amount varies widely from species to species. Also, some aspects of breeding biology (e.g., nest dispersion, laying season, and chick behavior) are treated in detail, while others (e.g., incubation behavior and site and mate fidelity) receive less attention. Vocalizations and displays of each species are described, based on their own observations, but there are few references to the descriptions of others, which makes comparison difficult. The drawings of displays (by Donald Watson) are not referred to in the text, so it is hard to tell which display is being shown. The black-and-white photographs merely illustrate the species described. In general, the authors took few of their many opportunities for comparison and synthesis, aside from an appendix of sonagrams of some species (including calls between parents and chicks) and a short chapter on spacing and dispersion.

I recommend this book for "wader watchers" (especially those who live or travel in Britain) who want a readable and enjoyable introduction to the breeding biology of these species. The authors' love of shorebirds comes through clearly, as does a plea for the preservation of shorebird breeding habitats, something that all wader watchers should care about. — Peter W. Bergstrom.

BIRDS OF SOUTH FLORIDA: AN INTERPRETIVE GUIDE. By Connie Toops and Willard E. Dilley. River Road Press, Conway, Arkansas. 1986: vi + 150 pp., 51 color photographs, 2 maps. $9.50.—This is a pleasant little book of five chapters introducing the birds, parks, and major environments of south Florida. The first chapter is a very brief discussion of the history of the south Florida avifauna and of its interactions with human civilization. Chapter 2 introduces the major terrestrial habitats of the area and discusses a few characteristic birds of each. Chapter 3 reviews the major parks, refuges, and wildlife sanctuaries and some birds of each. Chapter 4, comprising about half of the book, is an annotated list of the birds of the region, and Chapter 5 is a brief but lucid discussion of introduced birds in south Florida.

The definition of "south" Florida is a bit odd. Coastaly, coverage of the book extends north only to Fort Lauderdale on the Atlantic, and Sanibel Island on the Gulf coast, but north inland to include Loxahatchee Refuge, Lake Okeechobee, and even the Kissimmee Prairie.

The species list includes about 400 species and is illustrated by 41 high-quality photographs. The species accounts give one-to-three word descriptions of species abundance, and usually include telegraphic notes on behavior, migration, and preferred habitats. Often a number of places are listed where the bird is "most likely to be seen." The species list is extensive but not complete; a number of rare visitors are omitted, e.g., Ruddy Quail-Dove (Geotrygon montana), La Sagra's Flycatcher (Myiarchus sagrae); Fork-tailed Flycatcher (Tyrannus savana); and several seabirds. One or more localities may be listed for the rare and accidental species, but these lists are generally incomplete. A few of the comments on status are outdated or inaccurate, e.g., Fulvous Whistling-Duck (Dendrocygna bicolor) has
become much more common as a breeder than indicated; Snowy Plover (*Charadrius alexandrinus*) breeds in south Florida on the Gulf Coast; but overall the quality of information is very good.

This book will probably be most useful to birders visiting or planning trips to south Florida. It should also be useful to ornithologists wishing a quick familiarity with the south Florida avifauna.—*Wayne Hoffman.*

*Les Oiseaux des Régions Forestières du Nord-est du Gabon. Vol. 1. Écologie et Comportement des Espèces.* By A. Brosset and C. Erard, illus. by A. R. Devez. Société nationale de protection de la nature, 57 rue Cuvier, B. P. 405, 75221 Paris Cedex 05, France, 1986:297 pp., 54 fgs., index of scientific names. 250 French francs.—"This book, the first of a two-volume work on the birds living in the Ivindo River basin of northeastern Gabon, presents in a descriptive and analytical fashion most of our data on the biology of the species found there. In volume two we will discuss general topics, including community structure, social behavior, population dynamics, and ecological adaptations of birds to forest life" (translated from the authors' introduction, p. 3). This long-awaited publication represents the results of research carried out uninterruptedly in Gabon from 1963 to 1985 by a team from the Centre National de la Recherche Scientifique (C. N. R. S.) and the National Museum of Natural History in Paris. The senior author heads the ECOTROP research program of the C. N. R. S. ultimately responsible for all phases of the research in Gabon (which includes vertebrate taxa other than birds and invertebrates as well), and the junior author is Curator of Birds at the National Museum. Between the two of them, the authors have spent more than seventy months doing field work in the Ivindo basin. Their own studies were supplemented by results of research pursued by other investigators who spent several consecutive years in this region and whose field notes are incorporated in the present volume. It must be emphasized that the authors' research programs were not primarily faunistic but were designed to answer questions about the biology of selected forest birds, especially the Pycnonotidae (Brosset) and the Muscicapidae (Erard). This publication is therefore a by-product of this other research, only some of which has been published to date.

English-speaking readers must be warned that the thirteen-line English summary (p. 285) is quite inadequate to convey a sense of the contents or of the significance of this book. This text is, indeed, an annotated list of 424 species of tropical West African birds, but this is no ordinary annotated list. Most of the work leading to the present monograph (as well as to 30 other papers in the bibliography by one or the other, or both, of the co-authors, plus about 12 additional papers by other workers) has been carried out during 14 years on a 300 ha plot at a site called M'Passa near the town of Makokou (4000 inhabitants) in northeastern Gabon. The M'Passa plateau has permanent laboratories in or next to primary rainforest, in which three plots with quadrats have been established for long-term research on plants, invertebrates, and vertebrates. Species diversity is very high in this rainforest region: 473 species of plants and 364 species of birds have been identified on a 2 km² plot. Most field data were gathered in this restricted locality, but wisely the authors chose to extend the geographical scope of their report to the entire Ivindo basin, a 50,000 km² area covered mostly with primary tropical rainforest. The data come from visual observations, specimens collected (1400, deposited at the National Museum in Paris), banding (4000 birds belonging to 132 species), nest controls (1600 nests, not including those of several colonial groups such as *Ploceus*); breeding data (on 214 species), tape recordings of vocalizations, photographic documents, and raising of some species in captivity in France.

The book is divided into two chapters. In the first (pp. 9–24) are found a description of the Ivindo River basin, its climate, and its vegetation types (illustrated with black-and-white
photographs), and in the second, the bulk of the volume (pp. 25–285), a discussion of each of the 424 species definitely identified in this area. A bibliography and an index of the scientific names of birds end the book. In the species accounts more emphasis is given to passerines than to nonpasserines and to sedentary than to migrant species. The justification given by the authors is that the passerines or the sedentary species, especially the forest-inhabiting ones, are less well known than the others. While reading these species accounts, it is important to remember that the authors have not attempted to write "a series of species monographs," but instead they have presented only their "own data, insofar as they are original or complement usefully what was previously known." And furthermore: "When we refer to the basic literature, such as the work of Mackworth-Praed and Grant (1970 and 1973) and especially to the monumental Birds of Africa that is being published now, it is in order to complement it, or at times to contradict it" (p. 6).

Keeping this warning in mind, the reader will quickly appreciate the fact that this book (and the papers by the authors cited in their bibliography) constitutes probably the most significant piece of work on tropical African forest birds since the time of Chapin. It is impossible to cite here all the nuggets of invaluable information contained in the volume: they include thoughts about the systematic position of some species or genera, descriptions of nesting or display behavior, details about social life, and characteristics of habitats utilized or of foods ingested.

In spite of my overall praise for the published work and my admiration for the field data on which it is based, I do have a few criticisms or regrets. Given the fact that the research was pursued for so long and that one of the authors is a museum person, I regret that so few specimens were collected or preserved. For species after species we are told that one or two specimens only were preserved but that many more were not. What a loss of information. I wish in particular that the authors had made attempts to collect series of some of the more difficult taxonomic groups. Another point is the lack of information on weights, in spite of the note (p. 4) that after 1972 the weights of banded birds were rather systematically taken. Finally, I often wished while reading the book that the information was given in a more precise or quantitative manner. For example, the sample size of observations is too rarely indicated, so that it is difficult to judge whether some kinds of observations (relative abundance, habitat preferences) are based on just a few, or on the contrary, on hundreds of encounters with a given species. From the context of the text it is usually possible to guess at the relative frequency of observations, but this remains a subjective judgment on the reader’s part. It would be wonderful if the authors had prepared a bank of raw data that interested colleagues could consult or obtain copies of (for instance banding returns, nest cards, or weights).

In spite of these few defects this publication is a landmark in tropical African ornithology, especially of forest birds. I look forward to the synthetic generalizations promised for the second volume. — François Vuilleumier.

Conservation of Cameroon Montane Forests. Edited by S. N. Stuart. International Council for Bird Preservation, 219c Huntingdon Road, Cambridge, England, 1986:iii + 263 pp., 7 maps, 17 numbered text figures, numerous tables, gazetteer, references, no index. £10.—This paperback reports the ICBP Cameroon Montane Forest Survey of November 1983–April 1984 with contributions by S. N. Stuart, C. G. R. Bowden, M. O. Fedden, M. E. Gartshore, F. P. Jensen, H. L. Macleod, D. W. Thomas, and H. Tye. The survey worked in the highlands of western Cameroon—the habitat of eight threatened species of birds. Montane western Cameroon has 53 forest species (some live also on the Obudu Plateau of
Nigeria and the island of Fernando Po, where lack of recent observations is cause for concern). Of these, 20 (38%) are endemic species that live no place else. Four chapters discuss birds and provide informative species accounts with observations on behavior, ecology, range, and systematics. Shorter chapters give sketches of the itinerary, landforms, climate, vegetation, observations of bats, other mammals, and reptiles and amphibians, and recommendations and conclusions about conservation of the habitats. The aims of the survey were to determine the distribution, relative abundance, and habitat of the montane forest species, and the importance of the montane forests for conservation of the endemic birds.

The survey visited the southern slopes of Mt. Cameroon, the Rumpi Hills, Mt. Kupé, Mt. Manenguba, Mt. Nlonako (the first exploration by any biologists), and Mt. Oku and other remnant forests in the Bamenda area. The most critical area in Cameroon is the Bamenda highlands. No forests remain below 1500 m, and the forests on Mt. Oku are disappearing rapidly due to clearing for agriculture, firewood cutting, grazing by cattle, and fire. Four threatened species live in the remnant forests of the Bamenda highlands, and two, Bannerman’s Tauraco (Tauraco bannermani) and Banded Wattle-eye (Platysteira laticeps) live nowhere else on earth. “Mount Oku represents the most biologically unique and most seriously threatened of all the forests in Cameroon and urgent conservation measures are required.” Mt. Cameroon has the only continuous forest extending from sea level to a natural treeline in Africa, but projected commercial plantations at low altitudes may cut off dispersal routes for certain birds, and the value of the mountain for conservation depends on maintaining an intact habitat. The Mount Cameroon Francolin (Francolinus camerunensis) is restricted to Mt. Cameroon and is hunted, but it lives in habitat difficult of access and seems not to be in danger. The Rumpi Hills were only partly explored and further observations would be of interest. No White-naped Pigeons (Columba albinucha) were seen, although this is the only known locality in West Africa for the species. Mt. Manenguba is in bad shape; the authors suggest planting of eucalyptus for firewood for the local people to slow the destruction of the remaining patches of endemic forest. Mt. Kupé has four threatened species, including the endemic Mount Kupé Bush-shrike (Malaconotus kupeensis) and is avoided by the local people, so reasonably might be designated a national park because this would require no economic hardship on the people.

Birds were identified by experienced observers by sight, calls, and mist netting (1199 individuals, 112 species). The authors correct the sight identifications and records of other workers, but a few birds gave them their own problems, including the Icterine and Xavier’s bulbuls (Phyllastrephus icterinus/P. xavieri) and the Red-tailed Greenbuls (Criniger calurus/C. ndussumensis) where identifications are questionable for the second of each pair. The authors reported longer wings on some bulbul species than did Bannerman, so their P. xavieri, identified by wing length, is problematic. Nor did they get repeatable bill measurements for the Criniger, for which others report no difference in vocal behavior between calurus and ndussumensis and regard as conspecific thick- and thin-billed phenotypes. The chapter on netting includes ranges and histograms of measurements, but these are sometimes difficult to interpret because sex was not determined. Some species were larger at inland localities and at higher elevations, and it is uncertain whether the variation is geographic or altitudinal (both were suggested for Cameroon Mountain Greenbul [Andropadus montanus]).

The references cited are useful and reasonably complete for local distributions and relationships. The lists of bird species for several localities include nonforest and forest birds and would be useful for a visitor as well as for conservation purposes. Because montane western Cameroon is easy to visit, it is perhaps the best country in west Africa for anglophone ornithologists to travel and see African forest birds. It is hoped that the report will succeed in the ideal of its title. —ROBERT B. PAYNE.
ECOLOGY AND EVOLUTION OF DARWIN'S FINCHES. By Peter R. Grant. Princeton University Press, Princeton, New Jersey, 1986:xiv + 458 pp., 8 color and 55 black-and-white plates consisting of 123 photographs, 101 text figs., and 23 tables. $55.00 (cloth), $22.50 (paper). — Since their first scientific mention by Charles Darwin in 1841, the ubiquitous songbirds of the Galapagos and Cocos islands in the tropical eastern Pacific Ocean have been a perennial source of fascination for students of evolutionary biology. Given the patronym of “Darwin's Finches” by Percy Lowe in 1936, these 14 species of diminutive passerines have become famous out of all proportion to their size as classical examples of radiative adaptation. They are remarkable for their modest diversity in bill form, feeding habits and songs, and their striking homogeneity in patterns of plumage, nest, egg, courtship, and internal anatomy. Variation in beak structure within and between populations is often so broad as to blur species limits, a situation that originally led to considerable taxonomic confusion. It is not surprising, therefore, that generations of evolutionary biologists have been challenged by these birds in pursuit of a solution to that fundamental problem in biology, the origin of species diversity. The pervasive process of natural selection, and the product consisting of a plethora of Galapagos finches, were wedded in much of the reasoning embodied in Darwin's 1859 classic, “On the Origin of Species.”

Darwin's finches have undergone monographic treatment on average every 25 years, viz. Rothschild and Hartert (1899/1902), Swarth (1931), Lack (1945/1947), Bowman (1961/1983), and most recently by Grant (1986). The latter, the subject of this review, summarizes the basic facts and ideas of earlier workers, integrating many of them with the results of multifarious studies previously published in scientific journals by Peter Grant and his wife Rosemary, and a coterie of postdoctoral colleagues and talented graduate students, spanning the period of 1975 to the present. The upshot is a modern synthesis of contemporary evolutionary thought about Darwin's finches, which is as impressive for its intellectual breadth, thoroughness of treatment, and physical bulk, as it is for its beauty and readability. A major thrust of this attractive volume is Peter Grant's affirmation of the overall stability of the “house that Lack built” for Darwin's finches. In this endeavor he seems to be playing the role of David Lack's “bulldog” and scientific “ombudsman.” How convincingly Grant has struck a modicum of truth for certain contentious concepts remains to be seen.

The book is divided into a preface and 16 chapters, an appendix, references and author and subject indices. Each chapter, save the first, concludes with a helpful thumbnail summary. In the preface, Grant sets forth three reasons for his studying Darwin's finches: (1) The confusion about the significance of population variation in their beak sizes; (2) the lack of information on long-term changes in the modality of bill dimensions in island populations and its adaptive or nonadaptive significance; and (3) the need for resolution of the Bowman-Lack dispute concerning the importance of intraspecific competition in shaping variability in island populations of a species and interspecific competition in shaping the composition and structure of finch communities on the various islands.

Chapter 1 is an overview of the book, including a brief history of the scientific study of the finches: Darwin's perplexity due to insufficient materials with accurate place names; the evolutionary views of Harry Swarth and Erwin Stresemann, neither of whom had any notable experience with the live finches; and the historical importance of Stresemann's allopatric model of speciation for the finches, later adopted by Lack who inferred a process of species differentiation beginning in allopatry and continuing in sympathy through the process of interspecific competition. Grant freely admits that inferences about historical events in finch evolution cannot be inferred “with accuracy” (Grant's emphasis) from contemporary patterns of distribution, thereby acknowledging one of the criticisms levied by his arch critics, E. P. Connors and D. S. Simberloff.
Succeeding pages of the book treat of the following: general characteristics of the finches (Ch. 2 and 3); morphological patterns of the finches, including developmental features (Ch. 4 and 5); ecology of the finches, including food habits and bill shapes, fluctuating food supply, breeding ecology, mate choice, and avoidance of hybridization (Ch. 6 through 9); and an explanation of the evolutionary divergence of the group (Ch. 10 through 15). Chapter 16 is a recapitulation of the book with generalizations.

The book has a familiar "ring" about it because it mirrors in many ways the general plan set forth by Lack in his now famous 1947 classic, "Darwin's Finches." Grant covers much of the same ground as did Lack, even measuring once again the same museum specimens, performing similar (but much improved) field experiments on species recognition using stuffed specimens. Proceeding from where previous workers have left off, Grant's team has coordinated a multifaceted assault on Darwin's finches with an emphasis on their ecology, behavior, population dynamics, and evolution. The undisputed success of the effort is attributable to intensive, long-term field studies, employing imaginative experimental design and sophisticated statistical analyses.

Among the many new findings summarized in this volume, the following were of special interest to this reviewer.

Differences between species in size and proportion of adults arise during development by different patterns of relative growth. Relative growth in bill dimensions is fastest in those dimensions most pronounced in adults. The large billed ground finch (Geospiza magnirostris) appears to be unique in growing along an altered trajectory during the fledgling phase; initially bill depth increases faster than bill length as in other species, then the order of these rates is reversed.

The latter part of the dry season is identified as a period of potential food limitation for the finches. Seed biomass was lower on all islands at this time of year. Since the diets of co-inhabiting species on an island overlap then, the species are in competition for food, although competition is reduced as a result of the divergence of diets in the latter part of the dry season.

Finch populations differ in the degree to which they vary in continuously varying traits such as bill and body sizes. The directions of selection, as in G. fortis on Isla Daphne Major, change with the forces of selection so that small size and large size are alternatively favored. Over a long period of time the net effect of these oscillations is directional selection and may be roughly equivalent to a weak form of stabilizing selection.

Regarding species recognition and mate choice, through field experiments it was shown that with male and female discrimination of stuffed specimens, the bias is toward conspecifics. Both head and body size appear to be used in combination for correct species identification. Experiments using playback of recorded song indicate that Geospiza males know the difference between the songs sung by other members of the population, and the songs sung by other species in the same environment, even when these songs are structurally similar to their own. Song acts as a long-range auditory signal, and appearance, especially bill morphology, acts as a short-range visual signal, each transmitting information about the identity of the sender.

Addressing the basic problem as to how the finch species evolved, by examining the various subsets of this problem, Grant states that what few solutions have been proposed range from the confident to the speculative. It is likely, on the basis of current information, that the 14 extant species of finches are the only ones to have evolved.

The results of electrophoresis do not confirm Lack's assignment of greatest age to G. difficilis; G. scandens would appear to be closest to the tree-finches group. Using the numerical values for biochemical differences between species, the ancestral warbler finch split off from
the ancestral stock about 750,000 years before present. It is not known how long the Galápagos were tenanted by the original colonists before this initial speciation occurred. No species is known to have arisen in the last 50,000 years.

Grant proposes a 5-step model for the derivation of 13 species on the Galápagos. In essence, the model is that proposed by Lack and based on the idea set forth by Stresemann, namely that the derivation of 13 species on the Galápagos from a single ancestor was initiated by small differentiations of allopatric populations of a single form, followed by enhancement of differences when two such populations made secondary contact on an island through the dispersal of members of one to the island occupied by the other. The enhancement of differences in sympatry was driven by natural selection acting against individuals of the two populations which were so similar that they competed with each other for food, and breeding with each other with reduced reproductive success. Successive speciation events produced species adapted in very different ways to exploiting the environment for food, with different lineages radiating in very different directions from the common ancestral stock. He rules out the sympatric model of speciation as requiring a most unusual set of circumstances, evidence for which has not been uncovered in Darwin's finches. According to Grant the allopatric model owed its broad acceptance to the clarity with which observations were shown by Lack to fit the theory.

Grant freely admits that competition (discussed at length in Chapters 11 and 12) has been and continues to be the most contentious part of the allopatric model. He presents evidence that his group has developed which purports to indicate that competition is occurring at the present time, and it raises logical and empirical difficulties with the argument that differentiation always occurred entirely in allopatry. As first proposed by this reviewer in 1961, certain features of Darwin's ground finches are explicable in terms of their food supply, in a manner consistent with the complete allopatric model. For example, food supply determines not only diets but also which species occur on an island and their approximate abundance. The question now revolves around the current distribution of the finches. Are these distributions and diets determined by food supplies, regardless of whether competition has occurred in the past or not? Testing the competition hypothesis is said to be difficult for two reasons. First, the hypothesis deals with events in the past, and since we cannot reconstruct those events precisely, we cannot test the hypothesis directly; it must be tested through predictions of the assumptions upon which it rests. Second, since Lack's arguments were not expressed clearly, Grant put them into a testable framework. The observations to be explained are the distribution of species and the inter-island differences in beak size and shape; the hypothesis is that distribution and morphology were causally influenced by interspecific competition for food. The main assumption upon which the hypothesis rests is that the feeding niche of a population is reflected in, and hence adequately indexed by, the average beak characteristics, especially bill depth.

How precise an indicator of bill-biting potential is bill depth? Preliminary unpublished research in progress by this reviewer suggests that the physical forces exerted by living Darwin's finches at their bill base and tip do not correlate systematically with dimensions of bill depth, length, or width, nor with any combinations thereof. Bill depth is but one component of a three-dimensional musculoskeletal complex, which by itself does not reflect the functional potential in any precisely predictable way. Yet measurements of bill depth form not only a significant part of the data base used by Grant and his coworkers as an index of expected population density of finches but also for the range of preferred seeds of the ground finches. Their analysis is restricted to seeds preferred during the dry season, with little knowledge of why certain seeds in the total array presented by an insular flora are preferred over others, irrespective of their relative abundance. Palatability, determined by the presence of toxic substances such as alkaloids could, theoretically, cause a shift in seed
size/hardness preferences, and this, in turn, through natural selection could affect bill depth modalities of populations, unrelated to competing neighbors. Thus there is reason to question the validity of certain assumptions on which their methods are based. Nevertheless it is claimed that their ecological data have generally upheld the competition hypothesis by consistent agreement with its predictions, and therefore allow the rejection of Bowman’s alternative hypothesis that food supply alone has determined the morphological and distributional features of the finches. He asserts that competition has played an influential role in both allopatric and sympatric phases of the cycles of speciation of the ground-finches.

In a penultimate chapter, Grant discusses the phylogenetic relationships among the finch species. Phylogeny is inferred from estimates of selective forces involved in the transformation of one species into another. The so-called selective distances between species incorporate the time-dependence of morphological differentiation that arises from the retarding effects of genetic constraints upon the effectiveness of selection. As it turns out, the phylogenetic relationships inferred in this manner agree quite closely with those arrived at through a comparison of morphological phenotypes and biological properties.

Grant concludes the volume with a succinct capsulation of the principal points of earlier chapters, closing with a consideration of the extent to which the lessons learned from Darwin’s finches can be applied to the problems of evolution in other groups of organisms.

There are a few minor criticisms of the book, and the first of these concerns the pagination, or substantial lack thereof. Over 123 pages out of a total of 458 (i.e., over 25%) are unnumbered. Concerning matters scientific, Grant claims that finches in other parts of the world do not have a tommium of the maxilla forming an abrupt angle with the zygomatic bar but rather that it “projects straight out of the head.” Tree-finches are said never to build nests in cactus, which is not true for Isla Santa Cruz in the vicinity of Academy Bay. Grant implies that the island source of G. contosum on Isla Genovesa is either Daphne Major or Santa Cruz, based on superficial examination of wide-band sound spectrograms of their songs. Yet Bowman has clearly demonstrated that, due to extensive parallelisms, song structure in Darwin’s finches is a most unreliable clue to island source of colonists. The Galapagos mockingbird, Mimus (Nesomimus) parvulus is mislabelled N. galapagoensis on pages 268 and 272. Regarding the curious large-billed finches from the most northerly outpost of the archipelago, Isla Darwin, Grant states that they breed there, yet there is no evidence known to this reviewer to support this claim, and he is one of the handful of scientists to have ever set foot on top of the island during a breeding season.

Some things needing further study include a more intensive search for closest mainland relatives (sister groups) and extinct fossiliferous forms, clues to the nature of past changes in the Galapagos environment, and more detailed studies of life history characteristics of individuals and the dynamics of populations. With regard to the latter, the intensive field researches by Grant and his group, requiring patience, persistence and perspicacity, have yielded a bountiful harvest, showing once again how the small closely knit world of the Galapagos can be induced to yield insights into the origin of species.

The author and his research associates merit the highest of praise for the substance of this scholarly monograph which should prove to be a classical challenge and inspiration to a whole new guild of biologists. —Robert I. Bowman.
Liberia, Guinea, and the Ivory Coast. Its summit in Guinea is still one of the highest points in West Africa (1752 m). Had it been in Liberia, it would by now have been drastically whittled down, as has the rest of the mountain there, due to mining of the rich iron ore deposits since 1963. Mining activities and consequent human population pressures in what had been a sparsely populated forest have contributed, and are still contributing, to the rapid destruction of huge areas of natural vegetation, especially lowland and highland types of forest.

On behalf of the IUCN, Kai Curry-Lindahl (KCL) persuaded the mining company to fund research on and around the mountain before it was destroyed: he has been Chairman of the IUCN Nimba Research Committee since then. This is the report on the ornithology, particularly on the large and virtually complete series of 3400 bird skins, mostly collected by me and my helpers in 1967 and 1968. Peter Colston (PRC) works in the Bird Room of the British Museum (Nat. Hist.) where the specimens are housed, but he has had no field experience in West Africa. The title implies that this is a study of the birds of the mountain, but this is misleading: there is no truly montane avifauna, and most of the studies were in the lowland areas at about 550 m.

The whole is reminiscent of those faunal papers which were a feature of *Ibis*, in which it might very likely have been published in former times, when it would certainly have been more accessible. The text is in two main parts: "Mt. Nimba," including a 4-page essay on the biogeographic context by Malcolm Coe (MJC), the first investigator (in 1964); and "The Birds" comprising the bulk of the text (83 p.).

The color plate by Philip Burton is of the two "new" species: *Melignomon eisentrauti*, here called Coe's Honeyguide, also known as Eissentraut's or Yellow-footed Honeyguide (*Melaenornis annamarulae*) here called Anna's Flycatcher, also known as the Liberian or Nimba Flycatcher. I prefer Yellow-footed and Nimba, respectively, though the last could conceivably be confused with the new race of Olivaceous Flycatcher (*Muscipapa olivascens nimbae*) described on p. 85. Burton has given the flycatcher a slightly notched tail when it is actually rounded. In the review copy, at least, the plate is much too dark as are the three color photographs of captive birds by MJC—one of the *Melignomon*, one of the Golden-bellied Wattle-eye (*Platysteira concreta*) and one of the Blue-spotted Wood-Dove (*Turtur afra*) incorrectly called Lemon Dove (*Aplopelia larvata*). The other color photographs and 19 of the monochrome by KCL and Coe are of habitats and their destruction; those with dates being particularly useful. The other black-and-white photograph is by me of the Bare-headed Rockfowl (*Picathartes gymnocephalus*) at a nest—the altitude should be 750 m not 1000. The line drawings, by PRC, are an entirely unnecessary indulgence; they add nothing and in most cases are inaccurate—particularly toes, posture and proportions. The map (unacknowledged, but specially drawn by Jozeph Grounewoud) shows the contours of the Liberian part of Mount Nimba before mining started. The other text figure shows breeding and moulting seasons of some passerines, with the data in a table opposite. The other tables present a summary of the 117 species found at Mount Nimba which were previously not known from Liberia. The Swamp Flycatcher (*Muscicapa aquatica*) should be deleted—it was based on an early Coe specimen misidentified at the BM (NH) as a Garden Warbler (*Sylvia boriri*) (D. Goodwin, pers. comm.). On p. 17, *Andropadus ansorgei* should be corrected to *Criniger olivascens*. Nomenclature follows the two BM Atlases (1970, 1978) and so the Red-fronted Antpecker (*Parmoptila r. rubifrons*) is incorrectly called *P. jamesoni* (of 1890) *rubifrons* (1872).

The species accounts are based on sight records and specimens, which are briefly listed, and impermanent colors and stomach contents are summarized from my field notes, followed by very brief notes on status and habitat. The 19-page appendix is a summary of weights and measurements of the specimens; weights were taken by me on a Dial-O-Gram scale.
accurate to 0.1 g; some of the passerines weigh less than the 5 g generally accepted as the minimum passerine weight.

This collection has been called the best-prepared and most representative that the BM (NH) has received (by the late Con Benson, for instance), so I would like to correct the statements on p. 5. Almost all the birds were prepared by Joseph Mbonge Mwaki of Kenya who spent 18 months there in 1967–68 (not “for a period in 1968”). He trained Edward Yallah who gets the full credit here, although he has prepared the comparatively few specimens collected since then. An inspection of the skins pre-Mwaki, by Mwaki and post-Mwaki demonstrates his mastery of field taxidermy.

I am also reviewing this work for the new Afrotropical journal, Tauraco, in which I discuss the biogeography.

This hard-covered work is nicely produced and is virtually free of typos. For anyone with an interest in African and tropical avifaunas, this is a most useful set of data and another reminder that huge areas of irreplaceable natural areas are being destroyed.—Alec Forbes-Watson.

ARKANSAS BIRDS, THEIR DISTRIBUTION AND ABUNDANCE. By Douglas A. James and Joseph C. Neal, illus. by David Plank and Sigrid James Bruch. The University of Arkansas Press, Fayetteville, Arkansas, 1986:402 pp., 164 figs., including 31 black-and-white drawings, 19 color plates, and 19 color photographs of birds. $34.00.—Although this volume represents the fifth comprehensive work on the birds of Arkansas, the authors have pulled together something much more than a simple update on the knowledge that has accumulated since the last work of Baerg (1951. Univ. Ark. Agric. Exp. Sta., Bull. No. 258 [revised]). The current volume is not unlike (except for length) Oberholser’s “The Bird Life of Texas” (1974. Univ. Texas Press, Austin) in that it includes chapters on the history of Arkansas ornithology, Arkansas birds and the environment, Arkansas birds in prehistory, and finding birds in Arkansas. The introduction lays the groundwork for the contents of the volume, explaining the various sources of information and how they are used, the role of each author in Arkansas ornithology, and the role of each in preparation of the book; it also compares the number of avian species reported in each of the five works on Arkansas birds and how those numbers may differ, not just because of new knowledge.

The chapter on history begins with the explorations of De Soto in 1541, highlights the discovery of Traill’s (=Willow) Flycatcher (Empidonax traillii) by Audubon as the only species so described to science from the state, and then gives good coverage to the several important areas of Arkansas ornithology.

The chapter on birds and the environment is much more than an elaboration of the habitats that occur in the state. Climate, physiographic regions, and grouping of birds by habitat have a place in this chapter, but I found “Birds and their Habitats” far more interesting. This portion summarizes several studies on changes in bird populations with successional changes in woodland habitats of Arkansas.

I find the chapter on birds in prehistory interesting but somewhat of an enigma. Perhaps I am perplexed because this type of information, more of an anthropological nature than ornithological, pertains so much to birds in the Indian cultures of the area, rather than to the prehistorical presence of the birds in the state (although a table does summarize the presence of different avian species at the known archeological sites).

The three pages on finding birds in Arkansas gives too little information to be of much value to a person wishing to explore the avifauna to any extent.

The bulk of the book relates to the species account of the 366 species now known to occur, or to have occurred, within the boundaries of the state. The introduction to this
section defines the various terms used in the species accounts, explains why certain species have distributional maps, though most do not, discusses the maps on movements of banded birds, and lays a foundation for not considering subspecies: earlier work by Frances C. James “cast considerable doubt on the validity of the subspecies concept. . . .” This section also includes explanations of how various surveys and mapping techniques were used.

Each species account gives a brief statement of abundance and occurrence for the state. Following this, the authors discuss in greater detail seasonal abundance and distribution in which they frequently mention specific dates and locations in relation to arrival times, unusual numbers, or other facts of reported interest. A large number of the species have figures depicting the banding recoveries related to Arkansas birds; where over 150 such records exist, the authors have elected to use a clock-face mechanism for demonstrating the numbers from particular directions and distances. Unfortunately, 150 records is probably too high to begin this effort, as a number of the figures are obscured because of serious overlap. Nonetheless, this technique provides useful information and probably will be repeated in other state works if funds are available for the mass record search at the Bird Banding Laboratory.

The few species for which distributional maps are also presented have less than statewide distribution, and usually have rather unusual distributions or some other factor of interest. I found the two maps for *Picoides borealis* of particular interest in comparing the current situation with the distribution of 20 to 30 years ago. Even though *Icterus galbula* meets the authors’ criterion of not having a truly statewide distribution, the species lacked so few counties, and with no perceived reason for absence from those few counties, that I wondered why the map had been included.

The 31 black-and-white drawings and over half of the 19 color plates are by David Plank; he generally shows good talent, and most of the drawings were made at specific localities in the state. However, his rendition of the Wood Thrush (*Hylocichla mustelina*) leaves much to be desired. All of his illustrations are of songbirds. Sigrid James Burch painted the remaining color plates, all of nonsongbirds. This artist either lacks the training of Plank or is slightly less skilled. The book also contains 19 color photographs by various persons.

Generally, this is an excellent work for a state book. It has several innovations that others might emulate. My most serious complaint lies not with the authors, but with the publisher: the binding is very poor on my copy, not standing up to even moderate use.—Keith A. Arnold.

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**Conserving Biological Diversity in our National Forests.** By Elliot A. Norse, K. L. Rosenbaum, D. S. Wilcove, B. A. Wilcox, W. H. Romme, D. W. Johnston, and M. L. Scott. Prepared by the Ecological Society of America for The Wilderness Society. The Wilderness Society, Washington, D.C., 1986:116 pp., 20 unnumbered photos with captions, 1 fig. No price given.—National Forests are among the last places presenting long-range opportunities to maintain the integrity of forest life, but the National Forests are beleaguered by a philosophy of timber production as the major priority. This is a legacy of Gifford Pinchot, who along with President Theodore Roosevelt, was responsible for the establishment of the National Forest system. Since then, our National Forests have been a battleground between the philosophy of the wilderness, as espoused by John Muir, founder of the Sierra Club, and Pinchot’s utilitarian philosophies. The utilitarian approach still dominates, as evidenced by the management plans developed for the various National Forests.

The public, for whom the National Forests are held in trust, views the forest in a different light. As a result, Congress has mandated certain modifications in management of National Forests to maintain and enhance other amenities: wildlife, recreation, biological diversity, and maintenance of viable populations of vertebrate species.
Many, if not most, of the initial recent management plans written fail to take this holistic approach. The planners either may not be sympathetic to an ecosystem approach to management, lack the knowledge and expertise to develop such plans, fail to utilize their own ecologists and wildlife biologists in the planning process, or ignore the whole issue by continuing their past ways as witness the problems of the Tongass, the reluctance to maintain old growth in the Pacific Northwest and southern pinelands, keys to survival of the Spotted Owl (Strix occidentalis) and the Red-cockaded Woodpecker (Picoides borealis).

Legislation, however, mandates a public input into the National Forest management plans. The quality of this input varies. It is very difficult for the general public to assess critically these plans because it possesses even less ecological expertise than the planners. Yet public input can be effective as exemplified by the conversion of a strictly timber management, road-building plan for the Monongahela National Forest to one emphasizing wildlife and recreation.

This little book provides citizen conservationists, land managers, elected officials, and foresters a primer on ecological concepts relevant to forest planning. While the book will not make an expert out of the reader, it does provide enough ecological insights to permit a critical review of forest management plans, the purpose of this publication.

The book, well-written and easily understood, consists of nine short chapters. Chapter 1 explains the meaning of biological diversity and the reason for conserving it. Chapter 2 introduces the concepts of population, communities, succession, the role of long- and short-term disturbances, and the value of old-growth forest ecosystems. It introduces the basic ideas of population genetics, minimum viable populations, and fragmentation of habitats. Chapter 3 introduces the idea of ecosystem vs featured species management. Chapter 4, which should have followed Chapter 2, continues the discussion of habitat fragmentation and all its problems. Chapter 5 provides a brief review of silvicultural practices from thinning to harvesting.

Having provided this background, the authors move into the core of the matter, National Forest planning, the role of public participation, and the various legalities involved. Public participation in National Forest planning requires some idea of what to look for in these long-term management plans. The last chapters of the book tell you. They provide a balanced, nonadversative assessment, and ask the right questions. The list of questions posed is one that planners themselves should have on hand as a check-list. That would enable them to avoid oversights and meet the guidelines of forest management planning.

The last two chapters are case history studies. Chapter 8 is devoted to management or mismanagement of rare species and the conflicts between timber management and the wildlife species involved. The last chapter looks at the maintenance of biological diversity in the Yellowstone ecosystem involving the Park and adjacent National Forests.

Although the book is designed for those who have the opportunity to review National Forest plans, it has even wider application. It is the kind of primer on applied forest ecology relative to biological diversity that will provide keener awareness of the interactions between forest wildlife and their habitats and how they are affected by human intrusions. Anyone who is concerned about the future of birdlife and the effects of diminishing habitats should read this little book. It explains much about what is happening.—ROBERT LEO SMITH.

 PATTERNS AND EVOLUTIONARY SIGNIFICANCE OF GEOGRAPHIC VARIATION IN THE SCHISTACEA GROUP OF THE FOX SPARROW (PASSERELLA ILIACA). By Robert M. Zink. Ornithological Monographs No. 40, American Ornithologists’ Union, Washington, D.C., 1986:viii + 119 pp., 34 figs., 21 tables, appendix. $15.00 ($12.50, members). — All of systematics is divided into three parts. These include the inference of higher level relationships or phylogenetic analysis, the study of speciation, and the investigation of intraspecific variation. The latter
two areas were the major focus of systematists' interest during much of this century, but phylogenetic analysis has become dominant over the last 15 to 20 years. Its rise in popularity seems to be the result of theoretical and partisan disputes over methods, along with the development of new, including molecular, techniques for producing data. The investigation of speciation remains popular because of unresolved theoretical issues concerning modes of speciation, the dynamics of hybrid zones, and the definition of species. The debate about geographic variation is less audible in this era of macroevolution, heterochrony, and DNA sequences, but a few new issues have arisen here also. The theoretical issues that had traditionally been associated with intraspecific variation usually involved attempts to understand the beginnings of the process of speciation—issues such as the conversion of intraspecific variation to interspecific differences. Current interest also centers on the genetic basis for geographic variation, the time required for its evolution, and the relative roles of gene flow, natural selection, and random drift in its origin and maintenance. In this regard, the Fox Sparrow (Passerella iliaca) of the western U.S. is an exemplar of a species with remarkable, almost species-level, morphological variation among populations; it is the subject of Robert Zink's new AOU monograph.

Populations of Fox Sparrows in the montane chaparral of the Pacific Coast states and the riparian thickets of the Great Basin ranges vary in overall size, plumage color, and, especially, bill size and shape. For example, whereas mean body mass varies up to 30% among localities, mean bill widths and depths vary by as much as 50% among populations only a few hundred km apart. Two separate monographs (by Linsdale and Swarth) treated this variation in the 1920s. Zink's is the first comprehensive treatment of these birds since those earlier studies. It consists of statistical analyses of three data sets (skin measurements, skeletal measurements, and electrophoretic results) obtained from series of new specimens from 31 localities in California, Nevada, and Oregon.

Zink's approach was to search for patterns, in each of the three data sets, and then make inferences about causal processes by comparing these patterns. The electrophoretic data set indicated a lack of substantial differentiation among the morphologically diverse populations. In addition, clustering the genetic distances among samples resulted in a tree that made little geographic or ecological sense. These results led the author to conclude that either the divergence of the populations was recent or that there has been substantial gene flow among localities. Univariate and multivariate analyses of the skin and skeletal data sets were easier to interpret. The major components of variation in both cases were largely consistent with geography; that is, geographically proximal samples were morphologically similar. This was less true, however, of second order components of variation (second and subsequent principal components). Morphological variation was correlated with latitude and environmental variables, but was not consistent with the usual ecogeographic rules.

The investigation of intraspecific variation generally has become more statistically sophisticated over the last 20 years, and this study is no exception. In addition, it is the first monograph on avian geographic variation that treats electrophoretic and morphological variation in a single work. Zink is able to capitalize on that occasion; it was, for example, the contrast between the molecular and morphological data sets that allowed him to infer that the morphological divergence was recent and perhaps only ecophenotypic. His bold hypothesis that some or even much of the morphological diversity in the species may have been due to the influence of the local environment where the birds were fledged (the "Fran James effect") needs to be tested. This and the discussion of other topical issues, including the question of species status of well-differentiated forms (Zink thinks there are three species of Fox Sparrows), will be of interest to many readers.

Nevertheless, this is not the "complet" monograph; besides the minor matter of a mix-up that resulted in Figure 18 being replicated as Figure 24, several omissions are worth
noting. First, *P. iliaca* is highly polytypic; of the three subspecies groups—*schistacea*, *iliaca*, and *unalaschcensis*—only the first was examined in this study. Inclusion of representatives of the latter two taxa would have permitted the examination of the concordance of molecular variation, morphology, and geography over larger geographic and temporal scales. It is possible, for example, that the discordance Zink found between morphological and molecular variation was the result of an insufficient signal-to-noise ratio in the electrophoretic data due to recency of common ancestry. Second, in examining concordance among character sets, it would have been useful to possess information on plumage color and perhaps even on song variation. Third, although summaries of electrophoretic variation in each population are given in tables, summaries of morphological characters are not. The first two additions would have required significantly greater research time, but they would also have improved the monograph. These are quibbles, however; this work is as good as any recent monograph on geographic variation. The real problem is with the current state of that science.

Studies of intraspecific variation lack the cachet of phylogenetic and speciation analyses. I believe this is due to a lack of well-developed goals and hypotheses. With the widespread availability of multivariate and other computer packages, systematists are well-equipped to describe patterns of variation, their magnitude, and their statistical significance—the tactical machinery for the study of variation exists. But there is no universally agreed upon set of questions to be asked, and no overall agenda or research program. It is symptomatic of the state of affairs in this branch of systematics that Zink’s final discussion includes a series of unanswered questions rather than evidence supporting standard generalizations. This monograph does not tell a slick story; rather it accurately reflects present uncertainty. There is a challenge in this; those interested will want to read and reflect on this monograph.—George F. Barrowclough.

**Hawks at My Wingtip.** By Bill Welch. North Country Press, Thorndike, Maine, 1987: 148 pp., 39 black-and-white photographs and 22 figs. Soft cover, $7.95.—Mr. Welch provides an interesting narrative about following and studying hawk migration through the use of a powered glider during four fall migrations in New England. The book is easy to read and provides substantial information not readily attainable by ground-based observers. For example, we learn that Broad-winged Hawks (*Buteo platypterus*) have an air speed of about 25 mph while soaring in a thermal, and about 40 mph while gliding. Also the author provided air speeds (mph) of 41–58 for Turkey Vulture (*Cathartes aura*), 48 for Osprey (*Pandion haliaetus*), and 50 for a stressed Peregrine Falcon (*Falco peregrinus*). It was also confirmed that Broad-wings do thermal up into dense clouds and, more astonishing to me, that they emerge simultaneously to glide off in the migratory direction, rather than only a few at a time as they reach maximum soaring height, which (in New England) proves to be around 5000 feet. There is a comparison between thermal lift and ridge lift as it affects migrating hawks. We are also given hard data on glide ratios.

By way of criticisms, perhaps half of the photographs could have been deleted, as could most of the “Hawk Patrol” maps, the purpose of which is often unclear since reference to them in the text is seldom made. The author makes the curious statement that “the season for hawk migrations is documented” while “the exact dates are not.” He also applies the term “penetrating” to the mode of flight commonly known as gliding. The statement “hawks are sometimes reported migrating in extremely poor weather . . . after a long period of unfavorable weather has delayed the usual migratory flights” seems oxymoronic. In the listing of hawkwatching sites, geographical descriptions are sometimes lacking, e.g., “Hawk Ridge, Minnesota.” Some readers might not know that this site is in Duluth. There are a few, minor typographical errors; I counted three.
Also included are sections about the sport of hawkwatching, captive rearing, falconry, rehabilitating, and some personalities involved with raptors. There is a technical discussion on the mechanics of flight and four appendices dealing with hawkwatching, aerodynamic calculations (too technical for most laymen, including this reviewer), a glossary, and identification aids. The book is recommended reading for all raptor enthusiasts and students of avian migration.—Daniel D. Berger.

Voices of the New World Cuckoos and Trogons. Cuculidae and Trogonidae. By J. W. Hardy, George B. Reynard, and Ben B. Coffey, Jr. ARA 11, ARA Records, P.O. Box 12347, Gainesville, Florida, 1987: Monaural tape cassette. No price given.—As the comments accompanying this tape note, the recording of cuckoo songs is a difficult and trying task. Cuckoos generally do not engage in song bouts, and there may be long intervals between individual songs. Despite this obstacle, this new recording from ARA Records gives us the vocalizations of 26 of the 33 New World cuckoos. Missing are four species of the genus Neomorphus, Coccyzus cinereus, and Plata melanogaster, which are not known to have been recorded. Opisthocomus is included as a cuckoo (fide Sibley and Ahlquist) although the notes indicate that this is a debatable point.

The reverse side of the tape gives us the songs of the 25 New World trogons, which are easier to record than are cuckoos. Included are the only known recording of Trogon comptus and the recording of the Eared Trogon (Euptilotis neoxenus) made on its first appearance in the U.S.

The high standards, both of recording and reproduction, that we have come to expect from ARA are maintained here. Most of the recordings were made by the three co-authors, particularly the indefatigable Ben Coffey, but 14 others, including a Nobel Laureate, contributed one or more recordings. All are to be congratulated.

The recording data and other notes, usually found on the sleeve of a record, are here confined to the six 6 x 10 cm sides of the wrap-around cassette label. The fineness of print is guaranteed to send most people to their oculist. Besides the technical data, Hardy has made numerous comments on the possible significance of these vocalizations to the taxonomy of some of the species.—George A. Hall.

The Birdwatcher’s Diary. By Edgar M. Reilly and Gorton Carruth. Harper & Row Publishers, New York, 1987:218 pp., many sketches and maps. Soft cover. No price given.—If you are looking for an attractive gift for a fledgling birder friend this might be the answer. The diary portion consists of 52 lined pages available for keeping weekly observations and notes. However, the book is more than a notebook but is really a primer of bird watching and an introduction to ornithology.

For each week there is a short paragraph labeled “Activities” which suggests some things that might be done to expand one’s knowledge of birds, and a section with map, labeled “Comings and Goings” that highlights particular species. There is also discussion of a topic ranging from Migration, through Classification and Behavior, to “Group Birding.” These accounts, which are often several pages long, are good introductory chapters to a textbook on ornithology. A spot check of these accounts produced only a few ambiguities and no major errors of fact. Good references to further literature are given throughout, and a section called “Winter Nights Homework” lists books and journals that may be of value to the neophyte as he develops.

An attractive Checklist of the birds of Canada and the U.S., with spaces for annotations,
is provided. Throughout the book is profusely illustrated with maps and attractive sketches, although the artists are mentioned only in the Acknowledgments.—George A. Hall.

ABUNDANCE AND DISTRIBUTION OF THE BIRDS OF OHIO. Ohio Biological Survey, Biological Notes No. 19. By Bruce G. Peterjohn, Raymond L. Hannikman, Jean M. Hoffman, and Elliot J. Tramer. The College of Biological Sciences, The Ohio State University, Columbus, Ohio, 1987:iv + 52 pp., maps, and color photo cover. $5.00 (plus 20% postage and handling).—Ohio stretches from the foothills of the Appalachians to the beginnings of the prairies and there are a few relict boreal habitats in the northern part of the state. This alone would make for an extensive list of birds, but the number is further enhanced by the long Lake Erie shore which introduces an almost maritime flavor. Despite the legions of bird students in the state, there has not been a comprehensive treatment of these ornithological riches since Dawson's book in 1903. There have been only abbreviated checklists in 1950, 1968, and 1983 and the long out-dated Distribution of the Breeding Birds of Ohio (Hicks 1935). The publication before us is not a comprehensive treatment but continues the checklist format with more extensive annotations than in the past. Distribution is given by regions of the state, defined in a map, and abundance according to well-defined terms. Complete data as to date and place are given for the rarer species. A total of 368 species has been documented either by specimens (348) or photographs (20) in the state. An additional 19 species have been accepted as "Hypothetical" on the basis of observation with good documentation. Another 32 species are on an "Unaccepted" list, being represented by sight records with poor documentation or were possible escapes.

The annotations are terse, averaging 3-4 lines per species, but are informative. The almost obligatory bar diagram showing seasonal occurrences is given with the added convenience of having different bars for different regions, usually North and South.

In keeping with the checklist format there is no discussion of the physiography or phytogeography of the state, but a map of landforms is included, as well as a map showing the counties and the regions used in discussing distribution. The preliminary material explains the criteria of acceptance in detail.

This is a most useful addition to regional lists but bird students in the Midwest will await the Ohio Breeding Bird Atlas for which the field work is currently being carried out and we can hope for a comprehensive treatment in the future.—George A. Hall.

ALSO RECEIVED

ILLINOIS BIRDS: CORVIDAE. By Jean W. Graber, Richard R. Graber, and Ethlyn L. Kirk. Illinois Natural History Survey Biological Notes 126, Champaign, Illinois. 1987:42 pp., maps and graphs and one black-and-white sketch. No price given.—This is the eleventh fascicle in the series of short publications substituting for a formal state bird book. Nine species of corvids are discussed of which three nest in the state. The accounts of the Blue Jay (Cyanocitta cristata) and the American Crow (Corvus brachyrhynchos) are full of interesting detail, including a listing of all known winter crow roosts in the state. When completed, this series will constitute perhaps the most complete state book in existence.—G.A.H.


BIRD BEHAVIOR AND MORTALITY IN RELATION TO POWER LINES IN PRAIRIE HABITATS. By Craig A. Faanes. U.S. Fish and Wildlife Service, Room 148, Matomic Building, Washington, D.C. 20240. Fish and Wildlife Technical Report 7, 1987:24 pp., 10 maps and graphs. No price given.—A thorough examination of mortality at selected power lines in North Dakota. Waterfowl and gulls constituted 60% of the mortalities in spring and 4.9% in fall. Most mortalities occurred during migration seasons. Some recommendations to alleviate the problem are given.—G.A.H.

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Manuscripts intended for publication in The Wilson Bulletin should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Abstracts of major papers should be brief but quotable. In both Major Papers and Short Communications, where fewer than 5 papers are cited, the citations may be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the “CBE Style Manual” (AIBS, 1983). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 x 28 cm. Alterations in copy after the type has been set must be charged to the author.

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The male (the type, lower bird) and female of the El Oro Parakeet, *Pyrrhura orcesi*, a new parakeet from southwestern Ecuador. Painting by William T. Cooper.
PYRRHURA ORCESI, A NEW PARAKEET FROM SOUTHWESTERN ECUADOR, WITH SYSTEMATIC NOTES ON THE P. MELANURA COMPLEX

ROBERT S. RIDGELY AND MARK B. ROBBINS

ABSTRACT.—A new species of parakeet, Pyrrhura orcesi sp. nov., from southwestern Ecuador is described and named the El Oro Parakeet. This species is most closely related to the Maroon-tailed Parakeet (P. melanura). Pyrrhura orcesi is restricted to a narrow band of forest, between ca 600 to 1100 m in elevation, along the western slope of the Ecuadorian Andes. Its range is only ca 100 km in length, and, given the current rate of deforestation in the area, it soon may be threatened with extinction. Received 26 Mar. 1987, accepted 3 June 1987.

In August 1980 a field party consisting of R. S. Ridgely, P. Greenfield, and R. A. Rowlett was investigating remnant patches of cloud forest west of Piñas, Prov. El Oro, Ecuador, at ca 900 m on the west slope of the Andes. On 4 August, the group observed a flock of nine parrots, clearly members of the genus Pyrrhura, landing in the canopy. The flock was observed for about 15 min; all members of the flock displayed a red forecrown and a virtual lack of breast scaling. No known member of the genus shares such characters; however, no photographs or voucher specimens were obtained.

Not until June 1985 could a return expedition be organized, under the auspices of the Academy of Natural Sciences, Philadelphia (=ANSP) and the Museo de Ciencias Naturales in Quito, Ecuador. Members of the expedition spent three weeks during late June and early July in the region of the original discovery, found the parakeet to be relatively numerous in what forest habitat remained, and collected 12 specimens. In August
1986, a field party returned to southwestern Ecuador to determine the northern limit of the bird's distribution, and obtained four additional specimens at a site ca 100 km north of the original locality. In addition, a heretofore unrecognized specimen of the bird in the British Museum of Natural History, Tring (=BM) was brought to our attention by T. Schullenberg. Study of this material, and of specimens of related species in the genus *Pyrrhura*, convinces us that the new parakeet deserves recognition as a full species, which we propose to name:

*Pyrrhura orcesi* sp. nov.

**EL ORO PARAKEET**

**HOLOTYPE.**—Academy of Natural Sciences No. 177523; adult male, ca 9.5 road km W of Piñas, ca 900 m, 3°40'S, 79°44'W, Prov. El Oro, Ecuador, 21 June 1985; collected by Mark B. Robbins, original number 1541.

**DIAGNOSIS.**—A *Pyrrhura* parakeet most similar to *P. melanura*. Readily distinguished from all forms of that species by its obsolete scaling on the breast and sides of neck, its red frontal band, and its much greener crown (the feathers without any dusky-brown centers). Superficially resembles geographically distant *P. rhodocephala*, but differs strikingly in its smaller size, having only forecrown red (not the entire crown), green (not red) ear-coverts, red (not white) alula and median coverts, and much more green in tail.

**DISTRIBUTION.**—So far, known only from three localities, all on the west slope of the Andes of southwestern Ecuador in Provs. El Oro (the type locality and Piedras) and Azuay (7 km E of Naranjal, 2°40'S, 79°32'W), at elevations ranging from 600 to 1100 m. Presumably occurs in intervening areas at appropriate elevations, and where suitable forest remains (Fig. 1).

**DESCRIPTION OF HOLOTYPE.**—General coloration green, closest to Parrot Green (Color 60; capitalized colors from Smith 1975, 1981), but shinier and brighter than that color on face, crown, nape, back, rump, and abdomen; slightly darker and duller on the wing-coverts and breast. Pale buffy grayish marginations virtually absent from breast feathers, but somewhat more pronounced on sides of neck. Center of abdomen with slight maroon-red sullusion. Broad (ca 5 mm) frontal band Geranium (Color 12), extending back to just in front of eye. Outermost greater and median primary coverts, as well as the alula, Geranium Pink (Color 13), somewhat more intense on bend of wing. Outer webs of outer primaries blue, very narrowly edged with green. Tail above mostly Burnt Sienna (Color 132), with outer webs and base green; below mostly dusky with inner webs margined with Burnt Sienna. Soft part colors in life: irides dark brown; tarsi black; bill horn; eye ring pinkish-white.

**MEASUREMENTS (mm).**—Wing (chord) 123.2; tail 102.2; culmen from anterior edge of cere 16.4; mass 73 g.

**SPECIMENS EXAMINED.**—*Pyrrhura orcesi*: ECUADOR: type locality 11 (ANSP), 1 skeleton (photo of fresh skin in VIREO VO1-3-007-011); Prov. El Oro, Piedras, J (BM); Prov. Azuay, Naranjal, 3 (ANSP), 1 (Museo Ecuatoriano de Ciencias Naturales, Quito). *P. m. pacifica*: ECUADOR: Prov. Esmeraldas, San Lorenzo, 5 (ANSP), San Mateo, 1 (FMNH= Field Museum of Nat. Hist.), Lita, 1 (AMNH= American Museum of Nat. Hist.); Prov. Pichincha, Rio Blanco, 1 (ANSP); *P. m. melanura*: VENEZUELA: Amazonas, Cerro Duida, 7 (MCZ= Museum of Comparative Zoology, Harvard), Boca de Sina, 1 (MCZ), El Merey, 3 (MCZ); BRAZIL: Amazonas, Iauaretê, 1 (MCZ), Tahuapunto, 2 (MCZ), Lago Tefe, 1 (MCZ), Rio Mirapinimi, 1 (MCZ), Rio Mazan, 1 (MCZ); ECUADOR: Prov. Pastaza, Chicheroa, 1 (ANSP), Montalbo, 2 (ANSP); Prov. Napo, Limnoncocha, 1 (LSUMZ= Louis-
Fig. 1. Type locality of the El Oro Parakeet.

siana State Univ. Museum of Zoology, Baton Rouge), Archidona, 1 (AMNH); Prov. Morona- Santiago, Huila, [incorrect locality]; PERU: Dept. Loreto, Río Curaray, 2 (MCZ), 80–90 km N of Iquitos, 7 (LSUMZ), Río Nanay, 2 (FMNH), Apayacu, 1 (ANSP), Morado-Pamba, 2 (FMNH), P. m. souancei: ECUADOR: type, no locality, 1 (BM); COLOMBIA: Dept. Caquetá, Morelia, 5 (ANSP); Dept. Putumayo, Umbria, 1 (ANSP), Puerto Asis, 1 (ANSP), San Antonio, 1 (FMNH); Dept. Meta, La Macarena, 1 (FMNH); P. m. berlepschi: PERU: Dept. San Martin, Nuevo Lorcio, 2 (AMNH), Tarapota, 1 (LSUMZ); ECUADOR: Prov. Morona-Santiago, Cord. de Cutucú, 1 (ANSP), Macas, 1 (AMNH), 1 (photograph, VIREO, R10-1-005); Prov. Pastaza, Río Curaray, 1 [incorrect locality]; P. m. chapmani: COLOMBIA: Dept. Huila, La Plata (type locality), 4 (ANSP), La Candela, 3 (ANSP), El Isno, 4 (ANSP), San Agustín, 2 (ANSP); Dept. Cauca, Moscopán, 2 (ANSP), 3 (FMNH); P. rho docephala: VENEZUELA: Mérida, El Valle, 1 (ANSP).

ETYMOLOGY.—We are pleased to name this species in honor of Dr. Gustavo Orcés V., in recognition of his many contributions to Ecuadorian ornithology and his continuing encouragement of younger generations of field biologists. The proposed English name, El Oro Parakeet, refers to the province in Ecuador where this species was discovered.

REMARKS

Variation within the species.—Only very slight variation is apparent within adults of P. orcesi. Besides the holotype, only four other individuals (ANSP 177524, 177522, 177523, 177528) show even a hint of red on the
center of the abdomen; in all other examples, the abdomen is more or less uniform green. However, young birds (based on presence of bursa Fabricius in some individuals, and on begging behavior in others; ANSP 177526, 177530, 178081, 178083, plus 177533, which was preserved as a skeleton, but photographed before preparation; VIREO VO1-3-007-011) show markedly reduced red on the frontal area and have the red on the wing entirely or virtually restricted to the carpal edge (there is considerable variation, presumably due to molt stage). On one specimen (ANSP 177524), the entire 9th primary on the right wing is red.

Systematic relationships. — The closest relative of *P. orcesi* is the rather variable species *P. melanura*. The two species share relatively small size and overall plumage pattern, including tail and wing pattern and color. All races of *P. melanura*, however, show conspicuous narrow to broad pale tipping on the breast feathers and sides of neck, absent (or virtually so) in *P. orcesi* (see Fig. 2). All races of *P. melanura* do show a faint trace of reddish on the feathers just above the maxilla, most marked in *P. m. pacifica*, the race of *melanura* found on the western slope to the north of the range of *P. orcesi* (Fig. 2). This hint of color could argue for considering *orcesi* as merely the southwestern Ecuador representative of *P. melanura*. However, in none of the six available specimens of *pacifica* does this in any way approach the condition found even in young *P. orcesi* (in which the amount of red on the forecrown is reduced); furthermore, the color itself differs, being (in *pacifica*) closest to Brick Red (Color 132 A). In addition, while we are uncertain whether this has any taxonomic significance, the eye ring of *pacifica* is gray (Arndt 1983, pers. obs.), while that of *P. orcesi* is pinkish-white.

During the course of assessing the relationship of *P. orcesi* to the *P. melanura* complex, we critically examined specimens of *melanura* in American museums; and a number of problems came to light. Five subspecies of *P. melanura* have been described. Nominate, *souancei*, *berlepschi*, *pacifica*, and *chapmani* are known from various parts of western Amazonia or from the slopes of the northern Andes. Both *chapmani* and *pacifica* are isolated geographically and are relatively well differentiated. *Chapmani* differs from all other forms of *P. melanura* by virtue of its larger size in all measurements (see Table 1). It further differs in occupying a higher elevation zone than other races, ca 1600–2800 m (Forshaw and Cooper 1973); the lowest point at which it has been recorded is thus above the highest known elevation (1500 m, *berlepschi*; VIREO R10-1-005) for

---

**Fig. 2.** The Pyrrhura melanura superspecies complex. Clockwise from lower left: *P. orcesi*, range = red; *P. m. pacifica*, range = diagonal lines; *P. m. chapmani*, range = stippled; *P. m. melanura/souancei*, range = light gray; *P. m. berlepschi*, range = black. Thin red line represents 1000 m contour. Painting by Paul Greenfield.
Fig. 2. The Pyrrhura melanura superspecies complex. Clockwise from lower left, *P. orcesi*, range = red; *P. m. pacifica*, range = diagonal lines; *P. m. chapmani*, range = stippled; *P. m. melanura/souancei*, range = light gray; *P. m. bertepschi*, range = black. Thin red line represents 1000 m contour. Painting by Paul Greenfield.
Table 1
Selected Measurements (mm) of the *Pyrrhura melanura* Superspecies Complex

<table>
<thead>
<tr>
<th>Species</th>
<th>Wing chord</th>
<th>Tail length</th>
<th>Mass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Range (mean)</td>
<td>N</td>
</tr>
<tr>
<td>Orcesi</td>
<td>15</td>
<td>113.8-127.7</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(119.2)</td>
<td></td>
</tr>
<tr>
<td><em>Melanura pacifica</em></td>
<td>6</td>
<td>118.8-129.0</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(124.3)</td>
<td></td>
</tr>
<tr>
<td><em>M. melanura</em></td>
<td>21</td>
<td>119.6-133.9</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(126.6)</td>
<td></td>
</tr>
<tr>
<td><em>M. souancei</em></td>
<td>9</td>
<td>121.0-129.6</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(127.9)</td>
<td></td>
</tr>
<tr>
<td><em>M. chapmani</em></td>
<td>16</td>
<td>133.0-141.8</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(136.8)</td>
<td></td>
</tr>
</tbody>
</table>

any other form in the species. It might, in fact, be argued that *chapmani* deserves to be recognized as a full species (as indeed it was described; Bond and Meyer de Schauensee 1940), but we hesitate to do so in the absence of supporting evidence from other lines of investigation (e.g., biochemical).

*Pyrrhura m. pacifica* is also geographically isolated from other forms of *P. melanura*, being the only race found on the west slope of the Andes. It differs most obviously in its shorter tail (Table 1) and grayish eye ring (whitish to white in all other races of *P. melanura*; Arndt 1983, pers. obs.); in other respects it most resembles representatives of the species found far to the east in Amazonia, i.e., it has narrower breast scaling.

What is now known as *P. m. melanura* was described by Spix (1824) on the basis of two specimens taken at Tabatinga, a town in what is now Amazonas, Brazil, on the north bank of the Amazon near Leticia, Colombia. *P. m. souancei* was described as a species by Verreaux (1858) on the basis of three specimens to which he ascribed no locality, and with no reference to the description of the very similar *melanura*; none of the three specimens was designated as the holotype. Both descriptions of *melanura* and *souancei*, were accompanied by plates, rather crudely rendered; the birds depicted appear very similar. Sclater (1862) restricted the type locality of *souancei*, with no explanation, to “Río Napo.” We presume that Sclater had access to information, not available now, when he did so. In fact, the one specimen of the three syntypes that we have examined (BM 59.11.22.25) is marked “Río Negro.” The two forms were first considered conspecific by Chapman (1926), who correctly established
that *souancei* resembled nominate *melanura* but for its relatively wider pale breast scaling. Neither Chapman nor Peters (1937), however, seems to have addressed adequately the problem of *souancei*'s actual range. Peters listed it as “Amazonian Ecuador” (which at that time extended east to the Iquitos area in what is now northeastern Peru). Following this, specimens of this parakeet from anywhere in or near the Napo drainage have usually been labeled *souancei*.

Based on the available series of specimens from numerous localities, we believe that this is not the best treatment. Birds from the middle and lower Napo drainage, in fact, closely resemble birds from southern Venezuela and northwestern Brazil, nominate *melanura*: they have narrow breast scaling. Not until one gets relatively close to the Andes, or ascends their lower slopes, does one consistently find birds with relatively broader breast scaling. It is to this population that the name *souancei* should be applied; thus we restrict the type locality of *souancei* to the “upper Rio Napo.” We should point out that gene flow apparently occurs between these two forms.

These broad-scaled birds also appear to exhibit geographic variation. Several birds of a small series (N = 9) from western Caquetá and western Putumayo in southeastern Colombia seem virtually identical with the type of *souancei*. Southward along the base of the Andes, however, there occurs another population of birds with even broader, and consistently whiter foreneck scaling. This population was described by Salvadori (1891) as *P. berlepschi*, with the type locality of Chyavetas (=Chayahuitas, Dept. Loreto) in northeastern Peru south of the Rio Marañón. Still known from very limited Peruvian material, we believe that a recent specimen (ANSP 176701) taken on the western slope of the Cordillera de Cutucú in southeastern Ecuador, as well as a photograph of a netted bird from the nearby Upano River valley (VIREO R10-1-005) are referable to *berlepschi*, extending the range of this form ca 320 km northward. It should be noted that in the Colombian series there is also at least one bird (FMNH 286758) that approaches typical *berlepschi* in the width of its breast scaling. No such variation is apparent in the series of *berlepschi* from Peru and southern Ecuador available to us (5 of the 6 known specimens), but this may simply reflect inadequate material of *berlepschi*. Should variation in *berlepschi* prove to be comparable to that seen in *souancei*, we would synonymize *berlepschi* with *souancei*.

Two anomalous specimens deserve mention. One, AMNH 230883, taken by the Olalla brothers, is labeled as having been collected at “Boca Rio Curaray,” well within the range of nominate *melanura* (as defined above). Two other typical *melanura* (MCZ 137818, 137817) were obtained there on virtually the same date, but this particular specimen seems in every way identical to *berlepschi*. We suspect the locality is inaccurate.
Another specimen (AMNH 156769), is labeled as having been obtained at “Huilca” in Ecuador. The precise location of this town seems uncertain (see Paynter and Traylor 1977), but is seems unlikely to be in the “Macas Region,” as its tag is labeled, and the bird appears to be referable to nominate melanura. The latter may have been a cagebird (its rectrices are very heavily worn), perhaps transported over the Cordillera de Cutucú from east of the Andes (as RSR has observed local Shuar Indians doing with Pionites melanocephala and other parrots).

To summarize, we would recommend considering birds from virtually the entire Amazon basin as P. m. melanura, restricting P. m. souancei to a limited area near the base of the Andes in southeastern Colombia (and probably adjacent northeastern Ecuador), and P. m. berlepschi to a relatively small area on the east slope of the Andes in northeastern Peru and southeastern Ecuador. The extent of gene flow between souancei-berlepschi and nominate melanura presumably is unimpeded, although to date there is no specimen material conclusively demonstrating this. Likewise there is presumably a connection between souancei and berlepschi along the east slope of the Andes, also as yet not found; they may prove to be the same group.

A problem that needs to be addressed is the possible relationship of P. melanura and P. albipectus. This question came to light during our investigations in 1984 on the Cordillera de Cutucú in southeastern Ecuador, when we found a somewhat variable population of P. m. berlepschi on the lowermost slopes of the cordillera. One specimen was taken, and a significant amount of white on the breast of flock members was observed, with some showing almost all white. At higher elevations, what appeared to be pure flocks of P. albipectus were found; two specimens were taken. One interpretation of this distribution would be to consider albipectus as a partially localized upper-elevation replacement of P. m. berlepschi, but we hesitate to do this because of complications elsewhere (Robbins et al. 1987).

**Distribution, habitat, and ecology.**—The known range of this species is no more than 100 km in length and between 5 and 10 km in width, extending north from the type locality (Fig. 1) to just east of Naranjal, Prov. Azuay. Despite extensive searches, we failed to find orcesi north of the Naranjal site, and, in fact, no Pyrrhura was found at the appropriate elevations in the provinces of Cañar or Bolivar. Pyrrhura melanura pacifica is unrecorded south of Río Palenque, Prov. Los Ríos, ca 280 km north of the northernmost locality of orcesi. It thus appears that a gap exists between the ranges of orcesi and m. pacifica. Within this gap, at elevations where orcesi and m. pacifica should occur, a substantial amount of naturally occurring vegetation has been converted to orange groves and other agricultural use. Nevertheless, it appears that this gap may not have
been artificially induced, as a number of early collectors (e.g., Rhoads in 1911; Gill in 1921; Chapman et al. in 1922; see Bucay locality in Paynter and Traylor 1977) spent considerable time at appropriate elevations in this region without obtaining Pyrrhura.

We found *P. orcesi* only in a narrow band of humid, upper tropical zone forest, between 600 and 1100 m. The British Museum specimen (53.68.106), which L. Gomez collected at Piedras, however, is noted as having been obtained at 300 m. Perhaps at the time this specimen was taken (9 September 1939), suitable cloud forest extended lower than it does anywhere at present; Gomez obtained only one specimen, so perhaps the species was rare at that locality. At the type locality, forest canopy height on the more level areas exceeded 20 m, although average canopy height was lower on steeper slopes. During our investigation, the forest usually was enshrouded by clouds from predawn until about midday (VIREO RO8-7-014). Trees and the relatively dense understory were laden with epiphytes. Moisture is carried by westerly winds from the Pacific Ocean (ca 75 km west of the type locality). The forest at the Naranjal site was very similar to the El Oro site, except that it was even more fragmented by human activity.

At the El Oro site, at least six flocks of birds, comprised of from four to twelve individuals per flock, were observed. A highly conservative count gave us a total of between 55–60 birds at the type locality. Over twenty, in three different flocks, were recorded at the Naranjal locality. Flocks consisted of adults and young of both sexes. On 27 June 1985 in the early morning, Robbins observed a flock of four individuals foraging on fruit in the canopy of a tall tree. One of the individuals, a bird with no apparent red forecrown, was giving a distinctive, slightly higher-pitched, more raspy, and shorter call than the flight and contact calls of the birds it was with. As it called, its head, body, and tail were oriented horizontally, with its wings extended and constantly quivering. This behavior was directed at a nearby bird which had a broad red forecrown. On four separate instances the "red-fronted" individual regurgitated food to this bird. Attempts to collect the begging individual failed. At 12:00 on the same day, Robbins again encountered what appeared to be the same flock. Begging by a single individual was again observed. This bird (ANSP 177526) proved to be a female, in fresh plumage, with only a hint of a red forecrown. The throat and crop were filled with regurgitated fruit. The previous day another collected individual (ANSP 177533; VIREO VO1-3-007-011) with little red on forecrown, in fresh plumage, also had its throat and crop filled with regurgitated fruit. Both of these birds had less red in the alula and the outermost greater wing coverts than birds that had relatively broad red frontal bands.
Further evidence that birds with a reduced amount of red in the forecrown and on the bend in the wing are immatures comes from birds collected in 1986 at the Naranjal site. Two of the four birds collected (ANSP 178081, 178083) had the bursa present, and both of these birds had minimal amounts of red in the forecrown and the alula and outermost greater wing coverts. The other two birds that had larger amounts of red in the above regions did not have the bursa. Our 1985 series of parakeets unfortunately were not examined for the presence of bursa. No difference in soft part colors were noted between adults and immatures. Given that some young birds were begging food in late June, we speculate that the main breeding period for orcesi is from March through May.

At the type locality, the birds were observed feeding repeatedly at a fig (Ficus cf. macbridei; section Pharmacosycea) and on the fruit of Helio-carpus popayanensis (family Tiliaceae). At the Naranjal site, the parakeets were observed feeding only on the fruit of Hieronyma sp. (family Euphorbiaceae).

Conservation.—The natural forest habitat at the type locality and the Naranjal site has been reduced significantly by human activity (VIREO RO8-7-004, 006-009, 011, 018-024). At the El Oro site, between 10 and 15 large trees were being removed daily from a small tract of accessible forest (see Fig. 1); typically, once the larger trees are removed, the area is burned and cattle are brought in. Although orcesi was relatively numerous and appeared to be thriving in the patchy forest now found at both localities, significant further disturbance and fragmentation of the forest may eliminate vital nesting and feeding sites. Fortunately, there is still extensive, mostly inaccessible forest remaining between the type locality and the Naranjal site. We strongly recommend that a sizable tract of land in this area be preserved, not only to insure that a large population of the parakeet is protected, but also to protect other taxa that have distributions restricted to this region (e.g., the Ochre-bellied Dove [Lep- totila ochraceiventris]).

ACKNOWLEDGMENTS

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York Botanical Garden), the Aarhus Univ. Herbarium, Denmark, kindly identified botanical specimens. We are grateful to T. S. Schulenberg for bringing to our attention the presence of the Tring specimen of what proved to be the new parakeet. We are also grateful to M. Dolack for translating several articles. We thank the following people and institutions for the loan of their valuable specimens: M. LeCroy, American Museum of Natural History; J. Fitzpatrick and D. Willard, Field Museum of Natural History; J. V. Remsen, Jr. and S. Cardiff, Louisiana State Museum of Zoology; and R. Paynter, Jr., Museum of Comparative Zoology; and we also thank G. Cowles, of the British Museum, Tring for photographing the three types (and daring to send us one!) of souancei. We thank K. Bildstein, G. Graves, and K. Parkes for comments on the manuscript.

LITERATURE CITED


FRONTISPIECE

The male (the type; lower bird) and female of the El Oro Parakeet, Pyrrhura orcesi, a new parakeet from southwestern Ecuador. Painting by William T. Cooper.
GEOGRAPHIC VARIATION IN SEX RATIOS AND BODY SIZE IN WINTERING FLOCKS OF SAVANNAH SPARROWS (PASSERCULUS SANDWICHENSIS)

J. D. Rising

ABSTRACT. — I examined geographic variation in the sex ratio of Savannah Sparrows (Passerculus sandwichensis) in wintering flocks from 22 different localities. The percentages of males in relatively large samples (N > 20) range from 45 to 70%; overall, 55% of wintering birds collected were male. There is no discernible geographic pattern to the interpopulational variation in sex ratio. I also examined patterns of size (PC1) and shape (PC2) variation among 542 wintering Savannah Sparrows. The largest Savannah Sparrows of both sexes tend to winter in the east and in the north; the east-west trend is more pronounced than the north-south one. In both sexes, individuals with relatively small bills and large wing bones tend to winter in the west. I suggest that the variability in bill size reflects geographic differences in the seeds available in winter, for it is only during that time that Savannah Sparrows are primarily granivorous. Variation in the relative size of the bones of the pectoral girdle may reflect variation in the distances migrated (which are probably longer on average in the west than in the east).

For this data set a principal component analysis done on the raw data, using the matrix of correlations among variables, provides a more satisfactory result than an analysis using log-transformed data and the variance-covariance matrix. Canonical correlations analysis provides a clearer description between the relationships among morphometric and environmental variables than does stepwise multiple regression analysis. The latter technique, because it uses partial correlations, sometimes identifies variables as being significant that have low univariate correlations. For Savannah Sparrows, wing length is not a good measure of body size. Received 27 Jan. 1987, accepted 28 Dec. 1987.

Most studies of geographic variation in the size of birds have dealt with comparisons among breeding populations of nonmigratory species. It is generally assumed that patterns of variation in size and shape reflect adaptations of the birds to geographic variation in environmental conditions (James 1970, Power 1970, Johnston and Selander 1971, Niles 1973, Mengel and Jackson 1977, Aldrich 1984, Zink 1986), perhaps augmented by direct environmental influences (James 1983). Often, for birds, the average body size is greatest where the ambient temperature is lowest—the pattern described as Bergmann’s Rule. However, the percentage of migratory species that conform to Bergmann’s Rule is not significantly different from those that do not (Zink and Remsen 1986). Evidence supporting Bergmann’s Rule is often taken to reflect direct adaptations for temperature regulation (e.g., James 1970, Power 1970), but it may reflect...
adaptations to other environmental factors such as interspecific competition, prey availability, predatory pressures (Ray 1960, McNab 1971, Case 1978), the conditions under which the young were raised (James 1983), or various combinations of these.

It is easier to correlate body size with environmental factors in non-migratory species than in migratory ones, not only because the annual range of environmental conditions to which resident individuals are exposed can be determined, but also because the relative conditions among sites are generally similar from season to season: a site that is cold relative to others in summer is probably cold relative to others in winter as well. Consequently, most ornithologists have studied geographic variation in species that either are resident or that migrate little. There are, nonetheless, a few studies of size variation among wintering populations of birds. Ketterson and Nolan (1976) and Nolan and Ketterson (1983), for example, found no within-sex latitudinal variation in wing length in Dark-eyed Juncos (Junco hyemalis). They (1983) did find latitudinal variation in the body mass of juncos, with heavier birds tending to winter farther north; visible fat stores were also greater in birds wintering at higher latitudes, and they suggested that this, rather than variation in body size, probably explained the trend they found. James et al. (1984) found a clinal increase in median wing length (unflattened primary length; humerus length) among populations of male Red-winged Blackbirds (Agelaius phoeniceus) wintering in the southeastern U.S.

Here I report patterns of geographic variation among wintering populations of migratory Savannah Sparrows (Passerculus sandwichensis), and relate these to the variation in environmental conditions on the wintering grounds of the species. King et al. (1965) and Ketterson and Nolan (1979) reported that male western White-crowned Sparrows (Zonotrichia leucophrys) and eastern Dark-eyed Juncos tend to winter farther north than females. In both species males average larger in body size than females. On average, therefore, larger individuals of these species are wintering in the coldest parts of the wintering range. There is experimental evidence that migratory western male White-crowned Sparrows can fast longer than can females, presumably because of their greater mass (Ketterson and King 1977). This, however, apparently is not true for juncos and Tree Sparrows (Spizella arborea) (Stuebe and Ketterson 1982).

Ketterson and Nolan (1983) note that individuals wintering relatively farther north are closer to their breeding grounds than are others from the same populations that winter farther south, and therefore not only have a shorter distance to migrate, but also are perhaps better able to assess the conditions on their breeding grounds. This might permit more northerly wintering individuals to return and establish territories earlier.
Rising • GEOGRAPHIC VARIATION IN SAVANNAH SPARROWS

in spring than conspecifics wintering farther south. If so, it might select for males to winter as far north as possible, for in these species males compete for territories, and arrive on the breeding grounds well before females, probably as a consequence of this competition. They further suggest that individuals not constrained to winter in the north by other factors, such as the benefits of early return, may travel farther south to avoid higher densities in the north.

Savannah Sparrows breed across North America from Labrador to Alaska, and south to Massachusetts, central Ohio and Nebraska, in the Appalachians south to eastern Tennessee, and in the Cordilleras south into central Mexico and (formerly?) Guatemala (AOU Checklist 1983). With the exception of those birds that breed in southwestern saltmarshes, Savannah Sparrows are migratory. In winter, they are found east of the Appalachians, from Nova Scotia, and especially New Jersey south to Florida, and from Arkansas, Oklahoma and central New Mexico, central Arizona, and Oregon, south through most of Mexico. In winter, they are especially common from the coastal Carolinas south through Florida, west across southern Mississippi, and throughout Texas. They are moderately common, at least during some years, north to Oklahoma, and in southern New Mexico and Arizona, and very common in southern California and locally in the Mexican highlands. The approximate abundance and wintering range in the United States are shown in Fig. 1. I have samples from most regions in the United States where Savannah Sparrows are common in winter.

Using the data on wintering Savannah Sparrows, I address two questions: (1) do male Savannah Sparrows winter farther north than do females, and (2) do larger individuals (of either or both sexes) winter farther north than smaller ones. I also correlate interpopulational patterns of morphological variation with environmental variables in an effort to clarify the significance of morphological variability in the species.

An additional objective of this study is to use these data to assess empirically different methods of measuring “size” variation in a species. When many different variables are analyzed, as here, it is useful to create various combinations of these to simplify the perception of the patterns of interpopulational variation. Commonly, principal component analyses (PCA) are used to reduce the number of dimensions in multivariable studies. N components can be extracted from a matrix of N variables for each specimen; in morphometric studies of birds, most of the variance in the N variables usually can be explained in only two or three components (those with the largest eigenvalues). The PCA approach has advantages. It accounts for the covariation among the variables and reduces the number of “significant” dimensions. The components themselves,
Fig. 1. Map of the abundance of Savanna Sparrows (*Passerculus sandwichensis*) based on Christmas Bird Count data. The height of the peaks indicate the relative abundance. The dots indicate sites from which I obtained wintering samples. However, the two sites from High Island, Texas, coastal South Carolina, North Carolina, and Delaware are indicated by only a single dot. Contour map courtesy of T. Root.

however, can be difficult to interpret. PCI, in such studies, contains a great deal of information about overall size (large animals have large parts), but also contains information about shape (Gibson et al. 1984, Somers 1986). Mosimann and James (1979) recommend log transformation of data in morphometric studies, and the use of the geometric mean of the log transformed data as a measure of overall size, and of various ratios as measures of shape (e.g., bill length divided by bill depth). However, as Bryant (1986) notes, the use of a log transformation equilibrates variances within suites of highly correlated characters, but not among suites of such characters. If a data matrix contains two or more such suites of characters, log transformations may change the multivariate structure in the data matrix. Thus, Bryant recommends no single transformation of data when intercorrelations among the traits are likely to differ. McGillivray and Johnston (1987) use the sum of the unstandardized measures of an individual as a measure of body size. This approximates PCI scores derived from a matrix of correlations among raw measures, but gives greater weight to measures which relatively high variances.
Here, I present results from two PCA analyses, one using untransformed data, and the other using log transformed data. Traditionally, wing length (approximately the length of the longest primary wing feather) has been used as an approximate measure of body size. This is, in part, because it is easy to measure on museum study skins as well as on living birds—indeed, it is virtually the only measure of “size” that one can make on such material. Also, as Mosimann and James (1979:455) note, “wing length is easy to visualize.” Inasmuch as both skins and skeletons are available for most of the birds I examined here, I assess the value of wing length as a measure of body size in Savannah Sparrows. The wing feathers of these wintering sparrows show little sign of wear.

### MATERIALS AND METHODS

I obtained samples of migratory Savannah Sparrows from wintering flocks from several different localities (Table 1). Although some of these specimens were shot, the majority were caught in mist nets. None was captured at feeding stations or at otherwise baited localities. I think this procedure introduced minimal bias in the sex ratios in the samples. Each specimen was sexed, when possible. Of 568 sparrows collected for this research, only 26 could not be sexed; thus, bias due to any differences in the difficulty of determining the sexes could have only a slight effect on the results. (The unsexed birds were not used in any of these analyses, and are not included in the numbers in Table 1.) All birds were collected from mid-December through mid-February, except for 32 specimens from Dewey Beach, Delaware that were collected in early April. The April birds from Dewey Beach are probably birds that wintered there; at least, in sex ratio and size they are like Savannah Sparrows collected there in February. Collections were made from 1971 through 1979, but mostly between 1975 and 1979 (Table 1).

Each specimen was preserved as a skin and skeleton, and is in the Royal Ontario Museum, with the exception of those from Isabel Valley, California, which are in the Delaware Museum of Natural History. I measured 24 variables (Table 2) on the skeleton of each bird, and wing length (longest primary on the unflattened wing) on the skin. The size of broken or missing bones was estimated by multiple regression (BMD, Dixon 1983); birds for which wing length could not be measured (including the entire sample from Isabel Valley, California) were not used in analyses involving wing length. To summarize size variation, I used two different PCA models (using NTSYS/FACTOR, Version IV, Rohlf et al. 1982). First I calculated the first three components from a matrix of correlations among the unstandardized 24 skeletal measures. PCAs using raw data and correlation matrices have been widely used in morphometric studies (Schnell 1970, Johnston et al. 1972, Leisler and Winkler 1985). Second, I calculated the first three components from a covariance matrix among the log-transformed skeletal measures. Such an approach, which is particularly appropriate for species showing indeterminate growth, or when growth is specifically being studied, has been used widely (Fleischer and Johnston 1982, Zink 1986). Birds from all samples listed in Table 1 were used in the PCA. Additionally three specimens from Padre Island, Texas, and one from San Francisco, California, were included, for a total of 542 (299 males and 243 females). Following Mosimann and James (1979), I calculated bill length/bill depth for each specimen as a direct measure of bill shape, and in some analyses I used tibiotarsus and humerus lengths as direct measures of leg and wing lengths. Individuals from all samples were pooled, but the sexes were analyzed separately.
<table>
<thead>
<tr>
<th>Locality</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Date(s) collected</th>
<th>N</th>
<th>% Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>St. David, Cochise County, Arizona</td>
<td>32°30'</td>
<td>109°30'</td>
<td>30 Dec 1973</td>
<td>29</td>
<td>55</td>
</tr>
<tr>
<td>Isabel Valley, Santa Clara County, California</td>
<td>37°30'</td>
<td>122°15'</td>
<td>9 Nov 1974</td>
<td>19</td>
<td>(68)*</td>
</tr>
<tr>
<td>Dewey Beach, Sussex County, Delaware (winter)</td>
<td>38°45'</td>
<td>75°06'</td>
<td>21 Feb 1975</td>
<td>40</td>
<td>45</td>
</tr>
<tr>
<td>Dewey Beach, Sussex County, Delaware (April)</td>
<td>38°36'</td>
<td>75°06'</td>
<td>15-16 Apr 1974</td>
<td>32</td>
<td>47</td>
</tr>
<tr>
<td>Fieldsboro, New Castle County, Delaware</td>
<td>39°24'</td>
<td>75°42'</td>
<td>15 Dec 1977</td>
<td>14</td>
<td>(43)*</td>
</tr>
<tr>
<td>Gainesville, Alachua County, Florida</td>
<td>29°36'</td>
<td>82°18'</td>
<td>17 Feb 1975</td>
<td>23</td>
<td>48</td>
</tr>
<tr>
<td>Molino, Escambia County, Florida</td>
<td>30°42'</td>
<td>87°30'</td>
<td>19 Dec 1971</td>
<td>26</td>
<td>69</td>
</tr>
<tr>
<td>Basinger, Okeechobee County, Florida</td>
<td>27°18'</td>
<td>81°06'</td>
<td>18 Feb 1975</td>
<td>17</td>
<td>(24)*</td>
</tr>
<tr>
<td>Waynesboro, Burke County, Georgia</td>
<td>33°00'</td>
<td>82°00'</td>
<td>15 Feb 1975</td>
<td>13</td>
<td>(31)*</td>
</tr>
<tr>
<td>Jekyll Island, Glynn County, Georgia</td>
<td>31°06'</td>
<td>81°24'</td>
<td>20 Feb 1975</td>
<td>22</td>
<td>64</td>
</tr>
<tr>
<td>Mississippi State, Okitibe County, Mississippi</td>
<td>33°18'</td>
<td>89°00'</td>
<td>17 Feb 1979</td>
<td>35</td>
<td>63</td>
</tr>
<tr>
<td>Norman, Cleveland County, Oklahoma</td>
<td>35°06'</td>
<td>97°18'</td>
<td>28 Feb 1979</td>
<td>6</td>
<td>(83)*</td>
</tr>
<tr>
<td>Nags Head, Dare County, North Carolina</td>
<td>36°00'</td>
<td>75°42'</td>
<td>15 Feb 1978</td>
<td>14</td>
<td>(64)*</td>
</tr>
<tr>
<td>Harbinger, Currituck County, North Carolina</td>
<td>36°03'</td>
<td>75°48'</td>
<td>15 Feb 1978</td>
<td>23</td>
<td>58</td>
</tr>
<tr>
<td>Charleston, Charleston County, South Carolina</td>
<td>32°48'</td>
<td>79°54'</td>
<td>17 Dec 1977</td>
<td>26</td>
<td>50</td>
</tr>
<tr>
<td>Folly Beach, Charleston County, South Carolina</td>
<td>32°48'</td>
<td>79°54'</td>
<td>18 Dec 1977</td>
<td>12</td>
<td>(42)*</td>
</tr>
<tr>
<td>Clemson, Pickens County, South Carolina</td>
<td>34°45'</td>
<td>82°45'</td>
<td>13 Feb 1978</td>
<td>28</td>
<td>61</td>
</tr>
<tr>
<td>High Island, Chambers County, Texas (coastal)</td>
<td>29°18'</td>
<td>94°00'</td>
<td>19 Feb 1979</td>
<td>15</td>
<td>(33)*</td>
</tr>
<tr>
<td>High Island, Chambers County, Texas (inland)</td>
<td>29°18'</td>
<td>94°00'</td>
<td>20 Feb 1979</td>
<td>28</td>
<td>57</td>
</tr>
<tr>
<td>Goliad, Goliad County, Texas</td>
<td>29°00'</td>
<td>97°00'</td>
<td>21-22 Feb 1979</td>
<td>30</td>
<td>70</td>
</tr>
<tr>
<td>Ft. Davis, Jeff Davis County, Texas</td>
<td>31°00'</td>
<td>103°30'</td>
<td>26 Feb 1979</td>
<td>37</td>
<td>62</td>
</tr>
<tr>
<td>Graham, Young County, Texas</td>
<td>33°00'</td>
<td>97°30'</td>
<td>27 Feb 1979</td>
<td>12</td>
<td>(67)*</td>
</tr>
<tr>
<td>Crystal City, Zavala County, Texas</td>
<td>29°30'</td>
<td>100°06'</td>
<td>25 Feb 1979</td>
<td>37</td>
<td>54</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td></td>
<td></td>
<td>538</td>
<td>55</td>
</tr>
</tbody>
</table>

* Percentages based on small samples (N < 20) in parentheses.
Table 2
SPEARMAN CORRELATIONS BETWEEN PERCENT OF MALE SAVANNAH SPARROWS (PASSERUCULUS SANDWICHENSIIS) IN WINTER FLOCKS AND ENVIRONMENT

<table>
<thead>
<tr>
<th>Environmental variable</th>
<th>Correlation</th>
<th>Significance (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>-0.27</td>
<td>0.18</td>
</tr>
<tr>
<td>Longitude</td>
<td>0.30</td>
<td>0.16</td>
</tr>
<tr>
<td>Coldest winter temperature</td>
<td>0.00</td>
<td>0.50</td>
</tr>
<tr>
<td>Average winter temperature</td>
<td>-0.13</td>
<td>0.34</td>
</tr>
<tr>
<td>Average annual snowfall</td>
<td>-0.09</td>
<td>0.38</td>
</tr>
<tr>
<td>Average annual precipitation</td>
<td>0.09</td>
<td>0.38</td>
</tr>
<tr>
<td>Sparrow abundance</td>
<td>0.04</td>
<td>0.45</td>
</tr>
<tr>
<td>Sparrow diversity</td>
<td>0.17</td>
<td>0.29</td>
</tr>
</tbody>
</table>

In an effort to identify the possible adaptive nature of size and shape variation among wintering Savannah Sparrows, I correlated patterns of morphometric variation with geographic patterns of environmental variation, using stepwise multiple regression (SPSSX/REGRESSION, SPSSX 1986), and canonical correlations analysis (SAS/CANCORR procedure; SAS 1982). In multiple regression, the probability required to include an independent variable was set at 0.05. The measures of size and shape used were: PC1 and PC2 scores (from untransformed data), and in multiple regression, bill shape (length/depth), tibiotarsus length (skeletal measure of leg length), and humerus length (skeletal measure of wing length). The “environmental” variables used were: (1) coldest extreme temperature, (2) average temperature in the coldest month, (3) average annual snowfall, (4) average annual precipitation, (5) latitude, (6) longitude, (7) abundance of wintering Emberizinae, and (8) diversity of wintering Emberizinae. The climatic data are from the U.S. Department of Commerce (“Local Climatological Data” from nearest reporting station of comparable elevation); the data on abundance and diversity of Emberizinae are from Bock and Lepthien’s summary of Christmas Bird Count data (1976: Figure 3). Because the univariate measures of size contribute to the calculation of the PC scores, in canonical correlations analysis only PC1 and PC2 scores were used as dependent measures. Sexes were analyzed separately, and only data from localities where at least eight individuals were measured were used. There were 19 such localities for females, and 16 for males. Fewer than eight males were available from four sites where sufficient females were available, and sufficient females were not available from one locality where there were sufficient males. Thus 15 localities were used in analyses for both sexes, but the results are not directly comparable because somewhat different suites of localities were used for the male and female data.

Both canonical correlations analysis and multiple regression have been used to relate patterns of morphometric variation with patterns of climatic variation (O’Rourke et al. 1985, Zink 1986). Canonical correlations derive the linear functions of a vector of morphological variables with a vector of environmental variables that have maximal covariance. This may be preferable to multiple regression, which is more commonly used, because in multiple regression assumed independent (environmental) variables are entered into the equation on the basis of partial correlations, which can differ substantially in similar data sets (Pimentel 1979).

I used Spearman’s rank correlations to quantify the univariate relationships among the

...
PC scores and the eight environmental variables. I also used Spearman’s correlations between the percentages of males in the 13 samples in which the total sample size was greater than 20, and the latitude, longitude, and environmental variables listed above to describe those relationships.

RESULTS

Variation in sex ratios. — Overall, 55% of the Savannah Sparrows from wintering flocks that could be sexed are males, and although the percentage varies considerably among localities (from 45–70% in samples of more than 20 individuals; Table 1), there is no conspicuous geographic pattern. None of the Spearman correlations between the sex ratio and the environmental variables are even close to being significantly different (Table 2). In studies of breeding populations, males have been found to outnumber females. For example, Bédard and LaPointe (1984) found that, on average, about 60% (range 56–63%) of the birds in a breeding population at Isle Verte, Quebec, were males. It thus seems probable that males outnumber females in this species, but that there is no geographic pattern to the variation in the proportions of each sex in wintering flocks, at least within the latitudinal range covered by this study.

Principal component analyses. — Univariately, analysis of variance shows that there is significant interpopulational variation in all of the variables measured and for both sexes, with the exception of scapula length of females \( P = 0.08 \). Five of the 24 components from the PCA, based on a matrix of correlations among 24 unstandardized variables among 299 males and four from the 243 females have eigenvalues of 1.0 or greater. However, PC3, PC4, and PC5 from the male data have eigenvalues of nearly equal size (1.3, 1.2, 1.0), and thus there is little discernible structure in these three dimensions. Similarly, PC3 and PC4 of females are of similar magnitude (1.5 and 1.2), and cannot be reliably interpreted (Cattell and Vogelmann 1977, Gibson et al. 1984). Univariate correlations between the variables and PC1 are positive and large for both sexes (Table 3); thus, I interpret this component as being primarily a measure of overall size variation among individuals. PC2, for both sexes, contrasts bill size with wing size. An individual with a large value on this component has a relatively small bill and large flight apparatus (humerus, ulna, carpometacarpus, keel). Average PC1 and PC2 scores for 22 samples are given in Table 4.

From the PCA using the log transformed data and covariance matrix, PC1 explains 38.4% and PC2 12.7% of the total variance for the males, and PC1 explains 37.9% and PC2 13.5% of the total variance for the females. For both sexes, the loadings on PC1 are all of the same sign, indicating that it is a general measure of size. The scores of individuals on this axis approximate the geometric means of the 24 measures. In both
<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skull length</td>
<td>0.78</td>
<td></td>
<td></td>
<td>0.73</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Skull width</td>
<td>0.74</td>
<td></td>
<td></td>
<td>0.68</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Premaxilla length</td>
<td>0.53</td>
<td>-0.40</td>
<td></td>
<td>0.49</td>
<td>-0.44</td>
<td></td>
</tr>
<tr>
<td>Premaxilla depth</td>
<td>0.44</td>
<td>-0.39</td>
<td>-0.42</td>
<td>0.52</td>
<td>-0.31</td>
<td></td>
</tr>
<tr>
<td>Narial width</td>
<td>0.54</td>
<td>-0.30</td>
<td>-0.45</td>
<td>0.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Premaxilla width</td>
<td>0.56</td>
<td>-0.44</td>
<td></td>
<td>0.64</td>
<td>-0.38</td>
<td></td>
</tr>
<tr>
<td>Interorbital width</td>
<td>0.37</td>
<td></td>
<td>-0.37</td>
<td>0.41</td>
<td>-0.32</td>
<td></td>
</tr>
<tr>
<td>Mandible length</td>
<td>0.71</td>
<td>-0.35</td>
<td>0.33</td>
<td>0.68</td>
<td>-0.37</td>
<td></td>
</tr>
<tr>
<td>Gonys length</td>
<td>0.51</td>
<td>-0.49</td>
<td>0.34</td>
<td>0.48</td>
<td>-0.30</td>
<td></td>
</tr>
<tr>
<td>Mandible depth</td>
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<td></td>
<td>0.49</td>
<td>0.55</td>
<td></td>
<td>0.57</td>
</tr>
<tr>
<td>Coracoid length</td>
<td>0.82</td>
<td></td>
<td>0.30</td>
<td>0.82</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scapula length</td>
<td>0.76</td>
<td></td>
<td>0.33</td>
<td>0.71</td>
<td></td>
<td>0.38</td>
</tr>
<tr>
<td>Femur length</td>
<td>0.81</td>
<td></td>
<td></td>
<td>0.79</td>
<td></td>
<td>0.31</td>
</tr>
<tr>
<td>Femur width</td>
<td>0.46</td>
<td></td>
<td></td>
<td>0.45</td>
<td></td>
<td>-0.30</td>
</tr>
<tr>
<td>Tibiotarsus length</td>
<td>0.84</td>
<td></td>
<td></td>
<td>0.79</td>
<td></td>
<td>0.42</td>
</tr>
<tr>
<td>Tarsometatarsus length</td>
<td>0.81</td>
<td></td>
<td></td>
<td>0.77</td>
<td></td>
<td>0.46</td>
</tr>
<tr>
<td>Humerus length</td>
<td>0.80</td>
<td>0.34</td>
<td></td>
<td>0.78</td>
<td>0.33</td>
<td></td>
</tr>
<tr>
<td>Ulna length</td>
<td>0.78</td>
<td>0.45</td>
<td></td>
<td>0.80</td>
<td>0.33</td>
<td></td>
</tr>
<tr>
<td>Carpometacarpus length</td>
<td>0.71</td>
<td>0.39</td>
<td></td>
<td>0.69</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>Hallux length</td>
<td>0.72</td>
<td></td>
<td></td>
<td>0.65</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sternum length</td>
<td>0.75</td>
<td></td>
<td></td>
<td>0.74</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sternum depth</td>
<td>0.65</td>
<td></td>
<td></td>
<td>0.66</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Keel length</td>
<td>0.70</td>
<td>0.33</td>
<td></td>
<td>0.65</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Synsacrum width</td>
<td>0.70</td>
<td></td>
<td></td>
<td>0.64</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Correlations <0.30 are not included.
Table 4

<table>
<thead>
<tr>
<th>Locality</th>
<th>Male PCI</th>
<th>Male PC2</th>
<th>Female PCI</th>
<th>Female PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizona, St. David</td>
<td>-0.47</td>
<td>0.19</td>
<td>-0.31</td>
<td>0.25</td>
</tr>
<tr>
<td>California, Isabel Valley</td>
<td>-0.38</td>
<td>0.06</td>
<td>(-0.07)*</td>
<td>(0.18)</td>
</tr>
<tr>
<td>Delaware, Dewey Beach</td>
<td>0.68</td>
<td>-0.08</td>
<td>0.61</td>
<td>-0.30</td>
</tr>
<tr>
<td>Delaware, Fieldsboro</td>
<td>(0.85)</td>
<td>(-0.12)</td>
<td>(0.17)</td>
<td>(-0.30)</td>
</tr>
<tr>
<td>Florida, Gainesville</td>
<td>0.15</td>
<td>-0.08</td>
<td>-0.30</td>
<td>-0.33</td>
</tr>
<tr>
<td>Florida, Molino</td>
<td>-0.11</td>
<td>-0.11</td>
<td>(-0.20)</td>
<td>(-0.22)</td>
</tr>
<tr>
<td>Florida, Basinger</td>
<td>[-0.57]</td>
<td>[-0.20]</td>
<td>-0.10</td>
<td>-0.25</td>
</tr>
<tr>
<td>Georgia, Waynesboro</td>
<td>[0.32]</td>
<td>[-0.34]</td>
<td>(0.11)</td>
<td>(-0.13)</td>
</tr>
<tr>
<td>Georgia, Jekyll Island</td>
<td>0.38</td>
<td>-0.07</td>
<td>(-0.09)</td>
<td>(-0.13)</td>
</tr>
<tr>
<td>Mississippi, Mississippi State</td>
<td>-0.18</td>
<td>0.02</td>
<td>-0.32</td>
<td>0.13</td>
</tr>
<tr>
<td>Oklahoma, Norman</td>
<td>(-0.13)</td>
<td>(0.14)</td>
<td>[-0.29]</td>
<td>(0.23)</td>
</tr>
<tr>
<td>North Carolina, Nags Head</td>
<td>(0.57)</td>
<td>(-0.13)</td>
<td>(0.07)</td>
<td>(-0.10)</td>
</tr>
<tr>
<td>North Carolina, Harbinger</td>
<td>0.05</td>
<td>-0.10</td>
<td>0.03</td>
<td>-0.12</td>
</tr>
<tr>
<td>South Carolina, Charleston</td>
<td>0.28</td>
<td>-0.09</td>
<td>0.27</td>
<td>0.02</td>
</tr>
<tr>
<td>South Carolina, Folly Beach</td>
<td>-0.16</td>
<td>0.00</td>
<td>0.23</td>
<td>-0.07</td>
</tr>
<tr>
<td>South Carolina, Clemson</td>
<td>0.27</td>
<td>-0.07</td>
<td>-0.05</td>
<td>-0.05</td>
</tr>
<tr>
<td>Texas, High Island (coastal)</td>
<td>(0.54)</td>
<td>(0.15)</td>
<td>0.12</td>
<td>0.35</td>
</tr>
<tr>
<td>Texas, High Island (inland)</td>
<td>0.12</td>
<td>-0.03</td>
<td>-0.22</td>
<td>0.10</td>
</tr>
<tr>
<td>Texas, Goliad</td>
<td>-0.64</td>
<td>0.13</td>
<td>(-0.06)</td>
<td>(0.03)</td>
</tr>
<tr>
<td>Texas, Ft. David</td>
<td>-0.50</td>
<td>0.22</td>
<td>-0.52</td>
<td>0.23</td>
</tr>
<tr>
<td>Texas, Graham</td>
<td>(-0.33)</td>
<td>(-0.07)</td>
<td>[-0.68]</td>
<td>[0.39]</td>
</tr>
<tr>
<td>Texas, Crystal City</td>
<td>-0.32</td>
<td>0.17</td>
<td>-0.33</td>
<td>0.21</td>
</tr>
</tbody>
</table>

* Samples with N < 10 in parentheses; N < 5 in brackets.

sexes, PC2 is essentially a measure of interorbital width, the one variable not well “explained” by PC1 in any of the PC analyses (e.g., see Table 3). Although interorbital width has relatively low correlations with the other variables, the adaptive significance, if any, of variation in this feature is not apparent. In the log transformed data, PC3 contrasts bill size with pectoral element size, and is thus similar to PC2 in the raw data analysis. PC3 explains 9.8% and 11.3% of the variance among males and females, respectively.

The squared correlations among the first three components from each of the analyses (PCA/correlation matrix/raw data; PCA/covariance matrix/log transformed data), and wing length are in Table 5. The correlations between the respective PC1 scores are quite high for both sexes ($r = 0.92$ and 0.94). The correlations between the corresponding PC2 and PC3...
Table 5
RELATIONSHIPS ($r^2$) AMONG COVARIANCE AND CORRELATION COMPONENTS AND WING LENGTH IN WINTERING SAVANNAH SPARROWS (DATA FOR MALES ABOVE THE DIAGONAL, FOR FEMALES BELOW)*

<table>
<thead>
<tr>
<th></th>
<th>Cov1 (38.4%)</th>
<th>Cov2 (12.7%)</th>
<th>Cov3 (9.8%)</th>
<th>Cor1 (46.5%)</th>
<th>Cor2 (9.5%)</th>
<th>Cor3 (5.4%)</th>
<th>Wing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cov1 (37.9%)</td>
<td>-</td>
<td>0.00</td>
<td>0.00</td>
<td>0.88</td>
<td>0.07</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Cov2 (13.5%)</td>
<td>0.00</td>
<td>-</td>
<td>0.00</td>
<td>0.03</td>
<td>0.00</td>
<td>0.23</td>
<td>0.03</td>
</tr>
<tr>
<td>Cov3 (11.3%)</td>
<td>0.00</td>
<td>0.00</td>
<td>-</td>
<td>0.06</td>
<td>0.77</td>
<td>0.07</td>
<td>0.03</td>
</tr>
<tr>
<td>Cor1 (44.0%)</td>
<td>0.85</td>
<td>0.10</td>
<td>0.07</td>
<td>-</td>
<td>0.00</td>
<td>0.00</td>
<td>0.06</td>
</tr>
<tr>
<td>Cor2 (10.4%)</td>
<td>0.09</td>
<td>0.21</td>
<td>0.58</td>
<td>0.00</td>
<td>-</td>
<td>0.00</td>
<td>0.07</td>
</tr>
<tr>
<td>Cor3 (6.3%)</td>
<td>0.04</td>
<td>0.07</td>
<td>0.06</td>
<td>0.00</td>
<td>0.00</td>
<td>-</td>
<td>0.03</td>
</tr>
<tr>
<td>Wing</td>
<td>0.04</td>
<td>0.04</td>
<td>0.07</td>
<td>0.10</td>
<td>0.08</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* N (males) = 299 (268 for comparisons with wing length); N (females) = 243 (220 for comparisons with wing length).
Percentages of variance explained for females under variables in left-hand column, for males under variables across top.

values are quite low (range = 0.00-0.48). The correlations between PC2 (correlation matrix) and PC3 (covariance matrix), however, are high (0.88 and 0.76), indicating that they reflect similar shape variation. As previously stated, PC2 of the covariance/log matrix is a unique component summarizing variation in interorbital width. Some of this variation is incorporated into PC3 from the analysis of the correlations matrix of raw data, yet based on the percent of the total variation explained, PC3 is relatively unimportant (Table 3), and as mentioned above, cannot be reliably interpreted.

Wing length is essentially uncorrelated with any of the PC variables, but is significantly correlated with several of the original measures and mass (Table 6). Not surprisingly, the highest correlations with wing length are with various measures of the pectoral girdle, but even these correlations are not impressively high. In both sexes, wing length best predicts carpometacarpus length (the bone to which the primary wing feathers insert), but these correlations are only 0.47 and 0.45. At best wing length explains only about 20% of the variation in any bone measure, and, at least in Savannah Sparrows, wing length, though positively correlated with body size, is not a good measure of it, regardless of how estimated. Of the 139 studies of geographic variation in North American birds summarized by Zink and Remsen (1986), 80% used measures of study skins, and must have based assessment of body size on measures of wing length.

Because more of the total variance is explained by PC1 and PC2 from the correlation/raw data analyses than from the covariance/log analyses, I use PC scores based on the raw data in analyses of geographic variation.
Table 6
Correlations between Wing Length and 25 Other Measurements in Wintering Savannah Sparrows

<table>
<thead>
<tr>
<th>Variable</th>
<th>Females (N = 209)</th>
<th>Males (N = 251)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skull length</td>
<td>0.20</td>
<td>0.22</td>
</tr>
<tr>
<td>Skull width</td>
<td>0.25</td>
<td>0.18</td>
</tr>
<tr>
<td>Premaxilla length</td>
<td>0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>Premaxilla depth</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>Narial width</td>
<td>0.12</td>
<td>-0.06</td>
</tr>
<tr>
<td>Premaxilla width</td>
<td>0.13</td>
<td>-0.01</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>0.10</td>
<td>-0.03</td>
</tr>
<tr>
<td>Mandible length</td>
<td>0.16</td>
<td>0.18</td>
</tr>
<tr>
<td>Gonyx length</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td>Mandible depth</td>
<td>-0.02</td>
<td>-0.08</td>
</tr>
<tr>
<td>Coracoid length</td>
<td>0.30</td>
<td>0.27</td>
</tr>
<tr>
<td>Scapula length</td>
<td>0.34</td>
<td>0.25</td>
</tr>
<tr>
<td>Femur length</td>
<td>0.15</td>
<td>0.22</td>
</tr>
<tr>
<td>Femur width</td>
<td>0.13</td>
<td>0.04</td>
</tr>
<tr>
<td>Tibiotarsus length</td>
<td>0.14</td>
<td>0.23</td>
</tr>
<tr>
<td>Tarsometatarsus length</td>
<td>0.18</td>
<td>0.21</td>
</tr>
<tr>
<td>Humerus length</td>
<td>0.31</td>
<td>0.20</td>
</tr>
<tr>
<td>Ulna length</td>
<td>0.40</td>
<td>0.26</td>
</tr>
<tr>
<td>Carpometacarpus length</td>
<td>0.47</td>
<td>0.45</td>
</tr>
<tr>
<td>Hallux length</td>
<td>0.08</td>
<td>0.19</td>
</tr>
<tr>
<td>Sternum length</td>
<td>0.40</td>
<td>0.24</td>
</tr>
<tr>
<td>Sternum depth</td>
<td>0.30</td>
<td>0.24</td>
</tr>
<tr>
<td>Keel length</td>
<td>0.41</td>
<td>0.22</td>
</tr>
<tr>
<td>Synsacrum width</td>
<td>0.15</td>
<td>0.27</td>
</tr>
<tr>
<td>Mass (gm)</td>
<td>0.41</td>
<td>0.33</td>
</tr>
</tbody>
</table>

*Correlations > 0.11 are statistically significant (P < 0.05).

that follow. Also, as discussed above, the log/covariance analysis produced a PC2 that is essentially a measure of a single variable (interorbital width), whereas the interesting shape variation described by PC2 from the raw/correlation analysis is found in PC3 of the covariance matrix.

Relationship between size and environment.—For both sexes, there was one significant canonical axis. PC1, plus average winter temperature, snowfall, and precipitation are positively correlated with this axis for both sexes, although the standardized canonical coefficients between the axis and PC1 scores for males are not large (Table 7). In contrast, PC2 scores are highly negatively correlated with this axis. Thus, there is a weak tendency for relatively large birds to winter where it is relatively mild and mesic, and, because PC2 is negatively correlated with bill size and pos-
Table 7

Standardized Canonical Coefficients from Canonical Correlation Analysis of Wintering Savannah Sparrows (Passerculus sandwichensis)

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average PC scores</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC1 Score</td>
<td>0.51</td>
<td>0.29</td>
</tr>
<tr>
<td>PC2 Score</td>
<td>-0.73</td>
<td>-0.77</td>
</tr>
<tr>
<td>Climatic measures</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Latitude</td>
<td>0.34</td>
<td>0.29</td>
</tr>
<tr>
<td>Longitude</td>
<td>-0.39</td>
<td>-0.02</td>
</tr>
<tr>
<td>Coldest temperature</td>
<td>-0.49</td>
<td>-0.66</td>
</tr>
<tr>
<td>Average winter temperature</td>
<td>0.74</td>
<td>0.91</td>
</tr>
<tr>
<td>Average annual snowfall</td>
<td>0.30</td>
<td>0.23</td>
</tr>
<tr>
<td>Average annual precipitation</td>
<td>0.20</td>
<td>0.97</td>
</tr>
<tr>
<td>Sparrow abundance</td>
<td>-0.16</td>
<td>0.25</td>
</tr>
<tr>
<td>Sparrow diversity</td>
<td>-0.17</td>
<td>-0.04</td>
</tr>
<tr>
<td>Canonical correlation</td>
<td>0.94</td>
<td>0.95</td>
</tr>
<tr>
<td>Significance</td>
<td>(P = 0.001)</td>
<td>(P = 0.04)</td>
</tr>
</tbody>
</table>

Positively correlated with pectoral size, sparrows with relatively large bills and small pectoral elements tend to winter where it is relatively mild and mesic.

Multiple regression shows similar relationships, although to a certain extent different variables are emphasized because partial correlations are used instead of covariances (Table 8). For females, PC1 is positively correlated with snowfall, and in males negatively correlated with longitude. This effectively describes an east to west pattern of size variation in both sexes, with the largest birds found in the east or northeast (where snowfall is greatest). In both sexes, PC2 is negatively correlated with precipitation (Fig. 2), which is correlated with many other variables, such as longitude and the species diversity of wintering sparrows (Table 9). Relatively long-legged sparrows of both sexes are found in the north, and also (in males) in the east. Although the relationship between tibiotarsus length of females and the abundance of other sparrow species is identified by multiple regression as being highly significant, the univariate correlations are so low that it is doubtful that this is biologically important (Tables 8 and 9). Humerus length of males is negatively correlated with longitude (Tables 8 and 9). Both average PC1 and average PC2 scores for both sexes are highly correlated with longitude and (in males) with average annual precipitation, which is highly correlated with longitude. Other than
Table 8

<table>
<thead>
<tr>
<th>Morphological variable</th>
<th>Environmental variable</th>
<th>Simple r</th>
<th>Cumulative $r^2$</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females (19 locs.)</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>PC1</td>
<td>Average snowfall</td>
<td>0.56</td>
<td>0.31</td>
<td>7.7*</td>
</tr>
<tr>
<td>PC2</td>
<td>Longitude</td>
<td>-0.72</td>
<td>0.52</td>
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</tr>
<tr>
<td></td>
<td>Sparrow diversity</td>
<td>0.58</td>
<td>0.66</td>
<td>15.8*</td>
</tr>
<tr>
<td>Bill shape</td>
<td>Average temperature</td>
<td>0.61</td>
<td>0.38</td>
<td>10.3*</td>
</tr>
<tr>
<td></td>
<td>Longitude</td>
<td>0.49</td>
<td>0.53</td>
<td>9.2*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tibiotarsus length</td>
<td>0.59</td>
<td>0.35</td>
<td>9.3*</td>
</tr>
<tr>
<td></td>
<td>Abundance</td>
<td>-0.07</td>
<td>0.54</td>
<td>9.2*</td>
</tr>
<tr>
<td>Humerus length</td>
<td>None significant</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males (16 locs.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC1</td>
<td>Longitude</td>
<td>-0.79</td>
<td>0.63</td>
<td>23.5*</td>
</tr>
<tr>
<td>PC2</td>
<td>Average precipitation</td>
<td>-0.80</td>
<td>0.64</td>
<td>24.4*</td>
</tr>
<tr>
<td></td>
<td>Latitude</td>
<td>-0.37</td>
<td>0.75</td>
<td>19.0*</td>
</tr>
<tr>
<td>Bill shape</td>
<td>None significant</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tibiotarsus length</td>
<td>-0.69</td>
<td>0.48</td>
<td>13.0*</td>
</tr>
<tr>
<td></td>
<td>Latitude</td>
<td>0.53</td>
<td>0.66</td>
<td>12.4*</td>
</tr>
<tr>
<td>Humerus length</td>
<td>Longitude</td>
<td>-0.83</td>
<td>0.69</td>
<td>31.8*</td>
</tr>
</tbody>
</table>

*P < 0.05.
*P < 0.01.
*P < 0.001.

precipitation, however, other direct measures of the climatic environment are not significantly correlated with the PC scores (Table 9).

Thus, the best environmental predictor of PC2 variation is average annual precipitation (Fig. 2), although the correlation for the female data is reduced by several outlying points that may represent sampling artifacts. The females from High Island (coastal), Texas and Fieldsboro, Delaware, have the largest residuals, and these averages are based only on 10 and 8 individuals, respectively. The male sample with the largest residual is from Graham, Texas, and likewise is based on a small sample (N = 8). In males, PC2 scores also decrease latitudinally (Table 8), but univariately this relationship is not statistically significant (Table 9). “Bill shape” (length/width) is not correlated either with PC2 or precipitation, but in females is significantly correlated with temperature and snowfall (Table 9). Thus, sparrows with relatively small bills are found where it is relatively dry. Female Savannah Sparrows with relatively long, narrow bills (“bill shape”) are found where it is relatively warm, and in the west (Tables 8 and 9).
DISCUSSION

In contrast with studies of two other species of Emberizinae, eastern Dark-eyed Juncos and western White-crowned Sparrows, I find no evidence that male Savannah Sparrows tend to winter farther north than do females. The reason for this difference is not obvious. I have no data on sex ratios in populations of Savannah Sparrows that winter in Mexico (they winter commonly in the northern and central highlands), and thus it is possible that there is a latitudinal trend that I cannot detect. This seems unlikely, however, for two reasons: (1) the overall ratio of approximately 55 males to 45 females that I find is a reasonable reflection of the overall sex ratio in the species, and (2) I find no trend in the birds wintering north of Mexico. Unlike the White-crowned Sparrow and Dark-eyed Junco, which winter in weedy woodland edge and rank oldfields, Savannah Sparrows winter in open fields and would probably be more severely threatened by heavy snowfall. Savannah Sparrows, in fact, winter south of regions where there is persistent snow and, in general, farther south than White-crowned Sparrows and especially juncos. Thus, in the
Table 9
Spearman Rank Correlations among Variables Used in Canonical Correlation and Multiple Regression Analyses
(Correlations among 16 Male Samples are above the Diagonal and Those among 19 Female Samples are Below)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Coldest Average</th>
<th>Temperature</th>
<th>Snowfall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td></td>
<td>-0.35</td>
<td>-0.53</td>
<td>-0.56b</td>
<td>0.49a</td>
</tr>
<tr>
<td>Longitude</td>
<td>-0.43a</td>
<td></td>
<td>-0.02</td>
<td>0.04</td>
<td>-0.32</td>
</tr>
<tr>
<td>Coldest temperatures</td>
<td>-0.69c</td>
<td>0.22</td>
<td></td>
<td>0.88b</td>
<td>0.60b</td>
</tr>
<tr>
<td>Average wint. temperatures</td>
<td>-0.70c</td>
<td>0.17</td>
<td>0.90b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average snowfall</td>
<td>0.64c</td>
<td>-0.42a</td>
<td>-0.64b</td>
<td>-0.69c</td>
<td></td>
</tr>
<tr>
<td>Average an. precipitation</td>
<td>0.00</td>
<td>-0.52a</td>
<td>0.24</td>
<td>0.24</td>
<td>-0.13</td>
</tr>
<tr>
<td>Spar. abundance</td>
<td>0.51a</td>
<td>0.33</td>
<td>-0.58b</td>
<td>-0.67c</td>
<td>0.49a</td>
</tr>
<tr>
<td>Spar. diversity</td>
<td>-0.47a</td>
<td>0.50a</td>
<td>0.17</td>
<td>0.21</td>
<td>0.06</td>
</tr>
<tr>
<td>PC1</td>
<td>0.46a</td>
<td>-0.67c</td>
<td>-0.29</td>
<td>-0.18</td>
<td>0.27</td>
</tr>
<tr>
<td>PC2</td>
<td>-0.14</td>
<td>0.69c</td>
<td>-0.01</td>
<td>-0.07</td>
<td>-0.02</td>
</tr>
<tr>
<td>Bill shape</td>
<td>-0.49a</td>
<td>0.56a</td>
<td>0.49b</td>
<td>0.55b</td>
<td>-0.65c</td>
</tr>
<tr>
<td>Tibiotarsus length</td>
<td>0.61b</td>
<td>-0.63b</td>
<td>-0.46b</td>
<td>-0.34</td>
<td>0.38</td>
</tr>
<tr>
<td>Humerus length</td>
<td>0.00</td>
<td>-0.14</td>
<td>-0.08</td>
<td>0.02</td>
<td>-0.10</td>
</tr>
</tbody>
</table>

*P < 0.05.
*P < 0.01.
*P < 0.001.

U.S., the winter range of the Savannah Sparrow is more latitudinally compressed, and the average distances traveled in migration are greater than those of the other species of sparrows that have been studied. Possibly, within the region where Savannah Sparrows usually winter there is little size-differential mortality. As well, inasmuch as my data were gathered from several different winters, it is possible that in any given year there is a geographic pattern that is obscured by pooling information from several years.

The interpretation of patterns of size variation among wintering Savannah Sparrows is complicated because there is a high degree of intercorrelation among the various measures of environmental variation used. For example, the diversity and abundance of sparrows is highest in the southwest; snowfall is greatest in Delaware; precipitation shows an east to west pattern; and average winter temperature is highest in Florida. Thus east-west or north-south clines will be “explained” by several different measures of environmental variation that may or may not be of any significance to the birds. Nonetheless, some of the relationships are suggestive.

In both sexes, birds with relatively small bills and large pectoral skeletal
Table 9  
CONTINUED

<table>
<thead>
<tr>
<th>Precipitation</th>
<th>Abundance</th>
<th>Diversity</th>
<th>PC1</th>
<th>PC2</th>
<th>Shape</th>
<th>Tibiotarsus</th>
<th>Humerus</th>
</tr>
</thead>
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<tr>
<td>0.08</td>
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<td>-0.62b</td>
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<td>0.43c</td>
<td>0.28</td>
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<td>-0.72a</td>
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<td>0.48a</td>
<td>-0.84a</td>
<td>0.70c</td>
<td>0.38</td>
<td>-0.82c</td>
<td>-0.88c</td>
</tr>
<tr>
<td>0.25</td>
<td>-0.51a</td>
<td>0.17</td>
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<td>0.04</td>
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<td>0.08</td>
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<td>-0.22</td>
<td>-0.22</td>
<td>0.27</td>
<td>0.38</td>
</tr>
<tr>
<td>-0.61b</td>
<td>-0.53a</td>
<td>0.57a</td>
<td>-0.73c</td>
<td>-0.11</td>
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<td>0.52a</td>
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<tr>
<td>-0.50a</td>
<td>-</td>
<td>0.06</td>
<td>-0.40</td>
<td>0.43a</td>
<td>0.07</td>
<td>-0.44a</td>
<td>-0.33</td>
</tr>
<tr>
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<td>0.05</td>
<td>-</td>
<td>-0.42</td>
<td>0.52a</td>
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<tr>
<td>-0.57b</td>
<td>0.46a</td>
<td>0.63b</td>
<td>-0.27</td>
<td>-</td>
<td>-0.02</td>
<td>0.56c</td>
<td>-0.48c</td>
</tr>
<tr>
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<td>-0.24</td>
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<td>-0.11</td>
<td>-0.48c</td>
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<tr>
<td>0.13</td>
<td>-0.11</td>
<td>-0.32</td>
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<td>-0.34</td>
<td>-</td>
<td>0.86c</td>
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<tr>
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<td>-0.30</td>
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<td>0.56c</td>
<td>0.22</td>
<td>0.01</td>
<td>0.48c</td>
<td></td>
</tr>
</tbody>
</table>

elements winter in the west, where there is little rainfall and where several other species of sparrows commonly winter. In summer, Savannah Sparrows predominantly eat insects, whereas in winter seeds comprise the bulk of their diets (pers. obs.). In Darwin's Finches (Geospiza) bill size influences the efficiency with which birds can handle and crack seeds. Birds with large bills can eat both small and large seeds, although they may handle the small seeds less efficiently than birds with smaller bills. Geospiza with relatively small bills eat seeds of less varied sizes than ones with relatively large bills, and this is true both among and within species (Grant 1986). This is probably true for seed-eating birds in general (Pulliam 1985). The existence of an east-to-west cline in relative bill size of wintering Savannah Sparrows therefore indicates that there are differences in the foods available to them in different parts of their range, and specifically that large seeds are not so available in the west as in the east. This could be either because there is greater competition from other species in the southwest for relatively large seeds (the species diversity of wintering sparrows is high there), or because relatively few large seeds are produced there. If the variety of food produced is greater in mesic than in xeric habitats, there is support for either of these explanations in the data: PC2 scores correlate significantly with indices of sparrow abundance.
and diversity, that is, bill sizes are relatively small where other species of sparrows commonly winter, as well as where it is dry.

All of the longitudinal trends in geographic variation among wintering populations that I have discussed reflect similar trends among breeding populations (Rising, unpubl. data) in general, eastern Savannah Sparrows: (1) are larger than western ones, (2) have relatively larger and stouter bills, and (3) smaller pectoral appendages. Thus, the trends among wintering populations of Savannah Sparrows are consistent with the hypothesis that the breeding birds simply move south in winter, and north again in the spring. Although it is reasonable to assume that western-breeding Savannah Sparrows winter in the west, and eastern-breeding birds winter in the east, there is little direct evidence of paths of migratory movement for the species. There are, for example, only nine records of Savannah Sparrows banded during the summer and subsequently recaptured in winter, or vice versa. Of these, four are of apparently resident individuals from coastal California. The others are: banded 10 August 1932 in northern Michigan, and recovered 24 January 1933 in Alabama; banded 28 August 1954 in central Vermont, and recovered in December 1954 on Long Island, New York; banded in central Wisconsin 16 August 1956, and recovered in southern Maine on 25 December 1956; banded 25 July 1968 on Kent Island, New Brunswick, and recovered in eastern New York in early December 1968; and banded 10 February 1970 in east-central Florida, and recovered in July 1970 in New Brunswick. These banding data point to a north-south pattern, as well as some movement of birds from the interior to winter on the east coast.

The well-marked “Ipswich” sparrows, Savannah Sparrows that breed on Sable Island, Nova Scotia, are known to winter along the Atlantic coast, where they are virtually never found away from the dune grass of outer beaches (Stobo and McLaren 1975, pers. obs.). Ipswich sparrows are substantially larger than other eastern Savannah Sparrows. Indeed, there are a few Ipswich sparrows in my sample from Dewey Beach, Delaware (winter), although the inclusion of these birds has not significantly affected the results presented here. Other maritime breeding sparrows are somewhat larger than more inland ones (Rising, unpubl. data); if they, like the Ipswich sparrows, tend to winter along the coast, this could at least partially explain the longitudinal trend in body size and perhaps the latitudinal one as well. In the data presented here, there is some indication that larger individuals tend to winter closer to the coast than do smaller ones at the same latitude (Table 4). The two samples from North Carolina are from localities that are close to each other, one (Nags Head) in coastal dune grass and the other (Harbinger) just inland, in oldfield habitat. Similarly, the two samples from High Island, Texas, are from a coastal and
nearby inland site. In both cases, the birds in the coastal sample average larger than those from the inland sample, although the samples are small. The males from Folly Beach (coastal) South Carolina are small relative to those from Charleston (dump) and Clemson, but there are only five males in the Folly Beach sample.

If the conical bills of sparrows have evolved for granivory, I propose that winter selection has dominated the evolution of the cline in bill size (PC2 and to a lesser degree bill shape). Variation in the relative size of the pectoral elements could reflect differences in migratory distances as it is likely that western birds fly, on average, farther than eastern ones if they tend to move due south in the winter (it is about 4500 km from central Alaska to southern Arizona, and 3500 km from Ungava or southern Keewatin to central Florida).

Although it made little difference whether I used log-transformed data and the covariance matrix or raw data and the correlation matrix, more of the variance was explained by the first few (2 or 3) principal components in the raw-correlation analysis than in the log-covariance analysis. As well, the first few components from the raw-correlation analysis could be more easily interpreted as meaningful measures of size and shape than those from the log-covariance analysis. In a study such as this, the features measured are important. Wing length, for example, does not accurately reflect size or shape as defined by single measures of bones or PC scores. Although wing length may be the best measure of “size” available in many cases, my analyses suggest that it is a poor measure of size, explaining at most 20% of the variation in a long bone measure.

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LITERATURE CITED


ACTIVITY PATTERNS AND HOME-RANGE USE OF NESTING LONG-EARED OWLS

E. H. CRAIG, T. H. CRAIG, AND LEON R. POWERS

ABSTRACT.—A study of the movements of two pairs of nesting Long-eared Owls (Asio otus) was conducted during the spring and summer of 1982. Activity patterns, movements, and home-range use of the owls changed during the nesting season. The female incubated and brooded the young, while the male did most of the foraging, particularly when the female was attending eggs or very small nestlings. Mates shared a common core home range immediately around the nest site, but foraged in different areas away from the nest. The home-range areas of adjacent nesting pairs overlapped. Although changes in temperature significantly affected the movements of one of the female owls, wind speed, precipitation, and cloud cover appeared to have little influence on movements of the birds. During their nocturnal period of activity, owls were least active from 20:00-22:00 and 05:00-06:00.

Received 8 Apr. 1987, accepted 28 Sept. 1987.

Most research on Long-eared Owls (Asio otus) in North America has dealt with food habits, productivity, and nest-site selection (Armstrong 1958, Marti 1976, Craig and Trost 1979, Roth and Powers 1979, Marks 1986). Little information has been published on activity patterns, movements, and home-range.

We used radio-telemetry to study the activity patterns and movements of Long-eared Owls on the Idaho National Engineering Laboratory (INEL) in southeastern Idaho during the summer of 1982, in an attempt to obtain information on home-range, activity patterns, and movements of adult Long-eared Owls during the nesting season.

STUDY AREA AND METHODS

The INEL encompasses 231,600 ha of flat to gently rolling cool desert (Odum 1971) on the Upper Snake River Plain dominated by big sagebrush (Artemisia tridentata)-grass vegetation (Harniss and West 1973). The Big Lost River flows across the INEL, and the typical vegetation of the Snake River Plain is interrupted along the banks of the river by cottonwood trees (Populus sp.), which range in height to well over 9 m. There are few shrubs beneath the trees, probably because flow of the river is reduced or eliminated in late summer as a result of irrigation upstream and decreased snowmelt, although river hawthorn (Crataegus rivularis) and wild rose (Rosa sp.) do occur. Long-eared Owls nested in old Black-billed Magpie (Pica pica) nests in the cottonwood trees along the river. Adult owls were captured in mist nets at 3 nest sites during May and June 1982. Each captured adult was banded with a U.S. Fish and Wildlife Service band and fitted with a back-pack radio harness. The radios weighed 4-5 g (<2% of total body weight) and were attached with elastic straps that fit around the base of each wing. The range of the radios varied with weather conditions.

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but was generally about 3 km. Birds at 2 of the nests, approximately 3.5 km apart, were monitored for the entire nesting season (21 May–9 July). At the third site both owls abandoned their nest 2 days after we attached the radios on 22 May. The male was never located after this (including aerial searches), but the female was found about 3 km from the nest 5 days after nest abandonment.

The owls at one nest (3-pole) were tracked for 8 nights from late incubation until the young left the nest area; about a week after branching (the time when young owls that leave the nest perch in the surrounding vegetation). The owls at the second nest (KB5) were tracked for 9 nights from the time the young were about 12 days old until they left the nest area. Tracking was delayed at least 4 days after radio-tagging to allow the birds time to adjust to the transmitters. Radio locations were determined by triangulation using 2 portable towers (4.6 m high) equipped with out-of phase 5-element yagi directional antennae and a null combiner system (Telenics, Mesa, Arizona). Two people at separate stations and in radio contact took simultaneous readings on first one adult and then the other at a nest site at 10-min intervals throughout the night. Tracking began between 20:00 and 21:00 and continued through 05:00 to 06:00. Sunset occurred at about 20:30 and sunrise at about 06:15 (MDT). One nest was monitored each tracking night.

In addition to location, we recorded temperature, wind speed, cloud cover (recorded on a scale of 1–4), precipitation and general weather conditions at each 10-min interval. Regression analysis was used to examine possible relationships between owl movements and environmental factors. Because owl movements changed significantly during the nesting season, we analyzed data separately for each day. Regression analysis was also used to analyze the relationship between age of the young and time adults spent in the nest area.

Locations were plotted on a map of the study area and triangulation error was estimated with readings on both moving and stationary transmitters at known locations (after Springer 1979). Average locational error of a stationary transmitter at 0.5 km was ±24 m (±2.5° error). Readings taken on a transmitter 0.5 km away, moving along a known route at a velocity of approximately 6.5 km/h, yielded an average locational error of ±41 m (±5.8° error). These errors varied with the angle and distance of the owls from the tracking stations (Springer 1979). Because of possible locational error, we were unable to determine if owls were on the nest or adjacent to it; therefore, in data analysis birds were described as being in the “nest area.” Home ranges, or use areas, were determined using a modification of the grid system described by Rongstad and Tester (1969) and Laundré and Keller (1981). We included in our home range maps, however, all grids entered by the owls regardless of distance from the closest neighboring grid in which the owls were recorded. Grids were 300 m on a side (8.8 ha) with the nest the center of the grid system. Home ranges of female owls were more accurate estimates of actual use areas than those of males because males were frequently out of range of the tracking towers.

Distances moved were determined by measuring the minimum straight-line distance between successive radio locations. Distance data were analyzed using regression analysis. Movements per hour were analyzed by dividing the number of moves by the total number of radio locations per hour (expressed as a percentage). Hourly movement data were analyzed using a chi-square goodness-of-fit test with Yates’ correction for continuity (Zar 1974).

Food habits were determined from castings collected at nest sites. Castings were soaked in a weak NaOH solution and sieved through screen wire and 0.3-cm hardware cloth.

RESULTS AND DISCUSSION

Initially, both study nests contained 4 eggs; however, only 2 young branched from one nest (KB5), whereas at least 3 young branched from
the second nest (3-pole). The young at KB5 branched at 35 days, and the young at 3-pole branched at 24 days of age. Most other researchers have reported that young Long-eared Owls branch within 3 weeks of hatching (Armstrong 1958, Craig and Trost 1979, Hilliard et al. 1982, Wijnandts 1984, Marks 1986). The owlets at KB5 had scabs around their eyes and one disappeared from the nest 2–3 weeks after hatching.

**Influence of environmental factors on movements.**—There was no relationship between the distance the male or female moved each day and wind speeds up to 25 km/h, cloud cover, or precipitation ($P > 0.05$). We did not, however, monitor the birds during lightning storms, and owl behavior may have changed during these periods. Similarly, Delong's (1982) direct observations revealed no relationship between prey deliveries and wind speed (up to 20–27 km/h). In addition, he found no relationship between the rate of prey delivery by males and cloud cover, light precipitation, or temperature, but noted that prey deliveries were not made during extended periods of heavy rain.
Home-range use and activity patterns. - Owls at both nests frequently were located in open sagebrush areas close to the river (Figs. 1 and 2). The Long-eared Owls at KB5 were never recorded in a scattered juniper area 0.7 km southwest of their nest. Other researchers have reported that Long-eared Owls prefer to hunt in open, rather than timbered or shrub areas (Getz 1961, Sonnenberg and Powers 1976).

Incidental daytime observations and piles of castings indicated that the male owls generally roosted in the same tree or shrub within several hundred meters of their nests. Radio locations of the female at 3-pole indicated that she was in the nest area at daylight each night we tracked.
her. When the young at KB5 were 26 days old the female began to perch away from the nest at daybreak.

Owls became active as darkness approached, but from 20:00–22:00 owls moved significantly fewer times than from 22:00–05:00 ($P < 0.05$, KB5 male: $\chi^2 = 3.97$, KB5 female: $\chi^2 = 4.80$, 3-pole male: $\chi^2 = 16.89$, 3-pole female: $\chi^2 = 7.65$) (Fig. 3). The activity of the birds also was lower between 05:00–06:00, although the KB5 female was the only owl that moved significantly less ($\chi^2 = 8.24$, $P < 0.001$) during this time. DeLong (1982) observed a significant decrease in prey deliveries at Long-eared Owl nests from 20:00–21:00 and 05:00–06:00. He observed that delivery rates were highest during the first half of the evening, but not significantly higher until 2 h before sunrise. Periods of peak activity did not occur during the same time each night (see Fig. 3) and the activity patterns for the KB5 male may be biased because he was out of range much of the time.

At both nest sites the male and female shared a common core area (grids in a home-range entered by both adults) in the vicinity of the nest (Figs. 1 and 2), but often foraged in different directions away from the nest on a given night (Fig. 4). This may have kept adults at a nest site from competing for prey and may have served to maximize hunting efficiency. The home ranges of the KB5 and 3-pole birds overlapped slightly (Figs. 1 and 2) with the ranges of the females overlapping more (approximately 10% of the pairs' home-range) than those of the males (approximately 2% of the pairs' home-range).

The northern pocket gopher (*Thomomys talpoides*) and the Great Basin pocket mouse (*Perognathus parvus*) were the primary prey items (36.7% and 34.4% frequency of occurrence, respectively) at the 3-pole nest. The KB5 birds preyed on the Great Basin pocket mice, deer mice (*Peromyscus maniculatus*), sagebrush vole (*Lagurus curtatus*) and northern pocket gophers most often (45.7%, 17.1%, 17.1%, and 8.6%, respectively). Long-eared Owls are reported to be opportunistic in their food habits (Marks 1984, Craig et al. 1985). The difference in prey taken on the INEL supports

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Fig. 3. Activity patterns of mated Long-eared Owls at 2 nest sites on the Idaho National Engineering Laboratory. Movements are calculated as the number of times each owl moved from the previous radio location divided by the total number of radio locations each hour and expressed as percents. Dates of radio-tracking are indicated for each graph with approximate age of the young listed in parentheses. An asterisk indicates nights on which there was a significant difference between male and female movements. Shaded areas indicate the time of night (20:00–22:00) when all owls showed significantly fewer movements.
Fig. 4. Home range size and shape (black grids) of adult male and female Long-eared Owls at nest sites on the Idaho National Engineering Laboratory during individual nights throughout the nesting season. The open circles show the location of the nest and the numbers indicate the age of the young for each map. Dashed lines connect the use areas of the owls. Percent of total radio-locations that were in the nest grid are indicated for the female owls.

our radio location data that show the two pairs did most of their hunting in separate areas.

During incubation and until the young were approximately 12 days old the total home ranges of the females were relatively small ($\bar{x} = 7.0 \pm 2.4$ grids) and they spent 67–89% of their time within the nest grid (see Fig. 4). At this time, the males used a larger area than did the females, often moving out of range of our tracking towers. The males were out of range 40% of the time during incubation and when the young were 12 days old or less. Because of this, home range maps for the males underestimate actual use areas, particularly for the KB5 male. On the other hand, the KB5 and 3-pole females were out of range an average of 3.5% and 0.5% of the time, respectively, until the young fledged, and thus their home range maps are more accurate estimates of actual use areas.

The home ranges of the females more than doubled in size ($\bar{x} = 16.4 \pm 1.6$ grids) after the young were older than 12 days. In addition, at this time, the females spent less time in the nest grid and more in the remainder
of the home range area (Fig. 4). Home range of the 3-pole male appeared to decrease slightly during this time (Fig. 4), and he was also out of range less (11.5% of the time). The KB5 male continued to be out of range of our tracking towers and no trend could be seen. When nestlings were less than 2 weeks of age, females spent 70–80% of their time in the nest area (Fig. 5), but as nestling age increased, females spent less time and the KB5 male spent more time in the nest area. These data combined with the movement data suggest that females played an increasingly important role in provisioning the young as the nesting season progressed. The relationship of nestling age to time spent in the nest area was significant for the owls at KB5 (male: $r^2 = 0.63$, $F = 9.5$, $P < 0.025$; female: $r^2 = 0.84$, $F = 26.67$, $P < 0.0025$) but not for either owl at 3-pole (Fig. 5). The female at 3-pole disappeared, however, when the young were between 18 and 26 days old, and the fewer tracking days for this owl may have biased our data. The male owl at 3-pole successfully raised the young to branching age.

The average distance moved by the males generally decreased with the
progression of the nesting season, whereas the distances moved by the females increased, but the trends were not significant \((P > 0.05)\). A similar phenomenon was observed in the movements of a male Long-eared Owl tracked in southwestern Idaho by Hilliard et al. (1982). There was a significant difference in the moves/h of the male and female at 3-pole until the young were approximately 11 days old. During this time the female made few movements away from the nest area. Similarly, birds at KB5 displayed a significant difference in moves/h until the young were about 18 days old, and again after the young were 28 days old (Fig. 3), with the female moving out of the nest area infrequently. The KB5 nestlings may have required brooding by the female for a longer period of time than young at 3-pole, because of their physical condition and so she may not have moved from the nest as often. According to Delong (1982), female Long-eared owls incubate and brood the young and males provide most of the food for the family group. We found that at approximately 2 weeks of age when the nestlings were able to maintain body temperature (Wijnandts 1984), there was an increase in the size of the females’ home range, as well as in her number of moves and distance moved between radio-locations. These data suggest that at this time, female owls as well as males forage for food for the young.

ACKNOWLEDGMENTS

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LITERATURE CITED


HAWK MOUNTAIN RESEARCH AWARD

The Hawk Mountain Sanctuary Association is accepting applications for its twelfth annual award for raptor research. To apply for the $750 award, a student applicant should submit a brief description of his or her research program (five pages maximum), a curriculum vitae, and two letters of recommendation to Dr. Jim Bednarz, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, PA 19529. The deadline for applications is October 15, 1988. The Association’s board of directors will make a final decision early in 1989. Only students in degree-granting institutions are eligible to apply; both undergraduate and graduate students may apply. The award will be granted on the basis of a project’s potential to improve understanding of raptor biology and its ultimate relevance to the conservation of North American raptor populations.
ASPECTS OF THE WINTERING ECOLOGY OF PIPING PLOVERS IN COASTAL ALABAMA

Catherine M. Johnson and Guy A. Baldassarre

Abstract.—Piping Plovers (Charadrius melodus) wintering on the Alabama coast were studied from September–October through April 1984–85 and 1985–86. Time spent foraging dominated diurnal activities during all months (x = 76%) and was highest in December (90%). Tidal height was correlated negatively with foraging time and appeared to be the most important factor influencing activities. Time spent resting and preening was related inversely to foraging, and combined time spent in agonistic, territorial, alert, and locomoting activities was <5% during all months. Piping Plovers arrived on the study area in mid-July, and several individuals remained into early April. Observations of color-marked plovers indicated that individuals were least mobile from late November through late January. Of the plovers marked in 1984–85, 63% returned during 1985–86 despite the occurrence of two major hurricanes during the fall of 1985. Received 9 March 1987, accepted 12 Nov. 1987.

The Piping Plover (Charadrius melodus) is endemic to North America, breeding locally on the upper Atlantic coast, the Great Lakes region, and the Great Plains (Johnsgard 1981). Its wintering range extends along the Atlantic and Gulf coasts from North Carolina to Mexico and into the Bahamas and West Indies (Federal Register 1985). Unregulated hunting rendered this species near extinction by 1900 (Bent 1929); but the population began to recover following protective legislation. Since 1945, however, Piping Plover populations have been declining, primarily because of alteration of breeding and wintering habitats, human-related disturbance to nesting birds, and increased nest predation (Sidle 1984).

This recent population decline prompted the U.S. Fish and Wildlife Service to list the Piping Plover as a threatened and endangered species in January 1986. The species was assigned endangered status in the Great Lakes region where the population had decreased to 20–25 pairs by 1986 (M. R. Ryan, pers. comm.); threatened status was assigned throughout the remaining range. Despite this precarious status, however, there are few detailed studies of this species, and most research addresses breeding ecology (Wilcox 1959, Cairns 1982, Faanes 1983, Haig 1985, Prindiville 1986). Investigations during winter are sparse and focus primarily on population density and distribution (Haig and Oring 1985). This lack of

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winter data is significant because substantial annual mortality in migrating shorebirds occurs away from breeding areas (Baker and Baker 1973, Evans 1981). The specific objectives of our study were to determine activity budgets, movements, and site fidelity of Piping Plovers wintering in coastal Alabama.

STUDY AREA

Christmas Bird Count data for coastal Alabama from 1956–86 indicate that this area supports a population of wintering Piping Plovers that primarily uses only three sites: Dauphin Island, Little Dauphin Island, and Sand Island (Fig. 1). Most observations during the 1984–85 winter season were made along a 3-km beach and mudflat site on the north side of Dauphin Island because this location was the most frequently used feeding site of Piping Plovers in the area. Mudflats at Little Dauphin Island also were used for feeding by Piping Plovers, but these sites were exposed only during extremely low tides. Sand Island received use by plovers particularly after Hurricane Elena struck the area on 2 September 1985 and destroyed feeding sites on Dauphin Island and reduced avail-
ability of such sites on Little Dauphin Island. Sand Island then functioned as an alternate feeding site, thus approximately 35% of the 1985–86 time budget data were obtained from observations on Sand Island.

METHODS

Instantaneous sampling procedures (Altmann 1974) were used to observe Piping Plovers from September 1984 through April 1985 and October 1985 through April 1986. Plovers were sampled by dividing each day (sunset to sunset) into four equal time periods within which randomly selected individuals were observed for 5–15 min each, and their activities recorded at 15-sec intervals. Observations lasting <5 min were not considered for analysis. All observations were made using a 15–60x spotting scope and 7x binoculars, with the observer stationed at distances deemed not to affect plover behavior (30–50 m). Equal sampling during every time block of a given day was not possible at each study site because tidal fluctuations affected the number of plovers present; however, approximately 20 birds were observed per block per study site per week.

Activities were categorized as follows: (1) feeding—a peck at substrate or the extraction of a prey item; (2) running—raptid movement between a pause and feeding or two successive pauses; (3) waiting—a pause before running to feed or pause again; (4) foot-tapping—tapping a foot on substrate while in waiting position; (5) foraging—the sum of feeding + waiting + foot-tapping + running, which is referred to as the “stop-run-peck” feeding method characteristic of plovers (Pienkowski 1981); (6) locomotion—running not associated with foraging, walking, or flying; (7) preening—preening, bathing, and comfort movements; (8) alert—low, crouching posture with head held erect or cocked to one side, or head-bobbing not in association with another bird; (9) territorial—parallel-run display, head-bobbing (Cairns 1982); (10) agonistic—horizontal threat displays, striking with beak or wings, and ground or aerial chases (Cairns 1982); and (11) resting—with head tucked in plumage, standing on one leg or huddled in sand (resting usually occurred on dry sand). Environmental data recorded after observation of each plover included tidal height (estimated m above low tide), cloud cover (0–25%, 26–50%, 51–75%, 76–100%), ambient wind speed (km/h), ambient temperature, and substrate temperature.

For each plover observed, the percent time spent in each activity was obtained by dividing the number of recordings in an activity by the total number of recordings for all activities. Monthly activity budgets were determined by averaging time spent in each activity per bird by each time block and then averaging time blocks by each day. Differences in activity budgets among months of each year were determined using t-tests and, where not significant ($P > 0.05$), years were pooled to make monthly comparisons. ANOVA and Duncan’s multiple range test were used to determine significant ($P < 0.05$) differences among blocks, months, and observation sites (Steel and Torrie 1980). Pearson’s correlation analysis was used to examine relationships among activities and environmental variables (Conover 1980).

Piping Plovers were banded during both years using mist nets set at approximately sunrise and sunset. Birds were weighed to the nearest g and banded with a U.S. Fish and Wildlife Service leg band and colored plastic leg bands coded for individual recognition.

RESULTS AND DISCUSSION

Activity budgets.—A total of 769 observation periods of individual Piping Plovers was tallied during the 1984–85 and 1985–86 winter seasons for 100 h and 92 h, respectively. Activity patterns did not differ ($P >$
Foraging accounted for 76% of the time spent in all activities by Piping Plovers and was greater ($P < 0.05$) during autumn and midwinter than in spring (Fig. 2). This high rate of foraging may occur because Piping Plovers are visual predators selecting surface prey items, which may restrict feeding activities to daylight hours. The greater foraging effort in autumn versus spring could reflect feeding to replenish energy reserves depleted during migration and/or accumulation of reserves in anticipation of future energy demands.
of winter weather. Many species of shorebirds wintering at mid-latitudes accumulate lipid reserves during autumn to provide an energy source for use during severe weather or temporary food shortage in winter (Dugan et al. 1981). Alternately, Piping Plovers may forage more in fall to acquire reserves to survive the severe conditions associated with hurricanes, which primarily occur along the Gulf Coast in September and October. Hurricane Elena destroyed feeding sites of Piping Plovers at Dauphin and Little Dauphin in September 1985, thus individuals accumulating lipid reserves in early autumn may survive such storms by relying on that energy to move to alternate areas or to remain in the area until habitats recover. For example, of an estimated 30 Piping Plovers in the area prior to Elena, only 5–6 were counted following the storm. High winds occurring after hurricanes also might affect feeding efforts of Piping Plovers. Dugan et al. (1981) suggested that wind strength affected the Grey (Black-bellied) Plover’s (Pluvialis squatarola) ability to maintain weight, and thus fat reserves may insure against periods of harsh winds rather than low temperatures (Dugan et al. 1981). Strong winds also may interfere with the “stop-run-peck” feeding method of plovers by restricting the direction or speed of runs, or by reducing the visual cues of prey items (Evans 1976, Pienkowski 1983).

Plovers maintained a high foraging effort during midwinter, possibly because of higher energy requirements associated with winter conditions, even though winter is comparatively mild in the Deep South. Lower temperatures, high winds, and increased precipitation decrease activity and subsequent availability of many intertidal invertebrates at northern latitudes (Evans, 1976, Davidson 1981, Pienkowski 1981). The possible effect of lower temperatures in Alabama was reflected in the greater ($P < 0.05$) time plovers spent foraging during February 1985 when mean daytime temperatures averaged 11.1°C compared to February 1986 when temperatures averaged 13.9°C. Further, all significant correlations between temperature and foraging were negative (Table 1). Pienkowski et al. (1984) found that wintering Common Ringed Plovers (Charadrius hiaticula) spent more time feeding on days of lower temperatures and higher winds. In this study, correlations between foraging and wind speed also were positive where significant (Table 1).

The lower feeding time in March and April was unexpected because Piping Plovers arrive on breeding areas during these months (Wilcox 1959, Cairns 1977). Monthly censuses were not conducted during the study, but fewer birds were present in March, and most had departed by mid-April. Perhaps birds were rapidly leaving the area and/or migrants were passing through, thus lipid reserves may have been acquired earlier (January and February) and foraging efforts would be lower in March and April. Prey availability also could be more favorable during these warmer
Table 1

Pearson's Correlation Coefficients (r) by Each Month for Selected Environmental Variables and Foraging Activity of Piping Plovers Wintering in Coastal Alabama, 1984–86

<table>
<thead>
<tr>
<th>Month</th>
<th>Wind (km/h)</th>
<th>Cloud (% cover)</th>
<th>Ambient temperature (°C)</th>
<th>Temperature at 2 cm substrate depth (°C)</th>
<th>Tidal height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sep</td>
<td>-0.18 (42)</td>
<td>0.18 (42)</td>
<td>0.00 (42)</td>
<td>-0.03 (19)</td>
<td>-0.01 (42)</td>
</tr>
<tr>
<td>Oct</td>
<td>0.18 (68)</td>
<td>-0.08 (68)</td>
<td>-0.17 (68)</td>
<td>**-0.33 (68)</td>
<td>-0.18 (90)</td>
</tr>
<tr>
<td>Nov</td>
<td>0.00 (90)</td>
<td>0.15 (150)</td>
<td>**-0.27 (109)</td>
<td>-0.03 (19)</td>
<td>-0.18 (90)</td>
</tr>
<tr>
<td>Dec</td>
<td>0.12 (17)</td>
<td>0.20 (70)</td>
<td>0.08 (70)</td>
<td>0.11 (53)</td>
<td>-0.30 (17)</td>
</tr>
<tr>
<td>Jan</td>
<td><strong>0.35 (54)</strong></td>
<td>0.05 (129)</td>
<td>***-0.51 (129)</td>
<td>***-0.43 (75)</td>
<td>**-0.40 (54)</td>
</tr>
<tr>
<td>Feb 1985</td>
<td>0.15 (59)</td>
<td>0.10 (59)</td>
<td>**-0.29 (59)</td>
<td>**-0.32 (60)</td>
<td></td>
</tr>
<tr>
<td>Feb 1986</td>
<td>0.22 (36)</td>
<td>-0.24 (31)</td>
<td>*-0.44 (31)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mar</td>
<td>0.14 (68)</td>
<td>0.18 (166)</td>
<td>**-0.23 (112)</td>
<td>-0.01 (44)</td>
<td>***-0.50 (68)</td>
</tr>
<tr>
<td>Apr</td>
<td><strong>0.45 (21)</strong></td>
<td>-0.21 (34)</td>
<td>**-0.23 (34)</td>
<td>**-0.61 (13)</td>
<td>*-0.49 (21)</td>
</tr>
</tbody>
</table>

* Numbers in parentheses indicate sample size.

** P < 0.05; *** P < 0.01; **** P < 0.001; all other correlations were not significant.
months which would reduce foraging effort. This is supported by correlations indicating that plovers reduced foraging time when substrate temperatures were warm (Table 1).

Tidal height was correlated negatively with foraging and appeared the most important factor influencing foraging time of Piping Plovers during our study (Table 1). Rising tides gradually decrease exposed foraging space, and because tidal amplitude is small along much of the Gulf Coast, on-shore winds may delay receding tides (Evans and Dugan 1984). The substrate also dries with increasing time after exposure, and this reduces activity of intertidal invertebrates (Pienkowski 1981). Brown (unpubl.) noted that breeding Piping Plovers spent significantly more time during low tide on inner beaches with exposed muddy sandflats, but that they could be found in equal numbers on inner or outer beaches during high tides.

Haig and Oring (1985), noting that Piping Plovers used sandflats from January through March and beaches from August through October and March through May, concluded that habitat preferences were different during migration versus wintering. However, our data on substrate use (September through February, 1984–85) indicate that Piping Plovers wintering in Alabama did not exhibit these seasonal preferences. Observations of foraging Piping Plovers wintering in Alabama indicated similar use of protected mudflats or sandflats exposed at low tides; for example, foraging on dry, sandy beaches on the Gulf side of Dauphin Island accounted for only 13.3% of the time plovers were observed in that habitat. Indeed, Piping Plover use of the 6-km beach on this side of Dauphin Island was so low that the area was not considered an observation site. Plovers rather used mudflats or sandflats (both habitats were characterized by organic matter in the substrate) >85% of the time during each month ($\bar{x} = 93\%$), with no significant differences observed among months ($P > 0.10$). Plovers were seen on beaches during daylight hours in March and April, but these birds were nearly always roosting or preening. Thus, our observations indicate that sandflats, mudflats, and beaches serve different functional roles for wintering Piping Plovers. The two former sites are used for feeding, whereas sandy beaches are used for resting and probably roosting.

Combined time spent in alert, agonistic, territorial, and locomoting activities was $<5\%$ during all months (Fig. 2). Plovers were most alert during September (1.6%) and October (0.8%), possibly because migrating raptors concentrate in this region of coastal Alabama during the fall months (Imhof 1976). Human use of beaches on Dauphin Island also is high during these warm months, which could increase time spent in alert activity.

Agonistic activities were most common in April (2.6%) even though
Piping Plovers pair on the breeding grounds (Cairns 1982) and courtship displays were never observed at Dauphin Island. High rates of aggression also were observed during November and December, probably in association with territorial interactions. For example, combined time spent in territorial and agonistic activities largely involved intraspecific interactions (89%). Of all interspecific interactions (11% of the total), 29% involved Snowy Plovers (C. alexandrinus) and 24% involved Semipalmated Plovers (C. semipalmatus); 47% was in association with 6 other species.

Time spent resting and preening was related inversely to foraging activity. Preening was highest in February–April 1986, when birds were molting into breeding plumage. Locomotor activities were relatively consistent in occurrence, averaging 0.3% during all months (Fig. 2).

Site fidelity and local movements.—Of the color-marked plovers banded at Dauphin Island from October 1984 to February 1985, 63% (12 of 19) were recaptured or seen again the following year. This level of site fidelity was less than that of many other shorebirds returning to wintering areas (Evans 1981), possibly because two hurricanes during the fall of 1985 may have increased mortality and/or emigration to alternate wintering sites. Thus, 63% is probably a conservative estimate for Piping Plovers returning to wintering sites, but this falls within the range of estimates of return rates to breeding areas: 25% in New York (Wilcox 1959) to 75% in Manitoba (Haig 1985). The 63% return rate also can be considered a crude estimate of minimum annual survival, but the marked sample was small (19), and the proportion of juveniles to adults was unknown.

Plovers arrived on Dauphin Island in mid-July, and several individuals still were present in early April. Local movements varied among the 19 color-marked individuals during the 1984–85 winter season. For example, sightings of 9 individuals banded 1–14 November 1984 indicated that 4 stayed at least through late January 1985, whereas 4 were not seen again that season. Thus, it is difficult to determine which individuals were winter “residents,” because birds may be immigrating to, or emigrating from, the area. Eleven of 17 birds (65%) marked during October and November were still present in January. Numbers of Piping Plovers seemed most stable in the Dauphin Island area from late November to late January because 82% (9 of 11) of marked birds seen from 15–30 November were seen through late January. This indicates that winter censuses might best be conducted during December and January.

Overall, the relatively high site fidelity of Piping Plovers to wintering sites in coastal Alabama indicates that conservation efforts may be warranted at specific winter sites. Protection of preferred feeding areas from development and/or other human disturbance appears especially important because plovers spend a high proportion of the winter foraging. Ad-
ditionally, availability of several preferred sites within a general area may be important in limiting the effects of hurricanes or other natural disturbances on wintering Piping Plovers.

ACKNOWLEDGMENTS

The Dauphin Island Sea lab and personnel provided logistical and financial support throughout this study. Funding also was provided by the Mississippi-Alabama Sea Grant Fellowship Program, the Walter F. Coxe Research Fund of the Birmingham Chapter of The National Audubon Society, the Shell Company’s Foundation, Inc., and The Mobil Foundation, Inc. S. M. Melvin provided helpful comments on the manuscript.

LITERATURE CITED


FORAGING ECOLOGY AND HOST RELATIONSHIPS OF GIANT COWBIRDS IN SOUTHEASTERN PERU

SCOTT K. ROBINSON

ABSTRACT.—I studied the foraging ecology and host relations of a population of brood parasitic Giant Cowbirds (Scaphidura oryzivora) in the undisturbed Manu National Park of Amazonian Peru. Giant Cowbirds foraged mostly along rivers and lakes where they searched for arthropods, fruit, and nectar. Male cowbirds sometimes foraged on the backs of mammals on which they captured biting flies. The two potential host species, the Russet-backed Oropendola (Psarocolius angustifrons) and Yellow-rumped Cacique (Cacicus cela) defended their colonies against cowbird parasitism, regardless of colony location. Giant Cowbirds concentrated most of their visits on oropendola nests, which were sometimes left untended when the colony members were foraging together in a flock away from the colony. Yellow-rumped Caciques, however, seldom left their colonies untended and no cowbirds were known to fledge from cacique nests during the five years of the study. This situation differs markedly from that reported by Smith (1968, 1979, 1980) in Panama where Giant Cowbirds parasitized both oropendolas and caciques, and at least some hosts did not chase cowbirds away from their nests. I argue that the major difference between the two study areas is that in Peru, both caciques and oropendolas generally raise only a single young, which means that there can be no advantage to being parasitized as there is in Panama.

Received 29 July 1987, accepted 18 Dec. 1987.

One of the most remarkable examples of coevolution ever described is the relationship between the brood parasitic Giant Cowbird (Scaphidura oryzivora) and its colonial hosts, the Yellow-rumped Cacique (Cacicus cela vitellinus) and various oropendolas (Psarocolius spp.) in Panama (Smith 1968, 1979, 1980). Smith found that some Giant Cowbirds were not aggressively chased away from nests in colonies that were unprotected by wasp nests. These cowbirds laid nonmimetic eggs, and the nestling cowbirds cleaned botfly (Philornis spp.) larvae, which burrow into nestlings, from their nest mates (Smith 1968). As a result, parasitized nests fledged more host young on average than unparasitized nests. Cowbirds, however, were aggressively chased away from colonies protected by wasp nests, perhaps because the wasps provide protection against botflies. Only stealthy cowbirds that laid mimetic eggs could gain access to and parasitize nests in colonies protected by wasps. Smith concluded that it is to the hosts' benefit to allow their nests to be parasitized, but only in nests, unprotected by wasps. In response to this situation, the Giant Cowbird has evolved behavioral and egg-color polymorphisms.

In this paper, I describe the foraging ecology and host relationships of

1 Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820.
the Giant Cowbird in an undisturbed section of Amazonian Peru. At this site, Giant Cowbirds regularly visited colonies of two potential host species, the Yellow-rumped Cacique (*C. c. cela*), and the Russet-backed Oropendola (*Psarocolius angustifrons*), but were known to parasitize only the oropendola.

**STUDY AREA AND METHODS**

This study was conducted in the Manu National Park in the Department of Madre de Dios, southeastern Peru at 11°51'S, 71°19'W. All observations were made in the vicinity of the Cocha Cashu Biological Station, an area of undisturbed lowland floodplain forest of the Manu River. The study area includes an oxbow lake (Cocha Cashu) and a section of the Manu River (see Fig. 1). Terborgh (1983) described the vegetation and climate of the Cocha Cashu area.

This study was conducted during 24 months in the field, 1979–1984, as part of a study of the social behavior of the Yellow-rumped Cacique and other colonial Icterinae (Robinson 1984, 1985a, 1986a). I visited each active colony daily and recorded the phenology, fates, and positions of each nest (see Robinson 1985b). Caciques, oropendolas, and cowbirds were captured in mist nets placed near active colonies and roost sites. During the study I caught 8 cowbirds, 10 oropendolas, and over 700 caciques. All captured individuals were color-marked. Whenever cowbirds were observed at host colonies, I recorded the following data: date, number of cowbirds, host reaction, and any behavior patterns used by cowbirds to gain entrance to host nests. Contents of all oropendola nests and most cacique nests were not checked because they were too high, though I have checked nest contents of 106 low cacique nests. For this reason, I have no data on eggs, egg mimicry, or percentage of oropendola nests parasitized.

In 1982, as part of a larger census of the Cocha Cashu bird community (see Terborgh 1985), the locations and activities of any Giant Cowbirds observed were recorded in the 115-ha area shown in Fig. 1. The census area is crisscrossed by trails located 100–200 m apart, each of which was covered at least 20 times during the mid-August to mid-November census period. Once a week in 1982, I also paddled my boat around the entire lake and recorded the locations of Giant Cowbirds. Whenever I observed a cowbird foraging, I recorded its location, sex, height, and the substrate on which it was searching for prey. I used only the first observation from each independent sequence for statistical analyses.

**HOST SPECIES**

Russet-backed Oropendolas usually nested together with Yellow-rumped Caciques in the same or adjacent trees (Robinson 1985a). The two potential host species generally coexisted peacefully and often built their pendent, pouchlike nests close together, though in some years male oropendolas defended sections of colony trees against caciques (Robinson 1985a). Colonies were situated in isolated trees in the lake bed and in the forest (Fig. 1). Most colony sites provided protection against arboreal mammals such as monkeys, which often attacked colonies in less isolated positions (Robinson 1985b). Within colonies, caciques clustered their nests together and mobbed avian nest predators such as Cuvier’s Toucan (*Ramphastos cuvieri*) and the Black Caracara (*Daptrius ater*) (Robinson
Pig. 1. Map of study area showing locations of colonies of Yellow-rumped Caciques (closed circles), russet-backed Oropendolas (open circles), and mixed colonies (half open circles). Dashed line encloses area censused in 1982.

1985a). Oropendolas, however, often scattered their nests throughout a colony tree, perhaps because lone oropendolas, which are 2–6 times heavier than caciques (Robinson 1985a), are large enough to chase away most avian predators (Robinson 1986a). None of the colonies studied in 1981 and 1982 was located around wasp nests.

Cacique nests were generally continuously available to cowbird parasitism during the breeding season, while most oropendola nests were available for only brief periods (Fig. 2). Oropendola nesting was significantly more synchronous than that of the cacique (Fig. 2; Kolmogorov-Smirnov test, $\chi^2 = 16.4, P < 0.001$). The majority of oropendolas began nest-building within three of the 15-day periods (Fig. 2). In 1981, I estimated that 114 different female caciques nested on Cocha Cashu, compared with only 28 female oropendolas.
RESULTS

Foraging ecology.—Giant Cowbirds foraged in small flocks (Table 1) near water and generally avoided the forest interior (Fig. 3). Cowbirds were generalized in their diet, substrate use, and tactics used to catch prey. Cowbirds ate fruit (chiefly two moraceous species, *Ficus trigona* and *Cous-sapoa*), nectar (chiefly *Combretum* and *Quararibea*), and arthropods.

Casqued (*P. oseryi*), Crested (*P. decumanus*), and Olive (*P. yuracares*) oropendolas also occurred in the Cocha Cashu area. J. Leak (pers. comm.) observed no cowbird visits at two forest colonies of Casqued Oropendolas. However, I have no data on the relationships between Giant Cowbirds and the other two species of *Psarocolius*.
Cowbirds used three very different foraging tactics when searching for arthropods: (1) Terrestrial foraging. Cowbirds often walked along the shore of Cocha Cashu and along river beaches exposed during the dry season. When foraging along the lake shore, cowbirds both gleaned small prey from the surface and turned over leaves with their beaks. When foraging on beaches, cowbirds walked along the sand and gleaned small insects and probed in piles of driftwood. I have seen as many as 80 Giant Cowbirds foraging together along the beaches of the nearby Alto Madre de Dios River. The largest flock I ever observed on the Manu River consisted of 26 individuals. (2) Foliage searching. When foraging along the lake margin, cowbirds often searched branches and foliage up to 10 m above the water. Males generally searched branches more than females (Table 2, $\chi^2 = 10.84, df = 2, P < 0.001$), where they used their beaks to tear off strips of bark. Females searched significantly more living and dead leaves (Table 2) where they used their beaks to probe into curled leaves and extract hidden prey. (3) Foraging on mammals. Giant Cowbirds regularly foraged for insects on the backs of capybaras ($Hydrochoerus hydrochoerus$), a large aquatic rodent that occurs primarily in marshes along the edge of the lake (Fig. 3). Capybaras allowed cowbirds to feed on their backs, presumably because cowbirds eat the biting horse flies ($Tabanidae$) that swarm around capybaras during the day. In one 12-min observation period, a male cowbird caught 24 large (1.5–2.5 cm) tabanids. During part of this period, the capybara elevated its head at a 45° angle, closed its eyes, and allowed the cowbird to walk on its nose. Capybaras would not, however, allow cowbirds to probe in their fur; each time this happened, the capybara rolled over on its side, or shook itself. I also once saw a Giant Cowbird foraging on the back of a tapir ($Tapirus terrestris$).
Raid on host colonies. — Cowbirds usually visited colonies either singly or in small groups (Table 1). Before visits, the foraging flocks split up, some individuals staying behind and others moving towards colonies (Table 1; foraging flocks are significantly larger than flocks that visit colonies, $P < 0.001$, $x^2 = 40.2$).

Female Giant Cowbirds most often visited the nests of Russet-backed Oropendolas. Of 88 separate visits to active colonies witnessed, only two were directed at nests of the Yellow-rumped Cacique; all others were directed at oropendola nests. Similarly, cowbirds concentrated most of their visits on colonies when oropendolas were completing nests (Fig. 2). The frequency of cowbird visits differed significantly from the frequency of caciques completing nests during each period (Kolmogorov-Smirnov Test, $x^2 = 39.9$, $P < 0.001$). The distribution of cowbird visits did not, however, differ significantly from the frequency of oropendola nests completed during each period (Kolmogorov-Smirnov Test, $x^2 = 2.42$, $P > 0.20$).

Both caciques and oropendolas aggressively chased cowbirds out of colonies. Of 88 visits witnessed, cowbirds were chased away 74 times by oropendolas of both sexes and by male caciques. On 9 occasions, male caciques chased cowbirds away from undefended oropendola nests, which suggests that oropendolas may derive an antiparasitic benefit from nesting with caciques. On 8 of the remaining 14 visits, cowbirds left the colony before they either entered a nest or were chased away. Only 6 of the 88 visits resulted in a female cowbird’s entering an oropendola nest. All six visits occurred when the oropendolas were away foraging. One of these nests later fledged a cowbird. The most successful cowbird visit occurred when a flock of three females and a male flew into an undefended colony, and the females entered three nests in which incubation had just begun. There were no caciques nesting in this colony tree.

### Table 2

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Percentage</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Living leaves</td>
<td>4.8%</td>
<td>25.8%</td>
<td></td>
</tr>
<tr>
<td>Dead leaves</td>
<td>45.2%</td>
<td>54.8%</td>
<td></td>
</tr>
<tr>
<td>Dead branches</td>
<td>50.0%</td>
<td>19.4%</td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>42</td>
<td>31</td>
<td></td>
</tr>
</tbody>
</table>

Robinson • GIANT COWBIRDS IN SOUTHEASTERN PERU 229
When cowbirds visited colonies as a group, males sometimes seemed to lure oropendolas away from their nests, while females then entered the untended nests. On one visit, a male cowbird flew up to a group of oropendola nests where a male and female oropendola were sitting. The cowbird perched nearly vertically within less than 0.5 m from the male oropendola, and it puffed up its head and neck feathers, a display similar to that used during courtship (described in Skutch 1954). Both the male and female oropendola then started chasing the cowbird out of the tree. As soon as the chase began, two female cowbirds flew up to the untended nests and looked inside. The female oropendola returned before the cowbirds entered any of the nests. On five other occasions, I saw females approach nests when the oropendolas were chasing male cowbirds. N. Smith (pers. comm.) has observed similar behavior in Panama.

Three other group visits involved what appeared to be coordinated
efforts among female cowbirds. In each of these visits, one of the females entered a nest containing an incubating female, which resulted in a chase. The other female cowbirds then flew up to the nest as soon as the female oropendola was out of the nest. Each time the second female cowbird was about to enter the nest, she was chased away by male caciques. Chapman (1928) and Skutch (1954) also described group visits by cowbirds.

On two occasions, cowbirds entered oropendola colonies during attacks by a juvenile Bicolored Hawk (*Accipiter bicolor*), which frequently chased oropendolas. Both times, however, the oropendolas returned before the cowbirds entered any nests.

Cowbirds appeared to have considerable difficulty entering cacique nests. I twice saw female cowbirds in recently abandoned cacique colonies. These females poked their heads into six nests but only succeeded in entering one. One female cowbird appeared to become trapped halfway into a nest before giving up and leaving. The entrances in cacique nests may be too small for most cowbirds in Peru.

Giant Cowbirds appeared to have a minimal impact on their hosts in the Cocha Cashu area during this study. None of the 168 female caciques I observed with fledglings was feeding cowbirds, and only 3 of 24 oropendola families were feeding a cowbird. All 24 oropendola females fed only a single fledgling, whether it was a cowbird or an oropendola. Similarly, none of the 106 cacique nests I have checked during incubation contained a cowbird egg.

**DISCUSSION**

*Host relationships in Panama and Peru.*—The host relationships described in this paper differ considerably from the situation described by Smith (1968, 1979, 1980) in Panama. In Peru, Giant Cowbirds specialized on oropendolas and seemed to avoid the far more abundant Yellow-rumped Cacique. In contrast, cowbirds regularly parasitized both caciques and oropendolas in Panama and elsewhere in Central America (Skutch 1954, Smith 1968). In southeastern Peru, both caciques and oropendolas chased away cowbirds, regardless of whether or not their colonies were protected by wasps. Cowbirds used a variety of tactics to enter host nests, all of which involved stealth or possibly distraction. I never saw caciques or oropendolas passively allow a Giant Cowbird to enter a nest, even though many cacique nestlings have heavy botfly infestations, and none of the colonies I studied was protected by wasps or bees (Robinson, unpubl. data). In Panama, on the other hand, oropendolas show little aggression towards cowbirds in colonies that are unprotected by wasps. It is, however, difficult to separate the effects of cowbirds on caciques and oropendolas because Smith (1968) lumped the two host species together.
Why, then, do cowbirds specialize on oropendolas in Peru? The answer to this question may be related to the different social organization of the two potential host species. In Peru, most female oropendolas from a colony foraged together in a flock (Robinson 1986a, unpubl. data); males often accompanied these flocks (Robinson 1986a). As a result, oropendola colonies were often vacant when the flock was away foraging. During such times, oropendola nests were open to attacks by cowbirds. Cacique females, on the other hand, foraged singly or in small flocks, and generally did not leave the colony in a single flock (Robinson, unpubl. data). Dominant males consorted and defended each female separately, and low-ranking males spent much of the day singing and displaying in colonies (Robinson 1986c). As a result, large (>20 nests) cacique colonies were seldom vacant and were, therefore, protected most of the time. Oropendolas appeared to derive a considerable benefit from nesting with caciques. In this context, it is curious that oropendolas often nested apart from caciques and occasionally defended sections of colony trees against caciques (Robinson 1985a).

Why do caciques and oropendolas chase away cowbirds? Perhaps the major reason why there are no “dumper” cowbirds in the Cocha Cashu area is that both caciques and oropendolas generally only fledge a single young (Robinson 1986b, unpubl. data). In order to raise nestlings, cacique females greatly accelerated their foraging rate, lost weight, and even then generally only raised one young from a clutch of two (Robinson 1986b). These data suggest that females can only obtain sufficient food to raise a single young. Under such circumstances, there can be no benefit in raising a cowbird nestling even though botflies may pose a serious problem. It is unlikely that a cacique could raise both a cowbird and its own young, especially because cowbirds are larger than caciques (Robinson, unpubl. data). It is much more likely that a female oropendola could raise both a cowbird and an oropendola, especially because cowbirds are smaller, but I never saw a female oropendola with a mixed family. In contrast, both caciques and oropendolas routinely raised more than one young in Panama, and mixed families occurred commonly (Smith 1968). Smith artificially augmented clutches in Panama and found that caciques and oropendolas could raise more than two young. For unknown reasons, caciques and oropendolas may be less food limited in Panama than in Peru. It is also possible that the three other species of oropendolas in Amazonian Peru (P. yuracares, P. oseryi, and P. decumanus) have different relationships with the Giant Cowbird than the Russet-backed Oropendola.

Foraging ecology and brood parasitism.—Brood parasitism in birds is often associated with unusual diets and foraging tactics (reviewed in Hamilton and Orians 1965, Payne 1977, May and Robinson 1985). Brown-
headed Cowbirds (*Molothrus ater*), for example, historically followed herds of nomadic ungulates, a behavior that may have predisposed them towards the evolution of brood parasitism (Mayfield 1965). By parasitizing the nests of other species, Brown-headed Cowbirds could reproduce without staying for long in one place. Alternatively, the evolution of brood parasitism may have made such a nomadic niche possible. Giant Cowbirds also foraged with mammals, and most of their foraging is concentrated in a narrow belt along rivers and lakes in microhabitats that vary in availability with fluctuations in water levels. Within the available microhabitats, cowbirds wander widely, sometimes foraging one or more km from the colonies that they visit. The brood parasitic habits of the Giant Cowbird may make it possible both to reproduce and exploit temporally variable resources that are scattered along the narrow edges of rivers and lakes.

The evolution of host specialization in Giant Cowbirds. — Hamilton and Orians (1965) hypothesized that three conditions would favor the evolution of brood parasitism: (1) the potential parasite is closely related to the host, which increases the chances that the nestling diet will be appropriate, (2) the parasite is rare relative to the host, and (3) the host is a colonial nester because these species show reduced territorial behavior and their nests are easy to find. The Giant Cowbird association with both oropendolas and caciques clearly fits all of these criteria. Cowbirds are in the same subfamily as oropendolas, and both eat essentially the same kinds of food (Robinson 1985a, unpubl. data). Giant Cowbirds are considerably less common than their hosts and are restricted to bottomland areas along lakes and rivers. At least in Peru, neither oropendolas nor caciques appear to suffer high levels of cowbird parasites. Oropendolas and caciques are also very conspicuous and are located close to cowbird feeding areas, though oropendolas defend colonies against cowbirds. In addition, caciques and oropendolas place their nests in sites that are inaccessible to mammals and actively defend their colonies against most avian predators (Robinson 1985b). As a result, a high percentage of their nests escape predation and eventually fledge young. Over 40% of all cacique nests and 50% of all oropendola nests on Cocha Cashu fledged young (Robinson 1985b, unpubl. data), a very high percentage for a tropical bird (cf Oniki 1979, Skutch 1985). Oropendolas and caciques are, therefore, ideal hosts once their antiparasite defenses have been circumvented.

Colonies of caciques and oropendolas also support several other species of birds. Troupials (*Icterus icterus*) and Piratic Flycatchers (*Legatus leucophaius*) pirate oropendola and cacique nests and use them for their own eggs and young (Robinson 1985a). These two species parasitize the nest
building and predator defenses of caciques and oropendolas. Giant Cowbirds go one step further and parasitize both the nests and the parental care of their hosts. In Panama, Giant Cowbirds had further evolved a mutualistic relationship in which some cowbirds actually benefit their hosts by parasitizing them, while others lay host-specific mimetic eggs (Smith 1968). Oropendolas and caciques may also enjoy mutual advantages by nesting together, since both species mob predators, chase away cowbirds, and give loud alarm calls (Robinson 1985a, b, unpubl. data). These parasitic and mutualistic relationships are among the most complex ever described for birds.

ACKNOWLEDGMENTS

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LITERATURE CITED


SNAG PREFERENCES OF WOODPECKERS FORAGING IN A NORTHEASTERN HARDWOOD FOREST

STEPHEN K. SWALLOW,¹ RONALD A. HOWARD, JR.,² AND R. J. GUTIÉRREZ³

Abstract.—To assess the role of snags in cavity-nesting bird communities ornithologists need to identify the types of snags which foraging cavity-nesters select. Using data from a hardwood forest in central New York, this paper develops a logistic regression analysis of snags used for foraging by woodpeckers (Picidae) and compares these results to a companion study of snags used as nest-cavity sites. Snags used for foraging were in earlier stages of decay than snags used for nest cavities. Woodpeckers, however, exhibited less sensitivity to snag size and decay-stage when foraging than when excavating nest cavities. The importance of snags to cavity-nesters will depend both on the history of a particular forest and on the preferences which birds demonstrate for dead wood in various forms (such as snags, dead limbs, logs, etc.). Received 17 June 1987, accepted 18 Nov. 1987.

Many studies of cavity-nesting birds associate snag characteristics with the presence of nesting or roosting cavities to assess habitat quality. But basing descriptions of habitat quality on nesting or roosting sites alone may fail to consider other critical habitat components (Conner and Adkisson 1977; Mannan et al. 1980; Cline et al. 1980; Brawn et al. 1982; Carey 1983a, b; Davis et al. 1983; Raphael and White 1984; McComb et al. 1986; Sedgwick and Knopf 1986; Swallow et al. 1986). If sites used for nesting and roosting differ from those used for foraging, then habitat suitable for cavity sites may fail to include adequate feeding sites (see Conner 1980). This study addresses some habitat features important to the foraging requirements of cavity-nesting birds.

Some recent literature suggests that snags may not be essential to cavity-nesting birds. Several studies (Brawn et al. 1982, Carey 1983b, Sedgwick and Knopf 1986) suggest that live trees provide adequate supplies of dead wood (e.g., dead limbs) in many forests. However, snags remain as one potentially important and easily measured resource for cavity-nesters. Furthermore, while dead wood in the canopy may provide sufficient foraging or nesting substrate in some forests, forest manipulations to supply dead wood will likely prove most efficient when focused on snag (whole tree) management. In order to assess both the requirements of cavity-

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nesters for dead wood and to assess the role of snags in these bird communities, ornithologists need to identify those snags which foraging cavity-nesters select. While other sources of dead wood exist, this study concentrates on the snag resource.

Cavity-nesters, woodpeckers (Picidae) in particular, often leave identifiable foraging excavations on the tree boles. In this study, Hairy Woodpeckers (*Picoides villosus*) and Pileated Woodpeckers (*Dryocopus pileatus*) were the most common hewing species, while Red-bellied Woodpeckers (*Melanerpes carolinus*), Northern Flickers (*Colaptes auratus*), and Downy Woodpeckers (*P. pubescens*) were either less common or did less excavating. The first objective of the study was to differentiate between useful snags and snags not useful for foraging. The second objective was to compare factors which influence excavators' selection of snags for feeding or shelter. The study focused only on one major foraging method (excavation) used by cavity-nesters; foraging by other methods (e.g., gleaning and bark scaling, [Kilham 1965]) was eliminated.

**METHODS**

The data in the present study were collected at the Cornell Biological Field Station, Shackleton Point, Bridgeport, New York. In a 45-ha study area established during the summer of 1979, snags were sampled within 0.049-ha plots located by an unbiased procedure detailed by Swallow et al. (1986). The sample included snags in both mature sites (N = 10, age 90–110 years) and second growth forest sites (N = 51, age 25–45 years; total area of 0.49 ha and 2.5 ha, respectively) typical of central New York's maple (Acer spp.)-ash (Fraxinus spp.)-elm (Ulmus spp.) forest. The second growth forest sites developed on farmland abandoned in the mid-1930s, while adjacent mature forest sites were primarily old growth (post-Civil war) riparian sites. Second growth sites were in early aggradation, just becoming useful for cavity nesters, while mature sites were in middle to late aggradation, with greater supplies of dead wood. Carey (1983a) provides a brief introduction to forest development relative to dead wood supplies, while Swallow et al. (1986) quantify snag densities in the present study area. Snags were defined as any dead, standing woody stem >1.5 m tall and ≥10.1 cm in diameter at breast height (1.37 m).

Snag characteristics measured included dbh, total height, presence of external shelf fungi (*Fomes* spp.), number of limbs ≥7 cm in diameter at their origin and ≥1 m long, a subjective estimate of canopy closure above the snag (percent of a 3-m diameter circle occluded by canopy vegetation above the snag), percent of a snag's trunk covered by foliation (from nearby shrubs and trees) within 0.3 m of the trunk, wood density (g/cm dry weight of a 2.5–5 cm increment bore sample taken at breast height), snag species, forest type (second growth or mature), and percent (in quartiles) of the snag covered by bark. These variables measured snag size and/or served as indicators of the snag's stage of decay. Rather than using a *priori* definitions of decay stages (e.g., Cline et al. 1980), these methods allowed the data (i.e., the birds) to reveal those characteristics which best define the decay stage preferred for foraging.

Any snag with visible evidence of feeding by excavators (i.e., drilling or irregularly-shaped excavations) was classified as a "feeding snag." This bivariate classification separated snags not yet used for foraging by excavation from those which had been used and was compatible with logistic regression analysis (Hanuscheck and Jackson 1977:179–245, Press and Wilson...
Press and Wilson 1978). Qualitative observations during >500 man-hours of field work suggested that feeding snags continued to provide foraging substrate for hewing birds. This study did not discriminate among excavating bird species. Qualitative observations and field station records (Severinghaus 1979; unpubl. data of R. A. Howard and C. Welsh [1982] and of R. A. Howard and C. Hibbard [1983]) provided substantial knowledge of the hewing species present in or near the study area at the time of and immediately following this study. Hairy and Pileated woodpeckers were the most common hewing species and Red-bellied Woodpeckers were occasionally reported. Northern Flickers and Downy Woodpeckers were also common, but they forage most often by means other than hewing (see Conner 1980, 1981). In addition, Bull (1974:349-363) listed the Three-Toed Woodpecker (P. tridactylus) and the Black-backed Woodpecker (P. arcticus) as very rare, irregular winter visitants in central New York, but these species have not been recorded at the field station.

Among the snag characteristics measured, logistic regression analysis (Hanusheck and Jackson 1977:179-245, Press and Wilson 1978, Harrell 1980) identified the set most strongly (P < 0.05) associated with the presence of foraging excavations. Chi-square analyses, with expected frequencies computed from the border totals (Snedecor and Cochran 1967:250-253), aided interpretation of multivariate results.

A preference index (Fig. 1) aided interpretation of results pertaining to dbh. The numerator of this index expressed the excess in the relative use of snags in a dbh class beyond the relative availability of snags in that class; this numerator was Strauss' L (Strauss 1979, Raphael and White 1984:37-38). The denominator of the present index (Fig. 1) weighted Strauss' L by relative availability. This set of L statistics was not independent; therefore, only the logistic regression and chi-square analyses were used for tests of significance.

For clarity in the remaining sections, the paper refers to both roost or nest cavities as "nest cavities" and refers to the associated snags as "nesting snags." One snag may be both a feeding snag and a nesting snag.

RESULTS

All analyses reported herein employed the full sample of 388 snags; 234 snags (60%) had some foraging excavations, and 220 (57%) were elm snags. Elm snags comprised 77% (89 of 116) of the snags in mature forest sites. Elm (89 of 220) and ash (18 of 27) snags were located more often than expected in mature forest sites, while all (64) poplars (Populus spp.), all (13) red maples (A. rubrum), and nearly all (41 of 42) willows (Salix spp.) were in second growth sites ($\chi^2 = 77.59$, $P < 0.005$, 5 df).

The results of chi-square tests of association between the presence of foraging excavations on a snag and various explanatory variables, considered singly, are summarized in Table 1. Foraging excavations probably were not independent of the presence of shelf fungi, dbh, percent of bark remaining, snag species, and the presence of nesting cavities (Table 1).

Based on logistic regression analysis, the probability that a snag had feeding excavations was higher for elm snags, increased with the proportion of bark lost, dbh, degree of canopy closure, and number of limbs, but decreased with snag height (Table 2). Only variables in this logistic regression model were significant ($P < 0.05$) in the multivariate context; however, wood density would have entered the model next (with a neg-
Fig. 1. Preference for snag dbh by foraging woodpeckers. Preference index = (N feeding snags in dbh class/N feeding snags)/(N snags in dbh class/N snags) – 1. Dbh classes in cm are: 1 = 10.1–15, 2 = 15.1–20, 3 = 20.1–25, 4 = 25.1–30, 5 = 30.1–35, 6 = >35. N for each dbh class is, respectively: 165, 98, 55, 35, 16, 19.

Based on the same data set, Swallow et al. (1986:Table 1, Model 2) reported a logistic regression model for nesting snags. Only three variables entered the nesting snag model: dbh, bark cover, and snag height. In both the logistic regression model for feeding snags (Table 2) and the logistic regression model for nesting snags (Swallow et al. 1986:Table 1, Model 2), the coefficients for these variables (dbh, bark cover, and snag height)
Table 1
SIGNIFICANCE OF SNAG CHARACTERISTICS AS UNIVARIATE PREDICTORS OF THE PRESENCE OF FORAGING EXCAVATION ON SNAGS IN CENTRAL NEW YORK

<table>
<thead>
<tr>
<th>Variable name: levels</th>
<th>Feeding excavations present more often than expected for:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy cover: &lt;25%, 25% to &lt;50%, 50% to &lt;75%, ≥75%</td>
<td>No pattern (2.48, &gt;0.25, 3)</td>
</tr>
<tr>
<td>Total height (m): 1.5 m height classes between 1.5 m and 16.5 m (1.5 to 3 m, etc.)</td>
<td>No pattern (8.68, &gt;0.25, 9)</td>
</tr>
<tr>
<td>Fungal conks*: present or absent</td>
<td>Snags with conks (11.68, &lt;0.005, 1)</td>
</tr>
<tr>
<td>Dbh: 5 cm dbh classes between 10.0 cm and ≥35.0 cm</td>
<td>Larger diameter snags* (22.90, &lt;0.005, 5)</td>
</tr>
<tr>
<td>Dbh: &lt;20 cm dbh, ≥20 cm dbh.</td>
<td>Snags &gt;20 cm dbh (15.29, &lt;0.005, 1)</td>
</tr>
<tr>
<td>Bark remaining: &lt;25%, 25% to &lt;50%, 50% to &lt;75%, ≥75%</td>
<td>Snags with &lt;75% of their bark intact (24.28, &lt;0.005, 3)</td>
</tr>
<tr>
<td>Snag species: Ulmus spp., Acer rubrum, Fraxinus spp., Populus spp., Salix spp., all others</td>
<td>Ulmus spp. and &quot;other&quot; snags, less than expected for Fraxinus spp. and Populus spp. (72.22, &lt;0.005, 5)</td>
</tr>
<tr>
<td>Forest type: second growth or mature</td>
<td>No pattern (1.30, &gt;0.25, 1)</td>
</tr>
<tr>
<td>Roosting/nesting cavities: present or absent</td>
<td>Snags with these cavities (5.26, &lt;0.025, 1)</td>
</tr>
</tbody>
</table>

* Result of chi-square test of variable levels versus presence or absence of foraging excavations. Expected frequency of foraging snags was 0.60 at each level. N = 388. Chi-square test statistic, P, and degrees of freedom in parentheses.

b External shelf fungi (Fomes spp.).

c See Fig. 1.

d Tilia americana, Alnus spp., Quercus spp., Pyrus spp. were lumped in the "other" category due to small sample size (N < 5).

had the same sign. Notably, an indicator variable for the presence of foraging excavations did not improve (P > 0.05) the nesting snag model (after accounting for dbh, bark cover, and snag height); therefore, for the purposes of comparison, the two models were considered statistically independent.

The "logistic regression elasticity" measures the relative contribution of a dependent variable on the probability of bird use for a particular purpose (feeding or nesting). An elasticity measures the percentage change in the probability of bird use, given that a selected independent variable changes by 1%. For example, at the mean value of all independent variables, a 1% increase in dbh raises the probability that a snag contains foraging excavations by 0.19% and raises the probability that a snag contains a nest cavity by 1.3% (Table 3). An increase in snag height or bark coverage has a greater, adverse impact on a snag's probability of use for nesting than on its probability of use for feeding (Table 3).
Table 2
LOGISTIC REGRESSION MODEL\(^a\) FOR THE PROBABILITY THAT FORAGING EXCAVATIONS WERE PRESENT ON A SNAG IN CENTRAL NEW YORK

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>Coefficient (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>—</td>
<td>0.566 (0.796)</td>
</tr>
<tr>
<td>Snag species(^b)</td>
<td>0.567</td>
<td>1.01 (0.246)</td>
</tr>
<tr>
<td>Bark remaining(^c)</td>
<td>3.34</td>
<td>-0.542 (0.150)</td>
</tr>
<tr>
<td>Dbh (cm)</td>
<td>19.15</td>
<td>0.0467 (0.0219)</td>
</tr>
<tr>
<td>Canopy cover(^c)</td>
<td>2.76</td>
<td>0.327 (0.119)</td>
</tr>
<tr>
<td>Total height (m)</td>
<td>8.80</td>
<td>-0.00866 (0.00273)</td>
</tr>
<tr>
<td>Number of limbs</td>
<td>0.557</td>
<td>0.511 (0.197)</td>
</tr>
</tbody>
</table>

\(^a\) The probability that a snag contains feeding excavations = 1/[1 + exp\((-XB)\)] where XB is calculated by taking the product of each coefficient and the value of the corresponding variable, summing these products, and adding the intercept (Hanusheck and Jackson 1977:187-189, Harrell 1980). \(P < 0.03\) for all variables; nonsignificant intercept retained for completeness; model \(P < 0.01\).

\(^b\) Coded: Ulmus spp. = 1, other species = 0.

\(^c\) For the levels in Table 1, coded 1, 2, 3, 4, respectively.

Discussion
The high proportion of snags with foraging excavations reported here (60%) and similar results in the west (Raphael and White 1984:44) indicate that snags can be important foraging sites for several excavating bird species. Relative to excavators, this study makes no attempt to determine whether the snag resource is an essential component of the available dead wood. Such a determination requires data measuring the proportion of foraging effort which birds invest on various sources of dead and live wood relative to the availability of these substrates.

Observations of foraging activity (Kilham 1965, 1976; Conner 1981;...
Brawn et al. 1982; Raphael and White 1984:42–43) indicate that large cavity-nesters (e.g., Pileated and Hairy woodpeckers) forage on snags more often by excavation than by gleaning; this observation probably indicates that the present results are biased toward larger species. Furthermore, Kilham (1961, 1965, 1976) reports that Downy and Hairy woodpeckers remove only the outer bark while bark chipping, and that, after removing some bark, Pilated Woodpeckers almost always excavate in newly exposed wood. Thus, foraging behavior would not confound bark cover as an (imprecise) indicator of deterioration. Nevertheless, the present results suggest that, when foraging by excavation, birds select snags with less bark (older snags). Snags with most of their bark intact may still be selected by superficial foragers (Kilham 1965, Brawn et al. 1982, Raphael and White 1984:43–45).

The two broad characteristics considered most important in previous studies (e.g., Cline et al. 1980, Mannan et al. 1980) are snag size and decay-stage. Yet, few variables clearly measured either size or decay-stage. One important example is wood density. Wood density measured wood softness due either to decay or differences in tree species. However, after accounting for all other significant variables, wood density provided no significant \( P > 0.05 \) new information; that is, the variables in the logistic regression (Table 2) jointly described wood softness/decay-stage and other critical features of foraging snags better than wood density. This result lends additional support to the discussions below.

Other studies (Mannan et al. 1980, Brawn et al. 1982, Raphael and White 1984) found no preference for foraging on particular snag species. Kilham (1961, 1965, 1970) did document preferences of Hairy and Downy woodpeckers for foraging on elms and paper birches \( (Betula papyrifera) \); however, Kilham’s observations apply only to diseased or “defective” living trees (not snags) and only to superficial foraging methods (not excavation). Since elm snags constituted a high proportion of snags in mature forest sites in the present study, excavators’ selection of elm snags may have indicated selection of mature forest sites. Alternatively, since ashes, which were also associated with mature forest sites, were generally young snags (usually with almost all their bark, few or no conks, more often with small branches and twigs intact) and elms were in a more advanced state of decay, the selection of elms may have represented a decay-stage preference. The latter interpretation was consistent with evidence discussed by Swallow et al. (1986) and with the moisture hypothesis discussed below relative to canopy closure.

At first, canopy closure appears unimportant (Table 1). However, after accounting for other characteristics of feeding snags, the results show that canopy closure significantly improves the logistic regression model for
feeding snags (Table 2). This result demonstrates the need to understand the relationship between snags and cavity-nesters in a multivariate context.

The positive association between feeding excavations and canopy closure (Table 2) conformed with several alternative interpretations. Canopy closure could have indicated a preference for snags with some overhead cover, for snags with more advanced decay, or for mature forest sites. Mannan et al. (1980) and Brawn et al. (1982) found a general tendency for cavity-nesters to feed in older forest plots. This study, however, found no clear evidence of a preference for their foraging in older forest sites (i.e., the forest type variable was insignificant, at \( P > 0.05 \), in the logistic regression analysis). The "canopy closure indicated decay" interpretation remained most persuasive for two reasons. First, the death of a large tree creates both a snag and a canopy opening; therefore, the degree of canopy closure indexed time since the tree died. Second, a closed canopy (typical of mature sites) possibly created moist conditions which promoted decay. This evidence suggested that canopy closure and the selection of elm snags partially defined a decay-stage preference.

Raphael and White (1984:43-45) reported a discriminant function analysis similar to the logistic regression reported here (Table 2). Their results showed a similar relationship between the presence of feeding excavations and dbh, total height, and deterioration of limbs.

The results in this paper show that as bark loss increases and total height-decreases, the probability that a snag contains feeding excavations or nest cavities, or both, increases. These characteristics indicate deterioration of the snag. However, the number of limbs on a snag is inversely associated with decay stage (e.g., Cline et al. 1980) and is positively associated with feeding excavations (Table 2). These results support hypotheses (Mannan et al. 1980, Brawn et al. 1982) that, on average, snags become useful for feeding earlier in the decay process than when snags become useful for nest-cavity sites. Of course the relevant decay stages may differ across bird species.

The positive influence of snag dbh on feeding use (Table 2) indicates that foraging excavators may prefer large snags (especially snags > 20 cm dbh, Table 1 and Fig. 1). Two factors may account for this result: larger snags are likely to supply more prey for a given foraging effort (Raphael and White 1984:53) and both foraging excavators and their prey may encounter larger snags more often. This result underscores the importance of large snags for cavity-nesters (Brawn et al. 1982, Raphael and White 1984:53–54). However, future research should address the response of cavity-nesting birds to the distribution of dead wood among snags, dead portions of live trees, and fallen logs.
The dbh-bark-height similarities between feeding snags and nesting snags (i.e., signs on comparable coefficients agree) appeared as a significant univariate association between feeding excavations and nest cavities (Table 1). The presence of nest cavities was not significantly associated with the presence of feeding excavations in the multivariate context. Substantial differences between feeding snags and nesting snags were documented (i.e., relative influences of dbh, height, and bark cover quantified in Table 3 and the relative retention of limbs), yet these snag groups exhibited some similar characteristics.

A snag's suitability for both feeding and nesting depends on its size and decay-stage. Yet, while selecting snags as foraging substrate, woodpeckers appear more tolerant of size and decay-stage variation than they are while selecting snags as nest-cavity substrate; changes in key independent variables affect the probability of nesting use at a rate 4 to 7 times higher than similar changes affect the probability of feeding use (Table 3). This interpretation, however, remains sensitive to the assumption (supported by qualitative field observations) that excavations in a snag imply woodpeckers currently use that snag.

This study did not quantify any relationships between forest structure (e.g., species diversity, age structure) and foraging excavations. The occurrence of feeding excavations in 95% of the sample plots, however, provided some evidence that foraging woodpeckers accepted a broader range of forest structure/age characteristics than was accepted for nest-cavity sites (see Swallow et al. 1986; Conner 1980, 1981).

Although mature forest sites (in middle to late aggradation) may serve as a reservoir of suitable roosting/nesting snags (McComb et al. 1986, Swallow et al. 1986), the results reported here indicate that foraging on snags by woodpeckers extends proportionately into adjacent second growth forests (in early aggradation). Given that excavators may forage at long distances from nest sites (Kilham 1965, 1968, 1970, 1976), this observation is not surprising. Forests of both types supplied foraging substrate. In forest stands which produce suitable snags for both uses (primarily mature sites in this study), snags with similar characteristics may serve as feeding and nesting substrates. In particular, nesting snags may develop by normal decay from foraging snags. Research into snag dynamics and deterioration is clearly indicated, as is further research into forest development, from regenerative disturbances to steady state (see Carey 1983a), and the concomitant spatial and temporal distribution of dead wood.

Recent literature, particularly that which emphasizes nesting substrate, suggests that snags may serve only a minor role in support of cavity-nester populations (Carey 1983b, Carey and Gill 1983, Sedgwick and Knopf 1986). The role of snags may vary depending on a particular forest's
history and ecology, including not only the intensity of competition among snag-using birds, but also the management objectives of man. In some forests, whole, dead trees may prove the most easily managed and most useful form for a given volume of dead wood.

Rather than arbitrarily concentrating on single factors (e.g., habitat for nest cavities), an evaluation of the role of snags should consider the spectrum of services which a snag may supply. An integrated multivariate approach is beneficial in assessing preferences for feeding sites just as in assessing nest-site preferences. Logistic regression appears well suited for this purpose as it captures important ecological complexities but may be applied with relative ease (Brennan et al. 1986, Swallow et al. 1986).

ACKNOWLEDGMENTS

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LITERATURE CITED


ASPECTS OF THE BREEDING BIOLOGY AND PRODUCTIVITY OF BACHMAN'S SPARROW IN CENTRAL ARKANSAS

THOMAS M. HAGGERTY

Abstract. — Breeding Bachman's Sparrows (Aimophila aestivalis) were studied in central Arkansas from 1983-85. Although one case of polygyny was observed, Bachman's Sparrows were primarily double-brooded and monogamous, breeding from 17 April-26 August. All nests were built on the ground. Clutches (mode = 4) laid during the first half of the breeding season were significantly larger than those laid during the second half. Females incubated eggs for 13-14 days, and both synchronous and asynchronous hatching were observed. The average nestling and fledgling periods were 9.0 ± 0.3 [SE] and 25.0 ± 1.2 days, respectively. Both parents cared for nestlings and fledglings. Females started second broods 12.3 ± 2.3 days after first-brood nestlings fledged, while males continued to care for first-brood fledglings. When nests failed, renesting attempts were made, and some pairs attempted 5 nests in one season. The average number of nests per season was 3.1 ± 0.2, and the average time interval between failed nests and repeatlayings was 9.7 ± 1.6 days. The probability that an egg would produce a fledgling was 0.25. Predation was the major cause of nest failure. Nest success was not influenced by year, time of season, degree of nest concealment, habitat, or clutch size. On average, Bachman's Sparrow pairs produced 3.0 fledglings per year. Received 3 June 1987, accepted 5 Jan. 1988.

Although the breeding range of Bachman's Sparrow (Aimophila aestivalis) extends throughout much of southeastern United States (AOU 1983), recent literature indicates that the species is now very local and declining in many parts of its former breeding range (Tate 1986). The Nature Conservancy (Drilling 1985) has ranked Bachman's Sparrow as endangered in five states (Illinois, Tennessee, Virginia, Texas, and Missouri) and rare in three (Kentucky, North Carolina, and Oklahoma). To discover why breeding populations of Bachman's Sparrow have declined and to recommend appropriate conservation efforts, more should be known about the Bachman's Sparrow breeding biology. Although reports exist on various aspects of its nesting biology (e.g., Lloyd 1931, Brooks 1938, Nolan 1953, Meanley 1959, Weston 1968, Nicholson 1976, Hardin 1977, Hardin et al. 1982), sample sizes were small; individual birds were not marked, and estimates of reproductive success and productivity were lacking. This study was part of a larger investigation (Haggerty 1986), and its objectives were to: (1) obtain basic life history data from a marked population, (2) examine effects of various ecological factors on nest success
and clutch size, (3) determine major causes of nest failure, and (4) estimate annual productivity.

STUDY AREA AND METHODS

The research was conducted from April through September in 1983, 1984, and 1985 in Hot Spring County, Arkansas, approximately 19 km south of Malvern. Daily observations began during the second week of May and continued through the second week of August. Observations before and after that period were made weekly. Seven shortleaf (Pinus echinata) and loblolly (P. taeda) pine plantations were the principal study areas. Plantations were divided into two classes: (1) those that did not have a canopy, “old field tracts” (N = 5) and (2) those with a canopy dominated by pine trees, “pine forest tracts” (N = 2). Old field tracts had been clearcut and were between 0–4 years old, depending upon age of planted pines. Pine forest tracts were approximately 45 and 70 years old and had been thinned and control burned. Angle of slope of the study tracts ranged from 0 to 20 degrees, and the average size of the tracts was 35.0 ± 8.6 [SE] ha.

Adult sparrows were captured in mist nets, sexed by absence or presence of a cloacal protuberance and brood patch, and marked with an aluminum U.S. Fish and Wildlife Service band and a unique combination of colored leg bands. Nests were located by watching the behavior of adult birds. I visited nests with eggs every third day or until the yolk was no longer visible through the shell (usually around the seventh or eighth day of incubation), at which time daily visits were made. Egg width and length were measured with dial calipers to the nearest mm. Egg volume was calculated using the methods of Hoyt (Hoyt 1979). Once eggs hatched, nests were checked daily, and on day 5 (hatching day = day 0) of the nestling period, the young were color banded. For those nests that were located during the incubation or nestling periods, laying and hatching dates were approximated by aging nestlings and eggs. The degree of nest concealment was estimated by observing how much of the nest was exposed from the front (i.e., nest entrance), back, and right and left sides of the nest at three angular positions (10, 45, and 80 degrees) at a distance of 1 m. The following ratings were used at each position: 1 = ≤25% of the nest visible, 2 = 26–50% of the nest visible, 3 = 51–75% of the nest visible, and 4 = 76–100% of the nest visible. From those 12 points, an average nest concealment rating was obtained for each nest.

Since most nests were found after the laying period, the Mayfield method (Mayfield 1961, 1975) was used to determine egg success. The Johnson’s statistic (Johnson 1979) was used to test for differences between...
daily success rates of the incubation and nestling periods. The number of “equally good months” for breeding was calculated using the formula:

\[
\text{Months} = \exp\left(- \sum p_{i} \log_{e} p_{i}\right)
\]

where \( p_{i} \) is the proportion of nests initiated each month (MacArthur 1964).

Statistical analyses were performed using the SAS computer software system (SAS 1985). Means are presented as \( \bar{x} \pm SE \). Statistical significance was set at \( P < 0.05 \).

RESULTS AND DISCUSSION

Site fidelity.—Of 34 adults (18 males and 16 females) banded over a 2-year period, 6 (18%) returned to the tract where they nested or defended a territory during a previous year. A greater percentage of males (22%) returned than females (13%), but sample size was too small to test for significance. Return rates between years also differed, with 29% (5 of 17) of the adults banded in 1983 returning in 1984 and 0% (0 of 17) of the birds banded in 1984 returning in 1985, but again small sample size made testing for significance impractical. One male, banded in 1983 but not seen in 1984, returned in 1985. Of the 60 nestlings banded and known to have fledged, none was captured in subsequent years.

Mating system.—Bachman’s Sparrows have been reported to have a monogamous mating system (Verner and Willson 1969). Of the 31 territories that I studied, 28 contained monogamous pairs, one had a bigamous male, and two contained bachelors. Pairbonds were formed before I arrived on my study area in early May, so actual time of pairing was not known. Pairs usually remained together on the same territory throughout the breeding season. In one case, a pair was found together on the same pine plantation for two consecutive breeding seasons. In winter, Bachman’s Sparrows occur singly and in pairs (Lowery 1960), which may indicate that some pairbonds are permanent (Wolf 1977).

Breeding season and number of nesting attempts.—The nesting activities of 18 pairs and one polygynous male were monitored closely during the three field seasons. Most nesting attempts were thought to have been found, but unsuccessful nesting cycles that lasted only a few days may have been missed. Additional data were collected from 10 pairs not observed as closely.

Egg laying occurred between 17 April–26 August; a period of 132 days, but 85% of the clutches were started in May, June, and July (Fig. 1). A recent examination of Bachman’s Sparrow egg data slips (McNair 1987) found that clutch initiation occurred between 21 March–23 July (\( \bar{x} = 13 \) May, \( SD = 24 \) days, \( N = 190 \)). I found an average breeding season for
individual pairs of 69.1 ± 5.1 days (N = 19, range = 33–126), and the number of equally good months for breeding was 4.2 (127 days: see Methods). Female breeding season length was positively correlated with the number of nesting failures she experienced (Spearman’s rho = 0.83, P < 0.01, N = 19). Breeding season length is probably shorter in the northern portion of the species’ range (Hardin 1977, Wolf 1977).

Number of nesting attempts per season per female ranged from 1 to 5 (x = 3.05 ± 0.23, N = 20). Females usually laid second clutches before young of a previous brood became independent. Average number of eggs laid per female per season was 11.6 ± 1.0 (N = 20). Pairs raised at most two broods per season even though time for a third brood often existed. Although three broods per season has been reported (Burleigh 1958, Sprunt and Chamberlain 1949, Potter et al. 1980), it is unclear if individual birds were marked.

Nest placement.—Bachman’s Sparrows are ground nesters that build their nest at the base of grass clumps or other low vegetation (Weston 1968, Wolf 1977). In my study, all nests (N = 71) were built on the ground, and 50 (70%) were built at the base of Andropogon spp. grass clumps. Blades from these clumps were often woven into the nests and helped conceal them. The other 21 nests were located at the bases of various hardwood saplings, pine seedlings, forbs, and other grass species.

Clutch size.—McNair (1987) reported an average clutch size of 4.06 (SD = 0.62, range = 3–5, N = 196) for Bachman’s Sparrow. In my study the modal clutch size was 4, and the mean was 3.9 ± 0.1 (range = 2–5, N = 71). Clutches laid during the first half of the breeding season (x = 4.1 ± 0.1, N = 42) were significantly larger than those laid during the
second half ($\bar{x} = 3.7 \pm 0.1$, $N = 29$) ($t = 2.6$, $P = 0.01$, $df = 69$). Clutch size did not vary significantly among the three field seasons ($F = 0.05$, $df = 2.70$, $P = 0.95$) or between old field and pine forest tracts ($t = 1.03$, $df = 69$, $P = 0.31$).

**Egg characteristics.** — All eggs were white and had a short oval shape (Preston 1953). Of 50 eggs that were measured from 29 nests, the mean length, width, and volume were $19.82 \pm 0.92$ mm, $15.63 \pm 0.40$ mm, and $2471.78 \pm 191.40$ mm$^3$, respectively (see also Weston 1968). The average egg weight was $2.48 \pm 0.04$ g ($N = 47$).

**Laying, incubation, and hatching.** — Two females were monitored throughout the laying period. Each laid an egg a day, probably at dawn, and each began incubating the day the penultimate egg was laid (both laid 4 eggs). Only one nest was observed from the laying of the first egg through the hatching of the last egg. The fourth and final egg was laid on 7 July, and it hatched between 17:00-17:30 on 19 July, indicating an incubation period of 13 days. In another clutch that was discovered after the final egg was laid, the incubation period was at least 14 days. Meanley (1959) also reports an incubation period of 14 days, but in South Carolina a 12-day incubation period has been noted (Sprunt and Chamberlain 1949). Although males were seen and heard singing near the nest site during the incubation period, I never saw them at the nest (but see Gainer 1921) or carrying food to their mate. I marked no eggs to follow the hatching sequence in relation to laying time, but of 58 nests in which nestling measurements were made, 16 showed possible evidence of asynchronous hatching (i.e., had a runt in the brood) (see also Nolan 1953, Meanley 1959, Nicholson 1976). Two of the 23 nests observed throughout the hatching period had hatching intervals (i.e., time between the first and last hatching of eggs of the same clutch) that were between 24 and 48 h.

**Nestling and fledgling periods.** — The average nestling period was $9.0 \pm 0.2$ days ($N = 16$), and both parents cared for the young (see also Brooks 1938). The average fledgling period (i.e., time between when young fledged and when they became independent) was approximately $25.0 \pm 1.5$ days ($N = 9$ broods, range 21–30 days). Both parents were seen feeding fledged young, but males were seen more frequently with young, especially after the clutches of repeat layings were completed. All food deliveries took place on the ground, and during the latter half of the fledgling period, young often hopped behind their foraging parents: The length of a successful nesting cycle (i.e., period between laying of the first egg to fledging the last young) was approximately 51 d.

**Internesting intervals.** — The average interval between nests that fledged young and repeat layings was $12.3 \pm 2.3$ days ($N = 11$). The average interval between failed nests and repeat layings was $9.7 \pm 1.6$ days ($N =$
27). No significant difference was found between these two internesting intervals \( t = -0.86, \ P = 0.39 \). The length of the internesting interval was significantly shorter during the second half of the breeding season than during the first \( t = -2.95, \ P = 0.01 \). No significant relationship was found between the internesting interval length and clutch size \( \rho = -0.07, \ P = 0.64, \ N = 38 \), brood size \( \rho = -0.08, \ P = 0.64, \ N = 34 \), or nesting cycle length \( \rho = 0.19, \ P = 0.26, \ N = 38 \).

Nesting failure and success.—Reported causes of nest failure in Bachman’s Sparrows include snakes (Brooks 1938, Weston 1968), Brown-headed Cowbirds \( (Molothrus ater) \) (Blincoe 1921, Brooks 1938, Mengel 1965, Weston 1968) and American Crows \( (Corvus brachyrhynchos) \) (Weston 1968). In my study, failure of 38 nests was due to predation (95%) and Brown-headed Cowbird parasitism (5%) (Table 1). Predation was actually observed at only two nests, and of 36 nests that were depredated, all but one showed no signs of disturbance other than the absence of eggs or young. Of the 35 eggs that were lost (Table 1), 7 (20%) were removed by cowbirds and 28 (80%) were depredated. Of the 115 nestlings that were lost (Table 1), 90 (78%) were killed by unknown predators, 13 (11%) were assumed to have starved or died of unknown causes, 7 (6%) were seen being preyed upon by snakes, 4 (4%) were killed and partially consumed by an unknown mammal, and 1 probably died due to the presence of cowbird nestlings.

Nesting success, which is defined here as a nest that fledges at least one young, did not differ significantly among the three field seasons \( \chi^2 = 1.17, \ df = 2, \ P = 0.56 \), between the first and second halves of the breeding season \( \chi^2 = 0.05, \ df = 1, \ P = 0.82 \), between old field tracts and pine forest tracts \( \chi^2 = 0.04, \ df = 1, \ P = 0.84 \), or between large-brood nests (4 or 5 nestlings) and small-brood nests (2 or 3 nestlings) \( \chi^2 = 0.8, \ df = 1, \ P = 0.77 \). No significant difference in nest concealment was found between successful and failed nests \( t = 0.53, \ df = 65, \ P = 0.60 \).

Using the Mayfield method, the probability that a Bachman’s Sparrow egg would produce a nesting that fledged was 0.25. Although the daily success rate was greater for the incubation period (0.965) than the nestling period (0.919), the difference was not significant (Johnson’s statistic = 1.16, \( P > 0.20 \)) (Johnson 1979).

Annual productivity.—The average number of fledglings per nest attempt was 0.25 (probability an egg would fledge) \times 3.91 \text{(average clutch size)} = 0.98. Since the average number of nests per season was 3.05, the yearly production was approximately 2.99 \((0.98 \times 3.05)\) fledglings per pair. If we assume an adult mortality close to 50% (Ricklefs 1973), then the estimate of first-year survival needed to maintain a stable population would be 34\% \((0.50/1.49 \times 100)\). If, however, the adult mortality rate is
Table 1

Outcome of Bachman’s Sparrow Eggs and Nestlings in Central Arkansas, 1983–1985

<table>
<thead>
<tr>
<th></th>
<th>1983</th>
<th>1984</th>
<th>1985</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nests</td>
<td>15</td>
<td>26</td>
<td>25</td>
<td>66</td>
</tr>
<tr>
<td>Eggs laid</td>
<td>58</td>
<td>100</td>
<td>97</td>
<td>255</td>
</tr>
<tr>
<td>Eggs/nest</td>
<td>3.9</td>
<td>3.9</td>
<td>3.9</td>
<td>3.9</td>
</tr>
<tr>
<td>Eggs hatched</td>
<td>51</td>
<td>77</td>
<td>78</td>
<td>206</td>
</tr>
<tr>
<td>Eggs hatched/nest</td>
<td>3.4</td>
<td>3.0</td>
<td>3.1</td>
<td>3.2</td>
</tr>
<tr>
<td>Eggs failed to hatch</td>
<td>2</td>
<td>8</td>
<td>4</td>
<td>14</td>
</tr>
<tr>
<td>Eggs lost</td>
<td>5</td>
<td>15</td>
<td>15</td>
<td>35</td>
</tr>
<tr>
<td>Nestlings lost</td>
<td>24</td>
<td>44</td>
<td>47</td>
<td>115</td>
</tr>
<tr>
<td>Young fledged of eggs laid</td>
<td>27</td>
<td>33</td>
<td>31</td>
<td>91</td>
</tr>
<tr>
<td>Young fledged of eggs hatched</td>
<td>27</td>
<td>33</td>
<td>31</td>
<td>91</td>
</tr>
<tr>
<td>Young fledged/nest</td>
<td>1.8</td>
<td>1.3</td>
<td>1.2</td>
<td>1.4</td>
</tr>
<tr>
<td>Successful nests</td>
<td>8</td>
<td>11</td>
<td>9</td>
<td>28</td>
</tr>
</tbody>
</table>

* Nests that fledged at least one young. Values in parentheses are percentages.

82%, as indicated by site-fidelity data (see above), then 55% of the young would have to survive the first year to maintain a stable population. Post-fledging data were difficult to collect, and I have no accurate estimate of the fledgling period survival rate. All nests that fledged young were successful in producing at least one juvenile.

**Declining populations.** — Although this study gives no clear answers as to why Bachman’s Sparrows are declining in various regions of its range, it does indicate that in central Arkansas the annual fecundity and probability of egg success do not appear to be abnormally low. If other Bachman’s Sparrow populations have similar productivity rates, then the cause of population declines may be due to other factors such as a shortage of breeding habitat and/or a high adult mortality rate possibly caused by a shortage of wintering habitat.

**ACKNOWLEDGMENTS**

I am grateful to D. A. James and K. G. Smith for their encouragement and support. The help of M. and H. Parker with various aspects of my study is greatly appreciated. I also thank my wife, L. C. Haggerty, for her valuable assistance and moral support. The University of Arkansas Zoology Department and the University of North Alabama provided equipment and computer time. International Paper Company kindly allowed me to conduct my research on their property and the assistance of C. Self is appreciated. The comments of D. James, K. Smith, L. Best, C. Blem, P. Kittle, and an anonymous reviewer improved the manuscript. Funding was provided by grants from the Arkansas Audubon Society Trust, Sigma-Xi Grant-In-Aid for Research, the Arkansas Nongame Preservation Program, and the Chapman Memorial Fund of the American Museum of Natural History.
LITERATURE CITED


MENGEL, B. 1965. The birds of Kentucky. Ornithol. Monogr. 3.


Changes in the avifauna of the great smoky mountains: 1947-1983

David S. Wilcove

Abstract. — In 1982-1983, I repeated ten breeding bird censuses made by B. Fawver in 1947-1948 in the Great Smoky Mountains National Park, Tennessee and North Carolina. Populations of neotropical migrants did not show significant changes. In contrast, during this period, many of the same species of neotropical migrants had declined in small woodlots and urban parks throughout the eastern United States. These findings support the hypothesis that declines in woodlots result from the fragmentation of breeding habitat and demonstrate the importance of large parks such as the Great Smoky Mountains National Park for the preservation of neotropical migrants.

Among the permanent residents and short-distance migrants, the Blue Jay (Cyanocitta cristata), American Crow (Corvus brachyrhynchos), and Dark-eyed Junco (Junco hyemalis) showed substantial population increases during this period. All three species probably have benefited from human activity outside the park boundaries. Received 16 June 1987, accepted 8 Dec. 1987.

Investigators recently have called attention to long-term changes in bird communities in small forest fragments and urban parks throughout the eastern United States (Briggs and Criswell 1979, Robbins 1979, Butcher et al. 1981, Ambuel and Temple 1982). In most areas, breeding populations of forest-dwelling neotropical migrants have declined, while populations of permanent residents and short-distance migrants have either increased or remained stable (Whitcomb et al. 1981). Without comparable data from extensive, undisturbed forest tracts, it is difficult to judge whether the avifaunal changes in the small woodlots are a consequence of the small size and isolated nature of the fragments themselves, the loss of winter habitat for the migratory species, or some other factor (see Morse 1980).

Since 1947, observers in West Virginia have been monitoring bird populations within an extensive red spruce-northern hardwood forest. These censuses reveal a steady decline in the diversity and numbers of neotropical migrants (Hall 1984). However, this study covers only one type of forest (red spruce [Picea rubens]—northern hardwoods), and only 6.1 ha of forest are censused. More studies are needed to fully understand what is happening to bird populations in large forest tracts.

In 1982-1983 I repeated ten breeding bird censuses made by B. Fawver in 1947-1948 in Great Smoky Mountains National Park, Tennessee and

### Methods

**Study sites.**—In 1982 I relocated most of Fawver's field sites using directions in his thesis, old maps from the park library, and information provided by Fawver and long-time residents of the area. I rejected tracts showing obvious successional changes and tracts altered by road construction. Ultimately, I censused birds at 10 localities representing five types of mature forest (Table 1). In 1983, I returned to four of these sites to replicate the counts.

Fawver (1950) obtained detailed botanical descriptions of most of his study sites. These were qualitatively updated in 1982–1983. Brief descriptions of the study sites are presented below: The classification of forest types follows Whittaker (1956), and includes:

1. **Cove forests** (three sites). Found in moist stream valleys and north-facing slopes, cove forests are characterized by a high, mostly deciduous canopy consisting of large, widely spaced trees of many species. *Rhododendron* forms dense thickets along streams. Two of the study sites are located in the lower Ramsey Creek area (660–780 m, 12.8 ha) and one is in the middle Ramsey Creek area (910–1,040 m, 5.6 ha). All three sites were censused by Wilcove in 1948 and again in 1982.

2. **Hemlock-deciduous forests** (two sites). These sites occur in middle elevations (900–1,000 m) and are characterized by a mixed canopy of hemlock and deciduous trees, such as maple and oak. One site is the Spruce Flats area (900–910 m, 4.2 ha), which was censused by Fawver in 1948 and again in 1982. The Brushy Mountain area (1,220–1,370 m, 9.0 ha) was censused by Wilcove in 1948 and again in 1982.

3. **Chestnut oak forests** (two sites). Located in the lower elevations (860–1,000 m), these sites are characterized by a mixed canopy of chestnut oak and deciduous trees. The Bullhead Trail area (860–1,000 m, 4.8 ha) was censused by Wilcove in 1947 and again in 1982. The Greenbrier Pinnacle area (1,080–1,090 m, 11.0 ha) was censused by Fawver in 1948 and again in 1982.

4. **Red oak forests** (one site). Found at higher elevations (1,250–1,300 m), these sites are characterized by a mixed canopy of red oak and deciduous trees. The Greenbrier Pinnacle area (1,250–1,300 m, 7.5 ha) was censused by Wilcove in 1948 and again in 1982.

5. **Beech gap forests** (two sites). Located in the upper elevations (1,660–1,680 m), these sites are characterized by a mixed canopy of beech and deciduous trees. The Double Spring Gap area (1,660–1,680 m, 7.0 ha) was censused by Wilcove in 1947 and again in 1982.
the sites (Lower Porter Creek, Middle Ramsey Creek) are virgin tracts. Lower Ramsey Creek was logged sometime in the 19th century, but by 1947 was a closed canopy forest (Fawver 1950). By 1982, the trees were larger, the canopy more closed, and the understory reduced as compared to 1947.

(2) Hemlock-deciduous forests (three sites). Eastern hemlock (Tsuga canadensis) is the dominant tree species. At Spruce Flats, American beech (Fagus grandifolia) is a prominent component of the understory and canopy, while at Roaring Fork and Brushy Mountain, the understory largely consists of sweet and yellow birches (Betula lenta and B. alleghaniensis). Extensive Rhododendron thickets border the streams. All three sites are virgin tracts that have changed little since 1947–1948, judging from Fawver’s descriptions.

(3) Chestnut oak forests (two sites). This forest type is characterized by relatively small trees 6–18 m in height. The principal species include chestnut oak (Quercus prinus), northern red oak (Q. rubra), and pitch pine (Pinus rigida). Ericaceous shrubs form a dense, often impenetrable understory. Both sites had standing, dead American chestnut (Castanea dentata) trees in 1947–1948, which were gone by 1982. At the Greenbrier site, chestnuts comprised less than 5% of the trees (Fawver 1950), and their loss probably had insignificant effects on the forest structure. At the Bullhead site almost 30% of the trunks in 1947–1948 were standing dead chestnuts. They created a very open canopy, permitting an extensive understory of tree saplings and mountain laurel (Kalmia latifolia) to grow up (B. Fawver, pers. comm.). By 1982, the canopy had filled in with various oaks, and the understory was much reduced (pers. obs.; see also Woods and Shanks 1959, Mackey and Sivec 1973).

(4) Northern red oak forests (one site). In oak forests at higher elevations, northern red oak replaces chestnut oak as the dominant species, although the forests are otherwise similar (Whittaker 1956). At the study site, standing dead chestnuts accounted for less than 5% of the trees in 1947. Their subsequent loss probably had little effect on the forest structure.

(5) Beech forests (one site). In this unique forest type, American beech comprises over 90% of the trees. The trees are small (8–12 m tall) and widely spaced. Grasses and herbs cover the forest floor. The study plot is a virgin tract.

_Census techniques._—Fawver used two census techniques: spot-mapping of singing males (Kendeigh 1944, Robbins 1970) and cruising counts. In a cruising count, the observer counts all singing males within a predetermined distance on either side of a transect line. Several such counts are made, and the largest number of each species observed on any one count is assumed to be the population of that species. Fawver censused birds during June and July 1947 and from May through July 1948. I censused birds from 19 May to 27 June 1982 and from 31 May to 14 June 1983. At each site, I repeated the census method used by Fawver (Table 1). Spot-map sites were visited at least four times in 1947–1948 and 7–10 times in 1982–1983. In 1947–1948, the three cruising count sites were visited two, three, and five times, respectively; in 1982–1983, they were visited five, six, and six times, respectively. By increasing the number of visits to each site, I was potentially biasing the data in favor of recording larger populations (see Dickson 1978). However, studies of bird census techniques now recommend a minimum of 8 visits per spot-mapping site (Robbins 1970). Because I wanted the 1982–1983 data to be as accurate as possible for future replication, I increased the census effort.

_Statistical tests._—Three statistical tests were used to compare populations in different years: (1) the sign test was used to evaluate the direction of change (increase, decrease) of each species over all study sites; (2) the chi-square one-sample test (two-tailed) was used to evaluate overall population changes of major groups (e.g., neotropical migrants, residents, and short-distance migrants) in the individual study sites or across all study sites; and (3) the binomial test (two-tailed) was used in place of the chi-square test when sample sizes were too small (Siegel 1956). No attempt was made to assess the significance of population
changes of individual species within each study site, due to the small sample sizes typically involved. All statistical tests were performed on the actual census counts, and not the density (pairs/10 ha) values. The actual counts can be calculated from the density values using the plot sizes from Table 1. It should be noted that the increased census effort in 1982-1983 compared to 1947-1948 decreased the likelihood of recording statistically significant population declines.

RESULTS

Census results are presented as density estimates: pairs/10 ha (Tables 2-4). If only a small fraction of a species’ territory extended onto the study plot, or if that species was recorded less than three times on the plot, it was not included in the population tallies.

Neotropical migrants: overall numbers.—In 9 of the 10 study sites, the total number of breeding pairs of neotropical migrants did not change significantly between 1947-1948 and 1982 (Table 5). At the tenth site, Greenbrier Pinnacle red oak forest, neotropical migrants declined by 48% ($\chi^2 = 5.46$, df = 1, $P < 0.05$). This was largely due to the local disappearance of the Wood Thrush (Hylocichla mustelina) and Red-eyed Vireo (Vireo olivaceus), both formerly common breeders at this site. One locality (Roaring Fork hemlock-deciduous forest) experienced a significant decline in total pairs of neotropical migrants between 1982 and 1983 ($\chi^2 = 5.73$, df = 1, $P < 0.05$). Interyear population changes at the three other sites censused in both 1982 and 1983 were not significant (Table 5).

Neotropical migrants: individual species.—Only one species, Black-throated Green Warbler (Dendroica virens), showed a significant, widespread increase between 1947 and 1982 ($P = 0.032$, two-tailed sign test). However, it declined sharply between 1982 and 1983; in the four areas censused in consecutive years, the population declined by 50%, from 28 to 14 pairs. Two species (Northern Parula [Parula americana] and Indigo Bunting [Passerina cyanea]) not found in the study sites in 1947-1948 were recorded in 1982-1983. Northern Parula was recorded in three localities, and Indigo Bunting appeared in two localities. A number of species (e.g., Acadian Flycatcher [Empidonax virescens], Blackburnian Warbler [Dendroica fusca], Worm-eating Warbler [Helmitheros vermivorus], Kentucky Warbler [Oporornis formosus]) were either so uncommon or so localized that little can be said of their population status. Between 1947 and 1982, Solitary Vireos (Vireo solitarius) increased at one site (Middle Ramsey Creek cove forest), disappeared from a stronghold (Spruce Flats hemlock-deciduous forest), and appeared in two new localities (Bullhead Trail chestnut oak forest, Greenbrier Pinnacle red oak forest). Between 1982 and 1983, the species declined at Middle Ramsey Creek, returned to Spruce Flats in large numbers, and appeared for the
<table>
<thead>
<tr>
<th>Bird Species</th>
<th>Lower Ramsey Creek</th>
<th>Middle Ramsey Creek</th>
<th>Lower Porter Creek</th>
</tr>
</thead>
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<td>Ruffed Grouse (<em>Bonasa umbellus</em>)</td>
<td>0.8</td>
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<tr>
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<td>0.8</td>
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<td>0.8</td>
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* Neotropical Migrants are denoted by an asterisk.
## Table 2
**Continued**

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<th>Lower Porter Creek</th>
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<td><strong>Veery</strong> (<em>Catharths fuscescens</em>)</td>
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**Table 3**

**Bird Population Data for Hemlock-Deciduous Forest Study Sites. Numbers Represent Breeding Pairs per 10 ha. Neotropical Migrants Are Denoted by an Asterisk**

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<td>Barred Owl (<em>Strix varia</em>)</td>
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<td>American Crow (<em>Corvus brachyrhynchos</em>)</td>
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<td>Tufted Titmouse (<em>P. bicolor</em>)</td>
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<td>White-breasted Nuthatch (<em>S. carolinensis</em>)</td>
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<tr>
<td>Brown Creeper (<em>Certhia americana</em>)</td>
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<td>Winter Wren (<em>Troglodytes troglodytes</em>)</td>
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<td>Golden-crowned Kinglet (<em>Regulus satrapa</em>)</td>
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<tr>
<td>Vcery* (<em>Catharus fuscens</em>)</td>
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<tr>
<td>Wood Thrush* (<em>Hylocichla mustelina</em>)</td>
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<tr>
<td>American Robin (<em>Turdus migratorius</em>)</td>
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<tr>
<td>Cedar Waxwing (<em>Bombycilla cedrorum</em>)</td>
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<tr>
<td>Solitary Vireo (<em>Vireo solitarius</em>)</td>
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THE WILSON BULLETIN • Vol. 100, No. 2, June 1988
### TABLE 3  
CONTINUED

<table>
<thead>
<tr>
<th>Species</th>
<th>Spruce Flats</th>
<th>Roaring Fork</th>
<th>Brushy Mountain</th>
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</thead>
<tbody>
<tr>
<td>Red-eyed Vireo* (<em>V. olivaceus</em>)</td>
<td>1.0 3.6 6.0</td>
<td>7.7 2.6</td>
<td></td>
</tr>
<tr>
<td>Northern Parula* (<em>Parula americana</em>)</td>
<td>2.6 2.6</td>
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<tr>
<td>Black-throated Blue Warbler* (<em>Dendroica caerulescens</em>)</td>
<td>11.0 11.9 11.9</td>
<td>18.8 23.1 12.8</td>
<td>22.0 17.8</td>
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<tr>
<td>Black-throated Green Warbler* (<em>D. virens</em>)</td>
<td>14.0 21.4 7.1</td>
<td>17.5 17.9 14.1</td>
<td>10.2 28.9</td>
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<tr>
<td>Blackburnian Warbler* (<em>D. fusca</em>)</td>
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<td>10.0 5.1 5.1</td>
<td>3.2 3.3</td>
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<tr>
<td>Ovenbird* (<em>Seiurus aurocapillus</em>)</td>
<td>27.0 23.8 16.7</td>
<td>8.8 14.1 5.1</td>
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<tr>
<td>Hooded Warbler* (<em>Wilsonia citrina</em>)</td>
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<tr>
<td>Canada Warbler* (<em>W. canadensis</em>)</td>
<td>0.5 8.8 7.7 7.7</td>
<td>12.8 6.7</td>
<td></td>
</tr>
<tr>
<td>Scarlet Tanager (<em>Piranga olivacea</em>)</td>
<td>1.0 2.5 2.6 1.3</td>
<td>0.8 1.1</td>
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</tr>
<tr>
<td>Rose-breasted Grosbeak* (<em>Pheucticus ludovicianus</em>)</td>
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<tr>
<td>Dark-eyed Junco (<em>Junco hyemalis</em>)</td>
<td>4.0 10.7 8.3</td>
<td>10.0 11.5 9.0</td>
<td>5.0 8.3</td>
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### Table 4

**Bird Population Data for Oak and Beech Forest Study Sites. Numbers Represent Breeding Pairs per 10 ha. Neotropical Migrants Are Denoted by an Asterisk**

<table>
<thead>
<tr>
<th></th>
<th>Bullhead Chestnut Oak</th>
<th>Greenbrier Chestnut Oak</th>
<th>Greenbrier Red Oak</th>
<th>Double Spring Gap</th>
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</thead>
<tbody>
<tr>
<td>Ruffed Grouse (Bonasa umbellus)</td>
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<tr>
<td>Ruby-throated Hummingbird* (Archilochus colubris)</td>
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<td>0.9</td>
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<td>Downy Woodpecker (Picoides pubescens)</td>
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<td>1.0</td>
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<tr>
<td>Hairy Woodpecker (P. villosus)</td>
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<tr>
<td>Northern Flicker (Colaptes auratus)</td>
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<tr>
<td>Pileated Woodpecker (Dryocopus pileatus)</td>
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<tr>
<td>Eastern Wood-Pewee* (Contopus virens)</td>
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<tr>
<td>Great Crested Flycatcher* (Myiarchus crinitus)</td>
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<td>4.2</td>
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<td>1.4</td>
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<td>Blue Jay (Cyanocitta cristata)</td>
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<td>Black-capped Chickadee (Parus atricapillus)</td>
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<td>0.9</td>
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<tr>
<td>Carolina Chickadee (P. carolinensis)</td>
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<tr>
<td>Tufted Titmouse (P. bicolor)</td>
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<tr>
<td>Red-breasted Nuthatch (Sitta canadensis)</td>
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<td></td>
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<tr>
<td>Golden-crowned Kinglet (Regulus satrapa)</td>
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<tr>
<td>Veery* (Catharus fuscens)</td>
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<tr>
<td>Wood Thrush* (Hylocichla mustelina)</td>
<td>1.2</td>
<td>0.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>American Robin (Turdus migratorius)</td>
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<td></td>
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<tr>
<td>White-eyed Vireo* (Vireo griseus)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Solitary Vireo (V. solitarius)</td>
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<td>1.8</td>
<td></td>
</tr>
<tr>
<td>Red-eyed Vireo* (V. olivaceus)</td>
<td>11.8</td>
<td>8.3</td>
<td>5.5</td>
<td>2.7</td>
</tr>
<tr>
<td>Northern Parula* (Parula americana)</td>
<td>Bullhead Chestnut Oak</td>
<td>Greenbrier Chestnut Oak</td>
<td>Greenbrier Red Oak</td>
<td>Double Spring Gap</td>
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</tr>
<tr>
<td>Chestnut-sided Warbler* (Dendroica pensylvanica)</td>
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<td>1.3</td>
<td></td>
</tr>
<tr>
<td>Black-throated Blue Warbler* (D. caerulescens)</td>
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<td>3.2 3.2 3.2</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>Black-throated Green Warbler* (D. virens)</td>
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<td>2.1 2.2 0.9</td>
<td>1.2</td>
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</tr>
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<td>Black-and-white Warbler* (Mniotilla varia)</td>
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<td>7.3 7.3 5.4</td>
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<td>Worm-eating Warbler* (Helmitheros vermivorus)</td>
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<tr>
<td>Ovenbird* (Seiurus aurocapillus)</td>
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<td>9.0 6.2</td>
<td>2.5 1.3</td>
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<td>Kentucky Warbler* (Oporornis formosus)</td>
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<tr>
<td>Hooded Warbler* (Wilsonia citrina)</td>
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<td>8.5 5.0 5.0</td>
<td>1.2</td>
<td></td>
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<tr>
<td>Canada Warbler* (W. canadensis)</td>
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<td>1.0</td>
<td>1.3</td>
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</tr>
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<td>Yellow-breasted Chat* (Icteria virens)</td>
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<td>5.2 2.1</td>
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<tr>
<td>Scarlet Tanager* (Piranga olivacea)</td>
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<td>7.3</td>
<td>4.0</td>
<td></td>
</tr>
<tr>
<td>Northern Cardinal (Cardinalis cardinalis)</td>
<td>1.2</td>
<td>2.1</td>
<td>10.0</td>
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<tr>
<td>Rose-breasted Grosbeak* (Pheucticus ludovicianus)</td>
<td>10.5 5.2</td>
<td>8.5 1.8 1.8</td>
<td>8.3</td>
<td></td>
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<tr>
<td>Indigo Bunting* (Passerina cyanea)</td>
<td>8.3</td>
<td>1.8</td>
<td>18.7</td>
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<tr>
<td>Rufous-sided Towhee (Pipilo erythrophthalmus)</td>
<td>14.0 12.1</td>
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<td>5.3</td>
<td></td>
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<tr>
<td>Dark-eyed Junco (Junco hyemalis)</td>
<td>12.8</td>
<td>1.3</td>
<td>1.8</td>
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</table>
first time at the Greenbrier Pinnacle chestnut oak forest. Between 1947 and 1982, the Red-eyed Vireo appeared in two new localities (Middle Ramsey Creek cove forest; Roaring Fork hemlock-deciduous forest) and disappeared from a stronghold (Greenbrier Pinnacle red oak forest). Between 1982 and 1983, it declined sharply at Roaring Fork, but did not change appreciably elsewhere. No correlation between the population changes of the two vireo species was apparent.

Residents and short-distance migrants: overall numbers.—At nine localities, the total number of permanent residents and short-distance migrants did not change significantly between 1947-1948 and 1982 (Table 5). At the tenth, Greenbrier Pinnacle red oak forest, residents and short-distance migrants increased by 450% ($\chi^2 = 15.58$, df = 1, $P < 0.001$). This overall increase was almost entirely due to an increase in Dark-eyed Junco ($Junco hyemalis$) populations (see below). Breeding populations in 1983 did not differ significantly from 1982 values at any of the four sites that were censused in consecutive years.

Residents and short-distance migrants: individual species.—The Blue Jay ($Cyanocitta cristata$), American Crow ($Corvus brachyrhynchos$), and

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Table 5

**Populations of Neotropical Migrants and Other Birds (Permanent Residents and Short Distance Migrants) at Each of the Study Sites in the Great Smoky Mountains National Park. Numbers Refer to the Total Number of Breeding Pairs at Each Locality. Underlined Values Represent Significant ($P < 0.05$) Population Changes**

<table>
<thead>
<tr>
<th>Locality</th>
<th>Neotropical migrants</th>
<th>Other birds</th>
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</thead>
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<tr>
<td>Lower Ramsey Creek</td>
<td>53</td>
<td>54.5</td>
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<tr>
<td>Middle Ramsey Creek</td>
<td>19</td>
<td>25</td>
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<tr>
<td>Lower Porter Creek</td>
<td>36.5</td>
<td>34.5</td>
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<tr>
<td>Spruce Flats</td>
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<td>34</td>
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<tr>
<td>Roaring Fork</td>
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<td>67</td>
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<tr>
<td>Brushy Mountain</td>
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<td>57.5</td>
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<td>Bullhead Trail (Chestnut Oak Forest)</td>
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<tr>
<td>Greenbrier Pinnacle (Chestnut Oak Forest)</td>
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<td>30.5</td>
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<tr>
<td>Greenbrier Pinnacle (Red Oak Forest)</td>
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<tr>
<td>Double Spring Gap</td>
<td>13.5</td>
<td>7</td>
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</table>
Dark-eyed Junco have increased dramatically since 1947–1948. In 1947–1948 Fawver found breeding jays at one of 10 study sites (a chestnut oak forest). In 1982–1983, I found breeding jays at seven localities, including cove forests, hemlock-deciduous forests, and oak forests. This increase was significant ($P = 0.016$, two-tailed sign test).

Of the American Crow, Fawver (1950) noted “[it] was seen only in areas of cutover and farm lands at lowest elevations in and around the park. None was found in census areas.” In 1982–1983, I found crows at three sites. At Spruce Flats, I observed two adults and two fledglings, evidence of successful breeding. Elsewhere in the park, I saw crows almost daily along the roadside, especially at dawn.

Perhaps the greatest change in the avifauna was the increase of the Dark-eyed Junco. Fawver recorded it at six of the 10 study sites, where it was common only in the high elevation hemlock-deciduous and beech forests. In 1982, I found breeding juncos at nine of the study sites. The population increase was statistically significant ($P = 0.04$, two-tailed sign test). Today the Dark-eyed Junco may be the most common bird in the park after the Black-throated Blue Warbler (*Dendroica caerulescens*).

The absence of the Brown-headed Cowbird (*Molothrus ater*) is noteworthy. In over 9 weeks of field work, I never saw a cowbird inside the park, although they were common in cleared areas along park borders. Fawver did not record cowbirds at any of his study sites in 1947–1948.

**DISCUSSION**

Discussion of these data must begin with the caveat that they cover only two or three points in time over a period of 36 years. Populations of small passerines may show such tremendous short-term variability that significant changes are apparent only with much more extensive data. Also, by conducting more counts per study site, I may have biased the data in favor of recording larger populations in 1982–1983 versus 1947–1948. Therefore, conclusions from this study are at best preliminary.

**Status of neotropical migrants.** — There was no evidence of a widespread decline in neotropical migrants in the Great Smoky Mountains. As noted earlier, this is not the case for many small woodlots where populations of neotropical migrants have declined dramatically. Some of the species declining in small woodlots have not declined in the Great Smoky Mountains (e.g., Black-and-white Warbler [*Mniotilta varia*], Northern Parula, Ovenbird [*Seiurus aurocapillus*]). This suggests that declines in forest fragments may be due principally to the fragmentation process itself and not the loss of winter habitat. This idea is further supported by two additional lines of evidence. First, neotropical migrants in some fragments were declining as early as the late 1940s before Latin American defor-
estation was a critical problem (Wilcove 1985a). Second, until quite recently, deforestation was far more extensive in North America than in countries to the south. The settling of eastern North America during the 19th century saw the loss of perhaps half the original habitat available to forest-dwelling birds. In Latin America, extensive deforestation began with the post-World War II population boom. Recent estimates indicate that the amount of forest in Central America and the West Indies has been reduced by about 50% (Myers 1980), so that the amounts of breeding and wintering habitat may be roughly in balance. If so, the loss of winter habitat may not yet be a major factor in the decline of migratory passerines, although this will certainly change as more of the tropical forests are destroyed (see Wilcove and Terborgh 1984).

However, three factors make it impossible to interpret the present data as unambiguous evidence that tropical deforestation has not affected these birds.

First, any event that reduces the overall population of a species without destroying its breeding habitat will permit a reassortment of breeding pairs. Such a reassortment can take several forms, depending on the behavior of the birds and the quality of the breeding habitat (see Morse 1976). If tropical deforestation has reduced populations of these birds, the survivors may have moved into vacancies within large tracts such as the Great Smoky Mountains. Such behavior would greatly complicate any attempts to disentangle the relative contributions of tropical deforestation and temperate forest fragmentation.

Second, it is conceivable that neotropical migrants in the Great Smoky Mountains winter in regions of the tropics that have been less heavily affected by tropical deforestation. While it is not possible to eliminate this hypothesis, at least one study indicates that most breeding populations of neotropical migrants scatter widely within the wintering range of the species (Ramos and Warner 1980; see also Wilcove and Terborgh 1984). Thus, it is unlikely that the birds in the Great Smoky Mountains all happen to winter in parts of Latin America that have been spared from deforestation.

Third, the accumulation of small biases in my sampling methods might obscure a relatively small decline. I began censusing birds earlier in the breeding season than did Fawver, and I conducted more counts per study site. All other things being equal, both factors would tend to increase my population tallies compared with Fawver's. However, in 1982, only three individual birds were sighted that unambiguously could be categorized as transients: one Northern Oriole (Icterus galbula) on May 20, and two Swainson's Thrushes (Catharus ustulatus) on May 23. Neither species breeds in the park (Stupka 1963). Other typically late migrants such as
the Blackpoll Warbler (*Dendroica striata*) were not observed. Also, long-term census data from forest fragments show declines in breeding populations of neotropical migrants as great as 70% (Wilcove 1985a). Declines of this magnitude in the Great Smoky Mountains would probably be apparent despite the biases noted above.

Some of the trends involving individual species have interesting precedents elsewhere. Population fluctuations among vireos, similar to those noted in the Great Smoky Mountains, have been recorded in New Hampshire (Robinson 1981). The sharp decline in Black-throated Green Warblers between 1982 and 1983 matches observations by Hall (1984) in West Virginia, where this species shows pronounced population fluctuations based on censuses done at 5-year intervals.

**Residents and short-distance migrants.** — The increase in Blue Jays, Dark-eyed Juncos, and American Crows within the park may be due to human activities in the surrounding areas. Bock and Leptien (1976) report that the North American Blue Jay population increased by about 30% between 1962 and 1971. They attribute this increase to the growing popularity of winter feeding stations. The increase in the Great Smoky Mountains may represent a spillover from the burgeoning jay populations in more settled areas. The junco subspecies in the Great Smoky Mountains, *Junco hyemalis carolinensis*, is an altitudinal migrant (Stupka 1963); birds summering in the mountains descend to lower elevations during the winter. If the number of feeders around the park has increased since 1947, the juncos may be faring better during the winter, thus boosting their population. Since 1966, the U.S. Fish and Wildlife Service Breeding Bird Survey has recorded significant increases in crow populations in eastern North America (Robbins et al. 1986). Crows have probably benefited from forest fragmentation (Whitcomb et al. 1981) and waste corn left in fields after harvesting by machines (J. Terborgh, pers. comm.). Within the park, increased motor traffic has probably resulted in more road-kills, providing food for crows. The overall increase in nest predators such as the Blue Jay and American Crow in the Great Smoky Mountains is of concern, as nest predation has been linked to the decline of neotropical migrants in forest fragments (Wilcove 1985b).

**Conservation implications.** — The Great Smoky Mountains National Park has clearly been more successful at preserving populations of neotropical migrants than most small woodlots and urban parks. The results of this study suggest that any conservation plan for migratory birds should include at least some very large forest preserves (see also Askins et al. 1987). Within a large tract, such as the Great Smoky Mountains National Park, there is less chance of a shortage of food resources (Blake 1983) or a lack of critical microhabitats (Lynch and Whigham 1984), both of which are
potential problems in small woodlots. Rates of nest predation and brood parasitism are also lower in larger tracts (Wilcove 1985b). Moreover, the larger populations of birds in extensive forest tracts are less vulnerable to stochastic extinction factors (Whitcomb et al. 1981). Yet even a preserve the size of the Great Smoky Mountains National Park is not immune to the effects of human activity and land development in surrounding areas, as shown by the increase in jays, crows, and juncos (see also Janzen 1986). Suburban communities will continue to grow at the expense of forested lands. As a result, our national parks and national forests may become increasingly important for the preservation of breeding populations of neotropical migrants. This study was possible only because of the fortuitous availability of older census data. It is crucial to the development of conservation plans for these birds that regular censuses be established within large national parks and forests. These censuses would provide an invaluable baseline for long-term studies of nongame birds.

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LITERATURE CITED


CONSERVATION OF RIPARIAN ECOSYSTEMS IN THE UNITED STATES

Fritz L. Knopf, R. Roy Johnson, Terrell Rich, Fred B. Samson, and Robert C. Szaro

Riparian ecosystems include relatively mesic vegetative communities and associated faunas occurring between aquatic and more xeric upland sites. In eastern North America, these ecosystems often occur in broad zones and are referred to as floodplains or bottomlands. In the west, they are conspicuous as narrow belts of vegetation along ephemeral, intermittent, and perennial streams and rivers and are most obvious in steppe, shrubsteppe, and desert regions. Vegetation associated with streams has been referred to as the "aorta of an ecosystem" (Wilson 1979:82) because of its significance to the perpetuation of water, fish, wildlife, rangeland, and forest resources.

Historically, riparian ecosystems have been subjected to both subtle and dramatic perturbations from water management practices (Carothers and Johnson 1975, Curtis and Ripley 1975) (Fig. 1), agricultural conversions (Best et al. 1979, Conine et al. 1979), grazing (Cope 1979, Knopf and Cannon 1982), channelization (Barclay 1979, McCall and Knox 1979), and recreational development (Aitchison 1977, Schmidly and Ditton 1979, Johnson and Carothers 1982). Riparian systems represent areas of maximum potential conflict between users of timber, grazing, recreational, water, and wildlife resources (Thomas et al. 1979). Additionally, exotic woody species such as salt cedar (Tamarix pentandra) and Russian olive (Elaeagnus angustifolia) have naturalized extensively within western riparian ecosystems (Robinson 1965, Horton 1977, Olson and Knopf 1986b), displacing native woody species that provide valuable avian habitats but also providing additional habitats for selected species of wildlife (Knopf and Olson 1984, Hunter et al. 1985).

Riparian ecosystems have recently attracted much attention, especially relative to the management of public lands in the west. Within the last

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Fig. 1. Stressed stand of plains cottonwoods (Populus sargentii) along the (now dry) channel of the Cheyenne River near Wasta, South Dakota. (Photo. 21 Sept. 1982 by F. L. Knopf.)

10 years, conservation of riparian systems has been the topic of one international (Johnson et al. 1985), two national (Johnson and McCormick 1979, Sharitz and Gibbons 1988), and many regional (e.g., Johnson and Jones 1977, Graul and Bissell 1978, Cope 1979, Warner and Hendrix 1984) technical conferences.

THE RIPARIAN AVIFAUNA

Less than 1% of the western landscape of the United States is covered by riparian vegetation. However, this vegetation provides habitats for more species of breeding birds than surrounding uplands. Eighty-two percent of all species annually breeding in northern Colorado occur in riparian vegetation (Knopf 1985), and 51% of all species in southwestern states are completely dependent upon this vegetation type (Johnson et al. 1977). Loss of the riparian component in the southwestern states could potentially result in the loss of 78 (47%) of the 166 avian species that breed in the region (Johnson et al. 1977). In New Mexico, losses of 46%
of the species breeding in the San Juan Valley (Schmitt 1976) and 49% of the species breeding in the Gila Valley (Hubbard 1971) might be expected. Hubbard (1977:16) speculated that "these two New Mexico river valleys support 16–17% of the entire breeding avifauna of temperate North America." Similar relationships, although less dramatic, have been observed in the eastern United States (Dickson 1978, Best et al. 1979, Hair et al. 1979, Stauffer and Best 1980).

Riparian vegetation attracts a greater number and variety of bird species during migration than during the breeding season. Riparian systems may attract up to $10.6 \times$ the number of migratory birds found in surrounding upland sites in the spring (Stevens et al. 1977) and $14 \times$ the number of species recorded during fall migration (Hehnke and Stone 1979). These differences occur almost exclusively in the insectivorous bird foraging guild, with granivorous species being associated more with upland (Stevens et al. 1977) or altered (Heller 1978) sites. However, granivorous species do use riparian sites extensively during winter for foraging and thermal cover (F. B. Samson and F. L. Knopf, unpubl. data).

The disproportionately high value of riparian vegetation in providing habitats extends beyond birds to other vertebrates (Brode and Bury 1984, Cross 1985, Bury, 1988).

**U.S. PUBLIC LANDS POLICIES**

Riparian ecosystems managed by natural resource agencies historically have been subjected to policy directives favoring adjoining vegetative associations. Only recently have riparian systems received special emphasis based upon their unique attributes.

Federal land-management agencies of the United States presently operate under executive and legislative mandates for riparian conservation. Specific federal authorities for conserving riparian vegetation do not exist; however, guidelines for management of riparian ecosystems on public lands are provided in two Executive Orders. Executive Order No. 11988, entitled "Floodplain Management," recognizes the importance and unique nature of the nation's floodplains and requires agencies (to the extent possible) to avoid adverse impacts associated with occupancy and modification of floodplains. Further, agencies are to avoid direct or indirect support of floodplain development whenever a practical alternative can be identified. A second Executive Order (No. 11990, "Protection of Wetlands") directs agencies to take necessary actions to minimize the loss or degradation of wetlands and to provide leadership in preserving and enhancing the natural and beneficial values of these areas.

In addition to these executive orders, general guidelines for conserving riparian and other natural areas are provided in legislative bills including
The National Environmental Policy Act, Federal Land Policy and Management Act, Land and Water Conservation Fund Act, Fish and Wildlife Coordination Act, National Forest Management Act, Federal Water Pollution Control Act, and Public Rangelands Improvement Act. The extent to which individual public lands agencies have developed internal guidelines based on these executive and legislative authorities varies with the charge for wildlife conservation legislated to that agency.

**U.S. Department of Agriculture, Forest Service.**—The Forest Service (FS) manages 35,903,804 ha of land, of which 33,261,675 ha are in the contiguous states (U.S. Dept. Agric. 1982). Specific directions regulating floodplain and riparian management on FS lands are found in the National Forest Management Act (NFMA) of 1976 and NFMA implementation regulation 36 CFR Part 219. The regulations state that land dominated by riparian vegetation within 30 m of perennial streams, lakes, and other water bodies will be given special attention. Management practices that adversely affect water condition and fish habitat in these areas are to be avoided. Other factors (e.g., topography, vegetation type) should be considered in determining what management practices are acceptable in these areas.

The Forest Service Manual (U.S. Dept. Agric. 1980) recognizes the unique values of riparian areas and emphasizes their protection, management, and improvement during the planning and implementation of land and resource management activities. The policy is to manage riparian areas relative to legal mandates, including those associated with, but not limited to, floodplains, endangered species, wetland resources, and water quality. Specifically, the policy is to: (1) recognize the importance and values of riparian areas during the land management planning process; (2) recognize the importance and distinctive value of riparian areas when implementing management activities and give preferential consideration to riparian area resources vs other resources in cases of unresolvable conflict; (3) manage riparian areas under the principles of multiple use and sustained yield, while emphasizing protection of soil, water, vegetation, and fish and wildlife resources; and (4) identify riparian areas prior to implementation of any project activity.

The FS responsibilities for riparian area management differ with administrative level (U.S. Dept. Agric. 1980). The FS Chief is responsible for National Policy, the minimum-protection standard, coordination of research programs, and coordination with other federal agencies at the national level. The Regional Forester is responsible for: (1) ensuring that riparian areas are addressed in the land management planning process; (2) providing technical standards, guidelines, training, and quality control for the management of riparian areas (Forest Service Manual 1921.43);
(3) monitoring the effectiveness of measures implemented for the protection and improvement of riparian areas; and (4) defining more specific criteria to identify and delineate soils, land forms, and vegetation in riparian areas. The Forest Supervisor is responsible through the land management process for the inventory, management, and protection of riparian areas according to national and regional objectives and standards. District personnel in each forest do the groundwork which includes identifying riparian areas most likely to be influenced by a proposed activity, classifying resource values within riparian areas, and (with the assistance of specialists) assigning resource protection values.

An additional requirement of the Forest Service is to monitor and evaluate management activities applied within riparian areas and to coordinate with federal, state, and local agencies to ensure that all activities are conducted in an environmentally, socially, and economically acceptable manner. In general, a more intensive monitoring system is suggested for riparian areas in that they are more susceptible to multiple impacts than are terrestrial systems.

**U.S. Department of Agriculture, Soil Conservation Service.**—The Soil Conservation Service (SCS) does not manage public lands, per se, but serves as an advisory organization for private individuals. Recognition of the special value of wetlands as wildlife habitats has evolved over the course of the last 50 years in the SCS. Although wetlands programs have emphasized marshlands on the Great Plains, numerous projects have affected the conservation of riparian vegetation locally (Barry 1979). Nonetheless, specific written policies on riparian conservation have not been developed (D. E. Chalk, pers. comm.).

**U.S. Department of Defense, Army Corps of Engineers.**—Beyond federal mandates and legislation, the Corps of Engineers has no stated riparian policy or guidelines within the agency. The general philosophy of the Corps recognizes that riparian systems are important and should be considered in agency projects and mitigation efforts (J. O’Neal, pers. comm.); Corps projects are subjected to Fish and Wildlife Service (FWS) review.

**U.S. Department of Interior, Bureau of Land Management.**—The Bureau of Land Management (BLM) administers 190,206,390 ha of public lands, or about 20% of the surface area of the United States (Almand and Krohn 1979). Approximately 69,798,057 ha of this area are in the western contiguous states, and the remainder is in Alaska. As with the FS, wildlife conservation is one of many charges of the agency, and riparian issues have received more specific guidelines in policy and levels of management responsibility than other vegetative communities.

Four basic policies safeguard riparian ecosystems on BLM lands (Almand and Krohn 1979). These include: (1) avoiding adverse impacts on
riparian areas when possible; (2) avoiding new construction in riparian areas where a practical alternative is available; (3) preserving and enhancing riparian sites and regulating those uses causing irreparable damage; and (4) minimizing actions causing definable adverse impacts.

BLM published formal guidelines for management of riparian areas in the Federal Register in 1980 (44 CFR 36121). Those guidelines have been incorporated into the BLM Manual for operations. Briefly, the Director and Associate Director are responsible for integration of riparian conservation into Bureau policies: this responsibility generally is exercised through the Deputy Director for Lands and Resources. The Chief, Office of Budget ensures that appropriations requests conform to Executive Order 11990. State Directors and Division Chiefs ensure compliance with defined procedures for riparian protection and management, with actual inventories and monitoring of riparian condition being the responsibility of District Managers. District and Resource Area Specialists identify and evaluate riparian sites. Recommendations for project work, management changes, and monitoring are then developed. In Fiscal Year 1986, each state office of BLM developed a riparian area management strategy outlining the future inventory and management of all riparian areas. Implementation of this strategy will be a high priority within all BLM programs in the future.

U.S. Department of Interior, Bureau of Reclamation.—Much of the 3,026,325 ha (U.S.D.I. 1984) of land held by the Bureau of Reclamation (BOR) is managed by other agencies. Reservoir lands may be managed by state park and wildlife agencies or federal authorities (e.g., National Park Service). “Reclamation withdrawn” lands (those with water delivery or irrigation potential) are also frequently managed by other agencies, principally the BLM. Despite primary management at a site by other agencies, the nature of BOR’s activities relative to water resources results in a large measure of control over western riparian systems (Busch 1984). BOR projects designed to develop water resources are conducted in compliance with federal mandates, and the agency is a cooperator in riparian habitat and species management programs. However, BOR guidelines do not specifically address riparian or wildlife issues (D. E. Busch, pers. comm.).

U.S. Department of Interior, Fish and Wildlife Service.—The Fish and Wildlife Service (FWS) manages 36,584,591 ha of which 32,782,580 ha are within the National Wildlife Refuge System. The remaining 3,802,011 ha are managed for secondary interests (i.e., wildlife) on lands owned by other public agencies or through legal agreements, easements, and leases (FWS Realty Office Statistics, 7 July 1986). The FWS does not have specific policies relative to management of riparian vegetation for wildlife
habitats at the national level. Rather, riparian conservation and enhancement are accomplished within FWS programs to promote wildlife conservation by: (1) land acquisition, (2) environmental planning and regulatory processes, and (3) resource inventories and basic research (Hirsch and Segelquist 1979).

Most riparian efforts have arisen directly from the FWS's responsibilities for protection and management of migratory birds—particularly waterfowl. Refuges such as Santa Ana, White River, Columbia White-tailed Deer, Havasu, and Upper Mississippi River are comprised primarily of riparian vegetation and have been purchased, in part, to protect the unique diversity of wildlife on those sites. The FWS tasks associated with reviews of environmental impacts and recommendations for mitigation of resource losses on federally funded water resource projects often emphasize wetlands, including riparian, issues. This authority is granted through the Fish and Wildlife Coordination Act, and the FWS has primary responsibility for reviewing projects by the COE and BOR, specifically.

Riparian systems usually are classified within Resource Category 1 (all losses should be prevented) or 2 (agency should strive for no net loss). As Hirsch and Segelquist (1979) observed, however, such review is advisory in nature and lacks enforcement power.

U.S. Department of Interior, National Park Service.—National Park Service (NPS) lands are protected for natural, cultural, recreational, developed, or special uses. The NPS manages the natural resources of the Nation's parks to maintain and perpetuate their inherent integrity. Because the agency is dedicated to the concept of perpetuation of a total natural environment or ecosystem rather than of providing resources for specific users, the NPS generally has not developed policies regarding specific natural resources such as riparian areas.

ON THE LOCALIZED FOCUS OF RIPARIAN CONSERVATION

Factors contributing to the local diversity of avian species in riparian vegetation have been identified in numerous studies (Stauffer and Best 1980, Szaro 1980, and others) as have impacts of specific disturbances on avian habitats (Barclay 1979, Sedgwick and Knopf 1987, and others). These studies of riparian avifaunas and management activities generally have been local in nature, because broad conservation guidelines are difficult to develop for such variable systems (Szaro 1980). Thus, agency policies and guidelines generally direct conservation and enhancement actions at a specific site (project or management unit) based upon local evaluations.

We see two potential dangers in developing management policy upon a site-specific information base, especially when viewed from a national
perspective. First, local information can foster erroneous conclusions regarding the biological contribution of a specific association to the continental avifauna. This point was illustrated with the evaluation of conservation priorities examining beta and gamma levels of diversity (cf. Whittaker 1975) within forest bird communities at Jackson Hole, Wyoming (Samson and Knopf 1982). Whereas riparian vegetation provides habitats for many species of birds in northwestern Wyoming, most of those species either are cosmopolitan or on the periphery of their continental distribution. In contrast, the local forest type (lodgepole pine \textit{[Pinus contorta]} that has the poorest species richness provides habitats for a number of species that are regionally unique when viewed from a national perspective. Management emphasis upon habitats for riparian species at Jackson Hole would be at the expense of efforts to conserve the unique elements of the regional avifauna. National guidelines and policies, to date, assure that primary emphasis is on riparian vegetation within all projects—and potentially towards a continentally cosmopolitan avifauna at many sites.

A second potential danger stems from the tendency to view site-specific data as finite, bounded information. Riparian tracts along major river systems constitute corridors of habitat for birds. Bird communities are more similar among riparian than among upland vegetation types at sites across a watershed (Knopf 1985), and some species may migrate along riparian corridors seasonally (Wauer 1977). The tendency for birds to move within riparian corridors is fundamental to the cosmopolitanism issue, and a corridor of riparian vegetation can foster extensive faunal mixing where it crosses a historic, geographic barrier to avian dispersal (Knopf 1986). Current thinking relative to the conservation of landscapes has been preoccupied with the application of area components of island biogeography theory to patterns of population dispersion (Willson and Carothers 1979, Harris 1984, Risser et al. 1984, Norse et al. 1986) rather than on an approach that emphasizes animal redistribution as a function of dispersal capabilities and probabilities (e.g., Simpson 1965). Vertebrate conservation within riparian ecosystems, especially, needs to be based upon the perspective of whether local management programs create or sever dispersal corridors.

**SUMMARY AND RECOMMENDATIONS**

Riparian vegetation occurs on <1\% of the western North American landscape, yet it provides habitats for more species of birds than all other vegetation types combined. Riparian ecosystems tend to be subjected to extensive disturbance. Besides diversion of water from streams and the subsequent stress placed upon the vegetative community, these ecosys-
tems are subjected to agricultural conversions, grazing, channelization, recreational development, and colonization by exotic plants. Given the high value of riparian ecosystems relative to surrounding uplands as wildlife habitats throughout the West, we offer the following recommendations:

(1) The U.S. Congress assign enforcement powers to FWS for charges delegated within the Fish and Wildlife Coordination Act. FWS powers should extend across all federal agencies.

(2) Public agencies (state and federal) review user fees for riparian areas to assure that rates reflect the enhanced wildlife value that these systems provide.

(3) Each public land management agency develop specific, internal, procedural guidelines for addressing riparian issues to reflect regional-level planning rather than conservation or enhancement actions justified upon local criteria. In addition, each agency should voluntarily make their riparian policies public and assure the visibility of those policies.

(4) Respective agencies coordinate planned management actions within an identified drainage (Clark 1980, Mantell et al. 1985, Knopf 1986), preferably with responsibility for coordination being assigned to a designated individual with agency-wide authority.

(5) Agencies should develop new technologies to discourage the spread of exotics within native riparian ecosystems, with both state and federal agencies discontinuing subsidization of exotic woody species (Olson and Knopf 1986a) that have demonstrated the ability to naturalize within riparian communities and displace native species.

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SHORT COMMUNICATIONS

Evaluation of *Vermivora × Oporornis* hybrid wood-warblers.—By the late 19th century, the breeding birds of the eastern United States were thought to be well known. Hence, discovery of three apparently new species of wood-warblers in the 1870s, *Helminthophaga leucobronchialis* (Brewster 1874), *H. Lawrencii* (Herrick 1875), and *H. cincinnatiensis* (Langdon 1880), was considered remarkable. Perhaps more surprising was the subsequent insight that all three taxa were hybrids (Ridgway 1880, 1885; Brewster 1881). "H. Lawrencii" (Lawrence's Warbler) and "H. leucobronchialis" (Brewster's Warbler) were determined to be the hybrid offspring of the Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers, while "H. cincinnatiensis" (Cincinnati Warbler) was judged to be an intergeneric hybrid of *V. pinus* and the Kentucky Warbler (*Oporornis formosus*). In the era before Mendelian genetics, these were among the first recognized examples of hybridization in passerines. Brewster (1881:224) reflected the sentiments prevalent among his colleagues, "many of our leading ornithologists were incredulous as to its [hybridization] occurrence in a state of nature save among the Grouse and some of the Swimming Birds."

Hybridization between *V. pinus* and *V. chrysoptera* is now well documented (Parkes 1951, Gill 1980). The specimen of "H. cincinnatiensis" remains unique, and for over sixty years was the only known hybrid between *Oporornis* and *Vermivora*. In 1948, a puzzling warbler was collected in Cass County, Michigan. This specimen, which was compared with the type of *H. cincinnatiensis*, was provisionally considered a hybrid between *V. pinus* and the

<table>
<thead>
<tr>
<th>Character</th>
<th><em>O. philadelphia</em> (N = 15)</th>
<th><em>O. formosus</em> (N = 15)</th>
<th><em>V. pinus</em> (N = 15)</th>
<th>Hybrids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing chord</td>
<td>60.3-65.6</td>
<td>65.6-74.1</td>
<td>58.7-63.4</td>
<td>61.6 63.6</td>
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<tr>
<td></td>
<td>62.8 ± 1.7</td>
<td>69.4 ± 2.1</td>
<td>61.1 ± 1.3</td>
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<tr>
<td>Wing tip</td>
<td>9.7-17.2</td>
<td>13.6-20.8</td>
<td>13.5-16.0</td>
<td>14.2 16.0</td>
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<tr>
<td></td>
<td>13.2 ± 2.4</td>
<td>17.7 ± 2.0</td>
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<td>Central rectrices</td>
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<td>43.1-49.2</td>
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<td>41.1-46.8</td>
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<td>46.6 ± 1.9</td>
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<tr>
<td>Tarsus</td>
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<td>19.6-22.7</td>
<td>16.0-17.8</td>
<td>18.7 18.4</td>
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<td>20.6 ± 0.7</td>
<td>21.6 ± 0.8</td>
<td>17.0 ± 0.6</td>
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<tr>
<td>Culmen (from anterior edge of nostril)</td>
<td>7.1-8.5</td>
<td>7.9-8.6</td>
<td>7.7-8.7</td>
<td>8.0 NA*</td>
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<td>7.7 ± 0.4</td>
<td>8.2 ± 0.2</td>
<td>8.4 ± 0.2</td>
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*Measurement not available.*
Fig. 1. Dorsal (A) and lateral (B) views of *Vermivora pinus*, *Oporornis formosus*, and presumed *V. pinus × O. formosus* hybrids (all males). From left to right: *V. pinus*, "Michigan" hybrid; "Ohio" hybrid, *O. formosus*. The Michigan hybrid may be the progeny of an F₁ hybrid back-crossed with a parental *V. pinus*.

Mourning Warbler (*O. philadelphia*) (McCamey 1950). In this paper, I reevaluate the two presumed *Vermivora × Oporornis* hybrid specimens.

*Specimens examined* — "*Vermivora pinus × Oporornis formosus*" (Ridgway 1880), Cincinnati Museum of Natural History No. 26247 (formerly No. 1394 in the Frank W. Langdon Collection), male, collected at Madisonville, Ohio, on 1 May 1880 by Frank W. Langdon. "*Vermivora pinus × Oporornis philadelphia*" (McCamey 1950); Delaware Museum of Natural History No. 54985 (formerly No. 10381 in the George M. Sutton Collection), adult male, 11.4 g, testes greatly enlarged, collected at Russ Forest, Cass County, Michigan on 28 May 1948 by B. Frank McCamey.

I compared these specimens with large series of all North American parulid species in the National Museum of Natural History, Smithsonian Institution. Measurements (after Baldwin et al. 1931) of the two putative hybrids and a series of male *V. pinus*, *O. formosus*, and *O. philadelphia* were taken with dial calipers and rounded to the nearest 0.1 mm (Table 1).

I used principal components analysis (PCA) on untransformed variables to reduce the dimensionality of data and to facilitate the visualization of morphology in two dimensions. Unrotated principal components were extracted from correlation matrices (SYSTAT).

**Results** — Because of its close resemblance to both specimens, there is little doubt that *V. pinus* is one of the parental species of both hybrids. Ridgway (1880) and McCamey (1950)
Fig. 2. Bivariate plots of factor scores from Principal Components Analysis. Separate analyses were performed for the Michigan (A) and Ohio (B) hybrids.

described the plumage intermediacy of the hybrids. Intermediacy in color or pattern, although strongly suggestive, is insufficient to prove parentage. Because the identity of *V. pinus* as one of the parents seems to be indisputable, I focussed attention on characters that are absent in *V. pinus* but shared by a hybrid and one or more species of *Oporornis*.

Unequivocal evidence of species-specific *Oporornis* parentage is found only in the crown and facial plumage of the hybrids (Fig. 1). Both hybrids have a yellow forecrown as in *V. pinus*, but differ from that species and from *O. philadelphia*, in having small black spots above each nostril (more prominent in the Michigan specimen) clearly separated from the loral area by a yellow preocular stripe. Both hybrids have scattered black feathers, tipped with grayish olive, at the sides and rear of the hindcrown. Crown feathers of *O. philadelphia* are medium gray (base to tip) from nostrils to nape. The crown of *O. formosus* is black from the nostrils posterior to a point behind the eyes; feathers of hindcrown are tipped gray. Because crown feathers of *O. philadelphia* are uniformly gray, black spots above the nostrils and black crown feathers could only have been inherited from *O. formosus*. Other potential parental species (e.g., *Geothypis trichas*) lack black-based feathers on the hindcrown. Auricular feathers of the Ohio hybrid are black with dull yellow tips or lateral barbs. These form an obscured facial pattern nearly identical to that of *O. formosus* (the auriculaires of *O. philadelphia* are uniformly gray). Under magnification, black barbs can be observed on the edges of a few auricular feathers on the Michigan bird. Again, *O. formosus* is indicated to be the *Oporornis* parent of both hybrids. Neither hybrid exhibits any trace of the extensively gray or black bib found in *O. philadelphia*. Both hybrids have yellow undertail coverts (tip of covert to tip of tail: "Ohio," 12 mm; "Michigan," 14 mm) similar in length to those of *O. formosus* (range, 12.5–22.5; \( \bar{x} = 15.5 \) mm) and *O. philadelphia* (range, 12.5–18.0; \( \bar{x} = 14.2 \) mm) but longer than in *V. pinus* (range, 15.5–21.7; \( \bar{x} = 18.1 \) mm).

The remaining plumage (e.g., wings, tail) could have been inherited from *V. pinus* or
Table 2
Factor Loadings for the First Two Principal Components from Separate Analyses of the Hybrids

<table>
<thead>
<tr>
<th>Variable</th>
<th>Ohio</th>
<th>Michigan</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>Wing chord</td>
<td>0.90</td>
<td>-0.33</td>
</tr>
<tr>
<td>Wing tip</td>
<td>0.57</td>
<td>-0.78</td>
</tr>
<tr>
<td>Central rectrices</td>
<td>0.76</td>
<td>0.58</td>
</tr>
<tr>
<td>Outer rectrices</td>
<td>0.86</td>
<td>0.18</td>
</tr>
<tr>
<td>Tarsus</td>
<td>0.87</td>
<td>0.18</td>
</tr>
<tr>
<td>Culmen</td>
<td>NA</td>
<td>NA</td>
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</tbody>
</table>

Variance explained

<table>
<thead>
<tr>
<th></th>
<th>Percent</th>
<th>Cumulative</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ohio</td>
<td>63.8</td>
<td>86.2</td>
</tr>
<tr>
<td>Michigan</td>
<td>53.9</td>
<td>81.9</td>
</tr>
</tbody>
</table>

either species of *Oporornis* and provide no additional information. Plumage pattern and color comparisons indicate that both specimens are *Vermivora pinus × Oporornis formosus* hybrids.

**Morphological analysis.**—Except for tarsus length, measurements of the hybrids were within, or narrowly outside, the range of values for *V. pinus* (Table 1). This morphological similarity is aptly demonstrated by the plot of PCA factor scores (Fig. 2, Table 2). The bill of the Ohio hybrid was broken at the tip, so separate principal component analyses were performed for each hybrid. Factor scores for both hybrids fall well outside the envelope of scores for *O. Philadelphia*, corroborating the conclusion based on plumage. The Michigan hybrid falls within the envelope of scores for *V. pinus* whether or not “culmen length” is included in the analysis. The Ohio specimen, which is larger than the Michigan specimen in four of the five comparable measurements, occurs outside the *V. pinus* envelope, roughly between the centroids for *V. pinus* and *O. formosus*. This suggests a correlation between intermediacy in plumage and morphology and raises the speculation that the Ohio specimen is an F₁ hybrid, while the Michigan bird may represent the progeny of an F₁ hybrid backcrossed with a pure *V. pinus*.

**Discussion.**—The occurrence of a greater frequency of intergeneric than intrageneric hybrids has been cited as evidence supporting the hypothesis that reproductive isolating mechanisms are strongest among closely related species (Parkes 1978). Hybridization (i.e., the ability to interbreed) is thus viewed as a shared primitive character. An alternate view suggests that hybridizing parulids are closely related and are generically oversplit (e.g., Short and Robbins 1967). These hypotheses would appear to be mutually exclusive. The AOU checklist (1983), which attempted to approximate a primitive to derived sequence of genera within families, lists no fewer than nine parulid genera (*Parula, Dendroica, Catharopeza, Mniotilta, Setophaga, Protonotaria, Helminthis, Limnodytis, Seiurus*) in the sequence between *Vermivora* and *Oporornis* (see Parkes 1978, Avise et al. 1980). Clearly, a robust phylogeny of parulid genera must be determined to evaluate the evolutionary implications of *Vermivora × Oporornis* hybridization.

**Acknowledgments.**—I thank R. Davis and R. Kennedy (Cincinnati Museum of Natural History) and D. Niles (Delaware Museum of Natural History) for loaning the hybrid warblers.
Techniques for study of avian syringes.—In most birds, the syrinx is located within the thoracic cavity, dorsal to the heart and ventral to the esophagus (in hummingbirds and some storks it is along the neck). The syrinx and trachea are bound to the esophagus by membrane; removal of these together, using the esophagus as a 'handle,' reduces risk of damage to the delicate bronchi and preserves membraneous connections (e.g., the bronchidesmus). Removal of a syrinx from a museum specimen disrupts the heart arteries and the sternum and breast muscles along one side, but careful removal leaves a specimen largely intact and makes the syrinx available for future researchers. Dissection procedures described here follow Ames (1971:13) but are more detailed:
(1) With the bird on its back, expose the skin along the neck and chest along the bird's right side.

(2) With scissors, cut shallowly through the skin of the neck until the trachea is found, usually to the right of the vertebral column. Initial cuts higher along the neck minimize damage to the trachea. Expose the trachea to its entry into the thoracic cavity at the furculum.

(3) Cut the furculum and the cephal edge of the sternum just to the right of the midline. Continue this cut, straight and shallow, through the right sternum and breast musculature; deep cuts may damage the heart or syrinx. In some birds, e.g., some owls and goatsuckers, the syrinx may be removed through the furcular opening without damaging the skeleton. The syrinx can be removed from skeletal preparations by working through openings between the ribs or through the abdominal cavity after the viscera have been removed.

(4) Open the thoracic cavity enough to see both M. sternotrahealis where they extend from the trachea toward the thoracic wall. Note their precise position of insertion, then cut through each muscle near to the thoracic attachment.

(5) Cut through the trachea and esophagus (or just the trachea if the esophagus is not being removed) far enough above the syrinx to include all 'syringeal' features and to provide a handle for manipulation of the specimen. It is better to include too much trachea than too little. Cutting away connecting tissue, free the trachea and esophagus (or just the trachea) down to the level of the heart.

(6) Carefully cut through the major heart arteries, allowing the heart to be lifted up to the left, exposing the syrinx and bronchi. With curved-blade scissors, cut through the right bronchus where it enters the lung, the esophagus cephal to the syrinx (if the esophagus is also to be removed), and the left bronchus where it enters the lung. Include as much of the bronchi as possible; short bronchi may be the most common deficiency of syrinx specimens.

(7) Using forceps, pull gently on the esophagus and continue to cut away attached connective tissue from around the trachea, syrinx, bronchi, and esophagus until these can be removed easily. If the esophagus is to be left within the body, use forceps to pull on the trachea and cut the tissues between the syrinx and the esophagus as well as other restraining tissue. It may be advisable to bind the carcass closed with twine, thread, or cheesecloth before returning it to its storage jar.

(8) In most syrinxes, dorsal and ventral surfaces may be distinguished by the greater dorsal exposure of the internal tympaniform membranes and the ventral tendency of the paired M. sternotrahealis. If there is doubt (e.g., picid syrinxes approach dorsoventral symmetry), notch the caudal end of the trachea on the dorsal surface as a marker and note that this has been done.

(9) Place fresh syrinxes in buffered 10% formalin for several days (see Cato 1986:26). Blot excess formalin, and transfer to 70%-75% ethanol (ETOH) for storage. Syrinxes from fixed museum specimens may be put directly into alcohol. For long-term storage, small alcohol-filled vials including the syrinx and appropriate labelling should be placed within larger alcohol-filled containers. In the field, small labels bearing field catalogue numbers may be tied with cotton thread gently but securely around attached tracheae and esophagi and placed with other syrinxes in a single container.

(10) The specimen may be 'cleaned' at your convenience. Artifacts within the respiratory tract can usually be removed by squirting alcohol through the trachea with a syringe. Care must be used in cleaning; removal of connective tissue may expose important features but at the cost of others, including embedded muscle or nerves.

Osteological preparation.—Normally, the syrinx and trachea are removed from skeletal preparations and discarded. If included, delicate articulations usually are broken by larger bones within crowded skeleton boxes. Since most adult birds have ossified trachea and virtually all have ossified syrinxes, it is useful and appropriate to preserve the syrinx as a
skeletal element during the preparation of skeletal specimens. First, before removing the viscera from the body cavity, cut through the bronchi, esophagus, and associated membranes at the level of the lungs, leaving them attached to the dorsal body wall of the thorax. Second, submit the specimens to minimal dermestid activity (terrestrial isopods may be preferable in preparation of delicate skeletal material, Maiorana and Van Valen 1985). Third, store the syrinx and other delicate skeletal elements in a smaller box or envelope within the primary skeleton box.

Skeletal syrinx specimens lack muscles and membranes. Their cartilaginous components may change shape with drying. However, they are more convenient for some measurements and for S.E.M. photography. In addition, because of scarcity of whole alcoholic specimens (Zusi et al. 1982), skeletal materials may provide the only syringeal source for many species.

**Muscle staining.**—The myology of many syringes is simple, consisting of only two pairs of muscles, M. sternotrachealis and M. tracheolateralis. Other syringes, including those of Coliiformes, Trochilidae, Psittaciformes, and most Alcedinidae and Passeriformes, possess a more complex, intrinsic musculature (Cannell 1986). The number, length, and fiber direction of these muscles may be difficult to determine because they are often small, thin, or obscured by connective tissue. Examination may be facilitated by using an iodine stain to darken fibers. By immersing specimens in a solution of distilled water (100 ml), potassium iodide (2.0 g), and iodine (1.0 g) for several minutes, muscles become a dark reddish-brown (Bock and Shear 1972). This stain, fading under light, is reversible and nondestructive; hence, iodine-stained specimens may undergo subsequent staining procedures. The stock solution should be stored away from light.

**Clearing and staining for cartilage and bone.**—This procedure distinguishes between cartilage and bone and clarifies the configuration of all supporting structures. Hence, perception of syringeal structure is greatly improved. Here, procedures of Wassersug (1976) and Dingkerus and Uhler (1977) have been adapted specifically for use on syringes, but a similar treatment could be used on avian embryos or other small materials. Note that the process is destructive, obliterating details of muscle and membrane and potentially altering the overall configuration. Rare specimens should only be cleared and stained after important myological and membranous features have been recorded in detail. Even for common species, muscles and membranes should be examined and measurements of syringeal parts made before clearing and staining. No syrinx should be cleared or stained or submitted to any other destructive procedure without permission from the host institution. Pre-1940 museum specimens may not have been fixed; syringes from these should be placed in formalin for several days. These and specimens stored in isopropyl alcohol should be kept in ETOH for a week before initiating staining.

This procedure takes at least 4 days, but may be interrupted when materials are in water or alcohol, or by refrigeration during the enzyme step. Large syringes may require longer periods at some steps. Other factors, such as quality of fixation and preservation, will also influence results. Excess tissue, clotted blood, and the esophagus should be removed prior to staining. These directions make solutions of 150 ml, adequate for staining ten small-to-medium syringes in individual 20 ml scintillation vials.

1. Stain cartilage with alcian blue for 24 h (no danger of overstaining). *Alcian blue stain:* 30 ml glacial acetic acid; 120 ml 95% ETOH; 20 mg alcian blue powder. Color should not be so dense as to obscure position of specimen. Solution is unstable and must be made up fresh. This is a tenacious stain that should be handled carefully.

2. Rinse in 95% ETOH for several minutes (until specimen sinks). This solution is reusable.

3. Rinse in 50% ETOH for several minutes (until specimen sinks). This solution is reusable.
Rinse in distilled water.

Clear in enzyme solution for 5–6 h, or longer, until membranous parts are clear. Large or tough specimens may need to be cleared for several days. Specimens retaining blue stain after a day or so in enzyme solution may be put in 1% KOH for several hours; KOH and enzyme solutions may be alternated until membranous parts are clear. Note that KOH destroys myelin, and its use will inhibit nerve staining. This solution is temperature dependent; activity can be increased by mild heating (27°C is ideal) or virtually halted with refrigeration. *Enzyme solution:* 40 ml saturated aqueous sodium borate (distilled water saturated with borax); 110 ml distilled water; 2 g (½ teaspoon) trypsin. Stir gently until dissolved. This solution must be made up fresh.

Rinse gently in tap water (but not over open sink drain).

Stain for calcium phosphates with alizarin red S for 12–14 h (no danger of overstaining up to 24 h). *Alizarin red stain solution:* 10 ml 10% KOH stock solution (10 g of pellets per 100 ml distilled water); 190 ml distilled water; enough alizarin red S powder to color solution deep purple. Reusable until solution loses color or effectiveness is reduced.

Rinse gently in tap water, then dehydrate through a series of KOH/glycerin solutions (a to c, below). These are stable and may be reused until they become too colored. Leave syringes in each step for 5 or more hours.

a. 3:1 KOH/glycerin: 30 ml 10% KOH; 270 ml distilled water; 3 ml 3% hydrogen peroxide (bleaches pigments); 100 ml glycerin.

b. 1:1 KOH/glycerin: 30 ml 10% KOH; 270 ml distilled water; 3 ml 3% hydrogen peroxide; 300 ml glycerin.

c. 1:3 KOH/glycerin: 15 ml 10% KOH; 135 ml distilled water; 450 ml glycerin.

Store syringes in solution of: 90% glycerin, 10% distilled water; a few thymol crystals (inhibits mold and bacteria).

If results are unsatisfactory, specimens may be recleared or restained with alizarin red, but once in glycerin, specimens should be rehydrated back through the glycerin series (1:3, 1:1, 3:1) and washed in distilled water before further treatment; glycerin negates enzyme activity and may affect stain effectiveness. It is possible to re-stain for alcian blue but there is a chance of losing the specimen (G. Dingerkus, pers. comm.).

*Nerve staining.*—This procedure is adopted from Filipski and Wilson (1984, 1985), A. Savitsky (pers. comm.), and S. Gornak (unpubl.). It can be used independently, with the cartilage and bone staining procedure, or applied to previously cleared and stained specimens.

Material to be stained for nerves alone should first be cleared with trypsin (see step 5 above), then washed in distilled water. For integration within the cartilage and bone staining procedure, insert steps described below between steps 6 and 7 above. Specimens previously cleared and stained should be rehydrated, soaked in distilled water for several hours, and then submitted to the following procedure.

Three provisos accompany this technique. First, nerves removed during the initial ‘cleaning’ can no longer be stained. Second, KOH is destructive to myelin, so specimens treated with KOH may not provide effective nerve staining. Third, nerve staining may not be permanent; observed patterns should be recorded while still visible. Nerves can be re-stained but possibly with reduced effectiveness (rehydrate specimens before restaining).

1. Immerse in 70–75% ETOH for 30 min or more.

2. Immerse in Sudan Black B stain. Check frequently at first, then every 5–10 minutes; remove when nerves are a dense blue-black. Gentle agitation facilitates staining. *Sudan Black B stain:* dissolve 0.5 g Sudan Black B in 500 ml of 70% ETOH with the aid of a warm water bath. Filter solution before use.

3. Destain in 70–75% ETOH for 5 min or more, then rinse gently in tap water. (If staining for calcium, go to step 7 of clearing and staining procedure above.)
(4) Dehydrate through a KOH/glycerin series as in step 8 above.
(5) Transfer to 90% glycerin as in step 9 above.

Acknowledgments.—I thank A. Savitsky for information about nerve staining. Comments from C. Blem, M. Clench, C. Conway, T. Crowe, G. Dingerkus, W. Lanyon, and R. Zusi helped improve the manuscript; particular thanks are due W. Lanyon.

LITERATURE CITED


Avian Davian Behavior.—Dickerman (J. Mamm. 41:403, 1960) reported a field observation of a male Richardson ground squirrel (Citellus [= Spermophilus] richardsoni) copulating with a dead female which was lying on its side in a copulatory position. He termed the behavior “Davian behavior,” a facetious reference to a ribald Limerick about necrophilia. Here I make what is apparently the first report of Davian behavior in birds.

I observed several drake Mallards (Anas platyrhynchos) attempting forced copulation with a hen Mallard at 16:00 on 9 April 1987 on Sheldon Lake, Fort Collins, Colorado. After several minutes of constant pursuit, the hen was forced to swim to the shoreline of an island. She stopped at the water’s edge, apparently exhausted and unable to escape farther. She was immediately approached by two Chinese Geese (Anser cygnoides), one of which repelled the drakes to a distance of approximately 2 m. It then stood over, the hen in a pre-copulatory position and began to peck violently at the back of her head and neck. After approximately 5 min the hen became motionless in a copulatory posture, and she was not observed to move again; she was apparently dead at this point. The goose continued to peck for another
1–2 min before both geese walked away. Five male Mallards immediately swam to her, continued fighting among themselves, and began copulating with her body. This continued for approximately 7 min with a minimum of three different drakes participating. When the drakes swam approximately 3 m away, a Ring-billed Gull (Larus delawarensis) landed beside her and began pecking and tearing at her head and neck, occasionally grabbing her head and shaking it. In approximately 2 min, the five drakes returned, and two of them copulated with her body, but for a shorter duration than the first episode. After approximately 2 min they abandoned her body to the gull which began to tear flesh from her neck and back. The drakes did not return to her.

The proximate cause for this behavior can be explained in terms of the dead hen's lordosis position releasing copulatory behavior in the sexually aroused drakes. Schein and Hale (Anat. Rec. 128:617, 1957) demonstrated that a detached female head in an upright position is sufficient to elicit copulatory attempts in male domestic turkeys (Meleagris gallopavo). The adaptive significance of forced copulations in animals has been discussed by Crawford and Galdikas (Can. J. Psych. 27:215–230, 1986), but when it results in Davian behavior, it is difficult to explain in terms of individual fitness since apparently time, energy, and sperm are wasted. Although it was difficult to determine whether ejaculation occurred in all the copulations observed, post-copulatory tail-wagging behavior suggested that some of the drakes had ejaculated (McKinney and Stolen, Anim. Behav. 30:461–474, 1982). However, since this type of behavioral “mistake” apparently occurs infrequently, the fitness cost is too small to be selected against.—PHILIP N. LEHNER, Dept. Biology, Colorado State Univ., Fort Collins, Colorado 80523. Received 29 Sept. 1987, accepted 17 Nov. 1987.


Nest lining with sheep wool: potential negative effects on Cave Swallows.—Much discussion has centered on the energetic costs and benefits of construction and use of the avian nest. Investigators have discussed the insulative value of roosting (Kendeigh 1960) and nesting (Royama 1966) in cavities and the thermal homeostatic role of domed individual or communal nests (Ricklefs and Hainsworth 1969, White and Kinney 1974, White et al. 1975). Withers (1977), however, found little of this property in mud nests of Cliff Swallows (Hirundo pyrrhonota).

Bailey (1928), and later Bent (1968), documented the incorporation of domestic sheep wool into the nests of U.S. birds. Subsequently, van Riper (1977) reported the increasing use of wool in nest construction by six Hawaiian species and indicated that only nest bodies, and not linings, contained this material. In this and a subsequent work (Kern and van Riper 1984), the authors discussed wool's function as a binding, but not insulating, agent. Despite this framework of interest, few studies have attempted to correlate variation in natural nest morphology with concurrent variation in reproductive parameters in the field, although White and Kinney (1974), working under seminatural, relatively uniform environmental conditions, found an inverse relationship between nest insulating value and attentiveness in Ploceus cucullatus. Here, as part of our analyses of the influence of man on hirundinids (Martin 1980, Hamilton and Martin 1985), we report the use of wool as a lining material in the nests of Cave Swallows (Hirundo fulva), describe its physical contact with eggs deposited upon it, and attempt to relate this phenomenon to length of incubation period, clutch size, hatch, and nestling survival.

Our study sites were nine concrete culverts in Uvalde County, Texas, beneath a 17.7 km stretch of U.S. Hwy. 90 extending from 0.5 km W of the Nueces River to the boundary of
Cline, Texas. The culverts, oriented approximately N-S, are of similar single or multiple passageway construction; passages ranged from 1–14 in individual culverts and from 13.7–25.9 m in length, 1.5–3.1 m in width, and 1.5–2.8 m in height. Nests were open mud cups, built on the upper 15% of culvert walls. By utilizing such relatively uniform, darkened sites in south-central Texas, *H. fulva* recently has expanded its breeding niche, range, and numbers (Martin 1980).

Nests of *H. fulva* in 8 culverts had grass linings that incorporated little or no sheep wool. Culvert #37, in the central portion of this transect, was located near a sheep-shearing enclosure of a nearby ranch; nests in it were lined with considerable quantities of wool. Nests were visited and their contents marked and/or enumerated daily from 10 April to 3 June 1976; this period coincided with the first reproductive cycle for most *H. fulva*. We collected data on length of the incubation period from 31 nests (Table 1). After hatch, four nests were destroyed through human intervention; we arbitrarily excluded these from our subsequent tabulation of distributive statistics (Table 2, \( N = 27 \) nests). The Mann-Whitney \( U \)-test was employed in statistical comparisons; results were considered significant at \( P < 0.05 \).

In nests lined with wool, eggs tended to become embedded in separate, individual depressions near the bottoms of the nest cups, rather than remaining in tangential, exposed groups as in grass-lined nests. Incubation period was significantly longer in the sample of nests with thick wool linings \( (P < 0.025; \text{see Table 1}); \text{these groups did not differ significantly in clutch-size} (P > 0.9), \text{number of young hatched} (P > 0.5), \text{and} (P > 0.1) \text{number of young surviving to 18 days} \text{(two days prior to flight potential for this species, Martin et al. 1977).} \)

Within certain physiological limits, incubation periods vary inversely with temperature

### Table 1

**Frequencies of Occurrence of Clutches Having Various Incubation Periods in Nests of *H. fulva* with Different Lining Types**

<table>
<thead>
<tr>
<th>Incubation period (days)</th>
<th>Wool culvert</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>15-16( ^a )</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>16-17</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>17-18</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>18-19</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>

\( ^a \) Incubation of clutch through at least fifteen 24 h periods following clutch completion, possibly part of sixteenth period; longer incubation periods were scored similarly.

\( ^b \) This is the normal incubation period in *P. fulva* (Martin et al. 1977).

### Table 2

**Clutch-size, Hatch, Survival to 18 Days, and Percentages of *H. fulva* that Utilized Different Nest-lining Materials**

<table>
<thead>
<tr>
<th>Culvert</th>
<th>Clutch-size</th>
<th>Young hatched</th>
<th>Survived</th>
<th>% Hatched</th>
<th>% Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( x ) ( SE )</td>
<td>( x ) ( SE )</td>
<td>( x ) ( SE )</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wool culvert</td>
<td>6</td>
<td>4.17 ± 0.17</td>
<td>3.67 ± 0.33</td>
<td>2.17 ± 0.31</td>
<td>88.0</td>
</tr>
<tr>
<td>Other</td>
<td>21</td>
<td>4.14 ± 0.14</td>
<td>3.62 ± 0.16</td>
<td>2.81 ± 0.24</td>
<td>87.4</td>
</tr>
</tbody>
</table>
(Romanoff 1934, Nice 1954, Skutch 1976). Martin et al. (1977) and Martin (unpubl.) have established the normal incubation period of *H. fulva* eggs at 15–16 days. We have no evidence to indicate that environmental conditions or attentiveness differ in a systematic fashion among culverts included in our study. Our results indicate that because of the compressibility of wool, its use in nest linings by *H. fulva* appears to lengthen the period of incubation rather than to decrease it because of its insulating property (see Kern and van Riper 1984). We hypothesize that partially isolated eggs buried in individual nest-lining depressions may be separated too far for normal incubation patch contact or may be difficult to turn; hatch-synchronizing communication (if it occurs in *H. fulva*) also may be impeded.

Acknowledgments.—We thank Sallie Martin posthumously for her many contributions to and support of the project. Comments by C. van Riper III and C. R. Blem improved the manuscript. Research costs were paid in part by the National Geographic Society and the Texas Memorial Museum of The University of Texas at Austin.

LITERATURE CITED


ROBERT F. MARTIN AND DEAN HECTOR, Texas Memorial Museum and Dept. Zoology, Univ. Texas at Austin, Austin, Texas 78705. Received 15 Sept. 1987, accepted 24 Nov. 1987.
Interspecific interactions of Spotted Sandpipers.—Interspecific interactions have been studied in a number of avian groups. While most studies have dealt with interactions stemming from competition due to niche overlap (e.g., Bock 1969, Kalinoski 1975, Burger et al. 1979, Robinson 1981), few have investigated the effects of breeding status on interspecific interactions (e.g., Walters 1979, Stephens 1984). This study examines the effects of breeding status on interspecific interactions of Spotted Sandpipers (Actitis macularia), a species with a resource-defense polyandrous mating system and predominantly male parental care (Emden and Oring 1977). An “interspecific interaction” was defined as an agonistic encounter between a Spotted Sandpiper and an individual of another species.

A population of individually marked Spotted Sandpipers was studied on Little Pelican Island (LPI), Leech Lake, Minnesota (47°07′N, 94°22′W) from 1973 to 1987. Data on interspecific interactions were collected in 1976, 1977, 1979, and 1985. Observations began in early May and terminated in late July or early August when the birds left the island. See Oring and Knudson 1972, Oring and Maxson 1978, Maxson and Oring 1980, Oring and Lank 1982, 1986, and Oring et al. 1983 for further details on this population. The sandpipers were observed each day, weather permitting, from 3 m towers for an average of 6 h per day; 3 h beginning at sunrise and 3 h prior to sunset. The birds were most active during these time periods (Maxson and Oring 1980). Sandpipers were categorized by breeding status. Nonbreeding birds were not included in the analysis because individuals that failed to establish themselves as breeders never remained on LPI. “Unpaired” were all unpaired birds on LPI (prior to their breeding, exclusive of postbreeding birds). “Pre-laying” defined birds from the time of initial pairing to the laying of the first egg of a clutch. “Laying” is the time between laying of the first and last egg of a clutch; and “incubating” is the time between laying the last egg of a clutch and either hatch or destruction date of that clutch. “Brooding” is the time between hatching and fledging or loss of a brood, and “post-breeding” is any time spent on LPI after breeding activities ceased. Interspecific interaction rates for each bird in each breeding status were determined by dividing the number of interactions by the number of days spent in that status. We analyzed only interspecific interactions of adults of locally breeding species in order to minimize biases due to fluctuating migrant populations. Fluctuations in the population levels of resident species were negligible within seasons. Data from different years, however, were not combined due to possible variations in population numbers of resident species. Seasonal effects on interspecific interactions were minimal due to high predation and renesting rates (Oring et al. 1983).

Spotted Sandpipers interacted with a total of 20 species. Five species, Red-winged Blackbird (Agelaius phoeniceus), Killdeer (Charadrius vociferus), Common Grackle (Quiscalus quiscula), Song Sparrow (Melospiza melodia), and Yellow-headed Blackbird (Xanthocephalus xanthocephalus), accounted for 82% of male and 90% of female interspecific interactions (Table 1).

Rates of interspecific interactions of male Spotted Sandpipers were significantly related to breeding status in 1976, 1977, and 1979 (Kruskal-Wallis: 1976, adj $H = 14.011$, df = 5, $P < 0.025$; 1977, adj $H = 28.936$, df = 5, $P < 0.001$; 1979, adj $H = 19.164$, df = 5, $P < 0.005$). In all three years, the average interspecific interaction rate increased dramatically during brooding (Fig. 1). In 1985, interaction rates were high during brooding but moderately high rates during pre-laying eliminated significance (Fig. 1). For females, on the other hand, interspecific interaction rates were only related to breeding status in 1976 (Kruskal-Wallis, adj $H = 90.792$, df = 5, $P < 0.001$). In 1976, clutch loss was high; and few females engaged in either incubating or brooding activities (Maxson and Oring 1980). Therefore in 1976,
**Table 1**

**Frequency of Interspecific Interactions of Spotted Sandpipers**

<table>
<thead>
<tr>
<th>Species</th>
<th>1976</th>
<th>1977</th>
<th>1979</th>
<th>1985</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
</tr>
<tr>
<td>Red-winged Blackbird (<em>Agelaius phoeniceus</em>)</td>
<td>30 (21)</td>
<td>4 (22)</td>
<td>45 (30)</td>
<td>6 (38)</td>
<td>12 (20)</td>
</tr>
<tr>
<td>Killdeer (<em>Charadrius vociferus</em>)</td>
<td>83 (57)</td>
<td>9 (50)</td>
<td>27 (18)</td>
<td>4 (25)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Common Grackle (<em>Quiscalus quiscula</em>)</td>
<td>4 (3)</td>
<td>3 (17)</td>
<td>12 (8)</td>
<td>3 (19)</td>
<td>13 (22)</td>
</tr>
<tr>
<td>Song Sparrow (<em>Melospiza melodia</em>)</td>
<td>10 (7)</td>
<td>0 (0)</td>
<td>38 (26)</td>
<td>1 (6)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Yellow-headed Blackbird (<em>Xanthocephalus xanthocephalus</em>)</td>
<td>2 (1)</td>
<td>1 (6)</td>
<td>15 (10)</td>
<td>1 (6)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Purple Martin (<em>Progne subis</em>)</td>
<td>2 (1)</td>
<td>1 (6)</td>
<td>1 (1)</td>
<td>0 (0)</td>
<td>26 (43)</td>
</tr>
<tr>
<td>Brown-headed Cowbird (<em>Molothrus ater</em>)</td>
<td>8 (6)</td>
<td>0 (0)</td>
<td>5 (3)</td>
<td>1 (6)</td>
<td>1 (2)</td>
</tr>
<tr>
<td>Other species ^b</td>
<td>7 (5)</td>
<td>0 (0)</td>
<td>6 (4)</td>
<td>0 (0)</td>
<td>8 (13)</td>
</tr>
</tbody>
</table>

Fig. 1. Mean rates of interspecific interactions of male (M) and female (F) Spotted Sandpipers according to breeding status and year. Vertical lines show standard error of means. Unpair = Unpaired, Pre-lay = Pre-laying, Lay = Laying, Inc = Incubating, Brood = Brooding, and Post-Breed = Post-Breeding.
values for these two periods were abnormally low compared to other stages of the breeding cycle.

Within each year and reproductive status, rates of male and female interspecific interactions were compared using Wilcoxon two-sample tests. There was a significant difference between the sexes in only two cases, both during brooding (1976: \( U = 120, P < 0.001 \) and 1979: \( U = 235, P < 0.05 \)).

Among years, the species composition of LPI did not change drastically, but the percent of interactions that Spotted Sandpipers spent with particular species did change. In 1976 and 1977 a pair of Killdeers bred on LPI (Oring and Maxson 1984). Since Spotted Sandpipers and Killdeers occupy similar habitats, the opportunity for contact, and hence interactions with Killdeers, was high (Table 1). Of the other primary species with which the sandpipers interacted, variation in number and percent of interactions between years was due to variation of population sizes of these species.

In three of the four years, interspecific interactions involving males increased significantly during the brooding period (Fig. 1). Stephens (1984) suggested that “greater conspicuousness of the mobile chicks” and less direct protective contact between parents and chicks than between parents and eggs could lead to increased parental protectiveness. Gochfeld (1984, p. 358) noted that, in general, “adult shorebirds are more active in protecting chicks than eggs.” He provided two possible explanations for this change in parental behavior: (1) the stimulus of seeing the pipped egg or chick, and (2) a change in hormonal levels.

Increased levels of testosterone have been shown to increase aggression levels in many avian species (Trobec and Oring 1972, Searcy and Wingfield 1980). During brooding, however, male Spotted Sandpipers' plasma testosterone levels do not significantly change from incubation levels (Fivizzani and Oring 1986). Prolactin levels of brooding males also remain unchanged from incubation levels for at least three days post-hatch. It is unknown if they begin to change after this time (Oring et al. 1986). These results do not support Gochfeld's (1984) second explanation, at least for Spotted Sandpipers. While it may be true that a hatching chick provides the stimulus to alter the behavior of its parent, the mechanism by which this is regulated remains to be discovered.

We detected no effect of female Spotted Sandpiper breeding status on the rate of interspecific interactions. Although females occasionally provide parental care, such care is usually sporadic and consists of alarm calling and acting as a sentinel for the brood.

Maxson and Oring (1980) observed that intraspecific interactions were highest during the pre-laying stage but also increased during brooding. We observed no comparable increase in interspecific interactions during pre-laying. Intraspecific competition for mates has little if any effect on the frequency of interspecific interactions.

Although Spotted Sandpipers have a male-biased parental care system, we only found a difference in interspecific interaction rates between the sexes in two cases, both in the brooding period. In 1977 and 1985, the two years in which there was no significant difference between the sexes during brooding, the average interaction rate of males was indeed higher than that of females (Fig. 1). Of the 20 species with which Spotted Sandpipers interacted, only two, the Common Grackle (Maxson 1978) and Microtus spp. (Maxson and Oring 1978), were known to prey upon Spotted Sandpiper eggs and/or chicks. Red-winged and Yellow-headed blackbirds are also suspected of preying upon Spotted Sandpiper eggs (Oring, unpubl.).

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Sheldon, D. Bjerklie, S. Hennes, P. Dolan, R. Reese, M. Skwarok, and A. Fivizzani helped with field work. C. Gratto and M. Colwell provided helpful comments on the manuscript.

LITERATURE CITED


Adaptive perch selection as a mechanism of adoption by a replacement Bald Eagle.—Replacement of lost mates within the same nesting season has been recorded in 26 raptor species (Newton 1979). Only three species (Cooper's Hawk, *Accipiter cooperii*; Northern Goshawk, *A. gentilis*; and Peregrine Falcon, *Falco peregrinus*) have exhibited full adoption, i.e., incubation of eggs and/or rearing of young by an unrelated, replacement mate (Rohwer 1986). Neither mate replacement within the same season nor adoption has been recorded for Bald Eagles (*Haliaeetus leucocephalus*). Herrick (1932) describes two Bald Eagle mate replacements of 11 and 14 weeks' duration, but both occurred over winter (October–February), prior to nesting. Adoption may be adaptive for long-lived species, through establishment of a pairbond for future seasons, if: (a) following mate loss and nest failure, renesting within the same season is unlikely; (b) the probability of starting the next breeding season with an established pairbond is increased with adoption; and (c) experienced pairs tend to have higher breeding success than new pairs (Rohwer 1986).

In 1983, while monitoring a Bald Eagle nest in Arizona, we observed mate replacement and full adoption, which provided an opportunity to verify one aspect of adoption theory under natural circumstances. Given that habitat familiarization contributes to experience of pairs (see item c above), and that perch use is one mechanism of that familiarization process, we hypothesized that the replacement adult should perch more selectively as the season progressed, i.e., exhibit less movement between fewer perches. He should also use more perches in common with the original mate and fewer perches new to himself, if optimal or preferred perches with discriminating characteristics exist within the breeding area. In this paper, we present results of the perch analysis, along with documentation of the mate replacement and full adoption.

*Study site and methods.*—Observations were made at a cliff nest in central Arizona, 32 km east of Phoenix, Maricopa County. On-site surveillance of the nest was maintained 1 February–7 June 1983 as part of a USDA Forest Service volunteer nest watch program on central Arizona Bald Eagle nests (Forbis et al. 1985). The female (A1), the original male (A2), and the replacement male (A3) were differentiated by size, plumage, and behavior. A3 also had a U.S. Fish & Wildlife Service band. It was later determined to be a 4-year-old at the time of replacement, fledged from an adjacent breeding area 11 km away. To analyze perching in terms of habitat and behavior, we recorded both locations (perches) and the frequency of their use (perching frequency or observations). A perch location was tallied only once per month for each eagle using it, while a perching observation was recorded each time a perch was used. We defined A3's perches used by A1 or A2 within the same or
Results and discussion. — Incubation began about 25 January 1983. On 13 February, after incubation and a typical nest exchange, A2 disappeared. Over the next 7 days, A1 did not feed and was off the nest a total of only 25 min. A3 flew into the area on 14 February. He appeared restless when perching and made many short flights, changing perches often to new and different locations. A3 also frequently perched, roosted, and arranged nest material on a nearby, alternate nest. At first A1 watched A3 alertly, vocalized often, and chased him off when he came close.

Display flights (A3 flying by A1 with a stick, a fish, or with legs and feet extended) began on 16 February and increased in frequency through 20 February. On 17 February, A3 landed uncontested on the nest ledge. A brief courtship flight followed, wherein the two eagles presented talons and cartwheeled. The frequency and duration of courtship flights increased through the end of the month, with brief perching together-away from the nest and A1 initiating courtship activity by 21 February. A3's first stick delivery and first prey delivery occurred on 19 February. Soon thereafter, both birds commonly fed and arranged nest material together. Copulatory behavior first occurred on 24 February.

On 27 February, A3 began incubating or brooding (exact hatching date uncertain). We observed three nest exchanges that day and six on 28 February, which marked the onset of
normal nest attendance, indistinguishable from that of other established breeding pairs in Arizona. Three eaglets fledged about 16 May, after a typical 77-day nestling period (1983 population mean 79 days, Grubb and Forbis, unpubl. data). A3 fully participated in provisioning, feeding, and attending the young during this time.

This quick and successful mate replacement is indicative of a healthy population with a pool of nonbreeding adult eagles (Newton 1979). Bald Eagles in Arizona meet all three conditions set forth by Rohwer (1986) for adoption to be adaptive (Grubb and Forbis, unpubl.). Thus, A3, who as a 4-year old was likely seeking his first mate and nest site, could certainly afford to adopt and rear A2’s offspring in order to: (a) secure a viable breeding area, (b) obtain a proven mate for future nesting seasons, and (c) improve the likelihood of his own productivity the following year.

The dramatic difference in A3’s perching frequency over A2’s and the use of different perches by A3 were the first signs that replacement was occurring (Fig. 1). The progressive decline for A3 during the period indicates decreasing movement between perches. The pattern of total monthly perches for all three adults was similar, with A3 dropping from 64 perches in February to 20 in May. Only 12 (19%) of A3’s February perches were common to the other eagles, whereas in May, 10 of 20 perches (50%) were common perches. Conversely, the percent of new perches per month for A3 declined from 100% in February to 35% (11 of 31) by April.

We recorded approximately three times the perching observations (409 vs 141) at 1.6 times the perches (123 vs 78) for A3 as for A1 ($P < 0.05$, adjusted G-statistic, 3 df, Sokal and Rohlf 1981). Some of this difference may be due to sexual differences in behavior during nesting. However, we include A1’s data for comparison because: (a) during February, A1 and A2 showed similar perching patterns (47 observations at 40 perches and 39 at 32, respectively), (b) the frequency of perches and perching observations for A1 was relatively stable throughout the period, and (c) both perching measures for A3 progressively converged on A1’s figures until near parity by May (A3—40 observations at 20 perches; A1—34 at 18) (Fig. 1).

Results of our perching analysis for A3 evidence adaptive perch selection, which, as a mechanism of habitat familiarization and ultimately A3’s experience, should have improved his fitness for subsequent breeding seasons. No further perching data are available, but the A1-A3 pair successfully fledged 2 young in 1984 and have continued to produce 2–3 young per year since.

Acknowledgments.—We thank R. Orr and J. Kaiser, Mesa Ranger District, Tonto National Forest, for special field and administrative support that made these observations possible. K. Berger also assisted with field work. R. Bowman, W. Eakle, J. Hodges, and S. Rohwer provided helpful reviews of an earlier draft. USDA Forest Service, U.S. Fish and Wildlife Service, and Bureau of Reclamation funded this study through interagency agreement.

LITERATURE CITED


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Use of Red-winged Blackbird nest by a Prothonotary Warbler.—Apart from the use of old woodpecker holes, reports of cavity-nesting birds using nests (particularly open-cup nests) built by other species are rare. Interspecific nest use has more commonly been reported in open-nesting species (e.g., Finch, Wilson Bull. 94:582-584, 1982). We document here the first case of a Prothonotary Warbler (Protonotaria citrea), a cavity-nesting wood-warbler of swampy or riparian habitat, using an open-cup nest built by another bird species. Prothonotary Warblers have been known to nest rarely in some unusual man-made nest sites (Bent, U.S. Natl. Mus. Bull. 203, 1953), all of which resembled natural cavities to some extent. The nesting we report here occurred when all suitable natural cavities and nest boxes in the vicinity were unavailable due to an extremely high local density of Prothonotary Warblers.

The study site is located along the Tennessee River in Benton County, Tennessee. As part of a larger study on the reproductive ecology of Prothonotary Warblers (Petit, L., M.S. thesis. Bowling Green State Univ., Bowling Green, Ohio, 1986), nest boxes were erected in linear fashion along the river shoreline in densities of 0, 8, and 20 nest boxes per 300 m. On 1 June 1987, an unbanded male Prothonotary Warbler was observed on one of the high density nest box plots defending a small (0.08 ha) territory which did not encompass any of the 20 boxes present. Territorial boundaries were determined from >2 h of observation on that day. Vegetation on the territory consisted of a small knob of willows (Salix spp.) and buttonbush (Cephalanthus occidentalis) that extended into the river from the main contour of the shoreline. The male was apparently unmated, as no female was observed in his territory in 1 h of intensive observation. Probst and Hayes (Auk 104:234-241, 1987) found that 1-1.5 h of observation was sufficient to determine pairing success of Kirtland's Warblers (Dendroica kirtlandii). Six mated males also occupied territories on the plot, five of them within a 150 m length of shoreline adjacent to the male's territory. This represents a density of Prothonotary Warblers six times greater than that occurring naturally in this habitat (Petit 1986). Collectively, those 6 males defended all 20 nest boxes and two natural cavities on the plot, rendering them unavailable to the unmated male. There was one woodpecker cavity located within the unmated male’s territory, but it was occupied by Tree Swallows (Tachycineta bicolor).

The male was observed on several days during the following week, and on 9 June, an unbanded female Prothonotary Warbler was seen foraging within his territory. The female entered a Red-winged Blackbird (Agelaius phoeniceus) nest that was situated approximately 1 m above water in the crotch of a branch of a 2-m-tall buttonbush. The female remained on the nest for approximately 5 min before leaving to forage again. The nest contained 2 Prothonotary Warbler eggs, and it was lined with a thin layer of moss along the inner walls of the nest cup. During 1 h of observation (12:00-13:00), the female incubated three times...
for an average of 6.7 min/bout. Although some foliage was present above the nest, the female was still quite exposed to the midday sun and could be seen panting. We color-banded the male the same day. Sometime before 17 June the nest was depredated. Although the actual clutch size was not determined, incubation on 9 June meant that the clutch size probably was not >3 eggs, as Prothonotary Warbler females incubate once the penultimate egg is laid (Petit 1986). Average clutch size for this population is 4.6 and <10% of all clutches are ≤3 eggs (Petit 1986).

On 17 June we observed that the male had expanded his territory after three neighboring males had cased territorial defense while feeding fledglings. The expanded territory (based on the male’s singing posts) included five nest boxes and encompassed an area of approximately 0.15 ha. On 26 June an unbanded female was incubating 4 eggs in a nest box located within the male’s expanded territory. Although the identity of that female was not certain, the timing of clutch initiation and the fact that she was mated to the male suggest that she was his previous mate. The pair successfully fledged four young from that nest.

Measurements of the blackbird nest used by the warblers were compared with those of 20 other nearby nests of Red-winged Blackbirds, also built in buttonbushes in 1987. All measurements of the warbler nest were similar to those of blackbird nests except for inside depth, which was greater than the upper 95% confidence limit for the other 20 blackbird nests. This fact, along with the moss lining of the nest (Prothonotary Warblers use moss in their nests; Red-winged Blackbirds do not), suggests that the warblers altered the nest cup and made it deeper.

Lack of available natural cavities or nest boxes prompted use of the blackbird nest by the warblers. The question remains as to why the male would continue to defend an area that held no suitable nest sites. Possibly, the male had been “waiting” for a territory with suitable nest sites to become available, as is often the case in this population of Prothonotary Warblers (unpubl. data). Also, Prothonotary Warblers exhibit strong site tenacity (unpubl. data). If the male had nested at this site in a previous year, his tenacity could explain why he did not move elsewhere in search of cavities. When faced with severe nest-site limitation in habitat that is otherwise preferred, Prothonotary Warblers may utilize any site that adequately resembles a cavity, even if it is of lower quality, when the alternative would be to delay or forego breeding.

LJP’s research on Prothonotary Warblers has been supported by the Association of Field Ornithologists, Sigma Xi, Arkansas Audubon Society Trust Fund, the Reichhardt and Petit families, and a Causey Grant-in-aid of Research, University of Arkansas. Dr. W. Davis of Lambuth College kindly provided housing, and Acee Dairy, Fort Smith, Arkansas, donated milk cartons for nest boxes. We appreciate the very helpful comments of W. Buskirk, K. Petit, K. Smith, and D. Stauffer.—Lisa J. Petit and Daniel R. Petit,


Predation on overwintering wood borers by woodpeckers in clear-cut forests.—Few researchers have assessed the impact of woodpeckers on wood borers, a complex of insect species that burrow deep into the xylem of living trees and account for a $60–120 million annual loss of timber in the eastern United States (Donley and Worley 1976). In addition, few studies have discussed tree characteristics associated with locations of borers that were depredated, and no studies have assessed the impact of woodpeckers on wood borers in young, regenerating forests. This latter point is especially significant because of the contro-
SHORT COMMUNICATIONS

versial practice of clear-cutting and its effect on management practices. The purposes of this study were to document the extent of woodpecker predation on overwintering populations of red oak borers (Coleoptera; *Enaphalodes rufulus*) inhabiting regenerating stems in clear-cuts and to characterize attack sites of depredated and nondepredated borers.

**Study areas and methods.**—Our two study sites, located in The Wayne National Forest, Hocking County, Ohio, had been clear-cut about 1970. The 3.1-ha plots were located within larger (10–12 ha) clear-cut areas, but were bordered on at least one side by mature deciduous woodland (Petit et al. 1985). Slopes were steep (average grade 17%) and drained by ephemeral creeks. Canopy heights averaged approximately 8 m, and the sites were dominated by red oak (*Quercus rubra*), chestnut oak (*Q. prinus*), white oak (*Q. alba*), hickories (*Carya spp.*), flowering dogwood (*Cornus florida*), and maples (*Acer spp.*). The clear-cuts had not yet undergone self-thinning as evidenced by the high density of stems (approximately 9000 stems/ha).

The red oak borer has a 2-year life cycle (Donley and Acciavatti 1980). Eggs are laid on trunk surfaces during the summer, and hosts range from saplings to mature trees. As the hatched beetle larvae burrow through bark in August and September, they extrude from their entrance holes a fine, light-colored frass composed of sawdust and feces. Frass accumulation indicates the presence of active borers. By November, larvae are about 5 mm long and overwinter in a dormant condition within a burrow (about 1 cm³) just under the bark. The following summer, larvae grow to about 25 mm in length while they bore a 10–15 cm tunnel obliquely upward through the sapwood and heartwood. During the larva's second winter dormant period, woodpeckers must excavate approximately 3–7 cm into the trees to extract them. During the following spring and summer, surviving larvae pupate and then hatch as flying adults. The breeding cycle is synchronous throughout any given red oak borer population, with adults emerging every other year.

Our study focused on the second overwintering period when the borers were >3 cm deep in tree boles. Thus, results of borer mortality due to woodpeckers do not assess the impact of woodpeckers over the borers' entire life cycle. However, because many species of wood borers spend much of their larval stages deep within tree trunks and branches (e.g., Hay 1968, Borror et al. 1976), this seemed to be a reasonable time to study the proficiency of woodpeckers at removing the borers.

In August 1982, active red oak borer holes were located within each clear-cut. Some trees showed evidence of more than one borer attack. We marked each hole with plastic flagging tape placed 1–2 m from the infested tree. For each attack site, we recorded height above ground, diameter of trunk at the attack site, and direction (N, NE, E, etc.) on the tree bole. We searched for signs of woodpecker predation during the first week of April 1983. Woodpeckers dig characteristic conical holes when attempting to excavate borers (Hay 1972).

Differences in characteristics of trees with depredated and nondepredated borers were analyzed with *t*-tests, for diameter of the tree at a borer attack site and height of an attack, and with chi-square contingency tests for orientations of borers excavated on tree trunks.

**Results.**—Of 234 red oak borer attack sites located 10 to 456 cm above the ground, woodpeckers excavated 11 borers on each of the two plots (7.4% and 12.8% predation). These rates were not significantly different. Percentages of marked trees showing signs of woodpecker predation were also similar on both plots (9 of 79 trees [11.4%] vs 7 of 41 trees [17.1%]). The following analyses are based on pooled data.

Based on dimensions of the excavations and on bird censuses of the clear-cuts (see below), we infer that Downy (*Picoides pubescens*) and Hairy (*P. villosus*) woodpeckers accounted for all of the excavations. Woodpeckers did not excavate borers randomly with respect to their orientation on tree trunks. Eleven of 22 borers excavated had entered trees from the
west side ($\chi^2 = 15.7, \text{df} = 3, P < 0.005$). Also, frequency of predation did not differ between trees with one and trees with more than one borer attack ($\chi^2 = 0.42, \text{df} = 1, P > 0.50$).

Both trunk diameter ($t = 2.17, \text{df} = 232, P = 0.031$) and height of borer attack site ($t = 2.02, \text{df} = 232, P = 0.044$) differed between excavated and nonexcavated borer chambers. Depredated borers were found in smaller trunks ($\bar{x} = 8.3$ vs 9.8 cm) and higher on trees ($\bar{x} = 186.5$ vs 149.4 cm) than nondepredated borers. Because height was significantly correlated with diameter ($r = -0.20, P = 0.002$), there may have been an interaction between these two variables, such that the true relationship between woodpecker predation and its controlling factor was obscured. To control for this potential bias, we used logistic regression analysis (PROC CATMOD, SAS Institute Inc. 1985) to determine the simultaneous effects of the continuous predictor variables (height and diameter) on the categorical response variables (depredated and nondepredated). Results of our analysis showed that trunk diameter ($P = 0.049$) was a better predictor of predation than was height ($P = 0.073$).

Discussion.—The 9.4% capture rate of borers in this study was low compared to mortality caused by woodpeckers in other studies. For example, Solomon (1969, 1975), summarizing data for more than a dozen species of wood borers, found that woodpeckers depredated 13 to 81% of the marked borers. As in our study, Solomon (1969, 1975) recorded predation of most species over one winter. In a study of red oak borers in southern Ohio, Hay (1972) credited woodpeckers with 39% of the total mortality over a two-year period, with nearly equal predation rates between the first (33%) and second (30%) overwintering periods.

The low predation rate in our study may have been due to the study plots being in clearcuts. Dense vegetation and lack of large trees make these areas less profitable foraging sites in comparison to surrounding woodlands (see Conner and Crawford 1974, Conner and Adkisson 1975, Conner 1980). In fact, we sighted only 10 Downy and 4 Hairy woodpeckers in 25 pairs of censuses (one in each plot) over a six-month period from October to April. Relative abundances of these same species were more than two times higher in the surrounding uncut forests (Petit et al. 1985).

Another potential explanation for the low predation rate was that we studied the red oak borers only during their second winter. The depths at which the borers were located within the trunks during the second winter (3–5 cm) were much different than during the first winter period (1–2 cm, see Donley and Acciavatti 1980). Thus, woodpeckers may be able to excavate borers more readily during the beetles' first winter, but more data are needed to confirm this idea.

We have no answer as to why most borer larvae that were depredated had entered tree trunks on the west side of the bole. Regardless of the side of the tree which a borer entered, woodpeckers could excavate the chamber from any side of the tree. We did not quantify the orientation of excavation sites, but there appeared to be no pattern as to the side selected. Tree diameter affected the probability of borer predation. Solomon (1969) found that woodpecker predation of red oak borers was limited to trees < 15 cm in diameter. This relationship may be due to woodpeckers not being able to locate borers that are deeper within the boles of trees or to woodpeckers selecting small diameter trunks so as to reduce excavation time. Height of borer attack site also affected the chances of predation. Downy and Hairy woodpeckers may have selected those heights in which they were not vulnerable to ground predators and, yet, were not obstructed by the numerous branches higher on the tree trunk. This correlation, however, may have been affected to some extent by the interaction between diameter and height.

The low rate of borer mortality in this study suggests that, in regenerating hardwood clearcuts, woodpeckers may not be significant predators of borers overwintering deep within the boles of trees. This is not to say, however, that woodpeckers do not significantly reduce numbers of red oak borers during the first overwintering period (Hay 1972). The lack of
snags in clear-cuts may also be detrimental to populations of woodpeckers that may otherwise roost or nest there (e.g., Dickson et al. 1983; but see McPeek et al. 1987). This paucity of woodpeckers may, in turn, allow tree-damaging wood borers to remain relatively free of natural control provided by woodpeckers.

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LITERATURE CITED


Effect of previous occupancy on recruitment to territorial sites of male Blue Grouse.—Male Blue Grouse (*Dendragapus obscurus*) use territories primarily as areas for display and mating (Bendell and Elliott 1967, McNicholl 1978). During a 10-year study on Vancouver Island, British Columbia, some sites were used almost every year, whereas others were occupied sporadically (persistent and transient sites, respectively; Lewis and Zwickel 1981, also see Boag 1976). Male Blue Grouse that occupied persistent sites survived better than those on transient sites (Lewis and Zwickel 1981), and replacements preferentially settled on areas that had been occupied continuously when residents were removed (Lewis and Zwickel 1980). We inferred from this that persistent sites were of higher quality than transient sites. Since it seems advantageous to select the best sites for territories, what cues might young males use to distinguish between good and poor areas? Two possibilities are: (1) habitat differences between high and low quality sites, and (2) previous occupancy by another male. Here I examine the use of these two factors in territorial site selection by male Blue Grouse.

In a removal experiment (Lewis and Zwickel 1980), we shot original residents from 11 persistent and 11 transient territorial sites in early spring 1978. Throughout the rest of the spring and summer, all males were shot as soon as they were heard singing on a removal site. Males that took territories on the 22 vacant removal sites in 1979 still showed a preference for persistent sites, including 5 of 6 yearlings (Lewis and Zwickel 1980). These yearlings could not have been influenced in their choice of site by the presence of a previous occupant, since they hatched after residents were removed in 1978. Thus, they apparently distinguished between high and low quality areas on the basis of habitat. Persistent and transient sites did differ with respect to topography (Lewis 1981), so such cues seem to exist.

Although young males may use habitat features as an indicator of territorial quality, previous occupancy by another male could be used as an additional cue. Observations I obtained after conducting another removal experiment on Hardwicke Island, British Columbia, in 1982 enabled me to examine the effect of this factor on a male’s choice of territory. In spring 1982, 17 territorial males were present on my 95 ha study plot, and between 4 and 8 April 14 they were removed by shooting. All subsequent replacements to these sites were removed as soon as they were heard singing. The remaining 3 territorial males, and 11 that resided in areas immediately adjacent to the study plot, were left alive; 9 were individually color banded and 5 were unmarked. At least 8 of the 14 males that survived throughout spring and summer 1982 did not return in spring 1983 and are presumed to have died over winter. Seven of the vacant territories were occupied by new males in 1983, including the 3 within the study plot. In contrast, only 2 of the 14 vacant removal sites were occupied by new males in 1983. Rate of recruitment in 1983 was significantly greater to sites that had males on them in 1982 than to sites that had residents artificially removed (log-likelihood $\chi^2 = 8.91, P = 0.003$).

Quality of territorial sites on Hardwicke Island could not be determined prior to the removal experiment in 1982 because I lacked long-term occupancy and survival data as was available prior to the Vancouver Island removal experiment. Therefore, a possible explanation for the greater rate of recruitment to sites left vacant by overwinter disappearance is that by chance all were of high quality, whereas most of those vacated by artificial removal were of poor quality. However, 9 of the 14 removal sites had replacement males settle on them in 1982, suggesting that at least these 9 were good areas for territories. Rate of replacement in 1983 to sites that had been occupied throughout 1982 still was greater than to the 9 sites that were kept vacant artificially, and that likely were high in quality (log-likelihood $\chi^2 = 5.15, P = 0.023$).
Females may be attracted to the vicinity of a territory by the resident's singing. If males are more likely to take territories in areas where they previously encountered females, this might account for their preference for territorial sites that had been occupied previously. However, this likely was not a factor in the pattern of preference shown by new males in 1983. Despite the removal of most territorial males from the study plot in 1982, the density of females and their movement patterns were unaffected (Lewis 1984). The lack of replacement to removal sites in 1983 therefore cannot be attributed to a lack of females in those areas. The preference by recruiting males in 1983 for territories that had been used throughout 1982 suggests that selection of a territorial site can be influenced by the mere presence of a resident male the previous year.

Yearling male Blue Grouse are rarely territorial (Bendell and Elliott 1967, Jamieson and Zwicker 1983) but have home ranges that overlap the territories of a few adult males (Sopuck 1979, Jamieson and Zwicker 1983). As yearlings, they may evaluate the quality of all potential territorial sites within their home range. Results of my removal experiments suggest that features of the habitat and previous occupancy by another male are both used as cues when choosing a territorial site. Direct habitat assessment would seem the most reliable means of determining territory quality, since quality ultimately will be related to vegetative or structural features that affect survival and/or reproduction. However, this may not always be the most expedient means for selecting a territory, especially if the assessment must be done quickly (Stamps 1987). Additionally, little is known of the importance of social factors in territorial site selection, and they should not be overlooked when seeking to explain why some areas are used consistently and others intermittently.

Acknowledgments.—J. F. Neiderleitner and M. G. Sullivan assisted in the removal study on Vancouver Island, and S. J. Hannon and J. O. Murie made constructive comments on the manuscript. Field studies were conducted on lands leased to Crown Zellerbach of Canada Limited. The cooperation of their personnel, as well as the hospitality and logistic assistance of the Bendickson and Murray families on Hardwicke Island were very helpful and appreciated. Financial assistance was provided by the Canadian National Sportmen's Fund, the Natural Sciences and Engineering Research Council of Canada, and the University of Alberta.

LITERATURE CITED


Sopuck, L. G. 1979. Movements and breeding biology of the Blue Grouse in relation to


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Phenetic relationships among the warblers in the Dendroica virens complex and a record of D. virens from Sonora, Mexico.—Four species of warblers of western North America are closely related to the eastern Black-throated Green Warbler (Dendroica virens): the Black-throated Gray (D. nigrescens), Townsend’s (D. townsendi), Hermit (D. occidentalis), and Golden-cheeked (D. chrysoparia) warblers (Mengel 1964). These species seem to be related closely, but there is debate about their taxonomy. For example, D. townsendi and D. occidentalis hybridize where their ranges overlap in Oregon and Washington (Jewett 1944, Morrison and Hardy 1983) and may be conspecific. Mayr and Short (1970) regard D. chrysoparia as a subspecies of D. virens and suggest that D. virens, D. occidentalis, and D. townsendi comprise a superspecies complex, with D. nigrescens a close relative of the complex. The A.O.U. Check-list (AOU 1983:613) states that “D. townsendi, D. occidentalis, D. virens and D. chrysoparia appear to constitute a superspecies.” These opinions are based on the birds’ geographic distributions and a “largely subjective” evaluation of plumage patterns and song (Mengel 1964). Other than Morrison’s (1983) study of morphometric variation within D. townsendi, there are no published analyses of the size variations within this complex. The present analyses of the D. virens complex (including D. nigrescens), based on measurements of 21 skeletal features, provide information about the phenetic variation among these warblers, and confirm the identity of a skeletal specimen in the collection of the University of Kansas, Museum of Natural History (KU 37136). KU 37136 was collected 20 December 1956 by A. A. Alcorn 21 miles SSE of Nogales, Sonora. It was eviscerated in the field, dried, and sent to KU, where it was identified as D. virens before being prepared as a skeleton. It is not known who identified the bird, or on what basis (presumably plumage characters). Other than this individual, there are no specimens of D. virens from Sonora (S. M. Russell, pers. comm.).

Methods.—I measured the following specimens (adult males unless otherwise noted): 13 D. townsendi; 6 D. occidentalis; 35 D. virens (12 females); 18 D. nigrescens (2 females); 1 D. chrysoparia. With the exception of two specimens from Mexico (KU 37136 and one from Veracruz), all of the D. virens used were from the northeast, and thus on geographic grounds are not D. v. waynei. With the exception of D. virens, these were all of the adult male specimens of these species available in the following collections: Royal Ontario Museum, University of Michigan, Burke Museum University of Washington, University of Kansas, U.S. National Museum, and Delaware Museum of Natural History. I did not attempt to obtain samples of females (with the exception of D. virens) because only small numbers are available. KU 37136 is a male.

I measured 21 skeletal features (Table 1) on each specimen, as described by Robins and Schnell (1971), except that gonys length is their “minimum mandible length” (gonys with rhamphotheca removed), synsacrum width is width across the antitrochanters, bill length (skull) is length of the premaxilla from the base of the skull, and bill length (nost.) is length
of the premaxilla from the anterior edge of the nostril. I used only nearly complete specimens. If a specimen was missing only a few characters, I estimated missing values as the means for the appropriate species and sex. (The sample sizes given above were the numbers used in the analyses; other specimens were measured but were not used because of missing values.) KU 37136 was complete. I used principal component analysis (PCA) (NTSYS, 1982, program FACTOR) on a matrix of correlations among the untransformed characters to ordinate the 74 specimens.

Results.—Correlations between many variables and Principal Component 1 (PC1) are high. Several measures of long bones (femur, ulna, carpometacarpus), sternum, and bill length (mandible length, and perhaps skull length) have correlations >0.80 (Table 1). Therefore, this component can be interpreted as measure of overall size (including bill size), although it doubtless contains some information about shape as well (Somers 1986). Because the correlations are positive, the largest birds are to the right on the PC1 axis. PC2 primarily contrasts bill length with leg and toe lengths; PC3 contrasts bill and tarsometatarsus lengths with nasal bone and synsacrum widths (Table 1). PC2 and PC3 have approximately the same eigenvalues, and therefore it is not possible to interpret them precisely (Gibson et al. 1984), although they nonetheless give information on grouping the specimens. The first three components together explain 63% of the total variation in the data matrix.
Figure 1 shows the positions of the 74 specimens in the space defined by Principal Components 1 and 2. There is extensive overlap between *D. occidentalis* and *D. townsendi* and between *D. virens* (male and female) and *D. nigrescens*. *D. virens*, and especially *D. nigrescens*, are generally "smaller" (to the left on PCI) than *D. townsendi*-*D. occidentalis*. Likewise, female *D. virens* are smaller on the average than males, and the two smallest *D. nigrescens* are the only two females in the sample. The amount of size dimorphism in *D. virens* is similar to that of other *Dendroica* warblers (Rising, unpubl. data). The single specimen of *D. chrysoparia* is near, but outside, the cluster of *D. virens*. There is little overlap between the *D. virens*-*D. nigrescens* and *D. townsendi*-*D. occidentalis* groups. KU 37136
Fig. 2. Two-dimensional plot of phenetic relationships defined by Principal Components 2 and 3 (see caption to Fig. 1).

(“S”) clusters in the middle of male *D. virens* (as it was identified) and is outside the range of *D. townsendi*, the similar species most likely to occur in Sonora in December. Phenetically, KU 37136 could be *D. nigrescens*, but it is unlikely that the two would be confused on the basis of feather characters. There is extensive overlap among all of the species in the PC2 by PC3 space (Fig. 2). In that plot, *D. chrysoparia* again falls outside, but close to, *D. virens* space and is within *D. nigrescens* space. Again, KU 37136 is outside of the phenetic range of *D. townsendi*.

Discussion.—A superspecies complex consists of two or more allopatric species of “...relatively recent monophyletic origin which are much more closely related to each other than to any other species” (AOU 1983:xiv). Mengel’s (1964) scenario for the evolution of this complex assumes that these birds comprise such a complex. He proposed that all of the western members of the complex (perhaps excepting *D. chrysoparia*) were derived from
an eastern ancestor of present-day *D. virens*. He postulated a series of colonizations of the west of such “pro-*virens*” birds through the northern boreal forests, perhaps during major Pleistocene interglacial periods. He suggested that *D. nigrescens* was descended from the oldest of these western colonizations and *D. occidentalis* and *D. townsendi* from more recent ones. The present-day hybridization of *D. townsendi* and *D. occidentalis* certainly indicates a high degree of genetic similarity between these two taxa, and they doubtless have a recent common ancestor. *D. chrysoparia* may be a relictual population of a once more widespread eastern species, probably not much different from *D. virens*, or, alternatively, a remnant of a once widespread early western differentiate.

Phenetic similarity of the sort that I have quantified could easily be due to convergence. Nevertheless, these analyses show that there is a close phenetic similarity between *D. townsendi* and *D. occidentalis*, the two taxa in the complex that frequently hybridize. *D. virens* and *D. nigrescens*, the two taxa most distantly related to each other in Mengel’s scenario, are also essentially identical with regard to the features analyzed here; thus it seems appropriate to include *D. nigrescens* in the *D. virens* complex. The one specimen of *D. chrysoparia* falls close to the *D. virens* cluster, but it is more like *D. townsendi-D. occidentalis* on the PCI axis (which explains 47% of the variation among the specimens). Therefore, either hypothesis concerning its history is consistent with its phenetic placement. KU 37136 is confirmed as a specimen of *D. virens* from Sonora.

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**LITERATURE CITED**


Nesting success and incubation behavior of American Kestrels in central Kentucky.—Previous studies of the nesting success and incubation behavior of American Kestrels (Falco sparverius) reported that nest failure generally occurred before hatching and that 74-100% of hatchlings fledged (Hamerstrom et al. 1973, Balgooyen 1976, Craig and Trost 1979, Bloom and Hawks 1983, Coonan 1986, Bowman and Bird 1985). Male kestrels typically do 0-20% of all incubating (Willoughby and Cade 1964, Balgooyen 1976, Rudolph 1982, Wilmers et al. 1985). In the present study, we describe nesting success and incubation behavior of American Kestrels over three years in central Kentucky. This population has substantially lower nesting success and much more incubation by males than other populations described in the literature.

Breeding kestrels were observed during 1983, 1984, and 1987 on the Central Kentucky Wildlife Management Area (CKWMA) located 17 km SSE of Richmond, Madison County, Kentucky. Eleven nests were studied in nest boxes located on barns. Nest height ranged from 4 to 7 m. A removable door was placed at the back of each nest box so that contents could be checked from within the barn. It was often possible to observe kestrels through cracks in the doors without disturbing them. Nest boxes were checked for eggs or young no more than once per day. Date, time, and the sex of incubating birds were noted during each visit. Incubation by male and female kestrels was quantified by tallying the number of times each sex was observed incubating during 1983. Such incubation was assumed to begin only after clutches were complete.

Average clutch size for the three years (N = 10 clutches) was 4.2 eggs (mode = 4, SD = 0.91) (Table 1). Fifteen of 43 (34%) eggs failed to hatch (Table 1). One of these contained a fully developed embryo, and 14 were lost to predators. Nine eggs were lost from 4 nests between consecutive observations. At a fifth nest, 5 eggs were lost over a period of 7 days. Of 28 kestrel eggs that hatched, 12 young (43%) fledged from 3 nests (Table 1). Of 16 kestrels that hatched but did not fledge, one died (probably from an infection), while 15 were killed by predators. Thus, overall fledging success for three years was 12 fledglings from 43 eggs laid (28%) or 1.1. fledglings/active nest. In 1983, 2 of 5 nests were successful, yielding 9 fledglings (1.8 fledglings/active nest), in 1984, none of the 4 active nests produced fledglings, and in 1987, 1 of 2 nests was successful and produced 3 young (1.5 fledglings/active nest). Additionally, two adult females were found dead; one below a nest from which 4 eggs had disappeared, and the other within a nest from which 1 of 4 young was missing. Matted feathers on each female's head and neck may be an indication that snakes had tried to swallow them.

Incubation by individual males accounted for from 0% to 60% of total incubation (x = 32%). Males were not recorded incubating at two nests (N = 5 and 4 observations, respectively) while at three other nests males were recorded incubating in 3 of 5, 2 of 5, and 4 of 9 observations, respectively. Males performed 47% of the incubation (9/19 observations) for pairs in which males were observed incubating. Although incubation by male kestrels was common in 1983, they were never observed brooding (N = 15 observations of brooding adults).

Nesting success of American Kestrels in central Kentucky was lower than that published elsewhere. Unlike other studies, where nest failure typically occurred prior to hatching, mortality in the present study occurred both before and after hatching. This difference in nesting success probably was due to predation on both eggs and young by black rat snakes (Elaphe obsoleta) which are known predators of cavity-nesting birds. A black rat snake was observed consuming several nestling European Starlings (Sturnus vulgaris) from a nest box subsequently used by kestrels. In another case, a black rat snake was found inside a nest.
### Table 1


<table>
<thead>
<tr>
<th>Year</th>
<th>Nest box</th>
<th>First egg laid&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Clutch size</th>
<th>Number hatched</th>
<th>Number fledged</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>1</td>
<td>2 April</td>
<td>5</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>12 March</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
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<td></td>
<td>3</td>
<td>14 May</td>
<td>4</td>
<td>3</td>
<td>0</td>
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<tr>
<td></td>
<td>5</td>
<td>5 April</td>
<td>5</td>
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<td>0</td>
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<tr>
<td></td>
<td>6</td>
<td>26 May</td>
<td>4</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td>4.6</td>
<td>3.4</td>
<td>1.8</td>
</tr>
<tr>
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<td>1</td>
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<td>0</td>
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<td>25 April</td>
<td>5</td>
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<td></td>
<td>5</td>
<td>6 June</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<tr>
<td></td>
<td>6</td>
<td>30 May</td>
<td>4</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td>4.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.2</td>
<td>0</td>
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<td>1987</td>
<td>2</td>
<td>—</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>—</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td>3</td>
<td>3</td>
<td>1.5</td>
</tr>
<tr>
<td>Overall mean</td>
<td></td>
<td></td>
<td>3.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.5</td>
<td>1.1</td>
</tr>
</tbody>
</table>

<sup>a</sup> Back calculated using an interegg laying interval of 2 days for nests that contained >1 egg when first encountered.

<sup>b</sup> Based on completed clutches.

box from which two kestrels were missing. This seems to be the first instance where snakes have been found to be a major cause of nest failure in American Kestrels. The CKWMA may represent marginal breeding habitat for American Kestrels due to predation by black rat snakes on eggs and nestlings. Such predation totally eliminated kestrel reproduction during 1984, while in 1985 and 1986 no kestrels attempted to breed on the area.

In central Kentucky, male kestrels played an important role in incubation during 1983, perhaps because of food scarcity (Rudolph 1982). Packham (1985) suggested that incubation by male European Kestrels (*F. tinnunculus*) also was more important during years of food scarcity. Tall grass on the CKWMA may have protected prey, and one of two nests in which males apparently did not incubate was located on the edge of a large mowed area. Although male incubation was not recorded at one other nest, this male did enter his nest on two occasions after the incubating female flushed. In each case, he remained in the nest box for approximately 15 min.

Acknowledgments.—We thank C. Stinson, C. Blem, K. Smith, L. Petit, D. Petit, and N. Wilkinson for reviewing the manuscript. The research was supported by a Frank M. Chapman Research Grant from the American Museum of Natural History.

**LITERATURE CITED**

Sexual dimorphism in the voice of the Greater Shearwater.—Typically active at their colonies after dark, burrowing petrels may use calls to convey information given by visual signals in other diurnal seabirds. Recent studies of these calls have revealed that there is sexual dimorphism in some species (e.g., Little Shearwater [*Puffinus assimilis*], James and Robertson 1985a), and the call provides an immediate label of the bird's sex. In other species (e.g., White-chinned Petrel [*Procellaria aequinoctialis*], Brooke 1986), the sexes share two calls, one for sexual advertisement and another probably serving to discourage intrusion into the breeding burrow. Various intermediate vocal systems have also been described. For example in the British Storm-Petrel (*Hydrobates pelagicus*), the two sexes share a call, but in addition the male utters a sex-specific call (James 1984). However, the factors which dispose species to adopt a specific vocal system are not yet clear. The Manx Shearwater (*P. puffinus*) (Brooke 1978a) and the Little Shearwater (James and Robertson 1985a) have a marked sexual dimorphism in their calls. In both species the male call has a ringing quality lacking in the female, and sonograms of these calls are also distinct (Brooke 1978a, James and Robertson 1985a) so that human subjects, asked to assign a particular sonogram to the male or to the female group, may be 100% successful (Brooke 1978a). The closely related Cory's Shearwater (*Calonectris diomedea*) has an equally distinct sexual call dimorphism (Wink et al. 1982). The present note reports on dimorphism of the calls of Greater Shearwaters (*Puffinus gravis*).

Study area and methods.—The study was carried out in 1986 on Gough Island (40°21'S, 9°53'W) and Nightingale Island (37°24'S, 12°28'W), 420 km to the NNW, in the South Atlantic. The study period included the first two weeks of November, during the laying
The long and short phrases contained in each repeated unit are shown. The relative frequencies of F1 and F2 provide one means of distinguishing the calls of the two sexes (see text).

Period on Gough, and late November/early December during early incubation (Rowan 1952, pers. obs.) on Nightingale. Thus most, but not all, calls recorded on Gough were of males undertaking the first long incubation stint and similarly, playback tests were there directed at males. Conversely, on Nightingale, where I worked some three weeks after the peak of laying, females were incubating and provided most data. However, there were no significant differences in calls or in responsiveness to playback between islands, and henceforth the data are pooled.

Most birds handled in study burrows could be sexed by cloacal inspection (Serventy 1956). The calls of 12 males and 10 females were recorded on a Uher Report 1C tape recorder at 19 cm/s using a Uher microphone. All birds were incubating alone at dusk or at night when recorded. They were stimulated to call by playing a call of a Greater Shearwater of the same sex as themselves, either from the Uher or from a Sanyo M1170 dictaphone. Calls were analysed on a Kay 6061-B sound spectrograph using a narrow band filter.
Table 1

THE FREQUENCY OF RESPONSE OF INCUBATING GREATER SHEARWATERS TO THE
PLAYBACK OF CALLS. NOTE: PLAYBACKS TO BIRDS OF THE OPPOSITE SEX
DID NOT INCLUDE ANY PLAYBACKS TO MATES

<table>
<thead>
<tr>
<th>Sex of incubating bird</th>
<th>Call heard</th>
<th>No. of occasions bird</th>
<th>Responded</th>
<th>Did not respond</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Male</td>
<td>13</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>Male</td>
<td>Female</td>
<td>0</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>Male</td>
<td>0</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>Female</td>
<td>15</td>
<td>8</td>
<td></td>
</tr>
</tbody>
</table>

The recorded calls were played back at night at 39 burrows, 20 on Gough and 19 on Nightingale, to birds of known sex incubating alone. No bird experienced more than one playback per night, and no recording was played to a particular adult more than twice. In each test, the recording, usually lasting about 20 s, was played through once only, and I noted whether or not the incubating bird called in reply. No attempt was made to measure other possible responses, such as movement along the burrow towards the source of the sound.

Results.—Greater Shearwater calls usually consist of two principal phrases combined into a repeated call unit, and they are best described as vigorous unmelodious cries that crescendo in duetting pairs and during agonistic encounters. Though given mostly from the ground, calls were also uttered by flying birds. Calls began around 1600 GMT, reached a maximum as darkness fell (2000-2100), and then diminished in the next two hours. Birds in rafts approximately one km offshore from Nightingale also called.

Compared to Manx and Little shearwaters, the calls of male and female Greater Shearwaters were less distinct, both as sonograms (Fig. 1) and in the field. When five colleagues were given the 22 sonograms, one per bird, and asked to separate them into two groups, without it being specified how many should be assigned to each group, only two people (those with most experience of reading sonograms) achieved a satisfactory separation, with less than five birds placed in the "wrong" group.

In females (10/10) the fundamental frequency (F1; Fig. 1) of the shorter inspiratory phrase is lower than the frequency (F2) of the first harmonic of the longer expiratory phrase. The reverse is true in most males (9/12). The mean (± 1 SE) length of male units was 1.02 ± 0.045 s (N = 12), and of female units 0.76 ± 0.045 s (N = 10), a highly significant difference (t = 4.01, 20 df, P < 0.001). In fact calls with unit length greater than 0.85 s are very likely male (11 male and two female), whereas calls of shorter unit length are very probably female (eight female and one male).

Five of the recordings obtained were of birds (two males and three females) whose calls crescendoed during recording. From each crescendo, three sonograms were made. The sonograms revealed (by definition) changes in volume and also changes in the detailed frequency structure of each phrase. However, variation in unit length between individuals remained greater than that within individuals (one-way analysis of variance, $F_{4,10} = 46.5$, $P < 0.001$).

Differences in frequency structure and unit length provide a potentially powerful means of discriminating the calls of male and female Greater Shearwaters. No birds were misclassified by both criteria. Males normally responded when played a male call but were silent...
on hearing a female call (Table 1: $x^2 = 16.7, 1 \text{ df}, P < 0.001$). Conversely females responded to female calls but were silent on hearing male calls (Table 1: $x^2 = 12.0, 1 \text{ df}, P < 0.001$).

This study did not systematically investigate mate recognition of calls, known from other petrels (Brooke 1978a, 1986). However, on the two occasions a male's call was played to his mate (two different pairs involved), there was one response, whereas females never ($N = 13$; Table 1) responded to the calls of strange males.

Discussion.—The results of the playback experiments demonstrate that Greater Shearwaters can discriminate male and female calls. Such discrimination is potentially useful in mate selection (James 1985). Calling in response to the playback of the call of a bird of similar sex may occur because a bird's ownership of a burrow is more significantly threatened by the entry of another bird of its own sex (Brooke 1978a). The call may therefore serve as a "keep-out" function. Although it may generally not pay a shearwater to change mates (Brooke 1978b), it is arguably less important to keep out birds of the opposite sex; hence the lack of response in playback tests to calls of the opposite sex (Table 1).

Among petrels, sexual dimorphism in call may be related to whether or not the species calls in the air (James and Robertson 1985b, Brooke 1986). If correct, this relationship is supported by the Greater Shearwater results. This species has sexual call dimorphism, as evidenced by the statistical analysis and playback tests. However the extent of sexual dimorphism is manifestly less than in Manx and Little shearwaters (Brooke 1978a, James and Robertson 1985a). At colonies Greater Shearwaters seem to call less in the air than do Manx Shearwaters (pers. obs.), but critical data are not available. A detailed knowledge of the amount of time spent flying over the colony and the calling rates of flying and grounded birds of known status would be necessary to test whether or not the Manx Shearwater engages in more aerial calling than does the Greater Shearwater.

Another factor which may reduce the intensity of selection for strong sexual call dimorphism in the Greater Shearwater is this species' crepuscular habits (Rowan 1952, pers. obs.). On land, it lacks the strictly nocturnal habits of certain other petrels (e.g., Leach's Storm Petrel [Oceanodroma leucorhoa], Watanuki 1986), possibly because it is sufficiently large to be relatively secure from predation by Great Skuas (Catharacta antarctica). Consequently, some display takes place in light sufficient to allow visual signalling.

Acknowledgments.—Scientific research on Gough and Nightingale islands was carried out with the kind permission of the Island Council and Administrator of Tristan da Cunha. The logistic support of the South African Department of Environment Affairs made the visit to Gough possible, as did the cooperation of the South African Scientific Committee for Antarctic Research. I am very grateful for awards from the Foundation for Research Development, the Council for Scientific and Industrial Research, the British Ecological Society, and the Frank M. Chapman Memorial Fund. The captains and crews of the Tristan Investments vessels, Tristania II and Hekla, put me ashore on Nightingale and, more importantly, took me off! My thanks to N. Davies, A. Horn, M. Leonard, K. McComb, and R. Magrath for patiently sorting sonagrams. J. Cooper, A. Horn, and P. James helpfully commented on a draft of this paper, T. Harris loaned a microphone, and Tristan Islander C. Hagan cooked superlative chips in Greater Shearwater fat.

LITERATURE CITED


Wilson Bull., 100(2), 1988, pp. 323-324

House Sparrow and Chipping Sparrow feed the same fledgling Brown-headed Cowbird.—On 10 June 1986, on the campus of the University of Western Ontario, London, Ontario, I saw a Chipping Sparrow (Spizella passerina) and a female House Sparrow (Passer domesticus) successively feed a fledgling Brown-headed Cowbird (Molothrus ater). A Chipping Sparrow fed the cowbird, which I judged to be about a week out of a nest, at 09:07 EDT. Immediately after the Chipping Sparrow left, a female House Sparrow, carrying millet, appeared and fed the cowbird. At 09:15 a Chipping Sparrow, and at 09:16 a female House Sparrow, fed the cowbird. The House Sparrow flew to the roof of a nearby building where there were Potter traps baited with millet. She returned to feed millet to the cowbird at 09:22 and later, at 09:28, a Chipping Sparrow fed a caterpillar to the cowbird.

Seven days later, within 15 m of the site of the preceding event, I saw a Chipping Sparrow feed an almost fully grown cowbird five times between 10:30 and 10:35. From its size, the cowbird could have been the one observed on 10 June. I saw no House Sparrow upon this occasion.

The nest-parent of the cowbird was unknown, but it is likely that a Chipping Sparrow had reared the cowbird. Chipping Sparrows commonly nest nearby and are heavily parasitized (Scott, D. M., unpubl. data) by cowbirds. My students and I have more than 60 records of Chipping Sparrows feeding or attending fledgling cowbirds on the campus. Although House Sparrows nest on the campus in small colonies, I previously had never seen a House Sparrow feeding a cowbird.

This incident emphasizes the uncertainty of recording a species as a host solely upon the basis of an individual feeding a young cowbird (Klein and Rosenberg 1986). In the present case, one of the possible foster-parents, the Chipping Sparrow, is a common host (Friedmann 1963), and the observation about the Chipping Sparrow is not remarkable. However, the House Sparrow has only once been reported as rearing a nestling Brown-headed Cowbird (Mearns 1881, Friedmann 1963). I have found no other record of a House Sparrow nest...
containing a nestling Brown-headed Cowbird other than those of the nests used experimentally to study 6 nestling cowbirds (Eastzer et al. 1980), which all died before the age of 6 days. Nestlings of the Shiny Cowbird (M. bonariensis) also died in House Sparrow nests (Salvador 1983, Mason 1986). Mason (1986) and Eastzer et al. (1980) suggest that the nestling cowbirds died because of the inappropriate diet or mode of feeding provided by the adult House Sparrows.

There seem to be only three other records of House Sparrows feeding or attending fledgling Brown-headed Cowbirds (Ellis 1924, Imhoff cited by Friedmann 1963, and Stamm 1961). These observations, in the light of those made by Klein and Rosenberg (1986) and by Eastzer et al. (1980), do not establish conclusively that the House Sparrows were the nest-parents of the fledgling cowbirds. Thus, the House Sparrow may be a rarer successful foster-parent than formerly was thought.

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have a high degree of fidelity to the general area of their colony, as well as nest and colony fidelity as reported by Coulson and White (Bird Study 5:74-83, 1958). By 5 July 1987, all the nests that had been on the glacier had either fallen into the sea or become soggy piles of grass and mud as a result of melting of the glacier surface. Although their nests had disintegrated, some birds remained at the sites; one was rebuilding a nest in a new spot on the glacier.

I know of no other occurrences of glaciers displacing seabird colonies or of seabirds nesting on glaciers. However, kittiwakes have nested on snowbanks on the Pribilof Islands, Alaska, when snow covered part of the colony site. It is not known why they nested there (Hunt and Thompson, Wilson Bull. 89:616-618, 1977). Least Auklets (Aethia pusilla) and Crested Auklets (A. cristatella) have nested on snow on St. Lawrence Island, Alaska, when late snow covered areas of individuals' nest sites (Sealy, Auk 92:528-538, 1975). A few Herring Gulls (Larus argentatus) have nested on ice which covered their colony site at Lake Erie, near Port Colborne, Ontario. However, most birds waited until the ice melted to nest (Morris and Chardine, Can. J. Zool. 63:607-611, 1985).

Acknowledgments. — These observations were made during a project funded by the U.S. Fish and Wildlife Service. The manuscript benefited from readings by E. Flint, M. Hogan, V. Mendanahall, and K. Wohl and comments by B. Kessel and E. Murphy. — DAVID B. IRONS, U.S. Fish and Wildlife Service, 1011 E. Tudor Rd., Anchorage, Alaska 99503. Received 24 Sept. 1987, accepted 9 Dec. 1987.

Wilson Bull., 100(2), 1988, pp. 325-326

Boat-tailed Grackles nest in freshwater habitat in interior South Carolina.—On 21 May 1987, near Chicora, Berkeley County, South Carolina, I found a colony of Boat-tailed Grackles (Quiscalus major) on a 1-ha island in Lake Moultrie. The birds were nesting in a giant cutgrass (Zizaniopsis miliacea) marsh, about 5 x 20 m in extent, which grew at the edge of an island about 800 m from the lake’s edge. The colony had one adult (after-second-year) male and four females. I located eight nests, of which four had young, one had eggs and the others had either produced fledglings or had been depredated. Two nests were in buttonbush (Cephalanthus occidentalis) and were screened by giant cutgrass. The others were built in giant cutgrass. All nests were 1.0-1.8 m above 20-40-cm deep water. The inland nests resembled coastal nests that were built in cattail (Typha angustifolia and T. domingensis). As in many coastal colonies, the nests were built on a marsh island and were closely spaced. Four internest distances were 0.6, 0.8, 1.0, and 1.2 m. The grackles nested within 12 m of a Double-crested Cormorant (Phalacrocorax auritus) colony.

On 26 May 1987, I returned and found four adult male grackles. One male defended the nesting area, and the others displayed in tree-tops at the edge of the marsh. At least six females were present, but this may not have been a complete count, as they were feeding long distances from the colony. I also located another grackle nest in a cutgrass marsh on an island about 100 m from the first colony.

Outside peninsular Florida, Boat-tailed Grackles are known to nest only around brackish marshes (AOU 1983, Check-list of North American Birds. 6th ed., American Ornithologists' Union, Washington, D.C.). The breeding site reported here is 55 km from the Atlantic Ocean. The nearest known colonies are 25 km southeast in tidal areas, on the East Branch of the Cooper River. Although this is a minor inland expansion, it is significant in that use of inland freshwater marshes has not been reported outside Florida. If this is a change in habitat selection behavior, it may mean that Boat-tailed Grackles may continue to move
inland from the Atlantic coast. The large hydroelectric lakes in the Southeast may provide a corridor for such inland invasion, especially if marsh island habitats are available. Such an inland expansion would resemble that which has occurred in the closely related Great-tailed Grackle (*Quiscalus mexicanus*), which has penetrated as far inland as Nebraska (Faanes and Norling, Amer. Birds 35:148–149, 1981). I thank G. T. Bancroft and D. M. Forsythe for criticizing the manuscript.—William Post, The Charleston Museum, 360 Meeting Street, Charleston, South Carolina 29403. Received 22 Sept. 1987, accepted 8 Dec. 1987.

Wilson Bull., 100(2), 1988, pp. 326–327

**Ingestion of lead shot and aluminum bands by Bald Eagles during winter in Nebraska.**—The Bald Eagle (*Haliaeetus leucocephalus*) is a common winter resident along the Platte and North Platte rivers in southcentral Nebraska. Waterfowl are a major food of eagles during periods when fish are not readily available (Lingle and Krapu 1986). Eating ducks and geese can make eagles susceptible to lead poisoning, a significant cause of mortality of Bald Eagles in North America (Kaiser et al. 1980). Eagles ingest lead shot from waterfowl by eating shot imbedded in tissues or as part of the contents of digestive tracts. In this paper we describe the incidence of lead shot and Fish and Wildlife Service aluminum leg bands in regurgitated pellets of Bald Eagles along the Platte and North Platte rivers during the winters of 1978–79 and 1979–80. Documentation of aluminum bands in egested pellets was incidental to the evaluation of occurrence of lead shot.

**Study area and methods.**—Egested pellets were collected from 11 nocturnal communal roosts of Bald Eagles located along 370 km of the Platte and North Platte rivers in Nebraska. Pellets (*N* = 2858) were collected from the surface of the ground and snow below roost trees during 106 visits during 19 December 1978–28 March 1979 and 3 December 1979–14 March 1980. Each regurgitated pellet was examined for prey remains and the presence of lead shot. Food habits of Bald Eagles during winter in Nebraska were described by Lingle and Krapu (1986).

**Results.**—Of 2858 egested pellets, 1832 contained waterfowl remains (Lingle and Krapu 1986); 9 (0.3%) of the latter group also contained lead shot. Four and five pellets containing a single lead shot were found during 1978–79 and 1979–80, respectively. Of these nine pellets, three contained the remains of Mallards (*Anas platyrhynchos*), two contained Canada Geese (*Branta canadensis*), and four contained unidentified waterfowl. One pellet also had Ring-necked Pheasant (*Phasianus colchicus*) remains.

Other egested pellets contained 10 Fish and Wildlife Service aluminum leg bands: eight from Mallards, one from a Canada Goose, and one from a Green-winged Teal (*Anas crecca*). In addition, one web tag from a Canada Goose was found. The number of bands present in pellets reflects the importance of waterfowl in the diet during winter. Assuming each pellet represented the remains of an individual bird, the pellets contained the remains of 228 Canada Geese, 36 Green-winged Teal, 1059 Mallards, 14 Northern Pintail (*Anas acuta*), 4 Gadwall (*Anas strepera*), 3 American Wigeon (*Anas americana*), 1 Lesser Scaup (*Aythya affinis*), 3 Hooded Mergansers (*Mergus cucullatus*), 61 Common Mergansers (*Mergus merganser*), and 423 unidentified waterfowl (Lingle and Krapu 1986). These statistics probably overestimate the number of waterfowl consumed since several eagles may feed on a single carcass.

**Discussion.**—The incidence of lead shot in regurgitated pellets egested by Bald Eagles at nocturnal communal roosts along the Platte and North Platte rivers was lower (<1%) than at other studied sites in the midcontinent region. Griffin et al. (1982) reported 9% of the eagle pellets collected at Swan Lake NWR in north central Missouri contained lead shot.
At the Missouri site, eagles had access to large numbers of crippled and dead geese, which presumably were the primary source of lead shot. In South Dakota, Steenhof (1976) reported finding waterfowl remains in 285 of 363 egested pellets including 10 (2.7%) with lead shot. Based upon her observations, she concluded eagles obtained most of the waterfowl in upland fields. Likewise, at our Nebraska site, eagles ate waterfowl that had been feeding in upland fields (obtained by kleptoparasitizing other raptors [Jorde and Lingle, in press]). In March 1980, they also scavenged waterfowl that had died of avian cholera (Lingle and Krapu 1986).

Infrequent ingestion of lead shot by Bald Eagles in Nebraska probably stems from a low incidence of lead shot among waterfowl wintering along the Platte and North Platte rivers. The frequency of occurrence of lead shot in wintering waterfowl in Nebraska is not known; however, only about 1% of waterfowl wintering in the Texas High Plains region during the same period had lead shot in their digestive tracts (Wallace et al. 1983). It is probable that field-feeding Mallards obtained in lightly hunted uplands contain fewer lead shot than cripples or segments of the population feeding principally in wetlands where hunting activity and lead shot contamination are likely to be concentrated.

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Observations were made approximately 20 km NE of Mar Brava, the site of Duffy et al.'s observations. Olivaceous Cormorants roost (and presumably nest) in tall forest edge trees bordering a marshy lagoon in the interior of Peninsula Lacuy and feed, often in very dense flocks of 100 or more, in protected bays and nearshore waters along the marine coast.

While our observations of pursuit-plunging by Olivaceous Cormorants were very similar in detail to those of Duffy et al. (1986), we add that feeding by pursuit-plunging was initiated by surface activity of rapidly moving schools of small fish. On 15 January, Humphrey and López watched a solitary cormorant feeding about 100 m offshore by pursuit-plunging. The bird first scanned the calm water while swimming. When it saw a school of small fish agitating the surface it took off, flying a meter or less above the surface, and then in full flight, folded its wings and plunged at an oblique angle into the water in the middle of the school. It did this about a dozen times, sometimes flying only a few meters and other times up to 20–30 m or more. This bird had a low success rate; in a series of six plunges it caught a fish only in the last of them.

We saw Olivaceous Cormorants pursuit-plunging only in very calm water, and only when we could detect nearby fish surface activity. These observations suggest that pursuit-plunging is triggered by the surface activity of a school of fish and that the target of a pursuit plunge is the area below the surface activity rather than a specific fish. Pursuit-plunging in Olivaceous Cormorants involves active scanning, location of target surface activity, take-off and rapid flight low over the water, followed by a plunge into the water at the surface disturbance. This type of feeding behavior is exhibited by single individuals as well as large, rapidly moving flocks, as is the pursuit-diving (Ashmole 1971) so well-known in cormorants. We have not seen pursuit-plunging during our observations of Olivaceous Cormorants along the Atlantic coast of Patagonia, nor at three other localities we visited in Chile (Huillad, southeastern Chiloé Island; Ensenada Codihue and Calbuco, Llanquihue Province) where the species is abundant.

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The Birds of Canada. Revised Edition. By W. Earl Godfrey. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada, 1986:595 pp., 74 color plates, 102 line drawings, 386 distribution maps. $39.95 (available in the U.S. from Univ. Chicago Press, Chicago).—This new edition, despite its changed appearance, is basically the same valued reference work that has become familiar over the past 20 years (see Wilson Bull., 79:463-466, 1967, for George M. Sutton’s review of the original version). The new work is larger in size (582 text pp. vs 414), weight (2.35 kg vs 2.0), and scope, treating 578 species (plus 37 hypothetical spp. vs 518) of which 498 (501 by my count) are illustrated in color (vs 431). The extra size makes the book cumbersome to handle, and begs comment on the changed format, which may have been imposed by the designer or producer. The new version features two unequal-width columns, of which the left-hand is reserved (in most species) for the range maps and description of the range in Canada; the rest of the information—regardless of its length—is in the right-hand column. Blank spaces thus appear in both columns. The modified format avoids having different species in adjoining columns on the same page, a minor advantage, but it wastes space, and thus makes an already large book still larger. The narrower left-hand column means that the new maps are smaller and (for some species) less easy to read.

Most of the text is identical to the earlier edition, the main changes being where species and their descriptions have been lumped or, less often, split, and in the Distribution sections and the new species accounts. Reflecting the birders’ lust for rarities is the increased space given to extra-limital records of common species, as well as of the vagrants included for the first time; in a few cases (e.g., Varied Thrush [Ixoreus naevius]) the strays have received so much space as to unbalance the range account. Changes to the maps parallel those described in the text, with a few minor discrepancies where the text was changed but the map remains the same, or vice versa. Very few ranges are noted to have shrunk, in contrast to the many described and mapped as having expanded. In view of the many adverse impacts of man’s actions on the environment, including birds, one would expect the reverse. Perhaps we are reluctant to believe—or to publish—the evidence of our eyes when a species is no longer found in its former range? The nomenclature, species limits, and sequence generally agree with the 1983 AOU Check-list, with French names following Ouellet’s innovations. Many place-names in Quebec also have been changed to French versions, and a few in the north, to Inuit names; most—but not all—of these appear on the end-paper maps, now both the same (without the map of biotic zones in the earlier edition). All geographic names are spelled out, thereby lengthening the range descriptions. All measurements are now metric, and I found no changes in those given earlier.

Godfrey is up-to-date in taxonomy, accepting the splitting of Gavia pacifica from G. arctica, of Aechmophorus clarkii from A. occidentalis, and of Sphyrapicus nuchalis from S. varius, which were proposed since the 1983 AOU Check-list appeared. The splitting-off of Pluvialis fulva and the merging of the redpolls were evidently too recent to be incorporated in this edition which, with translation to allow simultaneous appearance of French and English versions, has been several years in the making. Godfrey’s is the first major handbook to accept the re-merging of Larus thayeri into L. glaucoides, even as in 1966, he was the first in recent years to accept L. thayeri as a separate species. Personally, I was glad to see Chen merged with Anser, a move long-overdue in the AOU Check-list.

As already noted, the textual descriptions and illustrations are largely unchanged from the earlier edition, and I have not attempted a new assessment of their adequacy. A number of new plates (e.g., of albatrosses and shearwaters) are included, and extra species were added
to several existing plates. I compiled a listing of apparent errors or discrepancies in or between the ranges in text and maps, which has been sent to the author. Most of these were minor, but a few of the more significant are noted below. The species range of *Melanitta fusca* does not include its distribution in Eurasia (the earlier edition had *M. deglandi* as a separate species). Various species (e.g., *Calonectris diomedea*, *Puffinus carneipes*) are surely of much more frequent occurrence than as described on the basis of specimen records. The locations of the Cape St. Mary’s and Funk Island colonies of *Sula bassanu*s again are misplaced; the 1979 population figure for this species is incorrect, actually 21,000 pairs. The description and map for American Black Duck (*Anas rubripes*) distribution are the same as in 1966, despite the nearly complete replacement of this form by the Mallard (*A. platyrhynchos*) in southern Ontario; there is still no mention of the introgression between these two forms, nor of the wide variation in speculum color of American Black Ducks. The mapped distribution of *Somateria mollissima* in Nova Scotia is both incomplete and inaccurate. The decline in *Haliaeetus leucocephalus* probably is no longer alarming, if it even continues. The disappearance of *Charadrius melodus* from southern Ontario is not mentioned, and allegations of its breeding on Sable Island (N. S.) have not been confirmed. The range described in the text for *Oporornis philadelphia* in British Columbia is not mapped, with a cryptic comment that it “require(s) confirmation and further study,” but *O. tolmiei* is not mapped for those areas either; if those reports are not to be mapped as either species, why are they mentioned at all? The mapped range of *Dolichonyx oryzivorus* in British Columbia now corresponds to that in the text (unchanged from 1966), but that shown in Alberta does not extend north to Whitecourt and Athabasca; it is mapped as breeding in southwest Newfoundland where the text calls it casual. Few of these (or the others) will cause difficulties except for specialists—and for people whose home ranges overlap a discrepancy. A new generation of amateur and professional ornithologists will appreciate having this important reference work updated and again in print.—Anthony J. Erskine.

**The Bald Eagle.** By Mark Stalmaster. Universe, New York, New York, 1987:227 pp., 80 line drawings, 16 color plates, maps, tables, and appendixes. $25.00.—Aside from the 1934 book on the Bald Eagle (*Haliaeetus leucocephalus*) by Francis Herrick (“The American Eagle,” Appleton-Century, New York) and that by George Laycock (“Autumn of the Eagle,” Scribners, New York, 1973), most other data on Bald Eagles exist as scientific papers or popular articles; this is the first synthesis book on the species. Stalmaster has done an admirable job in sorting through the vast literature. While I do not like each chapter having its own literature section at the back of the book (which makes it cumbersome to use), many unpublished reports and theses have been used to document the information. Thirteen chapters discuss such topics as Identification; Description and Adaptations; Breeding and Nesting Biology; Energy, Food, and Prey Requirements; Reproduction and Survival; Interactions with Humans; and Protective Management. Appendix 1, giving diets, nest structure, and reproductive data, is the most valuable appendix. The real contribution of this book lies in the array of topics covered and the literature sources provided for them, all brought together in one place. The writing style should appeal to people at most levels from high school to the professional. The editing has been good, and the text is largely free of error.

The art work, by Michelle LaGory, is excellent. Either the artist has an extensive personal knowledge of eagles or numerous good photographs for reference. Sketches in the Diet and Foraging Behavior and Winter Ecology chapters are particularly attractive.

While the cut-off date for gathering material is not stated, I presume it must have been in the early 1980s, as some valuable information from the last 2–3 years is not there. For
example, the Department of Veterinary Biology, University of Minnesota, where rehabilitation work has been done (p. 173) is now called the Raptor Research and Rehabilitation Program. The extensive work of the past 2-3 years by personnel of the George M. Sutton Avian Research Center in Oklahoma on hatching eggs and releasing nestlings for reintroduction is not mentioned. The northward migration into Canada of California-raised young shortly after fledging, as documented with radio transmitters within the past 2-3 years by Grainger Hunt and associates, is likewise not mentioned.

Since Stalmaster mentions correctly the nearness in relationship of the kites Haliastur to Haliaeetus, it would have been more appropriate to use that kite genus on the drawing of a phylogenetic tree (Fig. 2.1) rather than what appears to be a kite of the genus Elanoides. The breeding range map (Fig. 4.1) is poor, since it does not show eagles breeding down into Colorado, New Mexico, Arizona, and Baja California and does not agree with Fig. 4.2 that shows breeding by relative numbers of pairs per state.

It would be helpful if people working on Bald Eagles could arrive at a standardized terminology for various age plumages. Stalmaster used Juvenile Plumage A and B and Subadult Plumage C, D, and E for the various stages to the full adult, while in the recent Peterson Field Guide series on Hawks of North America (Clark and Wheeler, Houghton Mifflin, Boston, 1987) the terms White-belly I, White-belly II, and Adult Transition are used. It is not clear to me if in fact the same numbers of plumage gradations are recognized in these two most recent publications.

Since so little data have been assembled on other congeneric species elsewhere, except for perhaps two species, my preference would have been to see Stalmaster make better use of what has been done on those species. For example, another member of the genus with an extensive literature of similar type data to that given by Stalmaster, the African Fish Eagle (H. vocifer), has a rather well-documented plumage sequence through various stages leading to the adult after the fashion of H. leucocephalus which could have been compared to H. leucocephalus.

Overall, the book is excellent. The author has done a commendable job in his organization of the data and coverage of material. The style makes the book appropriate to all categories of libraries.—CLAYTON M. WHITE.

THE PARROTS OF LUQUILLO: NATURAL HISTORY AND CONSERVATION OF THE PUERTO RICAN PARROT. By Noel F. R. Snyder, James W. Wiley, and Cameron B. Kepler. Western Foundation of Vertebrate Zoology, Los Angeles, California 90024, 1987:xiii + 384 pp., 136 figs., incl. 87 black-and-white photos, 8 color plates in text, 1 on dust jacket, 104 tables, 12 chapters, literature cited, 36 appendices. Approx. 18 x 26 cm, cloth binding. $29.50.—This is a comprehensive monograph concerning everything that is known about Amazona vittata, the Puerto Rican Parrot, considerable discussion about what is not known or is speculative about the bird, much information about human events surrounding the bird’s history starting with Christopher Columbus in 1493, about other parrots, and about other species of organisms that live around the parrot and in various ways interact with it.

This book is a lavish production, one in which little if any expense has been spared, and one in which the authors are allowed not only to present their scientific results but often to do so in the context of extensive philosophizing and of vivid, descriptive accounts of bird-human encounters, scenery, and adventure. While the book is indubitably an important scientific report and reference work that will serve biologists concerned with endangered species, it is also a book to be read for entertainment. Skipping over tables and graphs, one can simply enjoy the text, much as one might enjoy an Alexander Skutch book.
From the front inside dust jacket: This is the first comprehensive study of the Puerto Rican Parrot and one of the few detailed studies of any wild parrot population. It describes the efforts to save a population once described as doomed to extinction. The first two chapters comprise a review of the population status of parrots in general, and provide an historical perspective for the decline of the Puerto Rican Parrot. Chapter 3 is devoted to a discussion of the species' taxonomic relationships to other West Indian parrots. Chapter 4 describes the Luquillo Forest of the Sierra de Luquillo, where the 30-odd remaining wild Puerto Rican Parrots live. Chapters 5–8 deal with behavior, food habits, nest sites, reproductive behavior, and the species' natural enemies. Chapter 9 quantifies the decline of the bird. Chapter 10 gives details of the history of conservation efforts. Chapter 11 discusses the captive breeding program, and chapter 12 brings us up to date on the status of the population.

The guts of this book are a highly quantified account of the Puerto Rican Parrot's natural history and attempts at conservation in the face of many factors of habitat destruction, direct human pressure in the form of hunting and capture for the pet trade, conflict with natural enemies such as the Pearly-eyed Thrasher (Margarops fuscatus) which usurps nest cavities, and Red-tailed Hawks (Buteo jamaicensis) which prey on adults (including captive-reared birds released to build up the wild population). The authors began their study in the early 1970s, pessimistic about wild survival of this species, and they end this book with a show of cautious optimism. The wild flock has ceased to decline (though it shows no great promise of multiplying); release of captives has had disappointing success but shows promise for the future; and the Luquillo Forest is a stable environment now, with considerable protection from poachers. If tropical storms do not level the whole scene, and if competition and/or hybridization with other introduced parrots do not become inhibiting factors (they are not now), there is hope.

In the concluding paragraph the authors write, "The Carolina and Puerto Rican parakeets are gone and can never reappear. . . . It is difficult to examine [specimens of them in museums] without a feeling of profound regret that these species might not have been lost if human concern for their survival had come a little sooner. The Puerto Rican Parrot is still with us and we firmly believe it can continue to survive, but only if that very same human concern does not falter in the years ahead."—JOHN WILLIAM HARDY.
Cedar Waxwing (*Bombycilla cedrorum*)? (There are hardly any scientific names in this section.) "Mohavian" or "Mohave Desert" species would be better termed Sonoran, despite the latitude. Dr. Behle’s grasp of extra-Utah distributions is apparently not so sure as that of within-state distributions, which are capably discussed in general terms.

The bulk of the paper reviews species supposed (now or previously) to have more than one subspecies in Utah. Species generally known to have only one race in Utah are usually not treated in detail, as they were in Behle’s earlier papers. Some species are quite complex, such as at least 5 races of *Branta canadensis* (if indeed all are conspecific), 4 of *Buteo jamaicensis* (*h. harlani* is truly a geographic race), 5 of *Bubo virginianus*, 4 (or 5?) of *Chordeiles minor*, 6 of *Eremophila alpestris*, 6 of *Melospiza melodia*, 6 (or 7) of *Junco hyemalis*, etc.

For most species discussed, there is a valuable review of previous literature (though here and there coverage is hardly adequate, or a bit misleading). References to the recent discussion of *Egretta thula* by Rea (1983, *Once A River*), to *Anser albifrons elgasi*, *Grus canadensis rowani*, *Icterus galbula parvus*, and *Molothrus ater buphilus*, and to the discussion of the Marsh Wren by Monson and Phillips (1981), as well as more references and discussion of problems in *Phoenicus* and *Carduelis trisits*, would give us more of a good thing. But "the present summary pertains only to those geographically-variable species that present problems in Utah." For other subspecies readers are referred (p. 3) to Behle et al. 1985; Hayward et al. 1976; and Browning 1974 and 1978 (not in bibliography). AOU Check-lists, seldom cited, are corrected for *Haliaeetus leucocephalus* and *Hirundo pyrrhonota*.

Problems needing further study are often noted and are summarized (p. 134). This summary does not include revisionary problems, such as *Parus gambelli* which "would now require the collection of vast numbers of chickadees in fresh fall plumage from multiple critical localities" (p. 1). There is still much to do!

Behle's conclusions tend to follow previous revisions in many cases, but there are important original contributions, such as for *Buteo jamaicensis* and *Agelaius phoenicus*. Behle’s "several western races" of *Catherpes mexicanus* (p. 78) must include northern Mexico, since only 4 (one highly doubtful) had been named from farther north before 1986, when I described one from Wyoming ("Known Birds of N. and Mid. Am.," Pt. 1:169). Otherwise, Mexican races are not considered. Since 5 assistants helped measure birds, it is disappointing to find few original measurements in critical species (e.g., *Branta canadensis* and *Corvus brachyrhynchos*).

It would have helped, in some cases, to have examined material in major eastern museums and to specify just what non-Utah material was seen and what plumages. In particular, I cannot believe that *Pooecetes gramineus affinis* (virtually unknown otherwise east of the Cascade Mts. and Sierra Nevada) is a "regular transient known from many specimens." These are listed: of the 14, 4 were taken 20 August (southern Utah) to 2 September; 7 from 8 to 18 September (1 in easternmost Utah); and 3 from 22 September to 2 October. Yet in Arizona, where breeding is less widespread and migrants easier to detect, the earliest transient *Pooecetes* are 24-28 August (Phillips et al. 1964, *Birds of Arizona*). Surely so many August-September birds had not already reached Utah from such a distant, unlikely area; migration dates needed closer attention. Most or all were surely local *P. g. altus*, as comparison with fresh August *affinis* would have shown. (All Utah reports were published, and all "affinis" taken, before Phillips et al. 1964 described *altus*.)

Behle summarizes the (supposed) distributions of races in surrounding states as well. Despite the above-mentioned unevenness, his book will be quite useful to all who deal with avian systematics (lower-level) and zoogeography of the western U.S.A. One wishes more states and provinces had equally long-time, independent, dedicated workers—with better material and more support for their basic researches. Such regional studies provide a basis for improved, more accurate check-lists, for which we hope.—ALLAN R. PHILLIPS.
ECOLOGY AND BEHAVIOR OF GULLS. By J. L. Hand, W. E. Southern, and K. Vermeer (eds.). Cooper Ornithological Society Studies in Avian Biology No. 10, June 1987:vi + 140 pp., numerous tables and figs. (order from J. R. Northern, Cooper Ornithological Society, Dept. of Biology, Univ. of California, Los Angeles, California 90024). $18.50.—This volume contains papers presented at an International Symposium during the joint meeting of the Colonial Waterbird Group (now Society) and the Pacific Seabird Group in San Francisco, California, 6 December 1985. The volume includes 11 papers, 10 abstracts, a Preface by F. A. Pitelka, and a valuable Symposium Overview by W. E. Southern.

The volume is divided into five major topics. Part 1 consists of four papers and two abstracts concerned with “Life History Strategy.” The papers consider constraints on clutch size, sex ratios and breeding patterns, survival and mortality factors, and the effects of increased population size on breeding success. W. V. Reid’s data and discussion of brood reduction in the Glaucous-winged Gull (Larus glaucescens) are fascinating. Equally stimulating is Fry et al.’s paper on the effects of chemical pollutants on gull reproductive anatomy. Spear et al.’s contribution presents some fine data on age-mortality characteristics related to competition and food shortage.


Part 3, “Foraging,” contains two papers and three abstracts on foraging efficiency and patterns, prey selection, diets, and predatory behavior. J. Burger's paper on age differences in foraging efficiency and age of maturity gives interesting data on the relation between foraging efficiency and the phenomenon of delayed maturity in 15 species of gulls she has studied in North America, South America, Europe, and Australia. J. R. Jehl, Jr., and C. Chase discuss the significance of gull predators to colony characteristics. It is a worthwhile introduction to the multiple effects of predation on animal aggregations.

Part 4, “Habitat Selection,” includes two papers and two abstracts. K. Vermeer and K. Devitos' paper on habitat and nest-site selection by Mew Gulls (L. canus) and Glaucous-winged Gulls is descriptive, whereas R. Pierottis' paper concentrates on the behavioral effects and reproductive consequences of habitat selection in Herring Gulls. The two abstracts introduce the topic of gull foraging and roosting distribution in the United States.

Part 5 contains a single paper by A. Ingolfsson on hybridization between the Iceland populations of Glaucous Gulls (L. hyperboreus) and Herring Gulls during the last 20 years.

The volume is of value to those interested in the biology of colonial nesting seabirds. It does, however, go beyond that group. As F. Pitelka alludes to in the Preface, the numerous principles and rules discussed in such detailed studies of single taxa (Laridae) are equally applicable to other main animal groups. For example, the significance of phenomena such as brood reduction, limitations on clutch and brood size, and the effects of habitat selection on reproductive success are not solely characteristic of gulls. The papers are generally of good quality and are important contributions with original data.

I strongly question the value of the abstracts in this volume. They contribute little useable material, and I have no idea why the editors chose to include them instead of insisting that the symposium participants submit their papers in full for publication. So far as this reviewer is concerned, the only use for such abstracts is to pad CV’s and the literature cited sections of papers written by other authors. Both uses are not quite cricket.

Despite the above, I recommend the volume for its major papers; they are based on recent research and current behavioral and evolutionary theory.—JOHN P. RYDER.
Penguins. Revised ed. By John Sparks and Tony Soper, illus. by Robert Gillmor. Facts on File Publications, New York, 1987: 246 pp. $19.95.—This is a revised edition of the first, published in 1969. In size, organization, and content it follows the first. Most of the text, in 8 chapters, is practically verbatim except where it has been updated to suit more recent findings or new concepts.

The illustrations are profuse. There are 4 pages of photographs in color and 30 in black-and-white, of which 12 each occupy a single page. Robert Gillmor’s many charming drawings embellish the book from beginning to end, including the margins of numerous pages. In this edition, Gillmor has a useful two-page color-spread of the entire penguin family showing associated species and comparative sizes.

I highly praised the first edition as the best book available for a review of the entire penguin family by means of an informative and readable text excellently illustrated. I praise this revised edition just as highly.—Olin Sewall Pettingill, Jr.

The Birds of the Southern Bahamas, An annotated check-list. By Donald W. Buden, Henry Ling Ltd., Dorset Press, British Ornithologists’ Union, London, 1987: 119 pp., 3 maps, 1 text fig., 7 tables, 1 index. £12. (Available prepaid from BOU, % Zoological Society London, Regent’s Park, London NW1 4RY, U.K.)—It seems that every 15-20 years there is an update on most regional avifaunas. The length of the span measures our knowledge (accuracy) and judgment (understanding) of changing faunas and the conditions that regulate change. Remote areas of the globe and even parts of the globe, yet so close to major populations, are no exception.

Buden has presented the essentials for a nutritious three course “avian biogeographer’s meal” which will, no doubt, be improved upon as some ingredients become more widely accepted and form the basis of a greater repast. Very few morsels are missing from the “appetizers” course. Even the area (km²) of individual islands or groups in the southern Bahaman archipelago (e.g., Acklins Island, Great and Little Inagua, the former being the best Caribbean nesting site of flamingoes [Phoenicopterus r. ruber], Mayaguana, Turks and Caicos Islands, and several other insignificant cays) has been lumped into the total for all the Bahamas necessitating further research for the reader. The discussion on paleontology, particularly interglacial sea level change, is very thought provoking, considering that the globe is faced with human-induced sea level rise during the next century. The fundamental reason this BOU Check-list No. 8 is so important is because the northern Bahamas have been examined more completely, leaving a void to be filled by the modern ornithologist-adventurer. Having recently spent 23 days afield in the Turks and Caicos Islands, I can state that adventuring is part of the recipe for gaining new information.

The analysis of the avifauna is quite complete and very informative, attesting to Buden’s lengthy association with the islands and his research on insular vertebrate speciation. While the bird life of the Bahaman archipelago may be Greater Antillean and North American in origin as a result of lowered sea level in the past, new and dramatic faunal changes may be expected in the near future to force new influences. This volume serves as an important portrait of these little-known, low-lying islands on the brink of irrepressible habitat alteration, not only locally but for the Gulf-Caribbean region.

The main course of Buden’s menu is the check-list itself, containing the status of 183 species recorded from the southern Bahamas. A conservative and thorough treatment includes sources dating from the early-1800s and acknowledged local reports to 1984, a record spanning more than 180 years. The extremely useful Summary of Status (pp. 94–107) and five plus pages of Literature Cited serve as a delectable “nut-shell” dessert.
This octavo-sized, paper-covered handbook may, however, suffer the rigors of travel and constant use, but not the passage of time. Perhaps the field-oriented observer should acquire a second desk copy. Professionals and amateurs alike will find Buden’s treatment of “The Birds of the Southern Bahamas” a benchmark for further evaluation of an avifauna which links the Antilles with North America and as a model for other regional lists. Bon Appetit! — ROBERT L. NORTON.

BEHAVIORAL ECOLOGY OF RED-TAILED HAWKS (BUTEO JAMAicensIS), ROUGH-LEGGED HAWKS (BUTEo LAGOpus), NORTHERN Harriers (CIRCUS CYaneuS), AND AMERICAN KESTRELS (FALCO sparveRIUS) IN SOUTH CENTRAL OHIO. By Keith L. Bildstein. Ohio Biol. Surv., Biol. Notes No. 18, Columbus, Ohio, 1987:viii + 53 pp., 39 figs., 39 tables, appendices. $5.00. — Little has been done to document the behavioral ecology of wintering raptors. Past reports have mainly been confined to anecdotal accounts of “playful” encounters, prey robbery, and interspecies predation. Daily activity patterns, hunting strategies, and dietary habits have been little studied. This publication attempts to fill the void by reporting on the behavioral ecology of sympatric hawks wintering in south-central Ohio.

The report is divided into sections describing the size and composition of the raptor community and its spatial distribution, habitat use, hunting behavior, feeding ecology, and agonistic interactions. Each section is essentially a separate article that deals with a different aspect of the community’s wintering ecology. There are numerous figures and tables of original data, and they are frequently compared with previous winter studies by F. and J. Craighead and G. Schnell in Michigan and Illinois. The information includes some very interesting observations on the behavior of wintering raptors such as food caching, kleptoparasitism, and temperature-dependent insect feeding. The report ends with an excellent General Discussion that includes estimates of niche overlap and a discussion of resource partitioning within the community.

My major criticism of the report is its inconsistent format. It begins by giving each section a separate Introduction, Methods, Results, and Discussion, but in the second half this format is abandoned. As a result, when feeding, hunting, and agonistic behaviors are discussed in the latter sections, the methods used to obtain data are not always made clear. Despite this drawback, this is a valuable publication that is replete with reference material pertaining to raptor behavioral ecology. For this reason, I would strongly recommend that it be included in reference libraries of raptor biologists and other ornithologists interested in the behavioral ecology of avian predators. — MARC J. BECHARD.

BREEDING WADERS IN EUROPE. Compiled by T. Piersma, for the Wader Study Group. Supplement to No. 48, Bulletin of the Wader Study Group, % Dr. S. R. Baillie, 8 Little London, Whitchurch, nr. Aylesbury, Bucks. HP22 4LE, U.K., 1986:116 pp., 36 numbered figs., 4 tables. £5 incl. postage and packing. — This regional review tries to provide population estimates of European breeding shorebirds and thereby promote sound conservation management of breeding habitat.

Besides the methods section, there are three basic parts to this report: an introduction, the population size estimates, and the extensive bibliography. The introduction (written by M. W. Pienkowski) provides a historical perspective on the report and discusses issues regarding international conservation of wetlands, particularly the Ramsar Convention initiatives. Annoyingly, it does not make any direct connection with breeding shorebirds until the fourth paragraph. The introduction ends by expressing hope that this report will lead
to additional and improved estimates of shorebird populations throughout Eurasia. This forms the main conclusion of the book.

The population size estimates are based on published information and from unpublished data solicited from national correspondents. Thirty-seven species are covered, representing a total of 6.5 million breeding shorebird pairs in the greater part of Europe, and an additional 100,000 pairs in Svalbard, part of Greenland, and Ellesmere Island. The Lapwing (Vanellus vanellus) is the most abundant species at 869,000 pairs, while the Terek Sandpiper (Xenus cinereus) is the most rare at 30 pairs. Some species, like Terek Sandpiper, appear rare because the area covered by this review is only marginally within their distribution. Unfortunately, the population size estimates for the total surveyed area are not consistently reliable. Due to varying coverage, methodologies, and nesting habits of different species, estimates cannot be readily compared among countries or species. As the compiler admits, some estimates are based on careful, comprehensive study, while others are little more than guesswork. Inadequate information for some areas undermines the overall value of the quantitative information contained in this book. However, it was the best job possible without substantial additional commitment in research time and funds.

Table 2 lists estimates, by country, for each species, but is hard to read and interpret. The print is small, and the lines are jammed together so that a straight edge is required to read it. Dashes are commonly used in the table without explanation. In North American journals, a dash is often used to indicate the absence of information. Dashes here apparently indicate zero breeding pairs, based on other information sources, as well as the use of a few question marks (also without explanation) elsewhere in the table. Another stylistic problem is the use of horizontal brackets to join counts in Great Britain and Ireland for Common Ringed Plover (Charadrius hiaticula) and Eurasian Woodcock (Scolopax rusticola). The upturned ends of these brackets seem to suggest that the numbers refer to the species listed above, when, in fact, they do not. For someone unfamiliar with the European avifauna, the data presentation in Table 2 could lead to erroneous interpretation. Also, “Luxemburg” is apparently used mistakenly in the table instead of Belgium; those data are mapped in Belgium, and their reference refers to an area of Belgium. Despite these superficial problems, Table 2 is valuable because it allows comparisons not otherwise possible.

The annotated species distribution maps (figs. 3-36) provide varying sized circles for each country that are proportional to the estimated total breeding population. Occasionally, a “+” symbol is used; it is not defined, although it clearly refers to very small breeding populations. These data might be better presented as densities rather than total numbers. Different shades depict subspecies. Scale of the circles differs among figs. 3-36, so direct visual comparison across species can be misleading. The figure legends provide information on geographic variation, subspecies, and the distribution of the species.

The immense bibliography (3374 entries) is organized into 66 sections. There are 326 references, under 8 topics, related to general biology of shorebirds. Then, 887 references on the breeding biology of particular species are ordered taxonomically. Finally, 2161 published surveys of breeding waders are listed among 21 countries or regions. Titles not in English, German, or French are translated, when possible, into one of these languages, unless they are considered too local in scope to be of general interest.

Despite the severe problem of inadequate population estimates for some areas, I applaud this effort. It is imperative to try to assemble estimates or indices of breeding populations, even if it requires some guesswork. The lessons in this book for North American ornithologists are clear. Certainly, we value undisturbed breeding habitat and are in good position to defend it against encroachment by human activities. The question is, are we prepared to engage in such conservation efforts? Do we know the status of our breeding shorebird populations? When areas like the Arctic National Wildlife Refuge are threatened by oil and
gas development, can we authoritatively predict the impact of such disturbance on breeding bird populations? The difficulties encountered by the Wader Study Group and the record of their achievement are instructive. Time is running out to save these species from increasingly severe competition for habitat with humans. Conservation biology is a crisis discipline, and we must sometimes make decisions based on marginal or incomplete information. Given the practical difficulties involved in surveying wide, uninhabited areas, perhaps developing a cost-effective and reliable methodology should be a priority. This report represents a very good beginning, but its greatest value is in demonstrating the need for yet more work. Quantification of species habitat preferences and of the pace and nature of ongoing habitat destruction would complement this effort. Hopefully this book will generate new interest among ornithologists worldwide to improve our knowledge of the status of breeding bird populations. —Elizabeth P. Mallory.


The purpose of the conference was to assemble a panel of experts who could offer a global perspective on the future of raptors. The proceedings begin with three papers on the regional status of raptors, and the tone set is generally one of guarded optimism. Ian Newton describes a “depressing picture in Europe” with a few remaining “bright spots,” thanks to a growing conservation movement and reductions in persecution and organochlorine pesticide use. Yossi Leshem’s statistics on raptor population declines in the Middle East (a former paradise for birds of prey) are both startling and depressing, but Leshem finds hope in the public education programs that are now underway in Israel. A more pessimistic view is offered by Robert S. Kennedy, who discusses the general implications of widespread tropical deforestation. According to Kennedy, more than 90% of raptor species are found in the tropics. Kennedy’s paper stops short of providing details of the specific problems faced by various raptors in the tropics.

The next two papers in the volume focus on raptor migration. Chandler S. Robbins’ analysis of North American banding data reveals that encounter rates (particularly with shot raptors) have declined in the U.S.A. and Canada but not in Latin America. Robbins’ concise summary of banding efforts, encounter rates, and causes of death from 1931 to 1980 is probably the only contribution in the volume that would have been suitable as a journal article. John R. Haugh’s chapter, “Raptors in Migration,” is a general review of the biology of raptor migration with a view of opportunities for future research.

The biological reports are punctuated with two philosophical contributions by Richard Olendorff (“Land Management for Raptor Conservation”) and James Brett (“Public Education and the Future of Raptors”). Noel Snyder has prepared the longest chapter in the volume, “The California Condor Recovery Program.” Despite two addenda, the information on condor population status is woefully out of date. The value of Snyder’s contribution will not be as a status report but as a historical reference about the procedures and politics during a critical juncture in the fight to save a species. Tom Cade’s chapter on “Reintroduction as a Method of Conservation” is a good general review of the subject, but it only touches on some of the more controversial issues surrounding raptor reintroduction (gene pools, the
merits of cross-fostering, and the introduction of exotic species, for example). Mark Fuller's introduction and Dean Amadon's synthesis round out the volume.

Because many of the contributions in it are "current status reports," Raptor Research Report No. 5 may not have the long-term value that earlier reports in this series have had. Report No. 5 seems less cohesive than earlier reports, partly because it is a conglomeration of scientific data, reviews, and philosophy. The report does not follow any standardized format. Some papers have abstracts; some do not. Some of the contributions have been revised for written presentation, while others are still in banquet-style prose. Literature cited formats are inconsistent, and I found numerous typographical and grammatical errors throughout the volume (even on the cover).

Nevertheless, the report contains information that can and should be used by persons working in the field of raptor conservation. Unfortunately, there has been little advertisement about this report. The report can be ordered from Jim Fitzpatrick, Treasurer, Carpenter St. Croix Nature Center, 12805 St. Croix Trail, Hastings, Minnesota 55033 U.S.A.—KAREN STEENHOF.

A BIRDWATCHER'S HANDBOOK. By Laura O'Biso Socha. Dodd, Mead & Co., New York, New York, 1987:182 pp., line drawings. $16.95 cloth, $7.95 paper.—Ornithology probably has benefited from the work of amateurs more than any other branch of science. Without the support of serious amateurs, professional ornithological societies and most ornithological field stations would be seriously hampered. The skills of some amateurs are so highly developed that the terms "amateur" and "professional" in ornithology really only have meaning as to how one earns a living. The present book seeks to increase the role of amateurs by encouraging beginning bird students to undertake scientific research. Unfortunately, in my opinion, it falls far short of accomplishing its goal.

I find several major problems in this book. Firstly, it is almost arrogant in its attitude toward scientific ornithology. Comments like "this book takes the scientific chill out of bird watching and ornithological studies, and puts the science of birding where it does the most good—in the hands of amateur naturalists" indicate that the author has some sort of ax to grind. Her occasional reference to "stuffy birders" reinforces that impression. Many of us will be astonished to learn from her book that "the scientific study of birds—ornithology—is based on bird watching" (emphasis the author's) and that "we already know the basic anatomy and physiology of birds."

Secondly, the book seeks to inform us about techniques used by field ornithologists. However, it often falls short of being very informative. For example, it only mentions three field guides in a section designed to lead us to identification references. A scientific bird watcher really should know of the existence of the great diversity of identification aids, including books covering specific groups, detailed identification techniques and keys (particularly for birds in the hand), and the "second generation" guides. Her coverage of banding techniques, recording of bird songs, and aviculture likewise is only superficial.

Thirdly, the author makes or permits errors in the text that suggest that she is not familiar with current ornithological literature. Names of birds erroneously given such as "Red-Tail Hawk," "English Sparrow," "Mallard Duck," and "Sawbill," give the impression that the author does not have a serious interest in ornithology. The poor editing of the text has resulted in at least one misspelling each of "Audubon" and "ornithologist." The author refers to the AOU Check-list and promises a citation to this which seemingly has been omitted. I do not believe that the National Audubon Society is mentioned anywhere in the book.
It seems to me that the author fosters a cavalier attitude toward federal regulations regarding birds. Statements such as “You may need to acquire the necessary government permits for keeping collections” do not convey to the readers the impression that possession of skins or parts of most birds is subject to strict federal regulation. Perhaps I have a personal bias in this regard, but it seems to me that the days of personal bird skin collections should be past. Likewise, the book did not leave me with the impression that bird banding permits should be restricted to investigators with serious projects. Instead, it seemed that the author felt bird banding was “fun” and that semi-serious, backyard banding was sufficient justification for obtaining a permit.

A number of figures are scattered throughout the book. These are not mentioned in the text, as far as I could tell. One diagram of the topography of a bird is so poorly labelled that it is nearly unreadable. Another, of outlines and heads of various birds, seems to me to be of little use, and has been reduced so much that details are hard to see.

Beginning ornithologists who really want to participate in the research process should be aware that modern ornithology routinely includes at least three important things: (1) a solid background in the literature of ornithology—careful reading of the current college textbooks (the author does not mention any of these), and the publications of the scientific societies, (2) development of an ability to design experiments and analyze data, and (3) the ability to write papers describing one’s work and an attempt to do so—research without publication is a little self-serving and circumvents the self-correction that peer review provides. The present book does not deal with any of these topics in a substantial way.

In summary, I cannot recommend this book. It may be true that any publication dealing with birds will sell a satisfactory number of copies to the public; however, this does not justify a poorly edited book containing only superficial information.—CHARLES R. BLEM.

THE ENDEMIC BIRDS OF MADAGASCAR. By T. J. Dee, cover illustration and 2 text illustrations by Richard Grimmett. International Council for Bird Preservation, Cambridge, England, 1986:vi + 173 pp., 26 maps. Price not given.—This report is an outgrowth of the recent (1985) I.C.B.P. publication “Threatened Birds of Africa and Related Islands—The ICPB/IUCN Red Data Book” by N. J. Collar and S. N. Stuart, in which the author assisted. The latter work treated only the threatened birds of Madagascar, a total of 28; here coverage has been extended to all 130 endemic species. The author’s use of “endemic,” as he himself admits, is somewhat loose. There are only 106 species strictly endemic to the island, i.e., found nowhere else, whereas he treats all species whose center of distribution is Madagascar. This additional group includes both birds that occur elsewhere in the Malagasy Region, e.g., Madagascar (Black) Bulbul (Hypsipeles madagascariensis) and Madagascar White-eye (Zosterops madaraspatana), and especially the large number shared with the Comoros, such as Blue Vanga (Leptopterus madagascarinus); and also birds that breed in Madagascar and migrate to Africa, such as the Madagascar Pond-Heron (Ardeola idae) and Madagascar Pratincole (Glareola ocularis). The inclusion of this extra category of what I call “near-endemics” in no way detracts from the book, in spite of rendering the title somewhat inaccurate; rather, the extra information is welcome since so little has been published on the island’s birds.

The principal emphasis of this work is on distribution and status. In each species account a paragraph is included on habitat, and an occasional remark on behavior, but it is not intended either as a field guide (no descriptions or illustrations) or a handbook (no life history data). Its objective, as one would expect of an I.C.B.P. publication, is to accumulate the data necessary for the implementation of a conservation policy for Madagascar. The author has attempted to cite every locality given in the literature for nearly every endemic species.
and as far as I can see, he has done an excellent job of it. The 130 species accounts fill 90 pages, giving an average of about two-thirds of a page per species. The bulk of each account comes under the heading "Status and Distribution," and consists principally of a catalog of the localities from which the species is known, complete with dates, authors, and citations.

The main body of the text is followed by several appendices, of which the most important are an 8-page gazetteer of locality names with coordinates, tremendously useful for any student of the avifauna, and a listing of current and proposed legislation concerning the protection of threatened species. At the back of the book are 24 maps showing ranges of selected endemic species.

Many of Madagascar's endemic birds are in desperate straits because of habitat destruction. The adoption of conservation measures has been hampered by lack of knowledge of their status. Hopefully the publication of this data base will at least go some way to solve the latter problem. Both I.C.B.P. and the author are to be congratulated on this production.—Stuart Keith.

**Birds in Minnesota.** By Robert B. Janssen. Univ. Minnesota Press, Minneapolis, Minnesota, 1987:352 pp., 22 color photos, 240 maps. $35.00 cloth, $14.95 paper.—As a sequel to "Minnesota Birds: Where, When and How Many" by Janet Green and Robert Janssen (1975), "Birds in Minnesota" is the archetypical state "bird book" for listers. The author notes that the number of species known from Minnesota has increased from the time of Roberts' (1936) monumental "The Birds of Minnesota" (just over 320 species), to 374 species in 1975, and the 400 species listed in the present book. Serious ornithologists may wish for a bit more detail, but the birder who intends to visit Minnesota will want a copy of this book. Each species known to occur in the state is listed in turn, along with a map of its occurrence and a description of its present abundance. Sight records are included for rarities, but only after close scrutiny of the report(s). Recent records are presented for less common species, and the status of species of concern is discussed. A good deal of useful information about where to find specific birds (and when) can be gleaned from the text. The copy I received (paperback) is well bound and relatively free of typographic errors. The color photos are of a few interesting species and are quite good.—Charles R. Blem.

**Wisconsin Birds. A Seasonal and Geographical Guide.** By Stanley A. Temple and John R. Cary. The University of Wisconsin Press, Madison, Wisconsin, 1987:364 pp., many maps and graphs. Cloth $27.50, Paper $9.95.—Breeding bird atlases are a current vogue among bird students, but this little volume represents a rather different approach to the task of mapping a region's bird life with the aid of amateur birders. Stanley Temple enlisted 431 members of the large and active Wisconsin Society for Ornithology who agreed to turn in a weekly checklist of all the birds encountered by them. Most of them faithfully turned in these checklists every week for five years. The checklists were in a format that could be read by an optical scanner, with the results being fed directly onto computer tapes or disks.

These observers were distributed throughout the state, which was then divided into 43 regions, each of which contained at least 10 people who had collectively contributed at least 250 checklists per year. The data were analyzed by calculating the weekly reporting frequency and the percentage of participants who reported the species during the week.

The bulk of the book is the visual presentation of these data for the 265 species most commonly found in the state. At the top of the page is a simple bar graph giving "Relative Abundance," which is really the probability of an observer seeing the bird in the state during
the year. This is followed by one or two range maps showing in which of the 43 regions the birds were found, with a system of hatching to indicate relative abundances. Permanent residents and birds present during only one season have one map, and birds whose distribution may change from season to season have two maps. There are then given two graphs showing the reporting frequencies throughout the year in Northern and Southern Wisconsin.

A second part of the text gives the season and county for the records of 98 species that were not reported at least ten times per year during the 1975–85 period. An appendix describes the details of the project.

Southern Wisconsin lies in the southern forest ecological region while Northern Wisconsin is in the northern forest region. Diagonally across the state from northwest to southeast there is a “tension zone” where the transition between regions occurs. Many of the range maps illustrate these three regions beautifully in so far as the distribution of birds is concerned. Thus this publication can be extremely valuable, not only for Wisconsin birders, but also for biogeographers elsewhere.

This represents a notable and successful attempt to harness the energies of amateur birdwatchers. Compared with the usual atlas project, the expense of conducting this one was minimal although the manpower and time involved was approximately the same. While the resulting distribution maps lack the fine-scale results of an atlas project, they are in no way inferior. In addition, this method gives year-round information on all common species rather than just information on breeding birds in the breeding season.

A comprehensive book on Wisconsin birds has been in preparation for some years, and this volume will both make the final preparation of that treatment easier and will serve as a more than adequate substitute until the major work appears.—GEORGE A. HALL.

The Carolina Parakeet in Florida. By Daniel McKinley. Florida Ornithological Society Special Publication No. 2, Gainesville, Florida, 1985:v + 64 pp., 1 map and cover drawing. $6.00 (obtainable from Treasurer, F.O.S., 1701 N.W. 24th St., Gainesville, Florida 32605).—It is a matter of great regret that for one reason or another Daniel McKinley has not been able to publish his long-term research on the Carolina Parakeet (Conuropsis carolinensis) as a single definitive (and also monumental) publication. The bibliography of the publication at hand lists 25 papers published so far. Most of these are in local publications, often hard for the average person to obtain. Be that as it may, we have here a very fine summary of the status of the Carolina Parakeet in Florida. Despite its English name, Florida was clearly the stronghold of the eastern race of the species.

McKinley has examined the numerous specimens and consulted the scattered literature to compile the records of the parakeet from the earliest days down to its extinction. Early travelers mentioned “Parrots” in Florida, but prior to the Civil War, there was little more information than this. William Bartram, George Ord, and Audubon said very little about the species. The first Florida specimens still extant were apparently collected in the 1850s. In the 1870s reports and collections increased. All the well-known ornithologists of the time made at least one trip to Florida and all collected parakeets. From 1870 on McKinley gives a detailed account of all known specimens and literature accounts. By 1880 some observers were commenting on the decrease in the species, and this served to attract more collectors. McKinley comments that from the reports from those years it would be easy but “—unfair to call the 1890s the decade when bird lovers of the world lined up for a chance to shoot the last Carolina Parakeet.” But collect they did. Frank M. Chapman shot 15 in March of 1889.

There is much disagreement and a host of confusing reports and rumors about the last bird to be seen in the wild. Chapman collected 4 in April 1904, although he did not publicize
this fact until the 1932 edition of his *Handbook* and these may have been the last collected, although a specimen of uncertain authenticity has a 1908 date. The species continued to be reported occasionally, even as late as the 1930s.

McKinley has cleared up a widespread misconception about the Carolina Parakeet. Apparently, in Florida at least, it was not an agricultural pest and was not widely shot for this reason.

Daniel McKinley has accomplished a prodigious piece of scholarship and succeeds in presenting it to us in a fascinating manner.—George A. Hall.

**BRIEFLY NOTED**

The **Bird Feeder Book**. By Donald and Lilian Stokes. Little Brown and Company, Boston, Massachusetts, 1987:vi + 85 pp. $8.95 (paper).—The subtitle, “An easy guide to attracting, identifying, and understanding your feeder birds” explains the purpose of this book, written primarily for the complete beginner.—G.A.H.


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Nine-year-old F₁ hybrid skua (Catharacta maccormicki × C. lomnbergi) on its breeding ground near the Antarctic Peninsula. Watercolor painting by David F. Parmelee.
THE HYBRID SKUA: A SOUTHERN OCEAN ENIGMA

DAVID F. PARMELEE

ABSTRACT.—Mixed pairs of South Polar Skuas (Catharacta maccormicki) and Brown Skuas (C. lonnbergi) were banded and observed during a 9-year study within a narrow zone of sympatry near the Antarctic Peninsula. A history of their territorial, mate, and other preferences disclosed that mixed pairs usually, but not invariably, reside near penguin colonies; male maccormicki usually, but not invariably, pair with female lonnbergi; some mixed pairs remained faithful, whereas members of others readily remated with the same or different species; nesting success in mixed pairs paralleled nesting success in maccormicki, indicating a major role of the male in securing food for the female before egg laying. Although hybrids resulting from mixed matings resembled lonnbergi in appearance, their mating, feeding, and migratory behavior resembled those of maccormicki. At least some F₁ hybrids were fertile, but matings between maccormicki and lonnbergi were less than expected by chance alone, and the two skuas were considered close but separate species. Field identification of hybrids was extremely difficult and likely will confuse observers along the migratory routes. Received 29 Nov. 1986, accepted 17 Mar. 1987.

Two widely recognized species of skuas breed in the Southern Ocean: the more southern South Polar Skua (Catharacta maccormicki) and the Brown or Subantarctic Skua (C. lonnbergi). Although these birds are allopatric over much of their vast breeding ranges, some pairs nest side by side within a narrow zone of overlap in the Antarctic Peninsula region (Watson 1975), the South Shetland Islands (Trivelpiece and Volkman 1982), and, more recently, the South Orkney Islands (Hemmings 1984) where a small number of mixed matings occur. The resulting hybrids pose questions concerning their influence on the gene pools of the two species. They also create problems in field identification of skuas, not only for biologists who study them, but also for the increasing number of enthusiasts observing birds either at sea or along the migratory routes of both Atlantic and Pacific shores of the Americas.
Peninsula, from which it is separated by Gerlache and Orleans Straits. The principal study area is located at Palmer, midway between Biscoe Point and the Joubin Islands.

For a period spanning 11 years, including the austral summer seasons (October–March) from 1974–75 through 1980–81, and from 1983–84 through 1984–85, the author and others observed mixed pairs and their hybrids in the vicinity of U.S. Palmer Station (64°46'S 64°03'W) on Anvers Island (Fig. 1) near the Antarctic Peninsula. In this report I attempt to identify and clarify some of the mystery surrounding the mixed matings and resulting hybrids.

**STUDY AREA AND METHODS**

Anvers Island, at the southern end of Palmer Archipelago, is covered with a thick, highly crevassed ice sheet except for the peaks of high interior mountains ranging up to 2822 m elevation, and the tips of low-lying peninsulas that jut into the sea. These peninsulas and the small offshore islands close by become mostly snow- and ice-free each austral summer and provide the breeding grounds for the skuas and other seabirds. The study area (Fig. 2) included both peninsulas and offshore islands which, with the exception of Bonaparte Point, were accessible only by means of outboard engine-driven rubber boats. Tides were not a concern, but whenever windblown pack ice moved into the area it hindered or prevented travel by boat. Several hundred pairs of South Polar Skuas that bred in many places throughout the Palmer study area were dependent on at-sea foraging for their principal food of fish.
Fig. 2. Palmer Archipelago Study Area. Parallel lines show locations of Adelie Penguin colonies on Cormorant, Christine, Torgersen, Litchfield, and Humble islands. Mixed pairs of South Polar and Brown skuas produced 24 hybrids on Cormorant Island (Site A), Hermit Island (Site A), Shortcut Island (Site A), Humble Island (Sites A, B, C, D), and Norsel Point (Site A). On Christine Island Site A, an eight-year-old F₁ hybrid mated with a South Polar Skua and produced an F₂ hybrid fledgling; for two seasons a male South Polar Skua and a female Brown Skua occupied but produced no progeny at Site B.

The much less numerous Brown Skuas (6 to 12 pairs) bred near and used Adelie Penguin (Pygoscelis adeliae) eggs and nestlings as a source of food.

Both South Polar and Brown skuas defended their nests boldly. As dive-bombing individuals were easily caught in hand nets thrust suddenly above one's head, the majority of nesting skuas were caught, banded, and frequently marked with combinations of colored bands for convenient field identification. Apart from the nesting areas, a few were caught in cannon or simple drop nets baited with food. As a rule adults were banded with numbered bands on the left leg, chicks on the right. Although we failed to catch some individuals, 16 individuals from mixed pairs were captured and marked at 10 sites within the study area (Fig. 2). Their hybrid offspring in turn were marked with a numbered metal band and a white plastic band on the right leg.

From one season to the next a concerted effort was made to keep track of the mixed and normal pairs of skuas. Their territories were mapped, and any change in occupancy was noted. As surviving adults often returned to the original territory and paired with former mates, changes were easily detected. Personnel at Palmer also noted the return of birds that
had been banded previously as chicks. Always, a watchful eye was kept for any returning hybrid.

HISTORY OF MIXED PAIRS WITHIN THE STUDY AREA

Within the study area, mixed pairs were not evenly distributed (Fig. 2). An abbreviated island-to-island summary of these pairs follows:

Cormorant Island


Christine Island

Site A.—Hybrid 877-36556 (banded when a chick on Humble Island by Neilson [1983] on 18 January 1976) was observed by me at Site A on 2 January 1984 when it was eight years old and mated with an unbanded South Polar individual of uncertain sex. C. Rimmer later confirmed the identity but not the sex of the hybrid (rebanded 1067-25309) and also banded its South Polar mate 1067-25708 on 16 February 1984; still later he banded their single F1 hybrid fledgling 1067-25841 on 24 February 1984, thus establishing beyond doubt the fertility of maccormicki-lonnbergi F1 hybrids. The mixed pair again occupied Site A in 1984–85 but produced no progeny; shell fragments at their nest indicated earlier loss of eggs. Before its rediscovery on Christine Island, the F1 hybrid was recovered from a fish net by E. Cunico at Parangual, Brazil, on 23 May 1980, when four years old and “released unharmed.”

Site B1.—Occupied by an unbanded South Polar male and unbanded Brown female in 1983–84, and 1984–85 but no evidence of nesting was recorded.

Hermit Island

Site A.—South Polar δ 977-31563 × Brown ♀ 977-31562 (banded at the site respectively on 15 and 11 February 1975) produced two hybrids each season in 1974–75 and 1975–76, but both adults were not seen since.
Shortcut Island

*Site A.*—Unbanded South Polar male × left-leg banded Brown Skua of uncertain origin produced one hybrid in 1975–76, but only South Polar Skuas have since occupied Shortcut Island. Site A was about 1.5 km from the closest penguin colony.

Humble Island


Brown δ 877-36911 was next recorded in 1977–78 on Litchfield Island where he participated in a trio (three adults occupying one nest) with two Brown Skuas that produced no young. In 1978–79, Site A was unoccupied, although visited occasionally by ♀ 877-36908, which did not mate that season; meanwhile δ 877-36911 died from fowl cholera on Litchfield Island. Site A was unoccupied in 1979–80 after ♀ 877-36908 abandoned it for Site C. It was also unoccupied 1980–81, but the site was occupied by South Polar Skuas 1983–84, 1984–85. Of the four hybrids produced at Site A, one later bred within the study area (see Christine Island above), and one was kept captive at Palmer Station where it eventually died.

*Site B.*—South Polar δ 877-31503 (banded at site on 10 January 1975 when mated to a South Polar female) produced two hybrids with an unbanded Brown female in 1975–76. In 1976–77, he mated with Brown ♀ 877-36958 (banded at site on 21 January 1977), but they produced no hybrid that season, and the South Polar male did not nest at this site again. Female paired next with a Brown δ (banded 1067-25059 at site on 24 January 1979), but only one young was produced from 1977–78 through 1980–81, and the male not seen since. When next observed in 1983–84, Brown ♀ 877-36958 (rebanded 1217-00939) was paired with South Polar δ 877-36651 (banded at site on 13 January 1984). They had no progeny that season, but produced two hybrids in 1984–85.


Site D.—This was a new territory not used by any skuas during the study before 1984–85, when it was occupied by South Polar ♂ 1057-10286 (previously banded at another Humble Island site on 9 February 1980 when mated to a South Polar female) × Brown ♀ 1217-00940 (banded at site on 24 December 1984). The pair produced two hybrids.

Norsel Point

Site A.—A previously banded (left leg) South Polar male of uncertain origin × Brown ♀ 1057-10449 (banded at site on 23 February 1980) produced one hybrid at the site in 1979–80. Brown female not seen since. Site A was about 0.7 km from the closest penguin colony.

MIXED MATINGS OUTSIDE THE STUDY AREA

Limited observations of mixed matings outside the study area included the following:

- At Biscoe Point (64°49'S 63°49'W), about 12 km east of Palmer Station, an unbanded South Polar male × unbanded Brown female had two eggs on 17 December 1984.

- At Dream Island (64°44'S 64°14'W), about 8 km northwest of Palmer Station, an unbanded South Polar male × Brown ♀ 1067-25104 (banded at site on 7 January 1984) produced two hybrids in 1983–84 and two in 1984–85. On an unnamed island adjacent to Dream Island, an unbanded South Polar male and an unbanded Brown female had two eggs on 31 December 1984.

On one of the many unnamed Joubin Islands (64°47'S 64°27'W), about 12 km southwest of Palmer Station, Neilson (1983), on 7 February 1977, banded two hybrids produced by an unbanded South Polar male and an unbanded Brown female.

RESULTS

Nearly a decade of repeated observations on mixed skua matings within and near the study area disclosed the following:

(1) Penguin-dependent Brown Skuas invariably nested near penguin colonies, whereas the fish-dependent South Polar Skuas and mixed pairs either nested near or far from the penguin colonies. Judging by the prey brought to the young, the mixed pairs residing far from the colonies were the least dependent on penguins for food.

(2) Within the study area, most Adelie Penguins resided in the triangle formed by Torgersen (8630 pairs, 8-year mean), Litchfield (579 pairs,
9-year mean), and Humble (2516 pairs, 8-year mean) islands (see Fig. 2). For reasons not understood, Humble Island with its modest population of both species of skuas had 45% of the mixed matings and produced 50% of all hybrids believed to have fledged, whereas nearby Litchfield Island, which had the largest population of both species of skuas, had no mixed pairs. The Brown Skuas of Litchfield hunted mostly on Torgersen Island, which had the largest penguin colony and, in many years, no nesting skuas. Nevertheless, the triangle referred to above was the heart of Brown Skua activity for all of Anvers Island, and where mixed pairing likely will occur.

(3) In 23 of 25 mixed pairings observed in the present study, a male South Polar Skua paired with a female Brown Skua. The only exception to this was at Site A, Humble Island. Other observers (Trivelpiece and Volkman 1982, Hemmings 1984) found only male maccormicki mated to female lonnbergi. Neilson (1983), who studied mixed pairing at Palmer, believed that an advertising male South Polar Skua on territory was joined by one of a surplus of Brown Skua females in search of a mate, especially before the arrival of many South Polar Skua females. This explanation may be oversimplified, for we now know that some Brown Skua females return to and remain at a nest site even when they have lost their mates. A few of these birds then form new pairbonds with South Polar Skua males, suggesting that occasionally a female may hold a territory and attract a male to it. Also, mixed pairs per se remained faithful to an established site for as many as four seasons, possibly longer. On the other hand, some individuals of both sexes readily changed territories and mated with members of the same or different species. In any event, it appears that the formation of mixed pairs is not strictly random.

(4) In observing marked skuas over a period of years, it is clear that both South Polar and Brown skuas show a trait that may best be described as sometime absenteeism, i.e., some individuals return to the breeding grounds and do not breed, or they fail to return altogether, but then later return and breed at old or new sites. With respect to mixed pairs, a site that is abandoned by the birds for one or more seasons may be reoccupied by either member of the pair that then mates with a new individual of the same or different species. We have not yet documented whether a mixed pair ever reunites following absenteeism.

(5) In the study area, the fish-dependent South Polar Skuas showed dramatic fluctuations in fledging success, whereas the penguin-dependent Brown Skuas did not (Parmelee et al. 1978). Nesting failure in mixed pairs paralleled that of widespread nesting failure in the South Polar Skuas, indicating the important role of the male in securing food for the female before egg laying (Pietz 1987). According to Pietz, the female Brown
Skua of a mixed pair nesting close to penguins on Humble Island preyed heavily on penguins; food records for its hybrid chicks were half penguin and half fish. Hybrid chicks observed by me far from the penguin colonies regurgitated only fish or krill, and the ground occupied by them had no penguin remains which invariably litter the nesting sites of Brown Skuas.

(6) We had so few observations on the one F₁ hybrid (sex unknown) × South Polar Skua nesting that we cannot say for certain where the birds hunted. It appeared that their food was derived from the sea, for they were not observed at a penguin colony near by, and within their territory we found no penguin remains.

(7) Palmer-banded South Polar Skuas have been recovered as far north as West Greenland in the North Atlantic, and Oregon in the North Pacific. Most South Polar Skuas, however, and one F₁ hybrid have been recovered along the coast of Brazil (Parmelee 1985). To date none of our Brown Skuas has been recovered outside the Palmer area. Unlike the South Polar Skuas, the Brown Skuas commence molting their flight feathers before departing the Palmer breeding ground (Neilson 1983), suggesting a short migration. On the basis of a single long-distance return, I know that hybrid skuas behave like South Polar Skuas in that they migrate at least as far north as Brazil.

MORPHOLOGY OF THE F₁ SKUA HYBRID

As a rule South Polar Skuas and Brown Skuas were easily identified in the field despite the fact that the large majority of maccormicki at Palmer and elsewhere along the Antarctic Peninsula are medium to dark plumaged. Not only did the species differ in behavioral characteristics (Parmelee et al. 1978, Neilson 1983, Pietz 1985, 1987), their morphology was quite distinct. Neilson (1983) took tarsal, culmen, gonys, and 7th primary measurements and weights of adults and showed lonnbergi to be the larger of the two. In the field, the larger body, heavier bill, and longer tarsus identified lonnbergi. Moreover, lonnbergi had a less variable plumage, characterized by somewhat rufous underparts and prominent yellow to white tipped back feathers that were lacking in maccormicki. Some South Polar adults showed a mottled rather than a uniform dorsum; most showed prominent golden hackles on the neck and, in flight, central rectrices that extended beyond the others.

By employing a nonparametric rank correlation test, Neilson (1983) showed that lonnbergi females had significantly larger tarsi, wing, and weight values than did their mates. On this basis we were quite certain of our sex determinations of live lonnbergi. Such measurements overlap between the sexes in maccormicki, and we were forced to rely on behavioral characteristics. Banded birds found dead during the 9-year study verified many earlier sex determinations.
Identifying the hybrid skua in the field, not to mention its sex, was quite a different matter. From the beginning we were puzzled by certain individuals whose size and plumage simply did not conform to our standards. The birds looked like small lonnbergi but behaved like maccormicki; some of these mystery birds were paired with South Polar mates, but none, to our knowledge, with lonnbergi mates. Once we began to observe mixed matings, we were convinced that hybrids likely were responsible for most of our problems in field identification.

Hybrid eggs and young measured by Hemmings (1984) were intermediate in size. Four eggs of one mixed pair measured by Pietz (pers. comm.) over two seasons were, however, typical of Brown Skua size: For samples of 16, 4, and 114 eggs, mean volumes \( V = 0.00048 \times 1 \times w^2 \) were 100, 102, and 84 cm\(^3\) for Brown, hybrid, and South Polar skuas respectively; the Brown and hybrid skuas differed significantly from the South Polar Skuas but not from each other, indicating that the size of the egg is not influenced by the male. One would expect that the size of the resulting hybrid may be intermediate to the parental types. Hemmings (1984) found that hybrid chick growth rates, with respect to weight and bill and tarsal lengths, generally fall between those of lonnbergi and maccormicki. Pietz (pers. comm.) also found that tarsal length in hybrid fledglings was intermediate and that the three groups differed significantly: For samples of 10, 3, and 11 chicks, means were 77.0, 70.0, and 67.0 mm for Brown, hybrids, and South Polar skuas, respectively. In outward appearance hybrid fledglings looked more like lonnbergi than maccormicki. A captive hybrid at Palmer Station continued to have the outward appearance of lonnbergi, although its development seemed abnormal, and it never learned to fly, possibly because of hand rearing.

C. Rimmer took several measurements of the eight-year-old F\(_1\) hybrid: culmen 54.3 mm, gonys 19.9, and tarsus 76.5. These measurements were intermediate between those taken at Palmer by Neilson (1983) for maccormicki (culmen 45–52, gonys 16–18, tarsus 63–72) and lonnbergi (culmen 52–59, gonys 20.5–22.5, tarsus 73–86). Overall, the hybrid had the appearance of a small lonnbergi, but its behavior with respect to mate preference, nesting, and migration pointed to maccormicki. Although additional examples of banded hybrids are needed to confirm this hypothesis, I believe that most, if not all, of the mystery skuas that plagued our studies probably were hybrids.

**DISCUSSION**

With few exceptions the behavioral distinctions between the two taxa were subtle. One obvious distinction mentioned earlier was the difference in their feeding behavior when breeding sympatrically. The Brown Skuas were so dependent on penguins for their food source that their breeding
schedules were attuned to those of their prey (Parmelee 1985). As a consequence, they bred early and within a relatively short time span, whereas, the at-sea foraging South Polar Skuas were not nearly so synchronized in their breeding, as is clearly reflected in their egg-laying dates that spanned a period of many weeks (Neilson 1983). Also, South Polar Skuas had a greater choice of nesting habitat, often far removed from the penguin colonies. This distinction breaks down, however, where the two species breed allopatrically, even as close as the west coast of Anvers Island where South Polar Skuas too depend on penguins (Parmelee 1985).

Pietz (1985) observed far more subtle differences while studying the two species within the Palmer Station study area. In examining several aspects of the skua long-call display, she found no significant species differences in call composition, call duration, or note duration. She did, however, find that the species differed significantly in four parameters. On the average, the notes of South Polar Skua had a faster repetition rate, lower pitch, lower average frequency, and more harmonics than those of Brown Skuas. Film analysis revealed that South Polar Skuas tended to lean farther back at some point in the long call display. Unfortunately, Pietz did not have the opportunity to observe the known F₁ hybrid discussed above.

I observed nothing in the behavior of known or suspected hybrids that clearly set them apart from the parental types. The hybrids resembled maccormicki in certain obvious behavior, particularly mate preference. It probably is no coincidence that our mystery birds recorded as probable hybrids were invariably mated to maccormicki, some of them nesting a long way from the penguin rookeries. Whether the hybrids select maccormicki mates through choice, or simply because those skuas far outnumber lonnbergi skuas in our study area is, at this time, a moot question. Nevertheless, if the pattern of F₁ hybrid skuas mating with maccormicki predominates, the influence of lonnbergi genes should diminish.

In another paper on Anvers Island skuas (Parmelee 1985), I stated that the Palmer study area appeared to be fairly typical of Short’s (1969) description of a zone of overlap and hybridization where secondary intergradation has occurred. Parental phenotypes far outnumbered the hybrids, and mixed matings were comparatively rare. Certain premating isolating mechanisms also were evident for keeping the two skuas apart, notably asynchronous arrival and breeding times. Ecologically, the two have different territorial and feeding strategies when sympatrically situated. Based on the number of breeding pairs of skuas in the study area, the expected number of mixed pairs through chance mating was calculated to be no fewer than 15 pairs—considerably more than the one to four pairs recorded annually during the 9-year study. The Anvers Island skuas
showed a very close though separate relationship and are thus best con-
sidered separate species even though there appear to be no postmating
isolating mechanisms with respect to hybrid fertility.

Of 15 banded hybrids believed to have fledged during the early part of
the study (1974–75 through 1978–79), including 14 within the Palmer
study area, there has been only one recovery (6%) of a returning hybrid
to date. This compares with the recovery rates of 2% for 541 Palmer
banded *maccormicki* chicks and of 3% for 80 *lonnbergi* chicks for the
same period (Parmelee and Rimmer 1984).

Apart from the breeding grounds where experienced observers have the
advantage of observing the birds closely on their territories, $F_1$ hybrid
skuas are extremely difficult to identify in the field. $F_2$ hybrids will prove
even more difficult. As it seems likely that the hybrids are long-distance
migrants, observers along the coasts of the Americas should be cognizant
of this problem.

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COLOR PLATE

The Frontispiece painting by David F. Parmelee has been made possible by an endowment established by George Miksch Sutton.
COMPARATIVE REPRODUCTIVE BIOLOGY OF KINGBIRDS (TYRANNUS SPP.) IN EASTERN KANSAS

MICHAEL T. MURPHY

Abstract.—Data on body size, timing of breeding, clutch size, egg weight and patterns of nestling growth are reported for sympatrically breeding populations of Eastern and Western kingbirds (Tyrannus tyrannus and T. verticalis) and Scissor-tailed Flycatchers (T. forficatus) in eastern Kansas. Body size and breeding dates were similar for the three species, but all other traits showed significant variation. Eastern Kingbirds laid the smallest clutches, the largest eggs, and their young gained weight fastest. The rate of weight increase by Eastern Kingbirds varied inversely with brood size. Scissor-tailed Flycatchers produced the largest clutches, the smallest eggs, and their young gained weight significantly slower than the young of Eastern Kingbirds. Western Kingbirds were intermediate in most respects. Variation among species in egg and clutch size represent fixed, apparently genetic differences. It is less clear whether variation in the rate of growth reflects phenotypic responses to stress or intrinsic species differences. Comparisons of tarsus growth indicate little variation among species, but primary development was faster in Western Kingbirds and Scissor-tailed Flycatchers than in Eastern Kingbirds. I propose that egg and clutch size vary independently among species in response to climatic stresses within the respective geographic ranges of each species. Received 23 July 1987, accepted 8 Feb. 1988.

Life histories are commonly viewed as sets “of coadapted traits designed, by natural selection, to solve particular ecological problems” (Stearns 1976). Implicit in this definition is the notion that life histories represent optimal solutions to ecological pressures impinging on reproductive success. Furthermore, it is often assumed that organisms operate at maximal rates and efficiencies (Calow and Townsend 1981), and that optimal amounts of energy are allocated to reproduction (Smith and Fretwell 1974). Hence, theory predicts the existence of compromises among such life history traits as reproductive rate and survival (Williams 1966, Charnov and Krebs 1974), number and size of offspring (Smith and Fretwell 1974, Brockelman 1975, Lloyd 1987), and number and rate of offspring development (Fretwell et al. 1974).

Recently, questions have arisen over the most appropriate taxonomic level for testing life history theory. Ideally, comparative tests should be made within species to control for genetic differences. However, attempts to test theory in birds through intraspecific geographic comparisons of reproductive traits have proved inconclusive (Hussell 1972, Murphy 1978,
King and Hubbard 1981, Jarvinen and Vaisanen 1983, Murphy 1983a, Winkler 1985, but see Blondel 1985). Except for timing of breeding and/or clutch size, most species showed little variation in reproductive characters among allopatric populations. Differences found to exist were often attributed to body size (Murphy 1978, King and Hubbard 1981), the physiological state of the female (Murphy 1978, Jarvinen and Vaisanen 1983, Winkler 1985), or to seasonal factors (Hussell 1972, Jarvinen and Vaisanen 1983, Murphy 1986a), suggesting that tests of life history theory within species may be limited by allometry, low genetic variability, physiology (Stearns 1980), phylogeny (Jones and Ballinger 1987), or gene flow (Slatkin 1987). Work on classes of animals other than birds indicate similar problems (e.g., Hart and Begon 1982, Brown 1983, 1985, Dobson and Murie 1987). Thus, although work at the population level is essential for identifying the causes for shifts in life history characters, the most profitable tests of theory may be made by comparing closely related species (Stearns 1980, Ekman and Askemo 1986, but see comments by Jones and Ballinger 1987).

As part of a larger study examining life history evolution in the Eastern Kingbird (Tyrannus tyrannus), I gathered reproductive data on Western Kingbirds (T. verticalis), and Scissor-tailed Flycatchers (T. forficatus) that bred sympatrically with Eastern Kingbirds over the same period in eastern Kansas. Bent’s (1942) life history summaries suggest that modal clutch size is 3, 4, and 5 eggs in Eastern and Western kingbirds and Scissor-tailed Flycatchers, respectively. Clutch size declines seasonally in kingbirds (Davis 1955; Murphy 1983a, 1986a; Blancher and Robertson 1985a, b, 1987), and at least in Eastern Kingbirds, differences in clutch size among years and among some populations can be accounted for by variation in timing of breeding (Murphy 1986a; see also Jarvinen and Vaisanen 1983 for the Pied Flycatcher Ficedula hypoleuca). Hence, one possible explanation for interspecific variation in clutch size is early breeding by Scissor-tailed Flycatchers and late breeding by Eastern Kingbirds. In this report I provide comparative data on timing of breeding, clutch and egg size, and nestling growth for all three species of kingbirds. I test: (1) the breeding date hypothesis, and, at the interspecific level, the theoretical predictions that inverse relationships should exist between: (2) egg and clutch size (Smith and Fretwell 1974, Lloyd 1987), and (3) number and rate of offspring development (Fretwell et al. 1974).

SPECIES AND STUDY AREA

Eastern Kingbirds (henceforth EKB) have the widest and northernmost distribution of the three species. They breed from the Yukon to south Texas and Florida, and from the Pacific northwest over all of eastern North America in habitats ranging from forest edge to
old field and pasture. Western Kingbirds (WKB) also breed in open habitats, including riparian forest, deserts and urban areas. In general, WKBs breed in drier habitats and are found mainly in western North America. However, over the past 50 years WKBs have spread eastward across the Great Plains. Scissor-tailed Flycatchers (STF) have the southernmost distribution, being restricted to grassland habitats in the southcentral United States (all distributional data from the A.O.U. Checklist 1983). All three species are migratory, breed monogamously, and normally raise a single brood per year (Bent 1942, Fitch 1950, Davis 1955, Murphy 1983a, Blancher and Robertson 1987). Diets and foraging behaviors during the breeding season are also very similar (see Murphy 1987), i.e., all three species typically hawk for flying insects. Likewise, all three build open cup nests that are usually placed 2 m or more above the ground (MacKenzie and Sealy 1981, Murphy 1983b, Blancher and Robertson 1985a).

Breeding ranges of the three species overlap in portions of Kansas, Oklahoma, and Texas. I collected data in Douglas County, Kansas, from 1980 through 1983. Additional data on adult body sizes were taken in June, 1986 from Douglas and neighboring counties. My principal research area extended west from the edge of Lawrence, Kansas, to Clinton Reservoir (38°57'N, 78°95'W), a distance of about 6.5 km. Habitats consisted of pastures, grassland with scattered trees, hedgerows, and, near the city and reservoir, parks and campgrounds. “Natural” habitats are described in greater detail elsewhere (Murphy 1986a). EKBs were the most plentiful species and bred in all the above habitats. WKBs were found only near human habitations, but were often very abundant in city parks, campgrounds, or other mowed areas. STFs were found almost exclusively in open grasslands and were the least abundant species. WKBs and STFs rarely bred in the same habitat, but EKBs were syntopic with both species.

METHODS

Field procedures.—Field methods have been described thoroughly in previous publications (Murphy 1983a, 1985a, 1986a, b). I did not make special attempts to locate breeding STFs or WKBs, but included them in my daily activities when nests were located. I used identical methods to record timing of breeding (=date of laying of the first egg in a clutch), clutch size, egg dimensions (maximum length and breadth) and weight, and nestling growth in all species. All weights and length measurements were measured to the nearest 0.1 g and 0.05 mm, respectively, with a 50-g Pesola spring scale and dial calipers. Dates of clutch initiation for nests found after egg laying were determined by backdating from events such as hatching of eggs or age-determination of nestlings (Murphy 1981).

Upon hatching (=day 1 of nestling period), I visited nests at regular intervals up to day 13 or 15 of the nestling period. At each visit I recorded the weight, tarsus length, and 9th primary length for each nestling present. Nestlings were marked individually by clipping toenails. Nest checks occurred daily in 1980. Nest predation increased in 1981 and 1982, presumably due to my disturbance of nests. I therefore attempted to decrease my impact on nest success by reducing the frequency of nest checks to every 1–4 days. I created broods of five EKB young in 1980 (N = 2) and 1981 (N = 1) by adding one nestling to broods of four. Transfers occurred by day 2 of the nestling period and were of same age individuals. Growth was also measured in a natural brood of 5 young in 1981. Except for one STF brood, no growth data were taken in 1983.

In 1983 and 1986 I collected adults of all three species using .22-caliber rifle and “dust-shot.” Immediately after the specimen was collected, I recorded body weight, wing chord length (unflattened), tarsus length, bill length (anterior edge of the nares to the tip), and keel length. The length of the keel was taken as the distance from the base of the sternum to the
base of the furcula, and was averaged from three separate measurements. Sex was determined from plumage characters (two outer primaries emarginate in males, only the outermost primary emarginate in females; Bent 1942).

Data analysis.—I determined fresh egg weight (weight on day of laying) for eggs measured during incubation using length and breadth measurements in the formula, egg weight \( W = [C(L \times B^2)] \), where \( L \) and \( B \) are maximum egg length and breadth, respectively. The conversion factor, \( C \), relating \( L \) and \( B \) to \( W \) was determined for each species separately from a sample of eggs weighed and measured on the day of laying. I took a random sample of 15 EKB clutches from each of the four years to compare to the cumulative four-year totals of the WKB and STF. Sample sizes in all analyses involving comparisons of egg size and nestling growth equal the number of nests from which data were collected. I used average weight, length, and breadth of all the eggs in a clutch in comparisons among species and years.

I computed growth curves for body weight and tarsus and 9th primary lengths for each brood. I then calculated each brood's average rates of weight gain using Crossner's (1977) weight-specific regression method. Crossner's technique permits simultaneous estimation of asymptotic weight \( A \) and rate of growth \( K \). I also computed the absolute rate of weight gain by regressing weight against age for the period when growth was approximately linear (days 3–11). Absolute rates of growth for the lengths of the tarsus and 9th primary were determined using the same method, but over different ages (tarsus, days 1–11; 9th primary, days 6–14). The resulting least-squares regression coefficients equalled the absolute rate of increase in weight or length.

I used standard parametric statistics throughout when the assumptions of the models were not violated. I checked distributions visually for normality, and used the F-max Test to determine if variances were homoscedastic. When variances proved to be heteroscedastic, I used a t-test \( t_s \) based on unequal variances (Sokal and Rohlf 1981) or substituted an appropriate nonparametric test. Most statistical analyses were performed using the BMDP statistical package (Dixon 1981). Statistical significance was accepted at \( P < 0.05 \). Specific tests are described in the Results.

RESULTS

Sexual size dimorphism and adult body size.—Patterns of sexual size dimorphism varied among characters. No dimorphism existed in tarsus length, bill length, or body weight; whereas in all three species keel lengths were 5–8% larger in males than females (Table 1). Wing chord lengths were significantly longer in males than females in 2 of 3 species. Sampling error resulting from small sample size was the probable cause for the lack of significant sexual size dimorphism in wing chord length of WKBs (Table 1).

Because of the lack of dimorphism in bill and tarsus lengths and weight, I combined the sexes for comparisons among species. Bill lengths varied significantly (Table 1) due to the short bills of STFs compared to both WKBs and EKBs (Sums of Squares simultaneous test procedure [SS-STP, Sokal and Rohlf 1981], \( P < 0.05 \) for both). Tarsus lengths also varied among species (Table 1). In this case STFs were the same size as WKBs and EKBs (SS-STP, \( P > 0.05 \)), but EKBs had shorter tarsi than WKBs (SS-STP, \( P < 0.05 \)). Weight differences among species were not significant.
### Table 1

**Morphological Comparisons among Adults of Three Species of Kingbirds Breeding in Eastern Kansas. Values Are Means (SD)**

<table>
<thead>
<tr>
<th>Sex (N)</th>
<th>Weight (g) Mean (SD)</th>
<th>Wing (mm) Mean (SD)</th>
<th>Tarsus (mm) Mean (SD)</th>
<th>Keel (mm) Mean (SD)</th>
<th>Bill (mm) Mean (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Eastern Kingbird</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male (32)</td>
<td>42.4 (3.64)</td>
<td>117.6 (2.28)</td>
<td>19.26 (0.79)</td>
<td>28.12 (1.01)</td>
<td>13.97 (0.69)</td>
</tr>
<tr>
<td>Female (34)</td>
<td>41.8 (2.69)</td>
<td>110.9 (2.49)</td>
<td>19.22 (0.75)</td>
<td>25.96 (1.31)</td>
<td>13.86 (0.77)</td>
</tr>
<tr>
<td><strong>Western Kingbird</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male (2)</td>
<td>41.2 (1.48)</td>
<td>125.8 (1.06)</td>
<td>20.20 (0.42)</td>
<td>28.68 (0.32)</td>
<td>13.65 (0.35)</td>
</tr>
<tr>
<td>Female (5)</td>
<td>45.8 (5.63)</td>
<td>122.1 (3.07)</td>
<td>20.16 (0.47)</td>
<td>26.49 (0.70)</td>
<td>13.91 (0.39)</td>
</tr>
<tr>
<td><strong>Scissor-tailed Flycatcher</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male (5)</td>
<td>40.7 (1.70)</td>
<td>121.9 (1.29)</td>
<td>19.24 (0.67)</td>
<td>28.07 (0.80)</td>
<td>13.48 (0.72)</td>
</tr>
<tr>
<td>Female (5)</td>
<td>40.4 (5.10)</td>
<td>111.6 (1.14)</td>
<td>19.96 (0.77)</td>
<td>26.64 (0.63)</td>
<td>13.13 (0.49)</td>
</tr>
</tbody>
</table>

Statistical Comparisons among Species (ANOVA)

<table>
<thead>
<tr>
<th>Sex</th>
<th>Statistical Test</th>
<th>F-statistic</th>
<th>df1</th>
<th>df2</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>ANOVA</td>
<td>2.6 ns</td>
<td>2</td>
<td>6</td>
<td>0.1 ns</td>
</tr>
<tr>
<td></td>
<td>t-test</td>
<td>21.1 ****</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>ANOVA</td>
<td>21.1 ****</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* P < 0.05, ** P < 0.02, *** P < 0.01, **** P < 0.001, ns = not significant.

* t-test for comparison of males and females within species.

* F-test from an analysis of variance (ANOVA) comparing species. Sexes combined when dimorphism was absent, but analyzed separately when it existed.

Within sex comparisons of wing chord yielded significant differences among species (Table 1). Female STFs and EKBs did not differ significantly (Table 1), but both had significantly shorter wing chords than WKBs (SS-STP, P < 0.001). Male differences were also significant (Table 1) because EKBs had shorter wing chords than both WKBs and STFs (SS-STP, P < 0.001). None of the within sex comparisons of keel length was significant (Table 1).

**Timing of breeding and clutch size.**—Breeding dates were variable in all species (Table 2; Fmax = 3.09, df = 2, P > 0.05). For this reason, I used nonparametric methods to test for interspecific differences in timing of breeding. Clutch initiation dates overlapped broadly in all three species (Table 2), with no evidence for early- or late-breeding on the part of any of the species (Kruskal-Wallis, H = 2.25, P = 0.40).

Clutch sizes differed substantially among species (Fig. 1 and Table 2), and in all three species clutch size declined seasonally (Table 2). Regression coefficients describing the relationship between clutch size and date...
Fig. 1. Interspecific variation in the frequency of different sized clutches in Eastern Kingbirds, Western Kingbirds, and Scissor-tailed Flycatchers breeding in eastern Kansas.

did not differ among species (analysis of covariance, $F = 2.14$, df = 2, 229, $P = 0.12$). Comparisons of clutch size among species after controlling for date effects showed that EKBs laid significantly fewer eggs than both WKBs ($t = 7.29$, $P < 0.001$) and STFs ($t = 8.78$, $P < 0.001$), but the difference between WKBs and STFs was not significant ($t = 1.57$, $P > 0.10$).

A potential complicating factor in the above species comparisons of clutch size is variation in food abundance among years. The availability of typical kingbird prey (Hymenoptera, Coleoptera, Orthoptera; Dick and Rising 1965) was significantly higher in 1981 than in other years (Murphy
**Table 2**

Reproductive characteristics of Western and Eastern kinhbirds and scissor-tailed flycatchers breeding in Eastern Kansas. Values are means (SE, N).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Eastern Kingbird</th>
<th>Western Kingbird</th>
<th>Scissor-tailed Flycatcher</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding date</td>
<td>11 June (0.84 d, 168)</td>
<td>9 June (1.61 d, 19)</td>
<td>10 June (2.96 d, 17)</td>
</tr>
<tr>
<td>Clutch size</td>
<td>3.37 (0.043, 214)</td>
<td>4.35 (0.209, 20)</td>
<td>4.69 (0.120, 16)</td>
</tr>
<tr>
<td>Seasonal decline*</td>
<td>-0.026 (0.0034, 200)</td>
<td>-0.066 (0.0270, 19)</td>
<td>-0.021 (0.0085, 16)</td>
</tr>
<tr>
<td>Egg weight (g)</td>
<td>3.90 (0.046, 60)</td>
<td>3.83 (0.091, 14)</td>
<td>3.41 (0.086, 17)</td>
</tr>
<tr>
<td>Egg length (mm)</td>
<td>23.48 (0.143, 60)</td>
<td>23.45 (0.269, 14)</td>
<td>22.59 (0.203, 17)</td>
</tr>
<tr>
<td>Egg breadth (mm)</td>
<td>17.50 (0.067, 60)</td>
<td>17.45 (0.156, 14)</td>
<td>-16.74 (0.151, 17)</td>
</tr>
<tr>
<td>Conversion factor</td>
<td>0.541 (0.0015, 57)</td>
<td>0.536 (0.0029, 7)</td>
<td>0.536 (0.0044, 10)</td>
</tr>
</tbody>
</table>

*Values given are regression coefficients from the least squares linear regression of clutch size on date. Y-intercepts and coefficients of determination for EKBs, WKBs and STFs, respectively, are 4.45 eggs ($r^2 = 0.233$), 5.77 eggs ($r^2 = 0.262$), and 5.57 eggs ($r^2 = 0.309$).
1986a), but periodical cicadas (*Magicicada* spp.) also emerged during the 1981 laying period (Murphy 1986a). Food was thus very plentiful, and I showed previously that clutch sizes of EKBs were largest in 1981 mainly as a result of early breeding (Murphy 1986a). Nonetheless, the only 5-egg EKB clutches and 6-egg WKB clutches were found in 1981, suggesting that food supply might have directly influenced clutch size. To investigate the potential impact of high food abundance in 1981 on the interspecific results described above, I examined residual clutch size (effects of laying date removed by the common regression equation, \( \text{CLUTCH SIZE} = 4.66 - 0.027\text{DATE}, r = 0.402, N = 235, P < 0.001 \)) using a two-way analysis of variance (ANOVA; BMDP2V) with the main effects being species and year of breeding. For the latter variable, I grouped clutches from 1980, 1982, and 1983 (i.e., “normal” years) and contrasted them with 1981 (i.e., high food abundance).

Comparisons of residual clutch size among the three species and two “years” showed that species effects were again significant \( (F = 55.2, \text{df} = 2, 229, P < 0.001) \), but effects of year were not \( (F = 1.87, \text{df} = 1, 229, P = 0.17) \). However, the interaction between species and year was significant \( (F = 3.23, \text{df} = 2, 229, P = 0.04) \), indicating that the three species responded differently across “years”. Pairwise species comparisons of clutch size (date-corrected) between 1981 (high food abundance) and the other years (low food abundance) showed that the only significant interaction effects was in the contrast of WKBs and STFs (two-way ANOVA, \( F = 5.33, \text{df} = 1, 31, P = 0.028 \)). Mean clutch sizes did not differ between species \( (F = 0.38, P = 0.54) \), but WKBs produced larger clutches in 1981 than in other years (5.0 eggs \( [\text{SD} = 0.89, N = 6] \) compared to 4.1 eggs \( [\text{SD} = 0.83, N = 14] \); \( t = 2.25, P = 0.04 \)), whereas the nonsignificant trend was for STFs to lay smaller clutches in 1981 (4.5 eggs \( [\text{SD} = 0.55, N = 6] \) compared to 4.8 eggs \( [\text{SD} = 0.42, N = 10] \); \( t = 1.23, P > 0.20 \)).

Because of the significant year-species interaction involving 1981 for WKBs and STFs, I compared date-corrected clutch sizes between species after excluding clutches from 1981. Results indicated that in “normal” years STFs produce significantly larger clutches than WKBs (Wilcoxon Two-sample, \( U_s = 102.5, P < 0.025 \)). This result held when the slightly smaller STF clutches of 1981 were included in the analysis \( (U_s = 151.5, P < 0.025) \).

**Egg and clutch weight.** —Conversion factors relating fresh egg weight to length and breadth (Table 2) were the same for all species \( (F = 1.34, P > 0.05) \), but average egg weights and linear dimensions varied among species (Table 2: ANOVA, \( F_{\text{mass}} = 13.0, P < 0.001, F_{\text{length}} = 4.1, P = 0.01, F_{\text{breadth}} = 12.7, P < 0.001 \)). Size differences were a result of the small eggs laid by STFs \( (\text{SS-STP}, P < \text{at least 0.01 for all 3 comparisons}) \). None
of the comparisons between EKBs and WKBs was significant (SS-STP, \( P > 0.05 \)). Egg sizes among EKBs exhibited significant annual variation, being largest in the year of high food abundance (1981, 4.0 g; Murphy 1986a). STFs also laid significantly larger eggs in 1981 (3.63 g, SD = 0.278, \( N = 6 \) nests) compared to other years (3.28 g, SD = 0.344, \( N = 11 \) nests; \( t = 2.13, \text{df} = 15, P = 0.05 \)). WKB eggs in 1981 (3.99 g, SD = 0.103, \( N = 5 \) nests) tended to be larger than in other years (3.75 g, SD = 0.401, \( N = 9 \) nests), but the difference was not significant (\( t = 1.29, \text{df} = 12, P = 0.23 \)).

Clutch and egg size varied independently in EKBs (Murphy 1983a), WKBs \( (r = 0.141, \text{df} = 12, P > 0.5) \) and STFs \( (r = -0.304, \text{df} = 14, P > 0.50) \), hence in all species total clutch weight (clutch size \( \times \) mean egg mass) increased with clutch size. Given the interspecific differences in clutch and egg size (largest clutches but smallest eggs in STFs), I compared total clutch weight among species to determine if reproductive expenditures at the time of egg laying were similar. They were not (Kruskal-Wallis, \( H = 20.9, P < 0.001 \)). EKBs produced the smallest clutch weight (\( \bar{x} = 13.0 \) g, SD = 2.71, \( N = 168 \); median = 12.6 g), followed by STFs (\( \bar{x} = 15.9 \) g, SD = 2.38, \( N = 16 \); median = 15.7 g), and WKBs (\( \bar{x} = 16.5 \) g, SD = 4.24, \( N = 14 \); median = 16.1 g). Differences between EKBs and the latter two species were significant (Wilcoxon Two Sample, \( P < 0.001 \) for both), but differences between WKBs and STFs were not (Wilcoxon Two Sample, \( P = 0.76 \)). None of the conclusions changed when data from 1981 (year of high food abundance) were excluded.

Nestling growth.—Average body weight and tarsus and 9th primary lengths for days 1–14 are given in Table 3 for EKBs for 1981 and 1982. Growth data for 1980 are presented elsewhere (Murphy 1981). Statistics on nestling WKBs and STFs over the same period are presented in Table 4. General patterns of development (Murphy 1981) are very similar in all species. Differences in size at hatching (weight and tarsus length) correspond well with egg size differences (Tables 2, 3, and 4).

Despite extremely different feeding conditions (Murphy 1986a), and highly different absolute rates of weight increase across years (Table 5; ANOVA, \( F = 20.8, \text{df} = 2, 28, P < 0.001 \)), weight-specific growth rate \( (K) \) did not vary with year in EKBs (Table 5; ANOVA: \( F = 1.19, \text{df} = 2, 28, P = 0.34 \)). Growth rates in the year of high food abundance (1981) were only 5.6% higher than in the drought year (1980). Growth rates in the drought year and an “average” year (1982) were nearly identical (Table 5). The three year average growth rate from 31 broods (\( K = 0.450, \text{SD} = 0.0398 \)) was also very close to the growth rate calculated from each year’s average growth curve for weight (1980, \( K = 0.444 \); 1981, \( K = 0.452 \); 1982, \( K = 0.455 \)). However, as would be predicted from the different absolute
### Table 3

Mean Daily Weight, Tarsus Length, and 9th Primary Length of Eastern Kingbirds Breeding in Eastern Kansas for the Years 1981 and 1982. Values Are Means (SD)

<table>
<thead>
<tr>
<th>Age</th>
<th>N</th>
<th>Weight (g)</th>
<th>Tarsus (mm)</th>
<th>Primary (mm)</th>
<th>N</th>
<th>Weight (g)</th>
<th>Tarsus (mm)</th>
<th>Primary (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day</td>
<td>1</td>
<td>20</td>
<td>3.7 (0.52)</td>
<td>6.65 (0.32)</td>
<td>6</td>
<td>3.4 (0.62)</td>
<td>6.43 (0.40)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>19</td>
<td>5.7 (0.72)</td>
<td>7.76 (0.40)</td>
<td>6</td>
<td>5.3 (1.04)</td>
<td>7.49 (0.56)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>14</td>
<td>8.2 (1.03)</td>
<td>8.96 (0.57)</td>
<td>8</td>
<td>8.0 (1.16)</td>
<td>8.80 (0.90)</td>
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<td></td>
<td>4</td>
<td>15</td>
<td>11.3 (1.38)</td>
<td>10.31 (0.87)</td>
<td>7</td>
<td>10.6 (1.65)</td>
<td>10.01 (0.81)</td>
<td>0.73 (0.49)</td>
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<td></td>
<td>5</td>
<td>11</td>
<td>14.8 (1.72)</td>
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<td>2.05 (0.86)</td>
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<td></td>
<td>6</td>
<td>10</td>
<td>19.1 (1.48)</td>
<td>13.68 (0.47)</td>
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<td>18.1 (1.13)</td>
<td>12.80 (0.38)</td>
<td>3.98 (0.68)</td>
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<td></td>
<td>7</td>
<td>8</td>
<td>22.4 (2.61)</td>
<td>14.79 (1.12)</td>
<td>6</td>
<td>20.9 (2.70)</td>
<td>14.00 (1.18)</td>
<td>7.17 (1.14)</td>
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<td></td>
<td>8</td>
<td>9</td>
<td>25.7 (1.62)</td>
<td>15.95 (0.64)</td>
<td>5</td>
<td>24.6 (0.98)</td>
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<td>30.1 (2.87)</td>
<td>17.13 (0.43)</td>
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<td>28.0 (1.33)</td>
<td>16.10 (0.83)</td>
<td>14.13 (0.74)</td>
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<td>31.5 (1.48)</td>
<td>17.54 (0.69)</td>
<td>5</td>
<td>30.3 (1.34)</td>
<td>16.94 (0.37)</td>
<td>19.06 (1.29)</td>
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<td>33.7 (1.57)</td>
<td>18.34 (0.52)</td>
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<td>32.4 (2.08)</td>
<td>17.62 (0.58)</td>
<td>22.96 (0.42)</td>
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<td>34.5 (1.75)</td>
<td>18.55 (0.49)</td>
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<td>33.2 (1.80)</td>
<td>17.84 (0.68)</td>
<td>27.98 (0.74)</td>
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<td>34.8 (1.43)</td>
<td>18.83 (0.63)</td>
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<td>33.9 (1.15)</td>
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<td>33.8 (1.63)</td>
<td>18.78 (0.58)</td>
<td>36.10 (1.92)</td>
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</tbody>
</table>
### TABLE 4

**Mean Daily Weight, Tarsus Length, and 9th Primary Length of Western Kingbirds and Scissor-tailed Flycatchers Breeding in Eastern Kansas. Values Are Means (SD)**

<table>
<thead>
<tr>
<th>Age</th>
<th>Western Kingbird</th>
<th>Scissor-tailed Flycatcher</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Weight (g)</td>
</tr>
<tr>
<td>Day 1</td>
<td>4</td>
<td>3.4 (0.67)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>5.1 (0.81)</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>6.9 (0.94)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>10.1 (2.48)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>12.9 (1.81)</td>
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<tr>
<td></td>
<td>4</td>
<td>18.0 (2.00)</td>
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<td></td>
<td>3</td>
<td>21.2 (3.04)</td>
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<tr>
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<td>23.5 (4.13)</td>
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<td>27.2 (3.87)</td>
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<td>4</td>
<td>31.1 (2.97)</td>
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<td></td>
<td>4</td>
<td>33.3 (1.71)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>33.9 (3.30)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>35.4 (2.18)</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>36.0 (2.27)</td>
</tr>
</tbody>
</table>
Table 5
GROWTH RATES FOR BODY WEIGHT, TARSUS LENGTH, AND 9TH PRIMARY LENGTH FOR
EASTERN KINGBIRDS (EKB), WESTERN KINGBIRDS (WKB), AND SCISSOR-TAILED
FLYCATCHERS (STF) BREEDING IN EASTERN KANSAS

<table>
<thead>
<tr>
<th>Species</th>
<th>Weight (mean [SD])</th>
<th>Tarsus (mm/day)</th>
<th>Primary (mm/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>K</td>
<td>g/d^b</td>
<td>Mean (SD)^b</td>
</tr>
<tr>
<td>EKB 80 (N = 16)^c</td>
<td>0.441 (0.045)</td>
<td>2.63 (0.354)</td>
<td>1.20 (0.044)</td>
</tr>
<tr>
<td>EKB 81 (N = 10)</td>
<td>0.466 (0.032)</td>
<td>3.34 (0.187)</td>
<td>1.24 (0.057)</td>
</tr>
<tr>
<td>EKB 82 (N = 5)</td>
<td>0.448 (0.033)</td>
<td>3.05 (0.098)</td>
<td>1.20 (0.046)</td>
</tr>
<tr>
<td>WKB (N = 4)</td>
<td>0.416 (0.029)</td>
<td>3.18 (0.302)</td>
<td>1.26 (0.112)</td>
</tr>
<tr>
<td>STF (N = 4)</td>
<td>0.394 (0.019)</td>
<td>2.92 (0.381)</td>
<td>1.20 (0.067)</td>
</tr>
</tbody>
</table>

^c 80, 81, and 82 refer to growth rates from 1980, 1981 and 1982.
^b Growth rate is the regression coefficient calculated from the least squares regression of weight, tarsus and primary length versus age for days 3-11.
^c N = sample size, which refers to the number of broods from which data were collected.

rates of increase, asymptotic weights differed widely according to year (ANOVA, $F = 18.8$, df = 2, 28, $P < 0.001$), averaging only 31.5 g in 1980 (SD = 2.24, N = 16 broods) compared to 36.2 g (SD = 1.15, N = 10 broods) and 34.9 g (SD = 1.28, N = 5 broods) in 1981 and 1982, respectively. Differences in the latter two years were not significant (SS-STP, $P > 0.05$). Nestlings starved in 5 of 17 nests in which initial and final brood size were known in 1980, versus 3 of 17 nests in 1981 and 1982 (G-test, $G = 0.16$, df = 1, $P > 0.05$). Yearly conditions had no influence on EKB tarsus or primary growth (Table 5; ANOVAs: tarsus, $F = 2.37$, 9th primary, $F = 2.14$; df = 2, 28, $P > 0.10$ for both).

Because weight-specific rates of growth in EKBs were insensitive to wide changes in food abundance, I directly compared species for weight-specific growth rates (Table 5). Differences were significant (ANOVA: $F = 4.71$, df = 2, 36, $P < 0.025$). STFs and WKBs grew at similar rates, as did WKBs and EKBs (SS-STP, both $P > 0.05$), but STFs grew significantly slower than EKBs (SS-STP, $P < 0.05$). Because asymptotic weight varied with year in EKBs, and because sample sizes were small for WKBs and STFs, I did not compare species for differences in the absolute rate of weight gain or asymptotic weight. However, asymptotic weights in the latter two species were similar to EKBs (WKB: 36.6 g, SD = 3.39, N = 4 broods; STF: 33.5 g, SD = 4.03, N = 4 broods).

Comparisons of the rate of tarsus growth (Table 5) indicated that tarsi grew at the same rate in all species (ANOVA, $F = 1.49$, df = 2, 36, $P > 0.05$). On the other hand, primary growth differed (Table 5; ANOVA, $F = 4.68$, df = 2, 36, $P < 0.025$). WKB and STF primaries grew at equal rates (SS-STP, $P > 0.05$), but the primaries of both species grew significantly faster than those of EKBs (SS-STP, $P < 0.025$).
Fig. 2. Variation in the rate of nestling weight gain with respect to brood size in kingbirds. Eastern Kingbird values are indicated by the solid dots. Average growth rate of Eastern Kingbirds ±2 SE are indicated at each brood size by the horizontal line and open box, respectively. The regression equation describing the relationship between growth rate (K) and brood size (BS) for EKBs (K = 0.503 - 0.0155BS, r = -0.398, N = 31 broods, P = 0.033) is plotted. Observations of growth rate in individual broods of Western Kingbirds (stars) and Scissor-tailed Flycatchers (enclosed open stars) are also plotted.

Mean clutch size and mean growth rate varied inversely in these species (see Tables 2 and 5). Among EKBs brood size and growth rate also varied inversely (Fig. 2; r = -0.398, N = 31 broods, P = 0.033), especially in the drought year (r = -0.608, N = 16 broods, P = 0.014). The relationship was not significant in 1981 and 1982 (r = -0.256, N = 15 broods, P > 0.10). Three of the four WKB growth rates fell within the range of variation for EKBs at the same brood sizes (Fig. 2). Indeed, 2 of 4 points were within ±2 standard errors (SE) of the appropriate EKB mean. When matched for brood size with EKBs, 3 of 4 STFs broods tended towards slow growth (Fig. 2). The only point to fall within ±2 SE of the appropriate EKB mean was the brood of five young (Fig. 2). Thus, the slower growth of STFs did not appear to be the result of the proximate “stress” of raising more young.
DISCUSSION

Body size.—Sexual differences in body size are similar in all species: bill and tarsus lengths did not vary with sex, but wing chord and keel lengths were 3–9% larger in males than females. Body weight did not vary with sex, but this was probably a result of the high variances in weight associated with variable fat stores and growth of female reproductive tissues (e.g., Ricklefs and Hussell 1984). The absolute and relative fat content of female EKBs exceeds that of males throughout the breeding season (Murphy 1986a), but lean dry muscle weight is substantially greater in males (Murphy 1985b). Therefore, overall structural “size” is greater in male than female EKBs and probably other kingbird species as well.

Neither weight nor bill length seem useful for detecting interspecific size differences. Weights are highly variable, and bill size is likely influenced by slight differences in feeding ecology and prey characteristics. Comparisons of wing chord and tarsus and keel (nonsignificant difference) lengths suggest WKBs are the largest species. EKBs and STFs appeared to be about the same size, except that wing chords were larger in male STFs. However, I doubt that wing chord is a good estimator of body size in these species since ecological factors have probably favored different wing shapes (Leisler and Winkler 1985). I suspect that a variable such as lean dry mass must be measured to test definitively for size differences, but at present, I have little evidence of interspecific variation in size.

Timing of breeding and clutch size.—Timing of breeding was the only reproductive trait which did not differ among species (see also MacKenzie and Sealy 1981). Data presented elsewhere (Murphy 1986a, b) suggest that initiation of breeding is energy-limited in EKBs, and given the similar breeding schedules for all species, it seems likely that timing of breeding is energy-limited in the other two species as well.

Clutch size differences appear to be genetically fixed and species-specific. On average, EKBs laid about 1.3 (39%) and 1.0 (29%) fewer eggs than STFs and WKBs, respectively (Fig. 1). The WKB average includes the significantly larger 1981 clutches. Excluding 1981, average EKB clutch size was 0.7 (20.8%) eggs below that of WKBs. The latter WKB average (4.1 eggs) is similar to the value reported for WKBs in Arizona by Blancher and Robertson (1987; 3.9 eggs, SD = 0.77, N = 73; t = 0.73, df = 85, P > 0.50) and is probably a more accurate measure of normal WKB clutch size. Fitch (1950) reported significantly smaller clutch sizes for STFs in Texas (3.9 eggs, SD = 0.81, N = 16; t = 3.46, df = 30, P < 0.01). The larger clutch sizes of WKBs (nonsignificant difference) and STFs in Kansas compared to Arizona and Texas, respectively, are consistent with known latitudinal and longitudinal gradients in clutch size variation in birds.
Murphy • REPRODUCTIVE BIOLOGY OF KINGBIRDS

(Ricklefs 1980, Crowell and Rothstein 1981). Such trends might “explain” the difference in WKB clutch sizes between Kansas and Arizona, but the difference between Kansas and Texas for STFs seems unusually large. Independent estimates of clutch size for STFs from museum egg sets (mean = 4.6 eggs, SD = 0.65, N = 220 clutches) suggest that Fitch’s (1950) estimate of clutch size is low.

Seasonal declines in clutch size occur in all three species (Table 2), and after controlling for effects of date, differences in clutch size persisted. The rate of decline in STFs (0.021 eggs/day) was similar to that of EKBs (0.027 eggs/day) and fell within the EKBs range of annual variation (Murphy 1986a). The rate for WKBs was greater (0.066 eggs/day), but did not differ statistically from either of the other species. The large WKB value probably resulted from sampling error due to small sample size as Blancher and Robertson (1987) reported a seasonal rate of decline in WKBs (0.018 eggs/day) that was much lower and closer to values for EKBs and STFs.

EKBs and WKBs appeared to respond positively to increased food abundance in 1981 by laying larger clutches. Most of the EKB response was due to earlier breeding, but after controlling for date, 1981 EKB clutches were larger than those produced in the drought year (P < 0.05, Murphy 1986a). Likewise, date-corrected clutch sizes of WKBs were larger in 1981 compared to other years. Unlike its congeners, STFs failed to lay more eggs in 1981. I suspect this resulted from differences in kingbird habitat use and differential availability of cicadas in each kingbird species breeding habitat. Mature trees, on which cicadas oviposit, were much more common in EKB and WKB breeding sites than in the grass-dominated habitats of STFs. Cicadas were no doubt less available to STFs than to either EKBs or WKBs. The larger STF eggs in 1981 presumably resulted from the increased availability of normal insect prey.

Egg size.—Differences in egg size were nearly as dramatic as for clutch size. Fitch (1950) commented previously that STF eggs were smaller than EKB eggs. My data confirm his statement, yet also show that STF eggs are smaller than those of WKBs. EKBs and WKBs produced eggs of nearly identical size. The small eggs of STFs are not due to small adult body size (Table 1). Small STF egg size may result from limited energy for clutch formation and trade-offs in number and size of eggs (i.e., Smith and Fretwell 1974, Lloyd 1987). This reallocation argument gains support from comparisons of total clutch weight for WKBs and STFs. Despite differences in clutch and egg size, the two species allocate very similar amounts of energy to clutch formation. However, given that small clutch size in EKBs is not matched by a further increase in egg size (compared to WKBs), I am doubtful of the applicability of the reallocation hypothesis.
Possible alternative explanations for the egg size differences are provided by a macrogeographic examination of egg size variation in EKBs. The smallest EKB eggs are produced within the geographic range of the STF, and from there egg size increases clinally with latitude (Murphy 1983a, 1985b). Small egg size in STFs may therefore reflect relaxation of selective pressures that are strong at high latitudes, and which EKBs experience regularly. One possibility is cold stress on eggs. Male kingbirds do not incubate, and large eggs at high latitudes may reduce the rate of heat loss from eggs when females are off foraging. Jarvinen and Vaisanen (1983) noted poor hatching success of small Pied Flycatcher (Ficedula hypoleuca) eggs at northern locations and suggested that selection for large eggs was strong at high latitudes. Alternatively, since the size of nestlings within the first week of hatching is primarily a function of the size of the egg from which they hatched (Murphy 1985a; Tables 2, 3 and 4), selection to minimize nestling heat loss may favor large eggs at high latitudes.

Nestling growth.—Pattern and rate of growth were similar in nestlings of the three species. Early size differences were determined by egg size, but as has been demonstrated for EKBs (Murphy 1985a), the influence of egg size waned as nestlings aged. Yearly variation in the growth of EKB tarsi and primaries was nonexistent despite variation in annual egg size and feeding conditions. Likewise, weight-specific rates of EKB growth did not vary with year, but did vary with brood size (Fig. 2), especially in the drought year. Asymptotic weights were also lowest in that year.

The similarity of EKB growth rates among years (Table 5), despite variable food regimes and small sample size in 1982, agrees with data for other species (Ricklefs and Peters 1979, King and Hubbard 1981) and suggests that the growth rates recorded for WKBs and STFs are sufficient for interspecific comparisons. Indeed, the rate which I calculated for WKBs in Kansas ($K = 0.416$) was very similar to the value reported by Blancher and Robertson (1984) from Arizona ($K = 0.414$). My interspecific comparisons indicated that EKBs grew significantly faster than STFs. Growth rates of only 1 of 4 STF broods fell within ± 2 SE of the mean growth rate of EKBs at the same brood sizes (Fig. 2), suggesting that nestling STF growth is intrinsically slower than that of EKBs.

Interspecific differences in clutch size.—The failure of timing of breeding to account for interspecific variation in clutch size leaves open the question of why clutch size differs among such equal-sized and ecologically similar species. Interestingly, the interspecific differences are opposite of what is considered the “usual” pattern for birds (Ricklefs 1980, Crowell and Rothstein 1981). The species with the northernmost distribution, the EKB, lays the fewest eggs whereas the southernmost breeding species, the STF, produces the largest number. A possible explanation is that inter-
specific clutch size differences reflect adaptation to climatic variability over North America. Northern and eastern portions of the continent experience cooler temperatures and more precipitation during summer than southern and western regions of North America (Climatic Atlas of North and Central America 1979), and evidence indicates that such weather impedes kingbird foraging success (Blancher and Robertson 1987, Murphy 1987). Previous experimental brood size manipulations have also shown that unlike broods of 3, broods of 5 young grow poorly and experience heavy starvation during extended periods of cool, wet weather (Murphy 1983c). Hence, attempts to raise large broods within most of the EKB’s geographic range possibly entails great risk to the survival of the parent’s entire seasonal reproductive effort. Threats of this magnitude are theorized to favor the production of smaller clutches which can be raised with greater certainty (G. Murphy 1968, Stearns 1976, Boyce and Perrins 1987).

If greater exposure to environmental uncertainty has selected for smaller clutch size in EKBs compared to its congeners, then EKB clutch size should vary geographically in a manner that mimics the interspecific differences, i.e., large clutches should be produced where EKBs breed with WKBs and especially STFs. Indeed, based on museum egg sets, EKB clutches are significantly smaller in eastern North America than in western and middle portions of the continent where they breed with WKBs and STFs (Murphy 1985b). However, EKB clutch sizes are still significantly smaller than clutch sizes of sympatric populations of congeners (Murphy 1985b, this study). Furthermore, although EKB clutch size varies little with latitude, the largest EKB clutches are produced at northern sites (Manitoba and Saskatchewan), which does not conform to predictions of the environmental uncertainty hypothesis.

Why intraspecific geographic patterns of clutch size variation are of lesser magnitude than interspecific patterns is unknown. Conceivably, adaptation of EKB clutch size to local conditions may be prevented by frequent dispersal and gene flow among geographically separated populations (Slatkin 1987). However, this seems unlikely given that EKB egg size shows strong geographic differentiation that is unrelated to food availability or body size (Murphy 1983a, 1985b). I also doubt that a lack of genetic variability is a problem because all species have been recorded to lay between 3 and 6 eggs (Fitch 1950; Davis 1955; Murphy 1983a, 1985b, 1986a; Blancher and Robertson 1985a, b, 1987). Presumably, at least some of this reflects underlying genetic variability (e.g., Noordwijk et al. 1981).

Clearly, further study is needed to answer the question of why clutch size differs among these species. Of particular need are estimates of age-
specific survival (Stearns 1976) and measures of dispersal and population genetic structure for all three species. The latter will permit inferences on the extent of recent past gene flow (Slatkin 1987). Parental time-budgets (see Hussell 1985) and food availability must also be measured among geographically separated populations of all three species. Finally, additional brood size manipulation experiments must be performed to assess the importance of stochastic variability in food supplies to the evolution of clutch size in the genus *Tyrannus*.

**ACKNOWLEDGMENTS**

Collection of the data contained in this paper would have been impossible without financial assistance provided by the Alexander E. Bergstrom Research Award of the Northeastern Bird-Banding Association, the Frank M. Chapman Fund of the American Museum of Natural History, and a Summer Fellowship from the University of Kansas Graduate School. Drs. P. Blancher and S. Rothstein provided critical and very helpful comments that improved my interpretations.

**LITERATURE CITED**


---. 1985b. Ecological and evolutionary aspects of the reproductive biology of Eastern


SPATIAL PATTERNS, FORAGING TACTICS, AND DIETS OF GROUND-FORAGING BIRDS IN A NORTHERN HARDWOODS FOREST

RICHARD T. HOLMES AND SCOTT K. ROBINSON

Abstract. — Seven species of ground-foraging birds bred syntopically in a northern hardwoods forest in New Hampshire. Spatial overlap was extensive, although some species were patchily distributed, apparently in response to local variations in habitat characteristics. Three groups of species were distinguished on the basis of their food-searching/foraging tactics: (1) those that hopped or walked slowly on the ground while searching and gleaning prey from the surface of the litter and nearby foliage (Ovenbird, Seiurus aurocapillus; Dark-eyed Junco, Junco hyemalis), (2) those that pried into substrates and searched methodically for hidden or buried prey (Wood Thrush, Hylocichla mustelina; Winter Wren, Troglodytes troglodytes), and (3) those that searched near and far substrates (up to 3 m) both on the ground and in the sapling, subcanopy, and, occasionally, canopy layers (Veery, Catharus fuscens; Hermit Thrush, C. guttatus; Swainson’s Thrush, C. ustulatus). Species within each of these three searching modes differed in macrohabitat occupied, microhabitat used, in relative use of prey-attacking methods, and/or in diet. Each species appears to use a unique combination of habitat characteristics (e.g., vegetation density on vertical and horizontal axes, food resources). Thus, bird foraging tactics and morphology combined with habitat structure constrain which species will be present in a given location and hence influence bird community patterns. Received 15 Sept. 1987, accepted 25 Feb. 1988.

Ecological relations of ground-foraging birds have been examined by Dilger (1956a, b), Morse (1971, 1972), Bertin (1977), Noon (1981), James et al. (1984), and others. Most of these studies have emphasized the importance of spatial segregation among guild members (James et al. 1984), morphological adaptations (Dilger 1956b), or the possibility that interspecific territoriality may play a key role in determining habitat use (Morse 1971, Noon 1981). Such analyses have largely been conducted at what Paszkowski (1984) called the “macrohabitat” level. Few attempts have been made, however, to understand the ways in which these species actually utilize their habitats, especially in terms of how and where syntopic species obtain food and what types of food are taken. An exception is the study by Paszkowski (1984) which showed that two thrush species in Wisconsin were generally similar in their macrohabitat use but differed in how they searched for food among height strata and vegetation types.

In this paper, we examine the spatial overlap, foraging behavior, and diets of seven species of ground-foraging birds that co-occur in a northern

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hardwoods forest in New Hampshire. These include four turdine thrushes (Wood Thrush, *Hylocichla mustelina*; Swainson’s Thrush, *Catharus ustulatus*; Hermit Thrush, *C. guttatus*; Veery, *C. fuscara*); a wren (Winter Wren, *Troglodytes troglodytes*), a paruline warbler (Ovenbird, *Seiurus aurocapillus*), and a fringillid (Dark-eyed Junco, *Junco hyemalis*). All seven forage for insects and other invertebrates mostly in forest litter and lower shrub levels. In multivariate analyses, these species cluster together into a ground-foraging guild based on foraging maneuver and substrate use (Holmes et al. 1979). In this paper, we address the degree to which these species actually co-occur within the study area, how they search for and capture prey, what food items are actually taken, and discuss what factors determine the ecological relations among these species in this forest.

**STUDY AREA AND METHODS**

This study was conducted between 1974 and 1978 on the 10-ha study plot in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, USA, described by Holmes and Sturges (1975) and Holmes et al. (1986). The study plot was located in unfragmented, second growth northern hardwoods dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). The forest floor was covered with a thick layer of dead leaves and other forest litter. The shrub layer (0.2-2 m) consisted of the seedlings and small saplings of beech and sugar maple, hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), mountain maple (*A. spicatum*), one common fern (*Dryopteris spinulosa*), and a variety of low-growing forbs. The sapling layer (2-8 m) contained the saplings of the dominant trees and some striped and mountain maple. The subcanopy (8-14 m) was relatively open compared to the denser overlying canopy (>14 m). Further descriptions of the forest are given by Siccama et al. (1970), Bormann and Likens (1979), and Holmes et al. (1986).

The vegetation of the study area appeared fairly homogeneous, although local variations occurred. The density of vegetation in the shrub and herbaceous layers varied with the topography and was influenced by the occurrence, frequency, and age of gaps created by fallen trees. Understory vegetation was particularly dense in the gaps and along a stream that crossed the plot near the north end. The southern half of the study plot was better drained, drier, and had a less dense shrub layer and a more open forest floor.

Birds were censused and their distributions mapped on the 10-ha plot between late May—early July in each year, 1974-1978. Censuses involved modified spot-mapping, systematic mist-netting, and observations of color-marked birds (Holmes and Sturges 1975, Holmes et al. 1986). The locations of all observed individuals, including chases, fights, and countersinging events, and of nests when found, were plotted on a gridded map of the study area and activity (=“territorial”) boundaries drawn. The distribution of each species on the study plot was then summarized by superimposing its territory maps for all five years and scoring the number of years that territories of that species covered at least 50% of each of the 40, 0.25-ha (50 × 50 m) quadrats which comprised the study plot (see Fig. 1).

Bird foraging behavior was quantified during June and early July, 1974-1978, using the protocol and techniques described by Holmes et al. (1979) and Robinson and Holmes (1982, 1984). Each time a bird was observed to attack a prey item, we recorded the substrate to which the maneuver was directed (litter, foliage of herbs, ferns, and trees, including seedlings
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Fig. 1. Spacing patterns of the seven bird species in the ground-foraging guild on the 10-ha study plot at Hubbard Brook, 1974-1978. Pattern (see key) in each of 40, 50 × 50 m, quadrants represents the number of years (0-5) that 50% or more of territories of each species overlapped that square (see text).

and saplings, bark, air), the type of attack methods used, and the height above ground. Prey-attacking maneuvers used by foraging birds were categorized as follows: glean, in which a walking or perched bird picked prey from the surface of a plant or the ground; probe, in which a bird's beak moved, disturbed, or entered the substrate (e.g., leaf litter, loose bark)
to obtain prey; hover, in which a flying bird snatched or grabbed prey from the surface of a substrate, sometimes after a slight pause or hover; jump-hover, in which a bird jumped from the ground and plucked prey, usually from the undersurface of a leaf; dive-glean, in which a bird perched above the ground on a low branch, log or rock, flew downwards, usually landing, and then grabbed (=gleaned) prey from the surface of the litter (equivalent to the ground-pounce of Holmes and Recher 1986), and hawk, in which a flying bird chased and captured air-borne insects.

Once a bird was observed foraging, we followed it for as long as possible. This was desirable for two reasons. First, ground-foraging birds were very difficult to observe in the dense shrub layer of this forest, so that once a foraging bird was located, it was opportune to observe it for as long as possible. Second, we felt long sequences might reveal more about the foraging behavior of these species than the initial observation which would likely involve a more conspicuous act and lead to biases in the results. In the analyses, we provide data in two ways: (1) those based on the first maneuvers of each sequence, and (2) those from the cumulative number of foraging maneuvers from all sequences. All statistical comparisons (χ² tests on frequency data), however, are based on the data from first observations only, following the rationale of Morrison (1984). Four to 18 individuals of each species were observed each season, the number varying with the species' abundance on the study area (see Holmes et al. 1986); no individual bird was observed more than once per day, and usually less than once per week. For all species, our data include observations from the entire breeding season over three years, which should reduce any effect of short-term fluctuations in resource availability on our sample.

We also gathered information on the patterns of hopping and flying employed by each species in their search for food. These were often difficult observations to obtain because of the dense shrub layer in the study area and the shyness of these ground-foraging species. Thus, most of such observations are qualitative. However, for the three *Catharus* thrushes, we were able to quantify, with reasonably large sample sizes, the frequencies at which they hopped and flew between perches while foraging and the distances flown between perches. By combining all of the sequences for each species, we calculated their overall hop and flight rates, following the procedures of Moermond (1979), Eckhardt (1979), and Robinson and Holmes (1984). For these species, we also estimated the distances and angles flown on flights terminating in hovering prey-catching maneuvers, as an index to the radius over which they searched for and captured prey (Robinson and Holmes 1982).

To determine diets, we caught birds in mist nets in areas with comparable vegetation structure 1–2 km away from the main study plot, and gave them an emetic, potassium antimony tartrate (1% solution, given 0.1 cm³ per 10 g body weight) following the techniques of Prys-Jones et al. (1974). Details of the method and our procedures in this operation are described in Robinson and Holmes (1982) as are several caveats concerning interpretations of such data.

RESULTS

Densities and dispersion patterns.—Ovenbirds, Wood Thrushes, and Swainson Thrushes, the most common ground-foraging species at Hubbard Brook (Holmes et al. 1986), were relatively evenly dispersed over the entire 10-ha study area, although the latter two species showed some concentration towards the north (Fig. 1). In contrast, Veeries were localized each year in the northern end of the plot (Fig. 1), primarily along the stream, while Hermit Thrushes occupied the southern half away from
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the stream where understory vegetation was less dense. Winter Wrens
and Dark-eyed Juncos were patchily distributed, with two or three regions
of the plot being used more frequently than the intervening areas (see
Fig. 1).

Males of all species sang frequently and actively chased intruders in
their defense of territory. All such interactions observed were with con-
specifics; no interspecific aggression was recorded in any year of the study
for any species. Despite the strong intraspecific responses, however, the
thrushes, especially the Wood Thrush, often trespassed on neighboring
conspecific territories. For example, on several occasions, individually
color-marked male Wood Thrushes were observed and caught in nets in
mid-breeding season up to 300 m from their home area and nesting site,
across one to several conspecific territories. Some of these individuals
were probably returning from long territorial conflicts which took them
far from their own territories; in other cases, the birds appeared to be
feeding and gave no vocalizations. From these few observations, it seems
that activity ranges of these thrushes may overlap intraspecifically, and
territories may not be very exclusive. Each thrush pair, however, did
concentrate its activity within a core area in which the nest was located,
and these activity centers were clearly evident from our composite field
maps. In contrast to the thrushes, individual Ovenbirds, Dark-eyed Jun¬
cos, and Winter Wrens were consistently present in the same areas through
each season and were frequently seen or caught near the sites where they
were originally netted or observed.

Use of vertical strata for foraging.—Although all seven species have
been classified as “ground”-foragers (Holmes et al. 1979), not all foraged
extensively on the ground (Table 1). There were statistically significant
differences between the frequency distributions of foraging heights for
each species when first and all observations were compared ($P < 0.001$
for each intraspecific comparison, Table 1). Since foraging heights in a
sequence are clearly correlated (Morrison 1984), we use only the data
from the first observations for our interpretations below.

Based on these first observations, all pairwise comparisons of foraging
heights among the seven species were significantly different ($P < 0.001,$
except for the Wood Thrush and Ovenbird comparison where $P < 0.05$).
The forest floor was used most frequently for foraging by all species except
the Winter Wren, which foraged more in the shrub layer (Table 1). Wood
Thrushes, Veeries, Ovenbirds, and juncos directed $\geq 65\%$ of their foraging
attacks toward prey in the ground layer, while Hermit Thrushes, Swain-
son’s Thrushes, and Winter Wrens foraged on the ground $< 50\%$ of the
time (Table 1). The shrub layer was the second most used stratum for all
species but the Winter Wren, for which it was the most frequently used
### Table 1

Vertically Distribution of Foraging by Birds in the Ground-foraging Guild at Hubbard Brook, Based on the First (1st) and All (All) Prey Attacks in Observed Sequences

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>1st (all)</th>
<th>1st (all)</th>
<th>1st (all)</th>
<th>1st (all)</th>
<th>1st (all)</th>
<th>1st (all)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Ground (0-0.2 m)</td>
<td>Shrub (0.3-2 m)</td>
<td>Sapling (2.1-8 m)</td>
<td>Subcanopy (8.1-14 m)</td>
<td>Canopy (&gt;14 m)</td>
<td></td>
</tr>
<tr>
<td>Winter Wren</td>
<td>52 (407)</td>
<td>37.7 (33.4)</td>
<td>54.7 (57.1)</td>
<td>7.6 (9.5)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>54 (204)</td>
<td>87.0 (92.2)</td>
<td>11.1 (6.8)</td>
<td>1.9 (1.0)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Hermit Thrush</td>
<td>41 (197)</td>
<td>46.4 (55.9)</td>
<td>26.8 (22.8)</td>
<td>17.1 (9.6)</td>
<td>7.3 (11.2)</td>
<td>2.4 (0.5)</td>
<td></td>
</tr>
<tr>
<td>Swainson's Thrush</td>
<td>123 (394)</td>
<td>46.3 (58.8)</td>
<td>20.3 (21.8)</td>
<td>13.0 (8.2)</td>
<td>10.6 (5.6)</td>
<td>9.8 (5.6)</td>
<td></td>
</tr>
<tr>
<td>Veery</td>
<td>27 (127)</td>
<td>70.4 (74.0)</td>
<td>22.2 (24.4)</td>
<td>3.7 (0.8)</td>
<td>3.7 (0.8)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Ovenbird</td>
<td>78 (482)</td>
<td>82.7 (88.4)</td>
<td>12.0 (10.0)</td>
<td>4.0 (1.4)</td>
<td>1.3 (0.2)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Dark-eyed Junco</td>
<td>102 (591)</td>
<td>64.7 (63.8)</td>
<td>19.6 (20.4)</td>
<td>11.8 (12.5)</td>
<td>3.9 (3.1)</td>
<td>0.0 (0.2)</td>
<td></td>
</tr>
</tbody>
</table>
stratum. Juncos and Swainson’s and Hermit thrushes foraged for prey in the sapling layer (2.1–8 m) more often than did the other species. Hermit and Swainson’s thrushes foraged higher than the other species in this group, especially the latter for which 10% of its prey attacks were in the forest canopy (Table 1).

Use of substrates for foraging. — All seven species took prey primarily from forest litter, foliage, and bark (Table 2). They differed significantly from each other, however, in their use of foraging substrates ($P < 0.01$ for each pairwise comparison among the seven species). The frequency distributions of substrate use differed significantly when first observations and all observations were compared ($P < 0.001$ for comparisons within each species). These differences were due mostly to more foliage- and less litter-use in the first-observation data than in the cumulative observations (Table 2). Since the act of attacking a prey on foliage, which usually involves flight, is probably more conspicuous, it would seem more likely to catch the observer’s eye, and hence bias the results. For the same reason, the extent of ground, air and herb-fern foraging was underestimated by use of first observations only. Because of these findings, we base the following descriptions of substrate use on the cumulative data from all sequences.

All species, except the junco and wren, direct >50% of their foraging attacks toward prey on or in the forest litter (Table 2). The apparent discrepancy between the data for the ground layer in Table 1 and the ground-litter substrates in Table 2 reflects the fact that some foraging in the ground layer was on herbs, ferns, and low seedling foliage. The Wood Thrush foraged most often in the forest litter and Winter Wren the least often. Veery, Swainson’s Thrush, and Hermit Thrush attacked prey frequently on tree foliage and to a lesser extent on tree bark (Table 2). Swainson’s and Hermit thrushes, Winter Wrens, and juncos attacked flying prey at low but measurable frequencies (Table 2). For the Winter Wren, 50.1% of all maneuvers were directed towards prey on bark (Table 2); of these, 50% were directed toward the bark on tree trunks and exposed roots, mostly near the bases of trees, 41% toward fallen dead wood, usually logs and branches lying on the ground, and the remaining 9% toward prey on the bark of twigs or branches near the ground.

Prey-attacking behavior. — The most frequently used prey-attacking maneuvers were probes, gleans, and hovers (Table 3). Based on first maneuvers only, the species differed significantly in their use of prey-attack maneuvers ($P < 0.001$ for all pairwise comparisons, except for Ovenbird and Winter Wren which differed at $P < .05$). The frequencies of foraging maneuver use also differed significantly between the first observation data and those from all observations within each species ($P < 0.001$ for each
<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>1st (all)</th>
<th>Ground/litter</th>
<th>Herb/fern</th>
<th>Foliage</th>
<th>Bark</th>
<th>Air</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter Wren</td>
<td>55</td>
<td>14.5 (18.2)</td>
<td>9.1 (6.4)</td>
<td>25.4 (21.2)</td>
<td>49.2 (50.1)*</td>
<td>1.8 (4.1)</td>
<td></td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>53</td>
<td>64.1 (85.6)</td>
<td>0.0 (2.0)</td>
<td>22.6 (8.9)</td>
<td>22.5 (25.7)</td>
<td>11.4 (2.5)</td>
<td>1.9 (1.0)</td>
</tr>
<tr>
<td>Hermit Thrush</td>
<td>40</td>
<td>30.0 (50.6)</td>
<td>2.5 (7.4)</td>
<td>27.5 (26.7)</td>
<td>27.5 (7.4)</td>
<td>12.5 (7.9)</td>
<td></td>
</tr>
<tr>
<td>Swainson's Thrush</td>
<td>112</td>
<td>41.1 (51.9)</td>
<td>0.8 (2.1)</td>
<td>37.5 (33.2)</td>
<td>17.0 (8.7)</td>
<td>3.6 (4.1)</td>
<td></td>
</tr>
<tr>
<td>Veery</td>
<td>25</td>
<td>36.0 (56.0)</td>
<td>4.0 (3.3)</td>
<td>44.0 (35.8)</td>
<td>16.0 (4.1)</td>
<td>0.0 (0.8)</td>
<td></td>
</tr>
<tr>
<td>Ovenbird</td>
<td>74</td>
<td>52.1 (65.6)</td>
<td>0.0 (0.0)</td>
<td>42.3 (29.4)</td>
<td>4.2 (3.3)</td>
<td>1.4 (1.7)</td>
<td></td>
</tr>
<tr>
<td>Dark-eyed Junco</td>
<td>96</td>
<td>39.6 (37.4)</td>
<td>14.6 (18.7)</td>
<td>37.5 (34.6)</td>
<td>7.3 (4.6)</td>
<td>1.0 (4.7)</td>
<td></td>
</tr>
</tbody>
</table>

* See text for further breakdown.
<table>
<thead>
<tr>
<th>Species</th>
<th>N (all)</th>
<th>N (1st)</th>
<th>Percent of prey attacks by maneuver type</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Probe (1st)</td>
</tr>
<tr>
<td>Winter Wren</td>
<td>52 (397)</td>
<td>28.9</td>
<td>50.0 (61.3)</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>51 (193)</td>
<td>56.8</td>
<td>21.6 (18.5)</td>
</tr>
<tr>
<td>Hermit Thrush</td>
<td>42 (232)</td>
<td>11.9</td>
<td>40.5 (43.9)</td>
</tr>
<tr>
<td>Swainson's Thrush</td>
<td>117 (377)</td>
<td>14.5</td>
<td>29.1 (25.1)</td>
</tr>
<tr>
<td>Veery</td>
<td>25 (136)</td>
<td>8.0</td>
<td>52.0 (40.6)</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>74 (456)</td>
<td>16.9</td>
<td>60.6 (62.3)</td>
</tr>
<tr>
<td>Dark-eyed Junco</td>
<td>99 (566)</td>
<td>7.1</td>
<td>59.6 (62.7)</td>
</tr>
</tbody>
</table>
intraspecific comparison). This was most likely related to the conspicuousness of the behaviors, since the maneuver which is accompanied by the most movement (hover) was recorded more frequently in the first observation data set for all species, while there was no consistent pattern for gleans and probes (Table 3). Hermit Thrushes were often first seen while hawking insects (Table 3). And, finally, the rarer prey-attacking maneuvers, such as jump-hover and dive-glean, were recorded more frequently in the full sequence data (Table 3). These findings indicate that data from the longer sequences provide more information concerning the range of foraging maneuvers used by these often secretive species. As a consequence, we base the following analysis of prey-attack behavior on the cumulative data.

Of these seven species at Hubbard Brook, the Wood Thrush was the only species to use the probing maneuver more than 50% of the time. It probed mostly among dead leaves on the ground surface, but occasionally dug deeper into the leaf litter; it also gleaned prey from the ground surface. Both the Ovenbird and Dark-eyed Junco frequently gleaned prey or, especially in the case of juncos, jumped to pluck prey from the undersurfaces of leaves they could not reach from the ground. Winter Wrens were primarily gleaners on all substrates, but also extensively probed bark on fallen dead wood and less commonly in the litter (see Table 2). They also hopped into knotholes and the cracks between exposed roots of upturned trees when searching for food.

The *Catharus* thrushes used more aerially-active foraging maneuvers, e.g., hovers, dive-gleans, and even hawking actions, and rarely probed, relative to other species (Table 3). Swainson’s Thrushes were often seen to perch on low twigs and branches and to search the litter below it, while Veeries sometimes perched on rocks or logs, especially near streams, and searched the banks and foliage on either side. When prey were spotted from these sites, both Swainson’s Thrushes and Veeries would dive to the ground and snatch the prey (i.e., dive-glean, Table 3). Lengths of hover flights averaged 1.1 ± 0.7 SD m (N = 58) for the Swainson’s Thrush and 0.8 ± 0.7 SD m (N = 13) for the Veery, which suggest (cf. Robinson and Holmes 1982) that they both visually searched substrates up to a meter away.

Search rates and locomotor patterns while foraging.—From qualitative observations, Ovenbirds, Dark-eyed Juncos, and Wood Thrushes, once in a foraging area, searched for prey primarily by hopping or walking along the ground; they rarely flew between perches used for searching. Ovenbirds walked more or less continuously, pausing only to glean prey, often with quick pecking motions, from the surface of the litter. Dark-eyed Juncos behaved similarly, except that they hopped rather than walked.
and seemed more deliberate in their gleaning actions. Winter Wrens methodically searched low substrates by hopping slowly, apparently examining crevices and other places for hidden prey. Wood Thrushes typically hopped several times in succession, then paused to visually search nearby substrates or to dig in the litter. In this respect, they foraged much like *Turdus* thrushes (Smith 1974, Paszkowski 1982).

The *Catharus* thrushes, particularly Swainson's and Veery, differed from other species in their search behavior by flying more often. While searching for food, they typically flew from one perch to another, hopped several times along a branch or occasionally on the ground, and then flew on to another branch to continue searching. Foraging Swainson's Thrushes changed perches, on average, by flying 6.1 times/min and hopping 5.0 times/min (N = 898 sec), while Veeries flew 5.8 times/min and hopped 6.5 times/min. (N = 240 sec). Thus, these two species flew and hopped about equally and had similar searching patterns. In contrast, Hermit Thrushes hopped more then they flew (2.6 flights/min, 17.6 hops/min, N = 235 sec). The distances moved in flights between perches while searching for food were similar for Swainson's Thrushes and Veeries, averaging 1.7 ± 1.2 m (N = 60) and 1.6 ± 0.9 m (N = 20) respectively (Hermit Thrushes not included due to small sample size).

**Diet.**—Diet samples were collected from mid-June to mid-July, and contained only animal, mainly insect, remains (Table 4). Coleoptera, most of which were adults, were the most frequently found item in all samples, probably because their body parts, especially elytra, persisted longer in the stomachs than those of other types of prey (Robinson and Holmes 1982). Also, the same major Coleoptera families were represented in samples from most bird species: Carabidae, Cantharidae, Scarabeidae, Curculionidae, Cerambycidae, and Elateridae (Table 4), all of which occur on the forest floor and on vegetation. Hymenoptera were represented primarily by ants and wasps (families Ichneumonidae and Braconidae). Lepidoptera were mostly larvae in the families Geometridae and Noctuidae (Table 4) which dominate the leaf-dwelling caterpillar fauna at Hubbard Brook (Holmes and Schultz 1988). Most Diptera in the samples were adult crane flies (family Tipulidae).

Diets of the five species, for which we had a reasonably large number of emetic samples, differed significantly at the ordinal level (*P* < 0.001 for all pairwise comparisons except the Veery and Ovenbird for which *P* < 0.05; analyses were not performed at family level due to small sample sizes in some categories). Comparisons among species indicate that Hermit Thrushes took relatively more Coleoptera, while Swainson’s Thrushes had the highest proportion of Hymenoptera, mostly ants (Table 4). Hermit Thrushes and Ovenbirds took relatively large numbers of Lepidoptera.
### Table 4

Diets of Birds in the Ground-foraging Guild at Hubbard Brook, 1974–1976, Based on Emetic Samples. Values Represent Percent of Each Taxon in the Sample of Identifiable Prey Items

<table>
<thead>
<tr>
<th>Taxa</th>
<th>N (n)</th>
<th>Wood Thrush 329 (60)</th>
<th>Hermit Thrush 82 (18)</th>
<th>Swainson's Thrush 186 (34)</th>
<th>Veery 101 (18)</th>
<th>Ovenbird 119 (30)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lepidoptera</td>
<td></td>
<td>11.9</td>
<td>19.5</td>
<td>9.7</td>
<td>12.9</td>
<td>19.3</td>
</tr>
<tr>
<td>Larvae&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>11.6</td>
<td>19.5</td>
<td>9.1</td>
<td>12.9</td>
<td>19.3</td>
</tr>
<tr>
<td>Adults</td>
<td>0.3</td>
<td>-</td>
<td>0.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>2.4</td>
<td>1.2</td>
<td>0.5</td>
<td>4.0</td>
<td>3.4</td>
<td>6.7</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>17.3</td>
<td>12.2</td>
<td>32.8</td>
<td>12.9</td>
<td>15.1</td>
<td></td>
</tr>
<tr>
<td>Formicidae</td>
<td>14.0</td>
<td>9.8</td>
<td>27.4</td>
<td>8.9</td>
<td>8.4</td>
<td></td>
</tr>
<tr>
<td>Other&lt;sup&gt;c&lt;/sup&gt;</td>
<td>3.3</td>
<td>2.4</td>
<td>5.4</td>
<td>4.0</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Coleoptera</td>
<td>38.0</td>
<td>64.7</td>
<td>44.7</td>
<td>41.5</td>
<td>36.1</td>
<td></td>
</tr>
<tr>
<td>Larvae</td>
<td>4.6</td>
<td>12.2</td>
<td>4.3</td>
<td>-</td>
<td>-</td>
<td>4.2</td>
</tr>
<tr>
<td>Adults</td>
<td>33.4</td>
<td>52.5</td>
<td>40.4</td>
<td>41.5</td>
<td>31.9</td>
<td></td>
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<tr>
<td>Carabidae</td>
<td>7.0</td>
<td>13.5</td>
<td>5.4</td>
<td>3.0</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>Cantharida</td>
<td>1.8</td>
<td>7.3</td>
<td>2.7</td>
<td>14.8</td>
<td>3.4</td>
<td></td>
</tr>
<tr>
<td>Staphylinidae</td>
<td>0.9</td>
<td>-</td>
<td>-</td>
<td>1.0</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>scarabidae</td>
<td>1.5</td>
<td>2.4</td>
<td>2.2</td>
<td>6.9</td>
<td>4.2</td>
<td></td>
</tr>
<tr>
<td>Curculionidae</td>
<td>4.0</td>
<td>7.3</td>
<td>2.7</td>
<td>1.0</td>
<td>5.0</td>
<td></td>
</tr>
<tr>
<td>Cerambycidae</td>
<td>0.9</td>
<td>2.4</td>
<td>2.7</td>
<td>2.0</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Elateridae</td>
<td>5.2</td>
<td>8.5</td>
<td>17.7</td>
<td>9.8</td>
<td>5.9</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>12.1</td>
<td>11.1</td>
<td>7.0</td>
<td>3.0</td>
<td>10.1</td>
<td></td>
</tr>
<tr>
<td>Diptera</td>
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<td>2.4</td>
<td>9.1</td>
<td>18.8</td>
<td>20.2</td>
<td></td>
</tr>
<tr>
<td>Larvae</td>
<td>2.7</td>
<td>-</td>
<td>-</td>
<td>5.9</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>15.8</td>
<td>2.4</td>
<td>9.1</td>
<td>12.9</td>
<td>20.2</td>
<td></td>
</tr>
<tr>
<td>Tipulidae</td>
<td>4.0</td>
<td>2.4</td>
<td>4.8</td>
<td>9.9</td>
<td>5.0</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>11.8</td>
<td>-</td>
<td>4.3</td>
<td>3.0</td>
<td>15.2</td>
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</tr>
<tr>
<td>Arachnida</td>
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<td>-</td>
<td>1.6</td>
<td>5.0</td>
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<tr>
<td>Mollusca</td>
<td>4.9</td>
<td>-</td>
<td>0.5</td>
<td>4.0</td>
<td>1.7</td>
<td></td>
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<tr>
<td>Other</td>
<td>5.2&lt;sup&gt;d&lt;/sup&gt;</td>
<td>-</td>
<td>1.1</td>
<td>0.9</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

* N = Number of identifiable prey items, n = number of birds from which emetic samples were obtained.

<sup>b</sup> Identifiable Lepidoptera larvae were mostly in the families Geometridae and Noctuidae.

<sup>c</sup> Adult flying Hymenoptera, including Ichneumonidae and Braconidae.

<sup>d</sup> Included several Diplopoda (millipedes) and Chilopoda (centipedes).

larvae, while Wood Thrushes, Veeries, and Ovenbirds fed more often on Diptera, especially tipulid adults (Table 4). Ovenbirds and Veeries both fed relatively often on Hemiptera, mostly leafhoppers, and spiders, while Veeries and Wood Thrushes took small snails (Table 4). Wood Thrushes also took measurable numbers of millipedes and centipedes which occur in the forest litter where this species concentrates its feeding. Also, one Wood Thrush sample had vertebrae of *Plethodon cinereus*, a common salamander that lives in the litter at Hubbard Brook.
Ecological relations among ground-foraging birds. — Even though all seven species in the ground foraging guild occurred syntopically on the 10-ha plot, some differences occurred in distribution and local habitat use, especially by the junco, wren, Hermit Thrush, and Veery. Although not quantified, the areas occupied most frequently by juncos had a more open understory with relatively dense herbs and ferns compared to the less occupied parts of the plot. Such areas occurred where the canopy was complete and had not been disturbed recently by tree falls. The wrens were often in or near the canopy gaps where understory vegetation was thickest and where upturned root systems provided suitable nesting sites. They have thus been responding, at least in part, to areas of local disturbance. Veeries and Hermit Thrushes concentrated their activities at opposite ends of the study area, the former near the north end where the shrub layer was relatively dense along the stream, the latter in better drained areas with more open understory. We have no evidence that their separation was due to interspecific competition (cf. Morse 1971, Noon 1981), and it may simply reflect differences between the species in habitat preferences (James et al. 1984). Veeries have been reported to occur in more mesic and thickly vegetated habitats (Morse 1971, Bertin 1977), such as those at the north end of our study area. Hermit Thrushes are usually considered a bird of forest interiors (Dilger 1956b).

Besides subtle differences in habitat selection, the species in the ground-foraging guild at Hubbard Brook also differed from each other in microhabitat use and/or in foraging behavior, which may be the basis for the significant differences in diet. Three major ways in which these species searched for prey (searching modes, sensu Robinson and Holmes 1982) can be distinguished, and within each of these, further differences occurred in foraging tactics, microhabitats searched for prey, and/or in body size.

(1) Near-surface searchers. Two species, Ovenbird and Dark-eyed Junco, searched for and gleaned prey from nearby substrates while walking or hopping more or less continuously along the ground. In this respect, their foraging patterns are analogous to those of the Dendroica warblers which use this same approach among tree foliage (Robinson and Holmes 1982). The junco searched more foliage and foraged more often in the vegetation strata above the litter than did the Ovenbird, which probably results in their capturing a greater number of caterpillars. Juncos also employed the jump-hover maneuver more frequently than did the Ovenbird, which was used to pick prey from foliage surfaces overhead. The slow, smooth walking gait of the Ovenbird and its rapid striking gleans resulted in the capture of adult Diptera and other active prey (Table 4) which may often be able to escape being caught when approached by birds
using other foraging methods. The longer and more pointed beak of the Ovenbird may increase its success in catching highly mobile prey. Thus, Ovenbirds and juncos, both of which use the ground and low shrub layer extensively, have unique searching and prey-capturing styles.

(2) Manipulative searchers. Another distinctive foraging pattern was exhibited by Wood Thrushes and Winter Wrens. Both species actively manipulated their foraging substrate to find hidden or buried prey. The larger Wood Thrush concentrated its foraging activities in the loose leaf litter, where it moved relatively slowly, probed and turned over litter, and took beetles, ants, adult tipulids, snails, millipedes, centipedes, and even small vertebrates. The Winter Wren also manipulated substrates to obtain prey, but did this by searching methodically among the fallen dead wood, root masses of upturned trees, and dense foliage near the ground, where it probed into crevices and under loose bark or gleaned prey from surfaces where they were hiding. In other sections of the forest, we have witnessed Winter Wrens probing clusters of dead leaves suspended in the shrub layer vegetation (S. K. Robinson, pers. observ.). In this behavior, the wren is similar to the Black-capped Chickadee (Parus atricapillus) which often concentrates its foraging on specific substrates (e.g., dead leaves) where it searches for hidden prey (Robinson and Holmes 1982). Although we do not have quantitative data on foods taken by Winter Wrens, we have observed them take spiders, harvestmen (Phalangida), and other invertebrates located on bark near the ground, suggesting that this searching of special substrates and foraging method lead to the detection and capture of prey different from those obtained by Wood Thrushes and other members of the foraging guild. The wren, being a much smaller species, probably takes smaller sized prey than the larger Wood Thrush.

(3) Variable-distance searchers. The three Catharus thrushes searched substrates both near and far from a particular perch and often took flight to catch more distantly sighted prey. In this respect, their searching behavior is similar to that of the canopy-foraging vireos and Rose-breasted Grosbeak (Pheucticus ludovicianus) (Robinson and Holmes 1982). Each thrush species, however, seemed to have a particular way of foraging that differed from the others. Veeries foraged more on the ground than its congeners and took a larger proportion of Diptera, especially adult tipulids which are often on the litter surface. Hermit and Swainson’s thrushes foraged from the ground layer to the canopy, but Swainson’s Thrushes were more arboreal, foraging more often among the canopy foliage. This is consistent with the morphology of these two species in that the Swainson’s Thrush has a shorter tarsometatarsus which is related to a more arboreal existence (Dilger 1956b). At Hubbard Brook, Hermit Thrushes gleaned prey from nearby substrates, while Swainson’s Thrushes did more
hovering and used the dive/glean maneuver more frequently. Finally, Hermit Thrushes took a larger proportion of beetles, particularly cantharids, while Swainson’s Thrushes fed more heavily on elaterid beetles and especially on ants (see Table 4), indicating that their different searching and foraging patterns led to differences in foods taken.

**Guild and community structure.**—The seven species of ground-foraging birds thus differ in one or more aspects of their use of space (horizontal or vertical), foraging behavior, and diet. The question that then arises is what determines the particular number and combination of ground-foraging species existing in this, or any, particular forest habitat? Why are there seven species in this forest at Hubbard Brook, and especially, why are there four species of thrushes, when this is an unusually high number (Noon 1981) to be found together?

The most parsimonious answer to these questions lies in the structure and resources of the Hubbard Brook forest during the period of study. Each species with its characteristic morphology and behavior may respond to specific features of the habitat, which in turn lead to their occurrence in a particular site. The study area at Hubbard Brook in the mid-1970s when this research was conducted was a second-growth forest, approximately 65 years post-logging. The forest contained a dense but somewhat patchy shrub layer, and thus represented a particular stage in mid- to late-forest succession following disturbance (Aber 1979). Forest stands with these particular plant species, vegetation characteristics, and the associated invertebrates may provide a particular set of microhabitats, food resources, or some combination thereof that allows each of the seven species to settle, feed, and reproduce successfully. At Hubbard Brook, as we have demonstrated, ground-foraging birds can make a living by searching for prey in the litter, on the surface of the litter, on herbaceous and low sapling foliage, and, for those with the morphological and behavioral capabilities of perching and moving through the trees, on the foliage of shrubs and saplings. In a forest with either a more open or a more closed understory, there would be different constraints or opportunities for species occupying this layer. In this context, it may be significant that the composition and abundances of species in the ground-foraging guild at Hubbard Brook has changed considerably since 1978 when this study was completed (Holmes et al. 1986). By the mid-1980s, the shrub and sapling layers had become denser, and all thrush species had declined in abundance, particularly the Wood Thrush which requires more open litter for foraging. These changes suggest the need for comparative studies of ground-foraging birds in sites differing in specific ways and or in habitats that have been experimentally manipulated. These would help to identify more clearly the proximal factors that are important in habitat selection and
in determining the requirements for each species. As far as we know, such comparative or manipulative studies have yet to be done for any ground-forging bird guild.

Our findings of ecological segregation among the coexisting species, and especially the complementary patterns in how they search for and capture prey and in foods taken, generally support predictions of competition theory (MacArthur 1972). It is impossible, however, to tell whether past competition has been important in the evolution of these habitat preferences and foraging patterns. We have no evidence for interspecific aggression or other forms of ongoing competition among the species at Hubbard Brook, although these are difficult to detect. The observations of habitat shifts of thrushes in Maine (Morse 1971) and the expansion of the Veery into spruce forests in the southern Appalachians where its congeners are absent (Noon 1981) suggests that competition might be important in certain situations, although Wiens (1983) and James et al. (1984) have questioned Noon’s conclusions.

As caveats to this discussion, it is important to note that other factors may also have important effects on the species composition and abundance of these ground-forging birds. One is a matter of the scale at which these species and habitats are viewed. For instance, our study site at Hubbard Brook was in deciduous forest, but a few hundred meters in elevation above our plot, the forest grades into a boreal, coniferous forest where Swainson’s Thrushes are more abundant (Sabo and Holmes 1983). Likewise, Wood Thrushes and Veeries are more common at lower elevations (see also Noon 1981). The presence of more preferred areas nearby might provide a source of birds that would settle in our study areas in years of high population density, and thus affect the relative abundance of species that we observed. Likewise, an examination of the abundance and resource use patterns of these species over such a habitat gradient might illustrate more clearly the habitat preferences, spacing patterns and foraging responses of these species. The present study was limited by analyses of only relatively few individuals occupying a single 10-ha section of forest and by not having information on the behavioral flexibility of these species in terms of their responses to different habitats or foraging opportunities. Such plasticity may differ among species, and play an important role in what habitats they occupy.

On an even larger scale is the influence on these species of events during migration or on their wintering grounds. The breeding densities of the four species of ground-foragers that winter in Central and South America (Wood and Swainson’s thrushes, Veery, Ovenbird) remained relatively constant at Hubbard Brook during the five years of this study (Holmes et al. 1986). However, densities of the three species that winter primarily
in the subtemperate regions of North America (Hermit Thrush, Winter Wren, Dark-eyed Junco) fluctuated strongly and synchronously, coincident with the occurrence of severe winter weather (Holmes et al. 1986). In fact, following the winter of 1977–78, the breeding densities of these three species at Hubbard Brook and in the northeastern U.S. as a whole, declined significantly for several years (see Holmes et al. 1986). Thus, following the arguments of Fretwell (1972), it is possible that the breeding densities of at least some of these species are kept below carrying capacity by winter mortality.

Concluding comments.—Our results support Moermond’s (1979) contention that the structure and characteristics of the habitat, including available food resources, will have a major influence in determining which species are present and how resources are used. The foraging tactics used by each species are in turn determined by their morphological and behavioral abilities (e.g., see Dilger 1956b for the thrushes considered here), which reflect selective pressures during their evolutionary history. Thus, foraging tactics, bird morphology, habitat structure, and historical events all interact in a complex way to determine which species will be present in a given location and thus determine guild and community structure.

Finally, on a methodological note, we found that the description of foraging behavior of these ground-foraging birds when based on initial foraging observations were often biased toward conspicuous maneuvers. Records from longer sequences provided a more complete description of the foraging repertoires of these species.

ACKNOWLEDGMENTS

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LITERATURE CITED


HABITAT SELECTION IN MEW GULLS: SMALL COLONIES AND SITE PLASTICITY

JOANNA BURGER¹ AND MICHAEL GOCHFELD²

Abstract.—We studied colony-site selection of Mew Gulls (Larus canus) in a small geographical area of south-central Alaska to: (1) determine if the plasticity in habitat selection in one region reflects the wide range of habitats used throughout their world-wide range, (2) ascertain the relative importance of physiognomic aspects of vegetation to nest-site selection in different colonies, and (3) quantify the communality of these characteristics among sites. We found colonies on grass, rock, sand, and earth, on rocky and sandy islands in lakes and rivers, on several types of marshes (floating vegetation, creek bog, muskeg and open grassy marsh), on a rock dike, on a roof, and in spruce trees. In all colonies, the gull’s habitat preferences differed from random with respect to some characteristics, but not necessarily the same characteristics in every colony. By comparing habitat choices among colonies, we identified the factors that were required for nesting or were ignored. The overall choice of nest-sites indicates narrow selection for some characteristics within a diversity of major habitat types, and indicates plasticity in colony-site choices, but not nest-site choice. This analysis provides a general method for assessing the relative importance of social and physical factors in colony- and nest-site selection. Received 22 Sept. 1987, accepted 22 Feb. 1988.

Selection of suitable breeding habitat is critical for most animals because it directly affects fitness (Partridge 1978, Cody 1985). Despite high mobility as adults, nest-site selection locks birds into a single location for weeks. Variation in reproductive success among habitats may be due to differential predation rates, environmental stresses (high tides, thermal stress), or social factors such as territorial disputes (Burger 1985). Faced by stress, a pregnant mammal can move to a safe location, and newborn mammals may be carried to safe sites. In most cases, however, avian parents are restricted to chosen nest sites for the duration of incubation, and except for precocial species, this commitment persists for several weeks after hatching. Habitat selection is critical particularly for birds with young that remain in or near the nest until fledging.

Available habitats often vary gradually along gradients, and populations distributed over a wide geographical range may benefit from behavioral plasticity with respect to colony- and nest-site selection. Birds with a wide geographic range may either use similar habitats in all regions or may select different sites from region to region (Cody 1985). Birds may select similar physiognomic characteristics despite differences in available vege-

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tation species, vegetation cover, substrate types, or other physical characteristics. Diversity of habitat preferences found over a wide geographic range suggests that a species might use a diversity of habitats within one geographic region. Birds may be plastic in their choice of overall habitat (marsh, forest, field), but require very specific features for suitable nest sites. Presumably, behavioral plasticity in general habitat choices is particularly advantageous in regions with short breeding seasons, limited or changing habitat, or both. In this paper we attempt to distinguish these levels of colony- and nest-site plasticity. Particular features of the habitat may be ignored, of minor importance, or of primary importance to a bird selecting a nest site. If the characteristic is completely unimportant, there should be no consistent relationship for that characteristic between the available habitat and where the birds nest (Fig. 1A, after Burger and Gochfeld 1986). If, however, the characteristic is important to birds in selecting a habitat, they could nest in areas with high values (Fig. 1B) or in areas with less of the particular features (Fig. 1C) than is available in the general area. If the characteristic is critical and the birds require specific characteristics, they may select a very narrow range of values despite the wider range of available characteristics (Fig. 1D).

Although this analysis could be used within a colony or nesting area, by comparing the mean value for nest-site characteristics with the mean for random points among several colonies, we believe it is possible to infer which characteristics are actually being selected by the birds, and what their preferences are. For example, in one colony with sparse vegetation, birds may select habitats with more vegetation than the average available, suggesting that they prefer heavily vegetated areas. However, in another colony with dense vegetation, they may select sites with less vegetation than average. In both cases, they may have selected sites with comparable vegetation cover. Our study examines habitat selection by comparing nest-site characteristics with random points (=available habitat) for several colonies.

The Mew Gull \( (Larus canus) \) provided an excellent opportunity to examine plasticity because it nests in a variety of habitats and has an extensive Holarctic distribution. In North America, Mew Gulls \( (L. c. brachyrhynchus) \) breed from western Alaska east to Hudson Bay, Canada (A.O.U. 1983), while the conspecific Common Gull \( (L. c. canus) \) nests across Europe and Asia from near the Arctic Circle south to the British Isles, Netherlands, the Black and Caspian seas, northern Mongolia, Kamchatka, and Kuriles (Godfrey 1979). In Alaska, Mew Gulls breed on many streams or lakes of the interior (Gabrielson and Lincoln 1959), and Sowls et al. (1978) estimated there were 5000 pairs of Mew Gulls in coastal Alaska, but their surveys did not cover the Anchorage area.
In this study, we examined plasticity in colony site selection in Mew Gulls in Alaska to: (1) determine if their choice of colony and nest sites in this area was as diverse as suggested from the literature, or whether a single population showed low plasticity, (2) determine the relative importance of physiognomic features of vegetation to colony- and nest-site selection, (3) determine the preferred or tolerated attributes that might influence habitat selection among colonies, and (4) determine whether certain characteristics are important in many different habitats. In a previous paper we examined nest-site selection in more detail and for additional characteristics (Burger and Gochfeld 1987). The main objective of this paper is to compare colonies to determine how gulls use each factor in colony-site selection.

In different parts of its range, *Larus canus* nests on a variety of substrates.
in a variety of habitats including grasslands, peat bogs, stone, rubble, sand, cliffs, and the tops of tree stumps (Dement’ev et al. 1951, Barth 1955, Hillis 1967, Isleib and Kessel 1973, Kumari 1976). *Larus canus* nests mainly in small colonies of up to 15 or 20 pairs (Bent 1921). In the interior of Alaska, Hurley (1931) found the species numerous on the Kuichak River with colonies up to 100 pairs, and Gabrielson and Lincoln (1959) and Sowls et al. (1978) mention only two coastal colonies as large as 250–300 pairs.

**METHODS AND STUDY AREA**

We studied 14 colonies of Mew Gulls within 250 km of Anchorage in south-central Alaska. Each colony was visited one to three times. We also observed two pairs nesting with terns in a lake and solitary pairs nesting in the tops of spruce trees. We made our observations from 26 June to 24 July 1985 during late incubation and early chick stages. At each colony site, we recorded a general habitat description, noted the dimensions of the colony and of the island or habitat type, and counted the number of adults and nests. For colonies with less than 30 nests, we collected data at all nest sites; for larger colonies (Hood Lake, Nenana River colonies A and B) we recorded data from 30 randomly selected nests. We used a table of random numbers to determine the coordinates of nests to be examined. Data collected at each nest included nest contents, distance to nearest tree or vegetation, height above water (or land), height of tree or vegetation, percent cover directly over the nest, percent cover in a one and five m circle around the nest, visibility of the nest from directly above, and visibility of the nest from five m. For the purposes of this study, vegetation height referred to plants that were not woody shrubs or trees, and tree height referred to woody shrubs and trees. Because the habitat varied among colonies, not all characteristics were represented at each colony.

At most colonies we identified a number of random points equal to the number of nests. The occupied area was treated as a rectangle, and the X and Y coordinates were selected from a random number table. At random points we measured the same characteristics as at the nests in that colony (Burger and Gochfeld 1986). We also used computer-generated random points to predict spatial features such as internest distance and distance to the edge of the colony. This Monte Carlo simulation procedure allowed us to streamline our collection of field data to the characteristics that were required at each site, thereby reducing the disturbance to the nesting gulls. The use of computerized Monte Carlo simulations to analyze complex events is now widespread (Ricklefs and Lau 1980). The simulations employ stochastic processes to generate “random” simulates analogous to the phenomenon being studied. From the simulation of 1000 replicates, we produced cumulative frequency distributions for nearest neighbor distance. The actual mean nearest neighbor distance for the colony was compared to the frequency distribution from which we could determine the likelihood of encountering a particular mean value if nests were indeed randomly distributed.

Within each colony, we compared the characteristics of the gull nests and random points to determine if gulls selected sites with particular features, compared to what was available. Among colonies, we compared the mean values for nests and random points (Fig. 1). Other nest-site characteristics and standard errors of the means can be found in Burger and Gochfeld (1987).

In this paper, we present mean values for nests plotted against the mean for random points for each nest-site characteristic in each colony. These comparisons reveal which
characteristics are being ignored, maximized (or minimized), or highly selected within a narrow range (see Fig. 1). For each characteristic we used a Sign Test to test the null hypothesis that nest sites do not consistently have a higher or lower value than the random points. That is, an equal number of colonies should fall above and below the line of equivalent values. Not all features were present at all colonies, so we plotted on each graph only colonies where the characteristic was relevant. The detailed descriptive data used to calculate these means are presented elsewhere (Burger and Gochfeld 1987).

RESULTS

Colony-site selection.—We found 14 colonies of Mew Gulls in our study area, as well as two pairs nesting on a lake and two isolated pairs nesting in spruce trees (Picea sp., Table 1). The number of nests per colony ranged from 2 to about 400 (x ± SD = 59.6 ± 105, median = 22). Mew Gulls nested on islands in lakes and rivers, on marshes and bogs, rock dikes, on a roof top, and in trees. Nesting substrates included dry ground, grass, branches, and floating vegetation (Table 1).

Most sites were at least partially isolated by some barrier from ground predators and human disturbance (Table 1). The dry ground colonies were isolated by a lake, creek, highway, or fence. Within Anchorage, gulls nested on several dirt dikes that were enclosed by 3-m high chain link fence which excluded large mammalian predators and people. The riverine colonies were well-protected by the swift moving Nenana River or less so by the slow moving water of Snow Creek. The bog and marsh colonies were protected by water or sphagnum of varying depths, all difficult to negotiate. The rock dike colony was protected by a fence, and the roof colony was also within a fence and access required climbing a 9-m ladder. However, such protection did not exclude avian predators.

Snow Creek had the least protection from predators. Its colony on a sandbar was surrounded by moving water, but a highway bisected the island allowing mammalian predators access to the island. Numerous coyote tracks on the island and preyed-upon eggs indicated predation. For all other riverine and lake colonies a boat or white water raft was required to get to them.

Nest-site selection.—Eight of 10 colonies had larger mean inter-nest distances than inter-random point distances (Sign Test, P < 0.05, Fig. 2A). Nearest neighbor distance ranged from 120 to 800 cm, with a mean of less than 300 cm. Only in the Rock Dike and Hood Lake colonies did the nesting gulls aggregate. In both cases, gulls were pressed into the central area of the colony by tidal waters and human pressures (Rock Dike) or by air traffic in the water (float planes at Hood Lake). In both colonies, a few pairs nested near the edges or center of the colony, so we included these areas in our selection of random points. However, if we excluded
Table 1

**Nesting Habitat of Mew Gulls in South-central Alaska, 1985**

<table>
<thead>
<tr>
<th>Type</th>
<th>Habitat</th>
<th>Location (abbreviation for figures)</th>
<th>Number of nesting pairs</th>
<th>Isolation</th>
<th>Predation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry ground</td>
<td>Grassy island</td>
<td>Hood Lake, Anchorage (HL)</td>
<td>400</td>
<td>Surrounded by lake</td>
<td>People–monofilament line</td>
</tr>
<tr>
<td></td>
<td>Small grassy islands with birch trees</td>
<td>Anchorage, Sullivan Park (SP)</td>
<td>.24</td>
<td>Surrounded by lake</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Earth dike</td>
<td>Anchorage Military Base (MB)</td>
<td>20</td>
<td>Fenced (3 m high chain link)</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Landfill</td>
<td>Anchorage, Airport (AL)</td>
<td>25</td>
<td>Creek and highway (people near)</td>
<td>Cannibalism on eggs</td>
</tr>
<tr>
<td>Riverine</td>
<td>Gravel island</td>
<td>Mt. McKinley, Nenana River A, (NA)</td>
<td>30</td>
<td>Swift-moving river</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Rock island</td>
<td>Mt. McKinley, Nenana River B, (NB)</td>
<td>75</td>
<td>Swift-moving river</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Sand bar</td>
<td>Seward, Snow Creek (SC) (Mile Post 18)</td>
<td>.80</td>
<td>Slow river and creek</td>
<td>Numerous coyote tracks, predated eggs</td>
</tr>
<tr>
<td>Wet ground</td>
<td>Wet marsh</td>
<td>Anchorage: Shell Oil plant floating nest</td>
<td>3</td>
<td>Water over 1 m deep</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Creek bog</td>
<td>Anchorage: Airport (CB)</td>
<td>12</td>
<td>Creek, water, and airport road</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Moss muskeg</td>
<td>Anchorage: Post Office (MM)</td>
<td>2</td>
<td>Water 1 m deep</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Open marsh</td>
<td>Portage Marsh (Mile Post 40 to Seward)</td>
<td>30</td>
<td>Shallow water (only site with shallow inundation)</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Open marsh</td>
<td>Potter's Marsh (Mile Post 10 to Seward)</td>
<td>18</td>
<td>Deep water</td>
<td>None</td>
</tr>
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</table>
### Table 1
#### CONTINUED

<table>
<thead>
<tr>
<th>Type</th>
<th>Habitat</th>
<th>Location (abbreviation for figures)</th>
<th>Number of nesting pairs</th>
<th>Isolation</th>
<th>Predation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock</td>
<td>Rock dike</td>
<td>Anchorage, Port (RD)</td>
<td>30</td>
<td>3 m high chain fence and guard</td>
<td>People</td>
</tr>
<tr>
<td>Roof top</td>
<td>Fine gravel</td>
<td>Anchorage, Port Authority (RF)</td>
<td>13</td>
<td>9 m high building</td>
<td>None</td>
</tr>
<tr>
<td>Trees</td>
<td>Spruce trees</td>
<td>Denali National Park</td>
<td>2</td>
<td>Tree</td>
<td>None</td>
</tr>
</tbody>
</table>
these marginal areas, internest distances would have been greater than
the mean distance between random points distances in these colonies as
well.

Flooding is a real danger in both marsh and dry land colonies adjacent
to water. In all cases, except for the Rock Dike colony, Mew Gull nests
averaged higher above water than the random points (Sign Test, \( P < \ 0.05 \), Fig. 2B). Nevertheless, the mean nest site in several colonies (Nenana A and B, Moss Muskeg, Rock Dike, Creek Bog) was less than 0.5 m above
water level. All of these colonies were exposed to tidal flooding (Rock
Dike, Portage Marsh) or storm flood (the other colonies). Mean slope at
random points in the colony sites varied from 0° (Portage Marsh, Moss
Muskeg) to 34° (Military Base), yet the gulls always selected sites with
lower slopes than the random points (Sign Test, \( P < 0.02 \), Fig. 2C).
However, they did not always have the option to nest in places with slopes
less than 10° because some colonies did not have flat places available
(Military Base). Even at the Military Base, however, they nested on the
flattest places, building up one side of the nest to make it level.

Mew Gulls in Alaska did not nest in completely unvegetated habitats
(except for the Roof colony), although vegetation cover was sparse (<10%
cover) in some colonies (Nenana A and B, Snow Creek, Rock Dike,
Military Base). Vegetation cover consisted of trees (willows, alder, birch)
and herbs (\textit{Lupinus}, grasses).

The mean distance to the nearest herbs was always equal or less for
nests than for random points (Sign Test, \( P < 0.05 \), Fig. 2D). Moreover
the mean distance of nests to herb vegetation was always less than 0.5 m
despite the available mean values of 0 to 6 m. Thus, distance to herb
vegetation is an example of a characteristic having a restricted range.
There was no clear pattern in the relationship between the mean distance
from nests to trees and from random points to trees among the colonies
(Sign Test, \( P > 0.10 \), Fig. 3A).

Vegetation height likewise showed a distinct relationship (Sign Test, \( P < 0.02 \), Fig. 3B). For nine of 10 colonies, mean herb height was greater
around nests than at the random points. Portage salt marsh was the
exception. However, marsh vegetation is usually higher where there is
tidal inundation (see Montevecchi 1978), suggesting that spots with short¬
ner vegetation would be those less vulnerable to tidal flooding.

Percent cover around the nest (within 0.5 m of the nest) was greater at
the nests than at random points for 9 of 11 colonies (Sign Test, \( P < 0.05 \),
Fig. 3C). Moreover, the cover over nests was generally greater than in the
area within 5 m of nests (Sign Test, \( P < 0.05 \), Fig. 4A). Nenana A, where
there was more cover near than over the nests, was the only exception.
Fig. 2A. Relationship of mean nearest neighbor distance to interpoint distance of random points. AL = Airport Landfill, CB = Creek Bog, RD = Rock Dike, MB = Military Base, PM = Portage Marsh, NA = Nenana A, NB = Nenana B, MM = Moss Muskeg, RF = Roof, SC = Snow Creek, SP = Sullivan Park.

Fig. 2B. Relationship of mean distance above water of nests and random points for Mew Gull colonies.

Fig. 2C. Relationship of the mean slope in degrees at nest sites and random points for eleven Mew Gull colonies.

Fig. 2D. Relationship of mean distance to nearest vegetation (in meters) for nests and random points for nine Mew Gull colonies.
**Fig. 3A.** Relationship of mean distance to nearest tree (in cm) for nests and random points for nine Mew Gull colonies (W = Willow, A = Alder, B = Birch). Symbols the same as in Fig. 2.

**Fig. 3B.** Relationships of nests versus random points for ten Mew Gull colonies with respect to mean vegetation heights (in cm).

**Fig. 3C.** Relationships of nests versus random points for 12 Mew Gull colonies with respect to mean percent cover around nests.

**Fig. 3D.** Relationship of nests and random points in eight Mew Gull colonies with respect to mean visibility from above the nest (percent).
Fig. 4A. Relationship of mean percent cover over nests to mean percent cover within 5 m of nests for 12 Mew Gull colonies in Alaska. Symbols the same as Fig. 2.

Fig. 4B. Relationship of visibility from above to visibility from 5 m for nests in 10 Mew Gull colonies.
Vegetation cover and height are features that determine protection from inclement weather and predators. However, visibility is a more direct measure of vulnerability to aerial predators. A nest that is highly visible from above presumably has a greater risk of aerial predation. Generally, visibility from above was less for nests than for the random points (Sign Test, $P < 0.05$, Fig. 3D). The Creek Bog was the only exception, because random points were usually within vegetation (low visibility), whereas all gull nests were on the top of tussocks (high visibility) secure from flooding but conspicuous.

We compared the visibility from above (exposure to aerial predators) with visibility from 5 m (exposure to ground predators such as coyotes, Sign Test, $P > 0.10$, Fig. 4B). In general, visibility was greater from 5 m (6 colonies) than from above (3 colonies), suggesting greater protection from aerial predators (see below). Mew Gulls selected areas with significantly more cover and taller grass and herbs.

**DISCUSSION**

*Plasticity in colony selection.*—Near Anchorage, Alaska, Mew Gulls nested in a wide variety of habitats including rooftops, marshes, bogs, sandy and rocky islands, dirt and rock dikes, and spruce trees. Vermeer and Devito (1986) also report Mew Gulls nesting solitarily on pilings in British Columbia. To our knowledge, this diversity of habitats is greater than that reported for any other gull in one geographical area and represents virtually the complete spectrum of gull nesting habitats except for deserts (see Howell et al. 1974) and true cliffs (Burger 1974).

The habitats where we found Mew Gulls nesting in south-central Alaska have been used elsewhere in its geographical range, but within smaller areas, *L. canus* generally uses only a few habitat types. The behavioral plasticity observed in Alaska may reflect a variety of selection factors including: (1) limited availability of preferred habitat, (2) small patches of preferred sites, (3) restricted breeding season forcing birds to select sites quickly, or (4) limited food resources restricting the location and size of colonies.

*Colony size.*—It is not apparent why Mew Gulls in Alaska and elsewhere form small colonies when most other gulls, even those nesting in highly disturbed sites, nest in larger colonies. Sowls et al. (1978) listed the population size of 41 coastal Alaskan colonies as ranging from 1 to 300 pairs (mean = 42 pairs, median = 20 pairs). About 10% of coastal colonies had more than 100 pairs. Turner's (1885) account of large Mew Gull colonies on cliffs in the Aleutians is surely erroneous as the habitat he describes is that of kittiwakes (*Rissa* spp.), and the recent coastal seabird surveys show virtually no Mew Gull nesting in the Aleutian chain (Sowls et al.
In Europe, the conspecific Common Gull does nest in larger colonies (Cramp et al. 1974).

Current theory suggests that patterns of habitat occupancy should be linked to variations in individual fitness and that preferred habitat should be fully saturated unless the species is rare (Fretwell and Lucas 1969). Competitive interactions with other species, however, may modify habitat use (Wiens 1985). If preferred habitats were limited gulls might nest in suboptimal habitats or even forego breeding.

One interpretation for the small size of Mew Gull colonies is that suitable colony sites are small. In Alaska, most of the larger inland colonies (Hood Lake, Nenana River, Snow Creek) had insufficient space for other pairs, and the availability of high spots free from flooding also may have been limiting.

In the intermediate-sized colonies, gulls either used most available space (Sullivan Park, Rock Dike) or used most suitable sites with vegetation (Anchorage Military Base, Portage Marsh). In Sullivan Park, for example, every island that was high enough to escape flooding had a pair of nesting gulls, and the larger islands had two pairs. In the Portage Marsh, nest sites were vulnerable to flooding and some nests had been washed out. To increase use of high sites, the gulls would have to tolerate increased density. At the Army Base, most of the dirt dike had no vegetation, and gulls nested only near vegetation. Of the intermediate-sized colonies, only the Landfill area appeared to have additional available space. However, that colony was suboptimal because it was not protected from mammalian access and contained a colony of Arctic Terns (Sterna paradisaea) that harassed the nesting gulls.

Likewise, the small colonies either had as many pairs as the available space permitted (Shell Oil plant) or the gulls used the few suitable sites above water levels (Creek Bog) or next to objects that would provide suitable protection from wind (Roof).

Another indication that limitation of suitable sites has selected for behavioral plasticity in colony site selection was the diversity of nest sites used in adjacent areas. For example, the Roof colony was 75 m from the Rock Dike colony, and the Roof colony may have represented overflow from the Dike colony. Secondly; the Creek Bog colony was less than 100 m from the Landfill colony, and gulls may have nested on the suboptimal Landfill colony because no more suitable sites were available on flood-free grass hummocks.

Another possible factor selecting for behavioral plasticity is that a restricted breeding season in Alaska forces gulls to select colony sites quickly and nest, so that young are fledged before temperatures drop in August. In contrast, conspecifics elsewhere have a longer breeding season. The
nesting areas we studied in Alaska were at 60–64°N latitude, while Common Gull nesting ranges in Britain, Germany, Poland, and Southern Sweden are mainly below 60°N latitude. Further, climatic conditions at the same latitude in Europe are milder than in Alaska because of the Gulf Stream. For example, tundra in Alaska occurs at 65°N latitude, while in Norway tundra is found at 70°N latitude. Over time, the colder climate and shorter breeding season in Alaska may select for sufficient behavioral plasticity to allow rapid, less narrow selection of colony sites compared to conspecifics in Europe. Further, gulls may nest in small colonies so the colony is less attractive or less visible to predators.

Lastly, limited availability of food resources could limit colony size in any location. However this seems an unlikely explanation for small colony sizes in Alaska, because gulls nested in different habitats within 100 m of each other where they were clearly using the same food resources. It is apparent that small scattered colonies are the norm for this species in Alaska (Gabrielson and Lincoln 1959, Sowls et al. 1978).

Overall, a few more pairs could have been inserted in most of these habitats, but in no case could the population have been markedly increased. Thus we suggest that a short breeding season, limited availability of colony sites, and the limited availability of nest sites free from the dangers of flooding, contribute to the pattern of the small colony size of New Gulls in Alaska.

Nest-site selection.—Plasticity of general colony-site selection may be possible only if the specific requirements of nest sites are met. In the following section, we examine whether there is behavioral plasticity in specific nest-site choices among colonies.

Gulls selecting nest sites could exhibit plasticity in their choice of social and physical features of the environment, or they could avoid nesting where site characteristics fall outside of a narrow range of preferred values. Some characteristics may be more important than others. Although comparing nest sites with available habitat in any one colony can be used to indicate statistical differences, only by comparing avian choices across colonies can one begin to distinguish which feature(s) of the environment the birds maximize or minimize, which they optimize, and which they ignore (refer to Fig. 1).

Once a bird chooses a colony site, it chooses a nest site within the colony. Thus the available range of characteristics is already fixed. By comparing several colonies where the range of values differs among colonies, we could examine the features selected under vastly different conditions.

Mew Gulls in Alaska selected nest sites that minimized some characteristics (slope, distance to vegetation, visibility from above), maximized
some characteristics (distance above water, nearest neighbor distance, percent cover around nests), optimized some specific characteristics (distance to vegetation), and appeared to ignore others (distance to trees, vegetation height).

The different patterns of habitat use clearly indicate that Mew Gulls responded differently to the social and physical features of the environment. Given a particular range of available slopes, distance to vegetation, and visibilities from above, they always selected the lower range of values. Similarly, they chose to be farther above water and from neighbors and to have greater cover around the nest than was generally available. Regardless of the dispersion of vegetation reflected by the range of available distances to vegetation, Mew Gulls always nested at mean distances of less than 0.5 m from vegetation.

We believe our analysis can be useful for examining habitat selection of a wide variety of organisms in many different situations. Further the method can also be used to examine plasticity in a variety of laboratory experiments where animals are provided with a range of choices.

The present study clearly indicates that, although Mew Gulls show plasticity in their choice of habitat for colony sites, they minimize, maximize, or optimize particular features (within colonies). This results in their using nest sites that are protected from inclement weather and predators under a wide variety of habitat conditions.

ACKNOWLEDGMENTS

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LITERATURE CITED


THE USE AND FUNCTION OF GREEN NEST MATERIAL BY WOOD STORKS

JAMES A. RODGERS, JR., ANNE S. WENNER, AND STEPHEN T. SCHWIKERT

Abstract.—Wood Storks (Mycteria americana) add greenery to their nests prior to egg deposition, and new additions decrease as the nestlings mature and develop self-thermoregulation at 1–2 weeks of age. With time, the accumulated nest greenery becomes coated with guano and matted down to conform to and line the inner surface of the nest. Wood Storks use many plant species to line their nests. We demonstrate that the greenery functions to insulate nest contents in a rather porous, twig structure. Nest greenery probably does not function to repel nest ectoparasites of Wood Storks. Received 5 Oct. 1987, accepted 25 Feb. 1988.

Several avian species, including Wood Storks (Mycteria americana), place green plant material in their nests (Holt and Sutton 1926, Bent 1926, Howell 1932, Matray 1974, Wimberger 1984). Although green material probably serves a function similar to the rest of the nest twigs, its specific role in Wood Stork nests is uncertain. Proposed functions of greenery include: concealment of eggs and nestlings from predators (Welty 1962, Collias and Collias 1984); shade for eggs and nestlings (Bush and Gehlbach 1979); nest sanitation by covering debris (Orians and Kuhlman 1956, Newton 1979); advertisement of nest occupation (Newton 1979); and insulation of eggs and nestlings from environmental extremes (Mertens 1977, Newton 1979, Collias and Collias 1984). Recently, Wimberger (1984) hypothesized that nest greenery may repel ectoparasites from nestling raptors (also see Johnson and Hardy 1962, Clark and Mason 1985). We know of no studies of variation in use of green plant material in nests in different parts of a species’ range, and only one experiment to determine the function of nest greenery (Clark and Mason 1985). Here we identify and compare intercolony variation in use of nest greenery in Florida Wood Stork nests, and we describe the results of two investigations of the possible function of such nest materials.

STUDY AREA AND METHODS

We studied six colonies in north and central Florida (Fig. 1). Location and species composition of the Dee Dot (No. 594004), Little Gator (No. 611024), Lake Yale (No. 612027), Moore Creek (No. 612007), Ochlockonee (No. 592003), and Pelican Island (No. 616007)
colonies may be found in Nesbitt et al. (1982) by colony number. Because Wood Storks pruned off leafy twigs, vines, and other herbaceous plants within and surrounding the colonies, it was impossible to quantify the surrounding habitats. However, qualitative descriptions of the habitat types are in Table 1. Colonies were visited every other week during May–June 1985 to identify plant species used in nests. For nest contents not readily visible, a mirror on a 7-m telescoping pole was used to identify nest greenery. Scientific and common plant names follow Kurtz and Godfrey (1962) and Lakela and Long (1970). Similarity in percent of plant species composition between and within colony habitats was calculated using Sørensen's Community Coefficient Index (Mueller-Dombois and Ellenberg 1974):

\[
\text{Similarity} = \frac{2C}{(A + B)} \times 100,
\]

where \(C\) is the number of species that the two sites share in common, and \(A + B\) is the total number of plant species in both colonies.

Common avian ectoparasites (e.g., mites and biting lice) are difficult to use in experiments because of their small size, susceptibility to desiccation away from their host, and the difficulties in counting and collecting them on live nestlings. Therefore, we used dermestid beetle larvae (Dermestid nidum) in an ectoparasite repellent experiment. Larval dermestid beetles are known ectoparasites of live Wood Stork nestlings (Snyder et al. 1984) that can cause severe external lesions. At the start of the experiment, 20 larvae (1.5–2.0 cm) were placed in the center of a 42 cm diameter pan (the approximate diameter of the greenery region of a stork nest). Equal amounts of dried carrion (approximately 30 g) were placed at

![Map of Florida showing Wood Stork colonies](image)

**Fig. 1.** Wood Stork colonies monitored in north and central Florida.
Table 1
VEGETATION OF WOOD STORK COLONIES AND SURROUNDING HABITATS. HABITAT TYPES
Follow Davis (1967)

<table>
<thead>
<tr>
<th>Colony</th>
<th>Colony site</th>
<th>Surrounding habitat</th>
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</thead>
<tbody>
<tr>
<td>Dee Dot</td>
<td>Cypress swamp</td>
<td>Longleaf-xerophytic oak woodlands</td>
</tr>
<tr>
<td>Little Gator</td>
<td>Cypress-hardwood swamp</td>
<td>Pine flatwoods-hardwood swamps</td>
</tr>
<tr>
<td>Lake Yale</td>
<td>Cypress swamp</td>
<td>Pine flatwoods</td>
</tr>
<tr>
<td>Moore Creek</td>
<td>Mangrove swamp</td>
<td>Coastal strand-mangrove swamp</td>
</tr>
<tr>
<td>Ochlockonee</td>
<td>Black gum swamp</td>
<td>Mixed hardwood-pine</td>
</tr>
<tr>
<td>Pelican Island</td>
<td>Mangrove swamp</td>
<td>Coastal strand-mangrove swamp</td>
</tr>
</tbody>
</table>

opposite sides: one sample was covered with moist paper towels (control), and the other side was covered with an equal amount (about 135 cm²) of vegetation (experimental) of the plant species that we had earlier determined were most commonly used by storks. The side on which the vegetation was placed was randomly determined for each trial. At 24, 48, and 72-hour intervals, the number of larvac on the carrion at each side were counted. Occasionally, larvac would disappear during the experiment. However, if the total number per pan dropped below 15 larvac, the test run was voided and repeated. Because we could not be certain whether fresh or desiccated vegetation would be responsible for producing repellents, we added one fresh sprig of greenery at each 24-hour interval. Control versus experimental results were tested using the binomial test for small sample sizes (Siegel 1956).

For a nest insulation experiment, two Wood Stork nests (average 75 × 65 cm wide × 20 cm deep) were removed intact from the Dee Dot colony immediately after the nestlings had fledged. These “intact” nests contained both dried greenery and guano. After the experiment described below was run on the intact nests, each nest was then carefully cleaned of all guano and dried greenery to produce the “clean” nests. These clean nests were very porous, but they still contained most of the small finishing twigs similar to the natural pregreenery nests. To reconstruct the “fresh” greenery nests, three small sprigs each of cypress (Taxodium distichum), Virginia creeper (Parthenocissus quinquefolia), red maple (Acer rubrum), live oak (Quercus virginiana), wax myrtle (Myrica cerifera), poison ivy (Toxicodendron radicans), and Spanish moss (Tillandsia usneoides) were evenly arranged in the center of the clean nests and lightly pressed flat (approximately 3–4 cm deep). These fresh greenery nests were allowed to air dry for seven days after their part in the experiment to produce the “dried” greenery nests.

The following experiment was conducted on each of these four nest types (i.e., clean, fresh, dried, and intact greenery nests) in the same manner. The nests were suspended 1 m above the ground in an outdoor, shaded, windless site. Three Wood Stork eggs (modal clutch size), blown and filled with paraffin, were placed in the nest and covered with a small, adjustable heating pad such that the upper surface of the clutch reached and stabilized at 39.5°C. This temperature was about 1°C less than the core nesting body temperature of adult storks (Kahl 1963) and represents a reasonable approximation of the temperature of the egg/stork interface. Inside the nest, the temperature at the egg/nest interface was monitored beginning when the ambient temperature was 32°C (approximately 18:00–06:00 EST). The average values for the two nests were used in subsequent analyses. Differences in nest temperature curves were analyzed using the Kolmogorov-Smirnov two-sample test (Siegel 1956).
To investigate further the insulation properties of Wood Stork nests, the overall thermal conductance \( h \) expressed as W m\(^{-2}\) °C\(^{-1}\) was determined for each of the above four nest types. The experimental apparatus and calculations are described by Skowron and Kern (1980).

**RESULTS**

**Nest composition.**—Wood Storks added green material to the upper surface of the nest after the main structure of dead twigs was completed, but in most cases before the eggs were laid (Fig. 2). Greenery continued to be placed in the nest through the incubation period, especially during nest relief ceremonies. Though greenery occasionally covered the eggs (1.2%; \( N = 1326 \) nest visits), we never saw nestlings hidden. By the time the nestlings were two weeks old and covered with thick downy plumage, the frequency of added greenery had decreased (Fig. 2).

Wood Storks used a variety of herbaceous and woody plant species for nest greenery that reflected vegetation both within the colony and surrounding habitat (Tables 1 and 2). In the coastal Moore Creek and Pelican Island nests, typical marine-estuarine vegetation of mangrove and cordgrass (Spartina alterniflora) was present. The introduced Brazilian peppertbush (Shinus terebinthifolius) and Australian pine (Casuarina equisetifolia), characteristic of upland, coastal areas in central and south Florida,
were found in nests, even though they do not grow on these islands. In addition, Moore Creek nests might have had more white mangrove (*Laguncularia racemosa*), but a severe January 1985 freeze killed the trees to the high water mark (see Provancha et al. 1986). The use of pigweed (*Amaranthus hybridus*) in nests may reflect its now common status as an understory plant since the mangrove canopy was defoliated.

Of the freshwater swamp colonies, Wood Stork nests at Dee Dot exhibited the most species of plants used for all nests, but Lake Yale possessed the greatest mean number of species per nest (Table 2). Of the three cypress-dominated sites (Dee Dot, Little Gator, and Lake Yale), only Dee Dot nests did not contain a high frequency of cypress. The low use of cypress by storks at Dee Dot probably reflects the poor, stunted tree growth at the site because of impounding for nearly 40 years. The lack of vigorous cypress growth may have forced the storks to prune the surrounding longleaf-xerophytic oak woodland habitat more frequently than at other colonies, thus resulting in the higher number of species used as greenery. Of all the freshwater sites, only the Little Gator nests did not contain wax myrtle, despite its abundance in the surrounding pine flatwoods. At Ochlockonee, where no cypress was present, the storks relied upon black gum (*Nyssa biflora*) as their only nesting substrate and a frequent source of nest greenery. Ochlockonee nests also contained more northern Florida species of vegetation for nest greenery such as loblolly pine (*Pinus taeda*) and southern red oak (*Q. falcata*). All nests at freshwater sites regularly contained Spanish moss.

Greenery was similar in the nests at the marine-estuarine Moore Creek and Pelican Island sites (*S* = 63.16%; Table 3), but differed from the other four colonies. However, both Moore Creek and Pelican Island possessed relatively low intracolony similarity of nest greenery with nesting substrate vegetation because Wood Storks use the surrounding coastal strand vegetation as a source of nest greenery. Likewise, nests at the four freshwater sites exhibited low to moderate use of within-colony vegetation (*S* = 20.00–50.00%), whereas storks often used the surrounding upland vegetation as sources of nest greenery (*S* = 23.53–63.76%).

**Ectoparasite repellent experiment.**—The results of the nest ectoparasite repellent experiment indicate that dermestid larvae are not repulsed by the most frequently used greenery species (black gum, cypress, red cedar [*Juniperus silicicola*], poison ivy, red maple, wax myrtle, water oak [*Q. nigra*], and Virginia creeper). For three species (black mangrove [*Avicennia germinans*], summer grape [*Vitis aetivalis*], and Spanish moss), there even appeared to be an attraction to the vegetation side of the experimental containers. Thus, these plant species probably do not function in repelling dermestid larvae from Wood Stork nestlings.
<table>
<thead>
<tr>
<th>Species</th>
<th>Colony</th>
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<tbody>
<tr>
<td></td>
<td>Dee Dot</td>
</tr>
<tr>
<td>Longleaf pine (Pinus palustris)</td>
<td>8.8</td>
</tr>
<tr>
<td>Loblolly pine (P. taeda)</td>
<td></td>
</tr>
<tr>
<td>Bald cypress (Taxodium distichum)</td>
<td>14.7</td>
</tr>
<tr>
<td>Red cedar (Juniperus silicicola)</td>
<td>4.3</td>
</tr>
<tr>
<td>Saltmarsh cordgrass (Spartina alterniflora)</td>
<td>4.3</td>
</tr>
<tr>
<td>Grass sp. (Paspalum sp.)</td>
<td>37.2</td>
</tr>
<tr>
<td>Spanish moss (Tillandsia usneoides)</td>
<td>22.5</td>
</tr>
<tr>
<td>Australian pine (Casuarina equisetifolia)</td>
<td>3.2</td>
</tr>
<tr>
<td>Southern willow (Salix caroliniana)</td>
<td>1.0</td>
</tr>
<tr>
<td>Wax myrtle (Myrica cerifera)</td>
<td>70.6</td>
</tr>
<tr>
<td>Turkey oak (Quercus laevis)</td>
<td></td>
</tr>
<tr>
<td>Laurel oak (Q. laurifolia)</td>
<td>7.1</td>
</tr>
<tr>
<td>Species</td>
<td>Colony</td>
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<tr>
<td>---------------------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td></td>
<td>Dec Dot</td>
</tr>
<tr>
<td>Water oak (Quercus nigra)</td>
<td>20.6</td>
</tr>
<tr>
<td>Live oak (Quercus virginiana)</td>
<td>6.9</td>
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<td>Southern red oak (Quercus falcata)</td>
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<tr>
<td>Glasswort (Salicornia virginica)</td>
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<tr>
<td>Pigweed (Amaranthus hybridus)</td>
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<tr>
<td>Sweet gum (Liquidambar styraciflua)</td>
<td>2.0</td>
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<tr>
<td>Red maple (Acer rubrum)</td>
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</tr>
<tr>
<td>Brazilian pepperbush (Shinus terbinthifolius)</td>
<td></td>
</tr>
<tr>
<td>Poison ivy (Toxicodendron radicans)</td>
<td>12.7</td>
</tr>
<tr>
<td>Dahoon holly (Ilex cassine)</td>
<td>2.0</td>
</tr>
<tr>
<td>Virginia creeper (Parthenocissus quinquefolia)</td>
<td>1.0</td>
</tr>
<tr>
<td>Summer grape (Vitis aetivalis)</td>
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<tr>
<td>Species</td>
<td>Colony</td>
</tr>
<tr>
<td>-----------------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Red mangrove (Rhizophora mangle)</td>
<td>43.6</td>
</tr>
<tr>
<td>White mangrove (Laguncularia racemosa)</td>
<td>7.4</td>
</tr>
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<td>Black gum (Nyssa biflora)</td>
<td>4.3</td>
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<tr>
<td>Water ash (Fraxinus caroliniana)</td>
<td>41.2</td>
</tr>
<tr>
<td>Black mangrove (Avicennia germinans)</td>
<td>96.0</td>
</tr>
<tr>
<td>Swamp primrose (Aster dumosus)</td>
<td>96.8</td>
</tr>
<tr>
<td>Marsh elder (Iva frutescens)</td>
<td>42.6</td>
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<table>
<thead>
<tr>
<th></th>
<th>Dee Dot</th>
<th>Little Gator</th>
<th>Lake Yale</th>
<th>Moore Creek</th>
<th>Ochlockonee</th>
<th>Pelican Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of nests</td>
<td>105</td>
<td>94</td>
<td>68</td>
<td>95</td>
<td>108</td>
<td>80</td>
</tr>
<tr>
<td>Number of species of plants</td>
<td>14</td>
<td>9</td>
<td>7</td>
<td>7</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>Mean ± SD (species/nest)</td>
<td>1.91 ± 0.98</td>
<td>1.66 ± 0.88</td>
<td>2.15 ± 0.91</td>
<td>1.98 ± 0.77</td>
<td>1.64 ± 0.82</td>
<td>1.35 ± 0.61</td>
</tr>
<tr>
<td>Range (species/nest)</td>
<td>0–5</td>
<td>0–4</td>
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</tr>
<tr>
<td>Colony</td>
<td>Dee Dot</td>
<td>Little Gator</td>
<td>Lake Yale</td>
<td>Moore Creek</td>
<td>Ochlockonee</td>
<td>Pelican Island</td>
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<tr>
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<tr>
<td>Lake Yale</td>
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<td>25.00%</td>
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<tr>
<td>Moore Creek</td>
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<td>11.76%</td>
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</tr>
<tr>
<td>Ochlockonee</td>
<td>34.78%</td>
<td>23.53%</td>
<td>62.50%</td>
<td>10.53%</td>
<td>20.00%</td>
<td></td>
</tr>
<tr>
<td>Pelican Island</td>
<td>8.70%</td>
<td>0.00%</td>
<td>12.50%</td>
<td>63.16%</td>
<td>11.11%</td>
<td>46.15%</td>
</tr>
</tbody>
</table>

**Insulation experiment.** — The experiment on the insulation properties of Wood Stork nests indicate that the clean nests barely functioned to maintain internal temperatures above ambient temperatures (Fig. 3). The clean nests were able to maintain the internal egg/nest surface temperature only 1.5–2.5°C above ambient temperature during the evening hours. In contrast, the three experimental nests with greenery exhibited higher insulation properties, especially the intact and dried greenery nests. No significant difference existed in the temperature curves between the intact and dried greenery nests ($K_D = 2.5, P > 0.05$) or between the dried greenery and fresh greenery nests ($K_D = 5.5, P > 0.05$), but the temperature curves for the intact nests were significantly higher than for the fresh greenery nests ($K_D = 7.5, P < 0.05$). The temperature curves of all three nests containing greenery (i.e., intact, dried, and fresh) were significantly higher than the clean nests ($K_D = 9.5, 8.0, 7.5$, respectively; $P < 0.05$). The fresh greenery nests had lower insulative value during the early hours of the experiment. This may be due to the initially higher water content of the fresh greenery and resultant greater heat transfer through evaporation. Nevertheless, after drying for more than two hours (initial temperature stabilizing period prior to 18:00 EST plus two hours of experiment), the moisture content and associated heat loss was reduced, and the insulative value was similar to the intact and dried greenery nests by the end of the experiment (Fig. 3).

In a further attempt to determine the insulating properties of the four nest types, they were held at 7.0°C in a refrigerated room. The internal egg/nest surface interface of the clean, fresh greenery, dried greenery, and intact nests stabilized at 11.1°C, 16.3°C, 16.6°C, and 17.5°C, respectively.

**Thermal conductance.** — The calculated thermal conductance ($h$) values for the clean, fresh greenery, dried greenery, and intact nests were 9.05
DISCUSSION

Although we observed some Wood Stork eggs that were concealed, few eggs and no nestlings were hidden by nest greenery in a way that would prevent predation. Storks are subject to raccoon (*Procyon lotor*) and Fish Crow (*Corvus ossifragus*) predation, but one adult stork is usually at the nest during predation attempts.
nest to defend its contents. Furthermore, as neither eggs nor nestlings usually are covered by greenery material, shading does not appear to be important as suggested for other avian species (Bush and Gehlbach 1979). Parent storks shade the nest contents with their bodies or outstretched wings during warm periods of the day. The development of thick downy plumage and self-thermoregulation by nestling storks at 1–2 weeks of age (see Kahl 1963:149) coincides with the noticeable decrease in the addition of greenery material (Fig. 2).

Adult Wood Storks regularly defecate over the edge of the nest; however, nestlings often defecate in the nest, suggesting the possible role of greenery material in nest sanitation during the nestling period (e.g., Orians and Kuhlman 1956, Newton 1979). Since greenery deposition is initiated prior to egg deposition and declines with increase in nestling age, its sanitation role is at best restricted to the early nestling period when the chicks cannot stand off the nest. Nest greenery tends to prevent guano from passing through the nest twigs and thus the nest and nestlings become soiled. This fact reduces the plausibility of the nest sanitation hypothesis with regard to guano. One advantage of greenery may be associated with the feeding of young stork nestlings. Parent storks regurgitate food boluses on the floor of the nest near the young nestlings (Kahl 1964). The nestlings must find and consume the rather small food items. Thus, greenery material retains food on the nest surface for consumption by nestlings and improves nest sanitation by preventing the loss of small food down into the nest during the early nestling phase.

Wimberger (1984) hypothesized that nest greenery use by raptors aids in repelling ectoparasites via release of secondary compounds during drying or decay of the plant material. Clark and Mason (1985) found that European Starlings (Sturnus vulgaris) chose plants whose volatile compounds are likely to inhibit arthropod hatching (but not adult stage mites) and bacterial growth. The nature of some of the vegetation used by Wood Storks seems to support this hypothesis (e.g., the aromatic or resinous species in Table 1: cypress, red cedar, poison ivy, Brazilian pepperbush, pine sp., wax myrtle). However, the vegetation species we tested had little effect on dermestids. Wood Stork nestlings are subject to infestation by dermestid larvae (Snyder et al. 1984, pers. obs.), five species of biting lice (Emerson 1972), and numerous species of mites (pers. obs.) further discrediting the effect of nest greenery on ectoparasites. Effect of green vegetation on biting lice, mites, fleas, calliphorid or hippoboscid flies, ticks, fungi, and bacteria should be investigated to clarify this point. Inasmuch as intercolony similarity in use of plant species is low (Table 3), the other nonaromatic or nonresinous plants used for nest greenery probably reflect the most commonly available plants in the surrounding uplands, including the nesting tree.
Nest greenery may function in maintaining the Wood Stork pairbond and structural integrity of the nest. After completion of egg laying, the pairbond must be maintained for about 12–16 weeks in order to fledge the young. Use of ritualized nest-building behavior (Kahl 1972) in the form of returning to the nest and passing greenery probably functions in maintenance of the stork pairbond. Green twigs used to line the upper surface are more pliable than the basal, dead twig structure of the stork nest. After drying, the greenery becomes a rigid, entangled, and relatively smooth surface and may aid in stabilizing the nest structure. Finally, guano-coated twigs are noticeably more rigid and form an adobe-like structure in the upper surface of the nest, further suggesting a role in construction.

Though greenery may serve more than one function, we believe the results of the insulation experiment support a conclusion that the primary function of nest greenery is to enhance insulation of Wood Stork nests, or perhaps of any species with a twiggy, porous nest. Greenery may accomplish this by itself or in combination with guano to plug holes in the nest and prevent loss of heat from the eggs and incubating parent bird. Nest insulation depends on the materials used in its construction, and these materials, in turn, may depend on what is available to the bird (Whittow and Berger 1977, Skowron and Kern 1980, this study). Skowron and Kern (1980) found that the most important aspect of insulation was nest density, whereas Mertens (1977) concluded that dry material provided better insulation than fresh vegetation. Nest greenery, especially when dried and associated with guano, provides material of relatively high density and results in increased insulation of Wood Stork nests. Thus, greenery may be important in reducing the energetic cost of incubation and early brooding.

ACKNOWLEDGMENTS

We are indebted to the following individuals, corporations, and agencies for access to their property: J. E. Davis, D. Wilson, L. Fain, Golden Gem Growers, Inc., and Merritt Island National Wildlife Refuge and Pelican Island National Wildlife Refuge personnel. R. Bjork assisted with the ectoparasite repellent experiment. E. Farber, Department of Mechanical Engineering, University of Florida, was especially helpful in the design of the experimental apparatus and calculations for thermal conductance. We are grateful to D. Maehr, M. Kahl, H. Kale, C. Blem, P. Wimberger, and K. Bildstein for reviewing earlier drafts of the manuscript, and T. Steele for typing the manuscript.

LITERATURE CITED


FACTORS AFFECTING PIRACY IN HERRING GULLS AT A NEW JERSEY LANDFILL

ELIZABETH HACKL AND JOANNA BURGER

ABSTRACT.—We studied piracy among Herring Gulls (Larus argentatus) at a New Jersey landfill. We determined rates of attack with respect to species, age, and size of food item and rates of success with respect to species, age, size of food item, number of birds pursuing in each chase, and duration of chase. Rates of attack were affected only by size of the food item; birds carrying larger items were attacked more frequently than birds with smaller items. Rates of success were affected by size of the food item and the number of birds pursuing in each chase. Birds carrying larger items were attacked by more pirates than birds carrying smaller items. The probability that the host would drop the item increased with increasing numbers of pirates. Consequently, larger items were lost more frequently. Received 26 June 1987, accepted 16 Feb. 1988.

Piracy, an opportunistic foraging behavior that includes both interspecific and intraspecific food theft, has been noted in several orders of birds, most notably the Charadriiformes (Brockmann and Barnard 1979). The incidence of piracy is greater under high food and host densities (Dunn 1973, Hulsman 1984). The pirate spends less time searching for a host, and the host, if it loses its food item, can replenish itself relatively easily. Behavior by both pirate and host must balance the energetic value of the food item against costs of obtaining or retaining food items (Hulsman 1984). Some of the factors that have been noted as important to this balance are age and species of host and pirate (Moyle 1966; Verbeek 1977a, b; Burger and Gochfeld 1981), the size of the food item (Dunn 1973, Fuchs 1977, Hulsman 1984), number of pirates involved in a chase (Hatch 1975, Hulsman 1976, Verbeek 1977b), and duration of the chase (Hatch 1975). The present study examines costs and benefits of retaining or obtaining a food item for both host and pirate Herring Gulls (Larus argentatus). We tested the following null hypotheses: (1) There are no differences in rates of attack on a host as a function of the host’s age, species, or the size of the food item carried. (2) There are no differences in rates of success for the host as a function of the host’s age or species, the size of the food item carried, the number of pursuers in each chase, or the duration of the chase. (3) There are no differences in rates of success for the pirate as a function of the pirate’s age or species, the size of the food item carried by the host, the number of pursuers in each chase, or the duration of the chase.

1 Dept. Biological Sciences, Rutgers University, Piscataway, New Jersey 08855. (Present address EH: 469 Grant Ave., Apt. C, Palo Alto, California 94306.)
METHODS

We observed gulls at the Edgeboro landfill in East Brunswick, New Jersey, from 16 October 1986 to 21 January 1987. Garbage was dumped at Edgeboro daily. Several ponds and fields within 500 m of the dumping surface provided areas for loafing and eating the items carried from the dump. We observed pirating behavior at both the loafing areas and at the dump. For each gull flying away from the dump with food, we recorded the following: date, time, age and species of the host, size of the food item, whether or not it was attacked, the number of attackers, the age and species of the attackers, the age and species of the successful pirate, the outcome of the chase, and the duration of the chase. The age of each gull was determined from the plumage. Young birds were those that had dark mottled coloration of the back and mantle. The head, neck, tail, and underparts had slightly lighter coloration but were thickly streaked with darker color. The tail had a dark terminal band or dark blotches. Subadult birds were those that were less mottled than young gulls. The head, neck, tail, and underparts were lighter than those of the young gulls but still had remnants of dark streaking. The tail band or blotches were smaller than in young gulls. Adult birds were those that had clear dark coloration of the back and mantle. The head and neck were white with hints of streaking. The tail and the underparts were entirely white (Dwight 1925).

The size of the food item was estimated in comparison with the length of the host's bill. The following are the bill length measurements used to normalize the size of the food item between different species: Greater Black-backed Gull (L. marinus), 6.3 cm; Herring Gull, 5.8 cm; Ring-billed Gull (L. delawarensis), 4.1 cm; and Laughing Gull (L. atricilla), 3.9 cm. Length measurements of the bill were taken from averages of measurements listed for male and female specimens of each species by Dwight (1925).

Gulls carrying items could fly to the ponds or to the loafing area adjacent to the dumping face or could be chased in the air. Piracy attempts in the air were recognized by the closely associated flying patterns of two or more birds. Piracy attempts on the ground were noted when one or more birds ran, with wings spread, towards the host. Data were recorded on both air and ground attempts. The result of the attacks were recorded with respect to the pursuers. Results of piracy included: an unsuccessful attempt = host retained the item; a lost attempt = pirates caused host to drop the item which was not recovered by any of the pursuers; and a successful attempt = one of the pirates (subsequently designated the successful pirate) obtained the food item.

The duration of a piracy attempt was measured by stopwatch from the tapes of the observations. Observations began when birds attacked the host. Observations for a chase ended when the item was eaten by the host, lost, or the pirates dispersed leaving the host with the item. Any secondary attack on the host was discarded to eliminate the complication of the previous outcome on the ensuing chase. Some data obtained from Greater Black-backed, Ring-billed, and Laughing gulls were included in this study for the sake of completeness. However, sample sizes were often too small for statistical analysis.

Data were analyzed using Kruskal-Wallis $\chi^2$ tests to distinguish differences among means. Pearson correlations were used to examine relationships between variables.

RESULTS

Types of piracy.—Gulls carried food items that ranged in size from 5 cm$^3$ to 100 cm$^3$ ($\bar{x} = 19.65 \pm 0.62$ cm$^3$ [SE], N = 401). Pirates tried to obtain a food item by grabbing it from the bill of the host or by grabbing the wings or the back of the host, causing the host to drop the item. Piracy attempts in the air varied from simple plunges at the host lasting only 1
sec. to more complex chases that could last for up to 100 sec. ($\bar{t} = 11.79 \pm 0.89$ sec [SE] N = 254). During ground attempts, a lunge from a neighbor was sometimes enough to displace the host, and at other times a tug-of-war over the food item ensued between the host and a pirate. The number of birds involved in both air and ground chases varied from 1 to 15 ($\bar{t} = 2.14 \pm 0.12$, N = 254). All host species were chased by conspecifics more often than by other species (Table 1). Chases were usually accompanied by vocalizations of the birds involved.

Rates of attack on the host.—Different species carried different sized food items from the dump ($\chi^2 = 12.26$, df = 3, $P < 0.006$, N = 401). Greater Black-backed Gulls carried larger food items than Herring Gulls ($\chi^2 = 2.04$, df = 1, $P < 0.04$, N = 376) or Ring-billed Gulls ($\chi^2 = 3.34$, df = 1, $P < 0.0008$, N = 44) but there was no difference between the sizes of items carried by Greater Black-backed and Laughing gulls ($\chi^2 = 1.90$, df = 1, $P < 0.06$, N = 39). Herring Gulls carried larger items than Ring-billed Gulls ($\chi^2 = 2.57$, df = 1, $P < 0.01$, N = 362). There was no difference in the size of items carried by Herring and Laughing gulls ($\chi^2 = 0.86$, df = 1, $P < 0.39$, N = 357) or by Laughing and Ring-billed gulls ($\chi^2 = 1.28$, df = 1, $P < 0.2$, N = 25). There were also no differences in the size of items carried by different age groups among Herring Gulls ($\chi^2 = 2.03$, df = 2, $P < 0.3$, N = 347).

All species were attacked at similar rates ($\chi^2 = 6.25$, df = 3, $P < 0.1$, N = 233). All Herring Gull age groups were attacked at similar rates ($\chi^2 = 1.17$, df = 3, $P < 0.5$, N = 209). Sample size was too small for analysis of the other species. In general, gulls carrying larger food items were attacked more often than gulls carrying smaller food items ($\chi^2 = 50.38$, df = 1, $P < 0.0001$, N = 401, Table 2). Specifically, this was true for Greater Black-backed Gulls ($\chi^2 = 6.08$, df = 1, $P < 0.01$, N = 29) and Herring Gulls ($\chi^2 = 46.29$, df = 1, $P < 0.0001$, N = 348), but not for Ring-billed Gulls ($\chi^2 = 0.73$, df = 1, $P < 0.4$, N = 15). Laughing Gulls were always attacked.

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>L. marinus</th>
<th>L. argentatus</th>
<th>L. delawarensis</th>
<th>L. atricilla</th>
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</thead>
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<tr>
<td>L. marinus</td>
<td>55.9%</td>
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<td>24.1%</td>
<td>69.4%</td>
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<tr>
<td>L. delawarensis</td>
<td>15.4%</td>
<td>15.4%</td>
<td>69.2%</td>
<td>0%</td>
</tr>
<tr>
<td>L. atricilla</td>
<td>0%</td>
<td>10.3%</td>
<td>0%</td>
<td>89.7%</td>
</tr>
</tbody>
</table>
Rates of success for the host.—There were no differences in the percentage of items retained and eaten by different host species when attacked ($\chi^2 = 2.44, df = 3, P < 0.5, N = 261$). There were also no differences in the percentage of items retained and eaten by different age groups among Herring Gulls when attacked ($\chi^2 = 2.45, df = 2, P < 0.3, N = 207$). All of the species and all of the age groups among Herring Gulls kept food items more than 50% of the time when attacked.

Herring Gull hosts lost large items more frequently than small items ($\chi^2 = 26.49, df = 7, P < 0.01, N = 207$). Sample size was too small for analysis of other species. Herring Gull hosts were also more likely to lose their food item when chased by increasing numbers of pirates ($\chi^2 = 26.02, df = 4, P < 0.001, N = 212$). The success of the host was not related to the duration of the chase ($\chi^2 = 1.79, df = 2, P < 0.4, N = 233$). Sample size was again too small for analysis of other species.

Rates of success for the pirate.—There were no differences in the frequency that each species was a successful pirate ($\chi^2 = 3.02, df = 3, P < 0.5, N = 479$) or in the frequency that each age group among Herring Gulls was a successful pirate ($\chi^2 = 0.047, df = 2, P < 0.9, N = 292$). Once a pirate attacked, the size of the food item was not related to the success of the pirate ($\chi^2 = 3.58, df = 2, P < 0.2, N = 254$). Nor was the duration of the chase related to the success of the pirate ($\chi^2 = 1.79, df = 2, P < 0.4, N = 233$). The number of pursuers for each chase, however, was related to the success of the pirate ($\chi^2 = 22.71, df = 2, P < 0.0001, N = 254$). More birds were involved in successful chases and chases in which the food item was lost to both the pirate and the host than in chases.

### Table 2

Ranges and Means of Item Sizes Attacked and Not Attacked for Different Species and Item Size to Bill Length Ratio

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Range (cm$^3$)</th>
<th>Mean (cm$^3$)</th>
<th>±SE</th>
<th>Bill length (cm)</th>
<th>Size/length ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. marinus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(not attacked)</td>
<td>11</td>
<td>10-25</td>
<td>16.36</td>
<td>0.65</td>
<td>6.3</td>
<td>2.5</td>
</tr>
<tr>
<td>(attacked)</td>
<td>18</td>
<td>10-100</td>
<td>31.67</td>
<td>5.03</td>
<td>5.0</td>
<td>5.0</td>
</tr>
<tr>
<td>L. argentatus</td>
<td>138</td>
<td>5-45</td>
<td>14.42</td>
<td>0.71</td>
<td>5.0</td>
<td>2.9</td>
</tr>
<tr>
<td>(not attacked)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(attacked)</td>
<td>209</td>
<td>5-70</td>
<td>22.99</td>
<td>0.87</td>
<td>4.6</td>
<td>4.6</td>
</tr>
<tr>
<td>L. delawarensis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(not attacked)</td>
<td>6</td>
<td>5-15</td>
<td>10.00</td>
<td>1.29</td>
<td>4.1</td>
<td>2.4</td>
</tr>
<tr>
<td>(attacked)</td>
<td>9</td>
<td>5-20</td>
<td>13.33</td>
<td>2.36</td>
<td>3.2</td>
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<tr>
<td>L. atricilla</td>
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<td></td>
</tr>
<tr>
<td>(not attacked)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(attacked)</td>
<td>10</td>
<td>5-25</td>
<td>15.50</td>
<td>2.03</td>
<td>3.9</td>
<td>4.0</td>
</tr>
</tbody>
</table>
in which the host retained the food item. There was also a positive correlation between the size of the food item carried by Herring Gulls and the number of birds pursuing in each chase \((r = 0.236, P < 0.001, N = 207)\).

**DISCUSSION**

Hypothesis 1 is supported with respect to the host’s species and age groups among Herring Gulls, but not with respect to item size. Hypothesis 2 is supported with respect to species, age, and duration of the chase, but not with respect to item size and number of birds chasing for each chase. Hypothesis 3 is supported with respect to the pirate’s species, age, the food item size, and the duration of the chase, but not with respect to the number of birds pursuing in each chase.

**Host and pirate frequency.** — It seemed likely that smaller species would be hosts more frequently than larger species and pirates less frequently than larger species, based on the greater strength (i.e., ability to carry larger food items) of the larger species. However, we did not find this to be true; all species exhibited similar frequencies as a host and as a successful pirate. This disagrees with the findings of Verbeek (1977b) who found species-related differences in the use of piracy and of Burger and Gochfeld (1981) who found both species-related differences and age-related differences in the use of piracy. The similar frequencies in our study might be attributed to smaller species being more agile flyers, capable of outmaneuvering larger species, making it more difficult for the larger species to harass the smaller species (Burger and Gochfeld 1981). Another possibility is that smaller species do not carry large enough items to warrant attack by larger species. Indeed, we found that smaller species carried smaller food items. Conversely, smaller species might have difficulty obtaining a food item from a larger species, even though the smaller species were capable of harassment, because of the greater strength of the larger species. Yet another possible explanation may be related to our finding that hosts were chased primarily by conspecifics. This preference by the pirate may have been more important in host selection than the size of the host. Stealing from conspecifics may be preferable because of equal strength, maneuverability, and energy needs.

It also seemed likely that the young, less experienced birds would be hosts more frequently and be pirates less frequently than older birds. We did not find this to be true. All age groups among Herring Gulls exhibited similar frequencies as a host and as a successful pirate. Adults may have been less likely to steal food from young birds because of the feeding relationship that existed between young and adult birds during the fledging period. Similarly, adult birds may tolerate piracy by young birds for the
same reasons. Moyle (1966) found that young Glaucous-winged Gulls (L. glaucescens) did not react, while subadult gulls did, to adult threat displays. Furthermore, adults were usually found in the company of younger gulls while they avoided the company of other adults.

Effects of item size.—In general, larger species carried larger food items away from the dump than those carried by smaller species, presumably because larger species are more aerodynamically capable of carrying larger food items and have greater energy requirements than smaller species. Birds carrying larger items were also attacked more often than those with smaller items. Similar results were found in studies of Arctic (Sterna paradisae) and Common terns (S. hirundo) (Hopkins and Wiley 1972). This preference is beneficial because of the greater energy gained from larger food items, and may be explained by greater visibility of larger items. A pirate must first find a host before attacking, and a large food item is more conspicuous than a small one.

Herring Gulls lost large food items more frequently to pirates than smaller items. It is more difficult for a host to hold a larger item than a smaller one. Larger items have a larger surface area and might be more easily grabbed whole or torn into pieces by a pirate (Burger and Gochfeld 1981). The greater loss of larger food items may also be attributed to the greater number of pirates in each chase involving larger items. This was found to be true for Arctic and Common terns (Hatch 1975), Lesser Black-backed (L. fuscus) and Herring gulls (Verbeek 1977b). A host evading one pirate has many directions in which to flee, but a host being chased by many pirates has far fewer choices. The more birds involved in the chase, the more intense the harassment of the host, causing it to drop food more frequently.

Costs and benefits to the host and to the pirate.—Larger food items contain more energy but are also more likely to elicit attack. One might expect hosts to carry food items at the best benefit/cost ratio between energy gained and vulnerability to attack. A very small item may never elicit attack but may also be too small to recoup the energy necessary for the trip to the dump. Conversely, a very large item may be worthwhile energetically but is more likely to be lost to a pirate. The optimal item size should be represented by the mean size of items successfully carried away from the dump, roughly 2.6 times the length of the host’s bill (Table 2, last column).

Pirates have a similar dilemma. Large items are energetically preferable, but usually elicit attacks from more than one bird. Theoretically, pirates should attack the host carrying the item size that is large enough energetically to balance the cost of competition among multiple pirates. This size should be greater than the mean size carried by the host because
larger items would be more worthwhile energetically. The mean size of items attacked was, indeed, larger than the mean size of items carried for both Herring Gulls and Greater Black-backed gulls (Table 2).

ACKNOWLEDGMENTS

We thank T. Casey and J. Applegate for carefully reviewing the manuscript, and M. Caffrey for computer aid.

LITERATURE CITED


ABUNDANCE OF GULLS AT TAMPA BAY LANDFILLS

STEPHEN R. PATTON

ABSTRACT.—I censused Herring, Ring-billed, and Laughing gulls (Larus argentatus, L. delawarensis, L. atricilla) at two landfills near Tampa Bay, Florida, from October 1981 to April 1984. Gulls were most abundant during mid-winter; Herring and Ring-billed gulls were nearly absent from landfills from May through October. At least 90,000 gulls foraged at seven bay-area landfills during January and February. Landfills appear to be an important food resource for all three gull species wintering on the west-central coast of Florida. Changing waste disposal practices from landfilling to incineration are likely to affect them greatly. Received 1 Aug. 1987, accepted 15 Jan. 1988.

Food resources at urban landfills have been implicated in increased abundance of gulls throughout North America and Europe (e.g., Drury and Nisbet 1972, Mudge and Ferns 1982, Patton and Hanners 1984). In some regions, gull populations apparently have reached a maximum, either because of human control measures (Coulson et al. 1982) or because a new carrying capacity has been reached (e.g., Drury and Kadlec 1974). Gull populations inflated artificially by waste disposal practices may threaten human health (e.g., salmonellosis, Butterfield et al. 1983), be a public nuisance (Blokpoel and Tessier 1986) or a hazard to aircraft (Blokpoel 1976). They also are agricultural pests (Blokpoel and Tessier 1986), and threaten other species of birds (Blokpoel and Tessier 1986). The objectives of the present study were to identify the seasonal patterns of occurrence of Herring, Ring-billed, and Laughing gulls (Larus argentatus, L. delawarensis, L. atricilla) at landfills in the Tampa Bay area and to assess the importance of these landfills to gulls. Census results presented in this paper provide a baseline from which the effects of changing waste disposal practices on gull populations in the Tampa Bay area can be assessed.

STUDY SITES AND METHODS

I censused gulls primarily at two landfills. Toytown landfill, Pinellas County, Florida, was visited regularly from October 1980 until it closed in May 1983. This 116-ha site was 4.5 km west of Tampa Bay and 19 km east of the Gulf of Mexico. The Hillsborough Heights landfill, Hillsborough Co., Florida, was studied from February 1982 to April 1984. This 63-ha site is 17.3 km northwest of Tampa Bay. I also censused all gulls at five other small Tampa Bay area landfills on a less regular basis during this study. Detailed site descriptions can be found in Patton (1986).

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From October 1981 to May 1983, I conducted one or more counts per month (x = 2.3) of all gulls on the active dumping surface of the Toytown landfill as well as at nearby gull loafing areas. Day-long visits to the landfill during the previous 12 months indicated that few gulls arrived at the landfill after 12:00 h and most gulls did not depart from the landfill or the surrounding loafing areas until after 15:00 h. Therefore, I started all censuses around 12:00 h, each lasting 1–2 h, depending on the number of gulls present. Although I suspect that daily variation existed in the number of gulls foraging at Toytown and Hillsborough Heights (e.g., Schreiber 1968, Kihlman and Larsson 1974), data presented in this paper provide a relative picture of the seasonal patterns of landfill use by each gull species.

For the purposes of this study, I recognized three age classes of Laughing and Ring-billed gulls, and four age classes of Herring Gulls using plumages described by Dwight (1925). The first day in June was chosen as the date when gulls passed to their subsequent age class because it approximates the date of hatching for all three species in North America (Schreiber et al. 1979, Southern et al. 1985); this date also has been used in other studies of gulls (Southern 1974a, b; Moore 1976). I estimated the age class distribution of each gull species at the landfills by recording the age classes of 5–20% of the gulls in each flock. In small flocks (< several hundred birds) I recorded the age classes of 50–100% of the individuals.

**RESULTS**

Gulls at the Toytown landfill exhibited seasonal changes in numbers of birds present and species composition (Fig. 1). Peak numbers of gulls present at mid-day in January and February were more than five times greater than the number of gulls present during the same time in May or June (Fig. 1). From May through October, more than 97% of the gulls present at Toytown were Laughing Gulls; less than 200 Herring and Ring-billed gulls were present during these months (N = 9 censuses). November and December marked a transition from the essentially monospecific assemblage of gulls in summer and the peak numbers of all three species observed in January and February. Between November and January, most of the increase in the number of gulls was attributable to an increase in the number of Ring-billed and Herring gulls (Fig. 1).

In January and February, all three species of gulls were at or near peak abundance at Toytown, with Ring-billed Gulls roughly equal in number to Laughing Gulls; the mean ratio of Ring-billed Gulls to Laughing Gulls was 1.0–1.1 (±0.2, SD) on 11 censuses in January and February of 1982 and 1983. Herring Gulls also reached peak abundance in January and February, but represented less than 18% of the total number of gulls. The number of gulls at Toytown decreased in March and April. By 19 April 1983, only 43, 8, and 18%, respectively, of the Laughing, Ring-billed, and Herring gulls present during the last week of February, remained at Toytown.

Prior to the closing of the Toytown landfill, about 15,000 gulls foraged at the Hillsborough Heights landfill in winter (11 February 1983 census, Table 1). Ring-billed and Laughing gulls were the two most common species (52 and 46%, respectively) and Herring Gulls made up the dif-
Fig. 1. Monthly censuses of gulls at the Toytown landfill, October 1981–May 1983. Vertical bars represent the average number of each species counted during each month. No censuses were made during November 1981 and August 1982. a—fewer than 200 Herring and Ring-billed gulls present.

ference (2%). After Toytown closed, the Hillsborough Heights landfill was censused regularly from June 1983 to April 1984. Following the closing, gulls at Hillsborough Heights exhibited a threefold increase between winter 1983 and winter 1984 (Table 1). The largest share of this increase was attributable to Laughing Gulls, which nearly quadrupled in number; Herring Gulls increased more than fivefold, but the number of Ring-billed Gulls only doubled. Total numbers of gulls at Hillsborough Heights in April 1984 were larger than in April 1983. Most of this increase resulted from a doubling in the number of Laughing Gulls present at Hillsborough Heights in spring 1984.

Herring Gulls were about 3.5 times more abundant at Toytown in January 1983 than at Hillsborough Heights in January 1984. During February, Herring, Ring-billed, and Laughing gulls were about 2.4, 1.7, and 1.8 times more abundant at Toytown in 1983 than at Hillsborough Heights in 1984. Laughing Gulls were less abundant at Hillsborough Heights during September through November 1983 than during the same months at Toytown in 1982 (Figs. 1 and 2).

After the Toytown landfill closed, gulls also increased at five of the six other landfills (Table 2). At the sixth site, the number of gulls present in 1984 was 27% of the total present in 1983 (Table 2). This was correlated with the loss of the primary gull loafing area adjacent to the landfill. In spite of the closing of the Toytown landfill in May 1983, the number of Laughing Gulls at Tampa Bay area landfills in January 1984 increased by about 19%, and that of Ring-billed Gulls increased by about 5% over
### TABLE 1


<table>
<thead>
<tr>
<th></th>
<th>Laughing Gull</th>
<th>Ring-billed Gull</th>
<th>Herring Gull</th>
<th>All species</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Winter</td>
<td>Spring</td>
<td>Winter</td>
<td>Spring</td>
</tr>
<tr>
<td>Toytown 983</td>
<td>24475</td>
<td>11500</td>
<td>27359</td>
<td>1600</td>
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<td>Hillsborough Heights</td>
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<td></td>
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<tr>
<td>1983</td>
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<td>5400</td>
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<td>1323</td>
</tr>
<tr>
<td>1984</td>
<td>26340</td>
<td>12150</td>
<td>17900</td>
<td>1425</td>
</tr>
<tr>
<td>Percent change</td>
<td>&gt;290</td>
<td>&gt;125</td>
<td>&gt;136</td>
<td>&gt;8</td>
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</table>

Fig. 2. Monthly censuses of gulls at the Hillsborough Heights landfill, June 1983–April 1984. Vertical bars represent the average number of each species counted during each month.

that recorded in the previous year. Only Herring Gulls showed a decrease (~2000 birds, 29%) between 1983 and 1984. Of the six landfills used by gulls in both years, two showed substantially larger increases in 1984 than the other four. The number of gulls at the Manatee County and Hillsborough Heights landfills increased by fifteenfold and fourfold, respectively. Perhaps not coincidentally, except for the very small Waste Aid landfill in Pasco County, these two landfills were the closest landfills to the Toytown landfill, and both sites were less than 22 km from nighttime roosting sites on Tampa Bay and the Gulf of Mexico.

Censuses of gulls at all Tampa Bay area landfills in January 1983 and February 1984 revealed that at least 90,000 gulls foraged at these sites (Table 2). Ring-billed and Laughing gulls made up 49–51% and 41–46%, respectively, of the total number of gulls counted at these landfills, whereas Herring Gulls accounted for only 5–8% of the total.

Juvenile Laughing Gulls comprised about 1% of the Laughing Gulls present at Toytown in July, but by September had increased to about 17% of the Laughing Gulls present; they remained near that percentage (12–17%) through February (Fig. 3). Numbers of juveniles decreased in April, when they represented only 7% of the total count (Fig. 3). From June to September 1982, the abundance of second-year Laughing Gulls decreased (Fig. 3), probably as a result of gulls passing through second prebasic molt into adult-like second basic plumage. For the remainder of the year, this age-class represented less than 2% of the total Laughing Gull count.
### Table 2

Census Data for Seven Landfills Before and After Closure of the Toytown Landfill

<table>
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<tr>
<th></th>
<th>Laughing Gull</th>
<th></th>
<th>Ring-billed Gull</th>
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<th>Herring Gull</th>
<th></th>
<th>All species</th>
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<tr>
<td></td>
<td>Before</td>
<td>After</td>
<td>Before</td>
<td>After</td>
<td>Before</td>
<td>After</td>
<td>Before</td>
<td>After</td>
</tr>
<tr>
<td>Toytown</td>
<td>19,500</td>
<td>-</td>
<td>22,450</td>
<td>-</td>
<td>5800</td>
<td>-</td>
<td>47,800</td>
<td>-</td>
</tr>
<tr>
<td>Hillsborough County</td>
<td>6750</td>
<td>26,340</td>
<td>7600</td>
<td>17,900</td>
<td>400</td>
<td>2200</td>
<td>14,750</td>
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</tr>
<tr>
<td>Manatee County</td>
<td>1200</td>
<td>9700</td>
<td>550</td>
<td>14,600</td>
<td>100</td>
<td>2000</td>
<td>1850</td>
<td>26,300</td>
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<td>3800</td>
<td>0</td>
<td>200</td>
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<td>11,500</td>
<td>3150</td>
<td>600</td>
<td>0</td>
<td>15,100</td>
<td>3450</td>
</tr>
<tr>
<td>Total</td>
<td>38,450</td>
<td>47,440</td>
<td>47,950</td>
<td>50,400</td>
<td>7375</td>
<td>5200</td>
<td>93,775</td>
<td>103,040</td>
</tr>
</tbody>
</table>
Fig. 3. Age class distributions of Herring, Ring-billed and Laughing gulls at the Toytown landfill, June 1982–May 1983. Vertical bars represent the average number of each age class estimated during each month. No census was taken during August 1982.
From June to September 1982, the only Ring-billed Gulls present at Toytown had just entered their second year. The first increase of adult- and juvenile-plumaged Ring-billed Gulls occurred in the Tampa Bay area during October, when they represented less than 1% of the total number of gulls. In November and December, the number of Ring-billed Gulls increased rapidly, with juveniles comprising a greater portion of this increase in November, and adults increasing more rapidly in December (Fig. 3). Both age classes approximately tripled in abundance between December and January. Ring-billed Gulls were at peak abundance in January and February with adults representing up to 86% (22 February 1983 census) of the gulls present. In spring 1983, their numbers decreased rapidly, from 14,200 on 29 March to 2500 on 12 April. The proportion of adults present at Toytown decreased during spring, compared to an increase in the proportion of first- and second-year birds. These results indicate that adult Ring-billed Gulls departed earlier than did first- and second-year gulls. By mid-April, adult Ring-billed Gulls were nearly absent from Toytown (<20 adults present) compared to more than 1400 first-year and 150 second-year gulls.

From May through October 1982, Herring Gulls were essentially absent from Toytown (Fig. 3). In October, the first juvenile-, subadult-, and adult-plumaged Herring Gulls arrived at Toytown, but they numbered fewer than 100. The number of Herring Gulls increased from about 350 on 19 October to 1150 on 12 November, but did not reach peak abundance until January. First-year Herring Gulls outnumbered adult Herring Gulls during every month but November from October 1982 through May 1983. Adults reached peak abundance in January and February, when they represented 34% and 44%, respectively, of the total number of Herring Gulls. As was true with Ring-billed Gulls, the proportion of first-year Herring Gulls increased in spring (67% in March, 86% in April), compared with a decrease shown by adults (19% in March, 1% in April). The relative abundance of second-year gulls remained the same in April as in March (9%), but this percentage was higher than for the winter season (6%). By May, fewer than 25 Herring Gulls remained at the landfill; most of those present (87%) were in their first year. Third-year Herring Gulls were uncommon during all months of the year, representing less than 6% of the total number of Herring Gulls at Toytown from November through April.

DISCUSSION

Migration patterns.—Banding data from Herring Gulls on the Great Lakes and northeast Atlantic coast indicate that Herring Gull migratory movements are initiated in November and December, and the southern
extremes of their winter range are occupied in January and February (Drury and Nisbet 1972, Moore 1976). Moore (1976) found that <1% of adult Great Lakes Herring Gulls winter as far south as the south Atlantic and Gulf coasts of the United States, but juveniles and subadults migrate farther than adults and winter on these coasts. Return migration northward is initiated in late February (Moore 1976, Southern 1980) with juveniles and subadults lingering at southerly latitudes into March and April.

Banding studies of Ring-billed Gulls on the Great Lakes have shown that fall dispersal from the breeding colonies begins in late July and August, with the major push towards southern localities occurring during November and December (Southern 1974a, b). Juvenile and subadult Ring-billed Gulls begin to arrive on the Florida Gulf coast earlier in fall and depart later in spring than adults (Southern 1974b). Peak numbers of Ring-billed Gulls occur in Florida during January and February (Southern 1974b, 1980). Most adult Ring-billed Gulls migrate back to their Great Lakes colony sites during March and April (Southern 1974a, 1980). These results parallel the pattern of Ring-billed Gull abundance I recorded at landfills.

Little is known about the seasonal distribution pattern of Laughing Gulls on the Florida Gulf coast. Banding data indicate that a substantial proportion of Laughing Gulls wintering in the Tampa Bay area are summer residents, but that wintering birds also come from breeding colonies located farther north on the Atlantic and Gulf coasts (Southern 1980, Patton, unpubl. data). First-year Laughing Gulls tend to migrate farther south than adults in winter (Patton, unpubl. data). This tendency may explain the drop in the relative abundance of first-year Laughing Gulls at Toytown between February and March. Also contributing to this reduction is the lower annual survivorship of first-year gulls compared with that experienced by adults (Ludwig 1967, Kadlec and Drury 1968).

The small number of Laughing Gulls present at Toytown in May (<5000 in 1982 and 1983) may be attributed to their presence at several colony sites in Tampa Bay. Laughing Gulls establish nesting territories and begin to lay eggs in mid- to late April; the peak of egg laying occurs during early to mid-May (Schreiber et al. 1979, Hanners, pers. comm.). During this period, both members of the pair remain near their territories (Hanners, pers. comm.), explaining their absence as loafers at the landfills.

**Interspecific comparisons.**—Although the timing of arrival and departure of Herring and Ring-billed gulls in the Tampa Bay area was similar, these species were markedly different with respect to the relative abundance of age classes in Florida. Whereas adult Ring-billed Gulls present at Toytown during January and February greatly outnumbered juveniles,
juvenile Herring Gulls were more abundant than adults during every month of the year except November. In contrast to Herring and Ring-billed gulls, more than 80% of the Laughing Gulls present at Toytown were adults during every month of the year.

A pattern that emerges from these results is that first-year gulls are proportionately more abundant in the southern extent of a particular species’ range. Tampa Bay is near the southern limit of the Herring Gull’s primary winter range in North America and near the center of the winter range for Ring-billed Gulls. By contrast, Laughing Gulls range widely through coastal Central and northern South America. Differences in the relative abundances of age-classes among these species reflect interspecific differences in the winter ranges of these species.

Closure of the Toytown landfill altered the distribution of gulls wintering in the Tampa Bay area. Laughing Gulls increased at three of five remaining bay-area landfills in 1984 following the closure of Toytown, and their total numbers increased by more than 9000 (23%). This overall increase at the landfills probably was attributable in part to their continued increase in number as a summer resident in the bay-area (Patton and Hanners 1984).

Ring-billed Gulls increased in number (5%) at five of six bay-area landfills in 1984 following the closure of Toytown; their increase was small compared with that shown by Laughing Gulls. Daily or weekly fluctuations in numbers of gulls present at landfills probably can account for most of this increase. Population size on their breeding range in the Great Lakes has been difficult to assess in recent years because record high water levels have caused major shifts in the distribution of gulls, and many gulls may have been unable to obtain sites for nesting (W. E. Southern, pers. comm.).

Only Herring Gulls decreased in number (29%) at bay-area landfills following the closure of the Toytown landfill. Records from Christmas Bird Counts suggest that Herring Gulls occur south of Tampa Bay in small numbers; and seldom fly far inland.

At least 90,000 gulls, primarily Laughing and Ring-billed, foraged at Tampa Bay area landfills in January 1983 and February 1984; more than 50,000 were at Toytown alone. Since this study was initiated, three waste-to-energy refuse plants have been built in Hillsborough and Pinellas counties. Similar waste management practices are being proposed in some of the adjoining counties. The amount of garbage being landfilled in the Tampa Bay area already has been reduced significantly, and further major reductions are anticipated during the next five years in spite of expected growth of the human population.

Burning urban waste greatly diminishes the need for landfills and, con-
sequently, two bay-area landfills have closed (Toytown, Hillsborough Heights). Those landfills that service areas with waste-to-energy plants bury primarily ashes produced by refuse incineration. Monaghan et al. (1986) demonstrated that partially incinerated waste was less attractive to Herring Gulls than garbage that had not been incinerated. My observations of landfills that bury completely incinerated garbage suggest that this material is unusable by gulls.

Changes in waste management practices in the Tampa Bay area are likely to have major consequences on the abundance and distribution of gulls on the west-central coast of Florida. The closure of the Toytown landfill in Pinellas Co., Florida, resulted in substantial increases in the number of gulls at neighboring landfills during the following year. As more landfills close and the amount of refuse that is landfilled without burning dwindles, gulls in west-central Florida will be forced to winter elsewhere or find alternative food resources. Ultimately, these changes may result in lower overwinter survival of all three species. The long-term consequences of changes in waste management practices that are taking place in the Tampa Bay area as well as in urban centers throughout North America may be significant declines in abundance of species whose populations previously were inflated by this abundant food resource.

ACKNOWLEDGMENTS

I thank J. Ryder, R. Schreiber, W. Southern, G. Woolfenden, my Graduate Committee, and the ornithology discussion group at the Univ. of South Florida for critically reviewing drafts of this manuscript. My studies have benefited greatly from discussions with L. Hanners, W. Hoffman, W. Southern, and G. Woolfenden. The help of L. Hanners with many of the censuses is greatly appreciated. This study was supported in part by a Chapman Memorial Grant (10044) and by the Hillsborough County Dept. of Solid Waste (Contract no. 54420).

LITERATURE CITED


REPRODUCTIVE ECOLOGY OF THE
RUDDY GROUND-DOVE ON THE
CENTRAL PLATEAU OF BRAZIL

RENATO CINTRA

Abstract.—The reproductive ecology of the Ruddy Ground-Dove (Columbina talpacoti) was studied between January 1982 and February 1983 in the Cerrado of the Central Plateau of Brazil. A total of 218 nests were found in 19 plant species, at heights ranging from ground level to 7.5 m. Nest construction was observed in all months except October. Some pairs reared a second clutch in the same nest in the same year. There was no significant difference between the sexes in nest defense behavior. The median clutch size of 200 nests was two. Fledglings remained with their parents for 25 days. One reached sexual maturity three months after hatching. The average daily mortality rate of eggs based on the Mayfield (1961, 1975) method was lowest (2.8%) in April–May and highest (8%) in November–December. The mean rate of daily egg mortality rate in all nests over the year was 4.4%. The total daily mortality rate of nestlings was (3.8%), ranging from (1.0%) in August–September to (5%) in February–March. There was a significant difference in the rate of predation on eggs and on nestlings. The highest rate of predation occurred during the peak of fledgling production. The probability of a nestling remaining in the nest until fledging was 63.3% and the probability of the nestling surviving from laying to fledging was 36.7%. At the end of incubation, there was an average of 1.2 eggs per nest and a mean of 0.7 nestlings per nest fledged. Received 24 Aug. 1987, accepted 5 Jan. 1988.

The Ruddy Ground-Dove (Columbina talpacoti) ranges from southern Texas (Shiflet 1975) to northern Argentina (Meyer de Schauensee 1966.) It can be found in natural habitats, such as forest, cerrado, and marshes, as well as on ranches and farms. Although the biology of the Ruddy Ground-Dove has been studied (Haverschmidt 1953, Skutch 1956, Carvalho 1957, Trollope 1974, Oniki and Willis 1983), little is known of the nesting ecology and reproductive success of the species. Much of the available literature is qualitative, and none involves studies over the entire breeding season. In the present paper I present quantitative data on nests, eggs, clutch size, nest defense, nestlings, fledglings, and breeding success of a population of Ruddy Ground-Doves in Brazilian cerrado.

STUDY AREA AND METHODS

The study was conducted between January 1982 and February 1983 on Fazenda Agua limpa, 30 km south of Brasilia, Brazil (15°55'S, 48°00'W). In Brasilia there are two climatic seasons: the dry season between June and September, and the wet season from October to May. The study area comprised 6.5 ha, of which 2 ha was coffee plantation (Cupressus sp.), and 2.5 ha cerrado (savanna woodland).

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Nests found before or shortly after egg laying were visited daily. The entire area was searched for nests every two days. Eggs, nestlings, and adults were measured using vernier calipers (0.1 mm) and pesola spring balances (0.2 g precision). The daily mortality rates and success probabilities of nests were calculated following Mayfield (1961, 1975), and I used only those nests with two eggs or nestlings. Food habits of nestlings were determined through direct observation of crop contents. To evaluate nest defense, dead frozen males and females in standing posture were put at varying distances from nests. The reactions of nest owners were observed through binoculars at distances of 20-50 m. Nestlings were banded with numbered metallic bands (IBDF-Cemave Brazil). Doves were captured in mist nets erected in places that flocks frequented. Statistical methods follow Snedecor and Cochran (1967) and Sokal and Rohlf (1981).

RESULTS

Nest characteristics.—I observed nest construction in all months except October. Nests constructed in September remained active until mid-October. Courtship was also observed in October. There was less nest activity during the final months of 1982, and in January 1983 the number of active nests increased again. The breeding season started in January and finished in September with few pairs nesting in November and December. Two hundred and eighteen nests were found from ground level (in cerrado) to a height of 7.5 m (in cypress), and from between zero to 4.5 m away from the center of the tree. Most nests (90%) were constructed in forks of horizontal limbs, which are quite common in cypress trees. Nests were constructed in 19 different plant species, and the distribution of nests among plant types differed significantly ($\chi^2 = 24.07; P < 0.0001; df = 17$) from that expected on the basis of the numbers of each plant species present (Table 1). The greatest number of nests occurred in cypress trees despite the fact that only 31.7% of the trees in the area were of this species. Of the other nests, 25.5% were built in coffee trees and the remaining were built in 17 different plant species. Four nests were built on the ground (Table 1). The principal material used in the construction of nests was the grass *Brachiaria plantaginea*. Three nests were constructed with roots and the others (N = 215) with stems and leaves of the grass *Brachiaria*. Only males were observed carrying material to nests. They made as many as 13 trips per min for up to 2 h at a time. Females arranged the material in the nest. Nest construction required an average of 4 days. The females roosted overnight in the empty nests prior to egg laying, and generally laid their first egg on the day after the nest was completed. They began incubation the following morning. Nests resembled small flat, elliptical shells. The mean external length of 27 nests was 109.8 mm ± 11.6 (range 91-135); the mean external width was 93.1 mm ± 13.1 (70-117); and the mean external height was 35.6 mm ± 8 (26-60). In nests the mean internal length was 68.5 mm ± 8.7 (55-80), the mean internal width was
Table 1

<table>
<thead>
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<th>Number of nests</th>
<th>Percent</th>
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<td>4</td>
<td>0.15</td>
<td>4</td>
<td>1.4</td>
</tr>
<tr>
<td>Limoio (Citrus sp.)</td>
<td>3</td>
<td>0.1</td>
<td>3</td>
<td>1.1</td>
</tr>
<tr>
<td>Laranjinha do cerrado</td>
<td>19</td>
<td>0.7</td>
<td>2</td>
<td>0.7</td>
</tr>
<tr>
<td>Milho (Zea mays)</td>
<td>50</td>
<td>1.8</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Jaqueira (Artocarpus integrifolia)</td>
<td>1</td>
<td>0.03</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Coração de negro (Connarus fulvus)</td>
<td>1</td>
<td>0.03</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Palmeira (Syagrus flexuosa)</td>
<td>1</td>
<td>0.03</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Bananeira (Musa sp.)</td>
<td>4</td>
<td>0.15</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Urucum (Bixa orellana)</td>
<td>2</td>
<td>0.07</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Ficus (Ficus elastica)</td>
<td>1</td>
<td>0.03</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Mexicrica (Citrus sp.)</td>
<td>1</td>
<td>0.03</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Jamelao (Eugenia cumini)</td>
<td>7</td>
<td>0.2</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Total</td>
<td>2728</td>
<td>100</td>
<td>271*</td>
<td>100</td>
</tr>
</tbody>
</table>

*Only 218 nests were used to calculate reproductive success.

5.93 mm ± 1.7 (55-60), and the internal height averaged 27.1 mm ± 3.6 (26-30).

I observed three pairs reusing nests. Successive clutches were produced up to three times in the same nest. The pairs only added a little more material on the upper part. Only successful nests were reused. If predation occurred, the nest was abandoned. Nearby new sites (<5 m away) were chosen in five cases.

Eggs and incubation.—Egg white differed significantly among eggs during the breeding season ($F_{6,140} = 188; P < 0.0005; df = 146$). The mean length of 85 eggs was 22.4 mm ± 0.10 (20-24.5 mm), mean width 16.8 mm ± 0.06 (15.2-18.5), and mean weight 3.41 g ± 0.05 (2-4.2 g). Of 218 nests, 91.7% contained two eggs (or nestlings), 7.8% contained one egg (or nestling), and 0.5% had three nestlings. The maximum number of clutches (each with two offspring) reared by one pair in the same year was four (N = 3).
Females began incubating after laying the first egg. The average period from the laying of the first egg to the hatching of the last egg in the nest was 12 days. Observations of two pairs indicate that the female incubates for approximately 18 h daily and the male for 6 h. The daily pattern of incubation at two nests was: at 07:00 h the female leaves and the male commences, at 11:00 h and 13:00 h the sexes switch, and at 15:00 h the female returns and remains until the following morning. Both the male and female displayed the same behavior before replacing the mate at the nest. After perching near the nest but on another limb, the incoming bird flew to the limb supporting the nest, walked to the nest where it remained still for a few seconds beside its mate. The sitting bird stood and walked to the limb’s tip and flew away while the other immediately sat upon the nest. Neither during the period of incubation, nor during the growth period of the nestlings, was the nest left unattended.

**Nest defense.**—In 6 of 21 tests of response to artificial birds the nesting bird attacked the model, jumping on its back and pecking its head. In 10 tests there was no reaction from the sitting bird. The nesting bird remained near the nest (1–2 m) on the ground while the model was present in 5 tests. Both reactions occurred in nests from the time of construction to when they had 5-day-old nestlings. The reactions of males to male models were not significantly different from the females’ reactions to female models ($\chi^2 = 0.24; P > 0.50; df = 1; N = 10$). Indifferent reactions to the model were more frequent between midincubation and the nestling growth stage (when the nest was guarded by the adults) than during the initial incubation period; however, the difference was not significant ($\chi^2 = 0.28; P > 0.50 df = 1; N = 10$). Intraspecific aggression was also observed in the field when neighboring males were seen batting their wings against one another while chasing each other in flights near nests under construction.

**Hatching, nestling, and fledgling.**—Hatching generally seems to be synchronized. After the eggs hatch, the parents carry the shells in their bills approximately 6 m (N = 2) from the nest. Hatchlings are altricial, their eyes closed at birth. Their naked bodies have a single narrow dorsal strip of buff colored feathers. The beaks are grey with a black narrow band separating the completely white tip. The white tip and the black band completely disappear when the young are ready to fledge. At 3 days after hatching, the nestling’s eyes open and the birds begin to chip softly (“pee-be”) (N = 10). Food is regurgitated by the parents on the first day when the nestlings receive only “crop milk.” On the following day they are fed small seed fragments (*Paspalum* sp., *Brachiaria plantaginea*, etc). The larger seeds (e.g., *Sorghum* sp., wheat, and rice), were observed in nestling crops after 4 days (N = 4). Analysis of variance showed no significant differences in the weight at hatching among the nestlings that: (1) hatched...
in different periods of the year ($F_{3,45} = 1.46; P > 0.10; df = 52$); (2) hatched in a nest alone or with one other nestling ($F_{2,49} = 0.16; P > 0.10; df = 52$); (3) hatched in nests localized in a coffee plantation or in a cypress grove ($F_{1,45} = 0.63; P > 0.10; df = 52$); (4) hatched in the dry or rainy season ($F_{1,38} = 0.48; P > 0.10; df = 90$). Measurements of one-day-old nestlings were: bill length 6.1 mm ± 0.03, N = 126; tarsus length 5.5 mm ± 0.1, N = 51; wing length 8.5 mm ± 0.1, N = 126 and body weight 3.2 g ± 0.1, N = 126. Nestlings remained in the nest from 9 to 15 days; $\bar{x}$ ± SD = 11.8 days ± 1.3 (N = 99). Fledglings had a bill length of 11.7 mm ± 0.07, N = 83; a tarsus length of 13.8 mm ± 0.26, N = 23; a wing length of 58.0 mm ± 0.74, N = 83; and a body weight of 24.8 g ± 6.0, N = 83. Up to the fifth day after leaving the nest, the fledglings still received regurgitated food from their parents (N = 3). After this, the fledglings began to peck the ground to pick up seeds. Fledglings left the nest with a weight that averaged 47% of their paternal parent's and 50% of their maternal parent's. Two young remained with their parents (who fed them frequently) for 25 days after leaving the nest (observations were made for one pair). Following this period, the young formed flocks and became independent.

Age at first reproductions.—One three-month-old male banded as a nestling was found incubating eggs in a nest, suggesting that sexual maturity can be reached within 3 months after hatching. Consecutive captures of one male (in the third, fifth, sixth, and eleventh month after having left the nest as a fledgling) showed that after only 3 months of age, it reached 97.7% of the average weight of an adult.

Adult weight.—Males were heavier and larger than the females (Table 2). Nesting males and females were significantly heavier (one-tailed $t$-test Male, $t = 5.5$, $P < 0.005$, df = 237; Female, $t = 4.5$, $P < 0.005$, df = 274) than those captured in nonbreeding flocks. During the breeding season, body weight differed significantly among adult males ($F_{9,200} = 5.21; P < 0.0005$; df = 209) and adult females. There was an increase in the body weight of both sexes in December, at the end of the breeding season (Fig. 1). In November, males weighed an average ($±SD$) 50.1 g ± 1.8, N = 18 and in December they weighed 53.5 g ± 3.62, N = 10. The corresponding average mass for females was: November 46.1 g ± 4.1, N = 13 and December 53.7 g ± 3.88, N = 2. The body weight of both sexes decreased when the new reproductive cycle began in the month of January (Fig. 1). The variation in weight of both sexes was greater during the rainy season than dry season (one-tailed $t$-test: Male, $t = 3.89$, $P < 0.0005$, df = 193; Female, $t = 1.97$, $P < 0.02$, df = 252).

Molt.—I found individuals molting (body wing molt was simply recorded as present or absent) throughout the entire breeding season. Of
<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Captured in flocks</th>
<th>Captured in nests</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult female</td>
<td>Adult male</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>247</td>
<td>46.0 ± 3.49</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>247</td>
<td>85.4 ± 2.63</td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>247</td>
<td>64.0 ± 5.94</td>
</tr>
<tr>
<td>Beak length (mm)</td>
<td>247</td>
<td>12.8 ± 0.49</td>
</tr>
<tr>
<td>Beak width (mm)</td>
<td>220</td>
<td>6.0 ± 0.30</td>
</tr>
<tr>
<td>Beak height (mm)</td>
<td>220</td>
<td>4.4 ± 0.28</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>220</td>
<td>15.3 ± 0.66</td>
</tr>
</tbody>
</table>
Fig. 1. Body mass of fledglings, adult females, and adult males during the breeding season of *Columbina talpacoti*. 
the total 218 individuals observed, 79 (36.2%) were males in molt; 24 (11%) were males not in molt; 88 (40.4%) were females in molt and 27 (12.4%) were females not in molt.

Diet. — Ruddy Ground-Doves collect seeds from the soil by pecking and swallowing them rapidly. They are capable of eating seeds ranging in size from 2 mm in length (wild *Paspalum*) to corn seeds 15 mm in length. A qualitative and quantitative analysis of the crop content of 15 fledglings and 35 adults (found dead during this study) showed that the Ruddy Ground-Dove is a seed eater, although two snails and one insect were found. The same general diet has been reported by Trollope (1974) and Schubert et al. (1965). The introduced grass *Brachiaria plantaginea* and the wild native gramineae *Paspalum convexum* were the major food items (Cintra et al., unpubl. data).

Predation. — There were no significant differences (level of 5%) in either the spatial location or height between predated and undisturbed nests. The mean height in the tree for predated nests was 2.0 m ± 1.29, N = 60 and for intact nests was 1.96 m ± 1.35, N = 72, while the average distance of predated nests from the tip of the branch was 0.96 m ± 0.74, N = 56 and intact nests was 1.0 m ± 0.63, N = 71. On two occasions I observed Curl-crested Jays (*Cyanocorax cristatellus*) eating eggs and nestlings of Ruddy Ground-Doves. The American Kestrel (*Falco sparverius*), the Aplomado Falcon (*F. femoralis*) and an unidentified snake were also observed taking nestlings. The two falcon species cited above and the Roadside Hawk (*Buteo magnirostris*) were also seen capturing fledglings from Ruddy Ground-Dove flocks.

Reproductive dynamics. — Although the percentage of active nests showed little variation (between 3 and 14%) among months throughout the year (Fig. 2D), there was a peak in fledgling production in July (Fig. 2A). The percentage of active nests decreased in the last months of the year (Fig. 3) and increased again in January 1983. The percentage of eggs laid and chicks hatched followed the same pattern (Fig. 2B, C). Of the 422 eggs laid, 67.3% hatched with success and 32.7% were lost. Of those lost, 70.1% were predated, 13.9% were deserted, 13.1% were infertile, 0.7% were lost due to my interference (when adults were flushed from their nests) and 2.2% were lost for unknown reasons. The highest rates of egg predation occurred at the beginning and at the end of the breeding season (Fig. 3C). There was a significant difference in the rate of predation on eggs (χ² = 26.7; *P* < 0.005; df = 11) during the breeding season.

Parental desertion of eggs occurred in six months of the year with the highest percentage in September (Fig. 3B). Egg infertility also occurred in six months. The period of highest infertility was in January, at the be-
Fig. 2. Percentage of fledglings produced (A), chicks hatched (B), eggs laid (C) and active nests (D) throughout the year.

Beginning of breeding season (Fig. 3A). Of 284 eggs that hatched, 37% of nestlings were lost. Of those, 75.0% were preyed upon in the nest, 10% were deserted and died, 7% died in the nest (probably due to rain) or fell from the nest, 3% died of disease, and 5% died for unknown reasons. The peak of hatchling predation occurred in August (Fig. 4D), in the month following peak fledgling production. There was a significant difference in the rate of nestling predation ($\chi^2 = 37.2; P < 0.005; df = 10$) during the breeding season. Parental desertion of nestlings occurred only between
May and September (Fig. 4C). Nestling loss due to rain occurred in four months (Fig. 4B) but not at high rates. Similarly, loss due to disease was minor (Fig. 4A).

Reproductive success.—The method proposed by Mayfield (1961, 1975)
Fig. 4. Percentage of nestlings lost during the breeding season of *Columbina talpacoti* due to disease (A), rain (B), parental desertion (C), and predation (D).
is based on nest exposure to predators. The unit of exposure that I use here is the nest-day. I calculated daily mortality rates (m) for eggs and nestlings. The daily mortality rate (m) is \( \Sigma i \) (where \( i = 1 \) if the nest was predated and \( i = 0 \) if the nest was not predated) divided by \( \Sigma d \) (d = number of days that each nest was exposed to predation). The survival rate is consequently \((1 - m)\) and the proportion of surviving nests after \( N \) days of exposure is \((1 - m)^N\). Hence the probabilities of survival based on nest exposure can be calculated given an incubation period of 12 days and nestling period of 11.8 days. Table 3 shows a daily mortality rate during incubation of 4.4% (daily survival rate of 95.6%) during 1982 and the first month of 1983, ranging from 2.6% in April–May to 8.3% in November–December. The incubation period is 12 days; so the probability of a nest remaining to hatching time is \((0.956)^{12}\) or 58%. For nestlings the daily mortality rate during the same period was 3.8% and ranged from 1.1% in August–September and November–December to 5.6% in February–March. Thus the probability of a nestling remaining in the nest until fledging is \((0.962)^{11.8}\) or 63.3%. Total nest success can be calculated by summing survival rates for the egg period and for the nestling period. By multiplying the probabilities of a nest surviving through each period we can calculate the probability of surviving from laying to fledging. In \( C. talpacot\) it is 0.580 \( \times \) 0.633 = 0.367 or 36.7%. I calculated that the mean number of young fledged per nest was 2.0 (mean clutch size) times 0.58 (probability of surviving through incubation), which equals 1.16 nestlings per nest at the end of incubation. Of these, 63.3% or 0.75 nestlings per nest can be expected to fledge.

**DISCUSSION**

Haverschmidt (1953) and Skutch (1956) reported that \( Columbina talpacot\) nested throughout the year. It is advantageous for pairs to nest principally during the rainy season and the beginning of the dry season, because of the abundance of cultivated seeds during these times. The grass \( Brachiaria plantaginea\), the principal food source of \( Columbina talpacot\) (Cintra et al., unpubl. data), produces seeds from January to June (Filqueiras; pers. comm.). Thus there exists a relation between the time of egg laying and food resource abundance. Food availability probably was not a problem for this population, because during the study period I never found a nestling that died from starvation. This population of \( C. talpacot\) nested near patches of \( Brachiaria, Paspalum\), and other grains available from the farms.

Ninety percent of the nests were constructed in forks of horizontal limbs. This preference may be due to greater availability of horizontal limbs in the cypress than in the coffee trees. Four nests were built on the ground. This is the first record of ground nests for the species.
### Table 3

**Variation of Daily Mortality Rate for Eggs and Nestlings of the Ruddy Ground-Dove Based on the Mayfield Method**

<table>
<thead>
<tr>
<th></th>
<th>Feb/Mar</th>
<th>Apr/May</th>
<th>Jun/Jul</th>
<th>Aug/Sep</th>
<th>Nov/Dec</th>
<th>Jan/83</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mortality of eggs</td>
<td>0.031</td>
<td>0.026</td>
<td>0.028</td>
<td>0.058</td>
<td>0.083</td>
<td>0.034</td>
<td>0.044</td>
</tr>
<tr>
<td></td>
<td>(34)*</td>
<td>(38)</td>
<td>(38)</td>
<td>(35)</td>
<td>(13)</td>
<td>(19)</td>
<td>(177)</td>
</tr>
<tr>
<td>Mortality of nestlings</td>
<td>0.056</td>
<td>0.020</td>
<td>0.026</td>
<td>0.010</td>
<td>0.010</td>
<td>0.045</td>
<td>0.038</td>
</tr>
<tr>
<td></td>
<td>(23)</td>
<td>(36)</td>
<td>(40)</td>
<td>(24)</td>
<td>(09)</td>
<td>(12)</td>
<td>(144)</td>
</tr>
<tr>
<td>Probability of success(^b)</td>
<td>0.34</td>
<td>0.57</td>
<td>0.52</td>
<td>0.43</td>
<td>0.31</td>
<td>0.38</td>
<td>0.36</td>
</tr>
</tbody>
</table>

* The numbers within parentheses correspond to sample sizes.

\(^b\) *P* = \((1 - m_{eggs})^2 \times (1 - m_{nestlings})^x\).  
 I = duration of incubation,  
 N = duration of period with nestlings in nest;  
 \((1 - m) = S = \text{daily survival rate.}\)
One adult always remained in the nest during incubation. I found no increase in intensity of intraspecific nest defense through the nesting cycle. Possibly my results were affected by sample size and the method that I used. Knight and Temple (1986) warned that "increased intensity of nest-defense behavior is largely a result of the methods used by the researchers." They suggested that repeated visits by observers modify the nest-defense behavior through positive reinforcement and loss of fear by nesting birds.

I found one male that reached sexual maturity in three months. This indicates that fledglings could be able to reproduce at the beginning of the following rainy season, or at the beginning of the next breeding season (January), when population density is low and there are fewer aggressive older individuals to inhibit nesting by younger birds.

Unfortunately, I observed parental care of only one pair after the young fledged. The two fledglings were fed by the parents until 25 days old.

Nesting adult males and females were significantly heavier than those in flocks. Possibly those adults that are reproducing are in better physical condition and/or are more mature than those in flocks. Individual weights of adult males and females differed significantly between wet and dry seasons. Murton et al. (1964) suggested that seasonal variation of body weight of adult doves could be adaptive because loss of body weight (and consequently loss of food reserves) occurs in the dry season when the balance between subsistence and resource level is critical. During the dry season, effects of environmental factors (such as low relative humidity, wind, and temperature) should result in a more intense water loss and, consequently, adult weight loss.

Some species of the predators (Falco sparverius, F. femoralis) also breed during the dry season, possibly as a result of the greater ease in finding their prey (cerrado vegetation is extremely dry in this period). As for young tropical birds, predation is the most important factor responsible for mortality of eggs and nestlings. Of the total dove eggs laid, 22.7% and 27.8% of the total number of nestlings hatched were destroyed by predators. These results are similar to those found by Skutch (1956) for C. talpacoti in Costa Rica. He found 24% nest success and 20% egg success. Carvalho (1957) found a slightly higher success rate in this species. Of 20 eggs, only 7 (35%) young fledged. In Surinam, Haoverschmidt (1953) observed that in three clutches with a total of 5 young, all left the nests. In the present study there was significant seasonal variation in the rate of predation on eggs and on nestlings. Fledgling production and percent of nests predated both peaked in July indicating that predation may be density dependent.
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LITERATURE CITED


CONSERVATION OF NORTH AMERICAN RALLIDS

WILLIAM R. EDDLEMAN, FRITZ L. KNOPF, BROOKE MEANLEY, FREDERIC A. REID, AND RICHARD ZEML

The Rallidae are a diverse group in their habitat selection, yet most North American species occur in or near wetlands. As a consequence, most species are subject to habitat enhancement or perturbation from waterfowl management programs. The overall effects of these management programs relative to rallid conservation have been assessed for few species, and there is a need for synthesis of such information. In the cases of some species or races, population status is not known, and suggested directions for conservation and management are needed. Rare, endangered, or status undetermined species or races often occur in areas where related species are classified as game birds, and the effects of such hunting on rarer forms are not known. Their generally secretive nature, the endangered status of several races and populations, and continued loss of habitat and threats to present habitat, warrant an examination of the conservation status of the North American taxa in this group.

In 1977, a committee of the International Association of Fish and Wildlife Agencies summarized available information on management and biology of American Coots (Fulica americana), rails, and gallinules in North America (Holliman 1977). That summary was intended to provide relatively complete information on conservation of these species, and also to provide guidance for research within the U.S. Fish and Wildlife Service’s (FWS) Accelerated Research Program for Webless Migratory Shore and Upland Game Birds (ARP). Subsequently, a number of rallid studies were funded under this program. The program was eliminated in 1982, following substantial research activities on North American rallids.

Since the demise of the ARP, additional research on rallids in North America has focused on an area the International Association of Fish and Wildlife Agencies report failed to cover in detail—that of endangered rallids in the U.S. and its possessions. Most of these studies have been

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7 U.S. Fish and Wildlife Service, 24000 Avila Road, Laguna Niguel, California 92656.
of threatened and endangered taxa in western coastal marshes. This report updates and summarizes information on North American rallids since the ARP report and identifies the major conservation problems of this group with the intent of focusing future efforts on these priority issues. Consideration of island forms occurring within U.S. possessions is beyond the scope of this report, mainly because of the special conservation problems associated with their insular distribution. The major topics include habitat requirements, effects of habitat and hunting management techniques currently practiced on wetland areas, and conservation of endangered and threatened populations. Research needs are identified. Habitats of the American Coot are similar to those of several waterfowl species, and the biology of coots is considered only as it is typical of rails in general.

GENERAL HABITAT REQUIREMENTS OF NORTH AMERICAN RALLIDS

Nine species of Rallidae regularly breed in North America: Sora (Porzana carolina), Virginia Rail (Rallus limicola), King Rail (R. elegans), Clapper Rail (R. longirostris), Yellow Rail (Coturnicops noveboracensis), Black Rail (Laterallus jamaicensis), Common Moorhen (Gallinula chloropus), Purple Gallinule (Porphyrio martinica), and American Coot (AOU 1983). Habitats used by North American rallids may be defined generally as wetlands with a well-developed zone of emergent vegetation. Within this vegetative association, rallids occur along a cline defined by flooding duration and water depth during the breeding season (Weller 1979). The Black Rail usually occurs in dense emergent vegetation, wet meadows, moist soil, or high marsh (Wilbur 1974, Repking and Ohmart 1977, Manolis 1978). Plants frequently found in these habitats include pickelweed (Salicornia spp.), saltmeadow cordgrass (Spartina patens), and salt-marsh cordgrass (S. alterniflora) in coastal marshes, and small bulrushes (Scirpus americanus and S. olneyi) in inland sites. Black Rails and Yellow Rails are most often encountered in wet prairie or grassland sites during migration.

Yellow Rails breed in wet meadows and shallow sedge marshes, especially in Carex lasiocarpa (Stahlheim 1974, Bookhout and Stenzel 1987). In Michigan, vocalizing birds were at sites with water ≤46 cm deep, but nests were at sites with water ≤10 cm deep (Bookhout and Stenzel 1987). The principal winter habitats are moist coastal grasslands and marshes.

Soras and Virginia Rails breed in freshwater emergent wetlands with shallow and intermediate water depths (Pospichal and Marshall 1954, Griese et al. 1980, Johnson and Dinsmore 1986). The cover requirements of these species appear to be similar (Johnson and Dinsmore 1986). During migration, both species use low areas of flooded annual grasses or
forbs, although Virginia Rails apparently prefer shallower sites for foraging than do Soras (water depth of <10 cm vs <20 cm) (Sayre and Rundle 1984). Habitats of Soras and Virginia Rails in winter are poorly known, but include both freshwater and salt marshes (Odom 1977, Zimmerman 1977).

King Rails use a variety of vegetative associations ranging from freshwater, brackish, and coastal salt marshes to shrub swamps and upland fields near marshes (Meanley 1969); they nest in portions of marshes with shallow (0–25 cm) water. Depths at foraging sites of King Rails are typically <10 cm, and drying natural swales are extremely important for foraging during the brood period. The similar Clapper Rail uses habitat ranging from coastal high and low salt marsh to freshwater marshes (Mangold 1977). Ideal coastal habitat for Clapper Rails includes extensive emergent vegetation, nearby tidal flats for foraging, and tidal influence (Lewis and Garrison 1983). Most nesting by Clapper Rails occurs in edges between tall and moderate-height cordgrass, but nests are also built in freshwater marsh edge (Massey et al. 1984) and in the bases of shrubs within the marsh (Abbott 1940).

Common Moorhens occur in the highest density in semipermanently flooded wetlands that have narrow-leaved, persistent, emergent vegetation, an abundance of submerged vegetation for food, and equal coverage of vegetation and water (Brackney and Bookhout 1982). Moorhen habitats include deeper and more open water than those of other rallids, and water depth at nests averages about 40 cm (Miller 1946). Purple Gallinules breed in wetlands similar to those used by moorhens, and the margins are overgrown with herbage and shrubbery (Ripley 1977). Wetlands used by Purple Gallinules frequently have extensive beds of floating-leaved plants. Nest sites of Purple Gallinules have denser vegetation and shallower water than those of Common Moorhens (Reagan 1977). The Common Moorhen and the Purple Gallinule regularly nest in southern ricefields (Helm et al. 1987).

TRENDS IN WETLAND LOSS

Wetland loss unquestionably is the greatest continent-wide threat to rail populations. Originally, >87 million hectares of wetlands existed in the contiguous United States, but by the mid-1970s only 46% of these habitats remained (Shaw and Fredine 1956, Tiner 1984). The rate of loss continues at >160,000 hectares annually. The most threatened habitats include palustrine and riverine wetlands that are also most important to rails. Agricultural development is responsible for 87% of recent national wetland losses; urban, industrial, and reservoir development account for the rest (Tiner 1984).

Inland freshwater wetlands have been drained disproportionately, mainly
because of agricultural activities. Certain areas have undergone extensive losses, such as the natural wetlands of Iowa and California's Central Valley; <6% of the original wetland area in each area exists today (Bishop 1981, Gilmer et al. 1982). Other areas important to rails, such as Lake Erie marshes that have lost >50% of their original area since 1954 (Weeks 1974), have not been so heavily affected. The most extensive wetland losses that affect rail habitats occurred from the 1950s to the 1970s in Louisiana, Florida, Texas, Arkansas, and Mississippi (Tiner 1984). Coastal salt marshes in the East, despite some losses, remain largely unchanged (Meanley 1985). About 800,000 hectares of salt marshes occur from Maine to Key West, and several hundred thousand hectares are on the Gulf Coast. Conversely, >150,000 hectares of the salt marsh in the San Francisco Bay area have been destroyed, and the remainder is currently threatened by urbanization (U.S. Fish and Wildlife Service 1984). Rail habitats in the greatest jeopardy of loss or perturbation are (1) estuarine wetlands in the coastal zone, (2) Louisiana's coastal marshes, and (3) Florida's palustrine wetlands (Tiner 1984).

The recent passage of the 1985 Farm Act offers alternatives to wetland drainage for increased agricultural production. The "swampbuster" provision of this act provides for withholding federal agricultural subsidies from landowners who drain wetlands to produce crops. This provision would actually save federal monies, because the cost of retiring the land ($760/hectare) would be cheaper than the estimated crop subsidy payments on land areas drained. Initial rules for implementing the provision defined wetlands and specified that landowners who altered wetlands were ineligible for Farmer's Home Administration loans for a period of 10 years. Difficulties arose when final rules were proposed by the U.S. Department of Agriculture (USDA). First, drainage districts were not mentioned in the legislation, so landowners could legally finance wetland drainage through these entities. Second, the law exempted wetlands for which drainage work had "commenced" before 23 December 1985. This definition was questionable, and USDA was considering defining "commenced" as any area where plans existed for drainage, thus opening the way for continued unrestricted wetland drainage. Final rules published on 17 September 1987 defined drainage as "commenced" if some earth-moving had occurred, if a substantial amount of money had been committed to contractors, or if substantial purchase of supplies for drainage had been committed before 23 December 1985 (J. Goldman-Carter, pers. comm.). The rules limited this potential loophole in the legislation.

Other recently passed legislation will raise additional monies for wetlands acquisition by the U.S. Fish and Wildlife Service (FWS). Among the provisions of the Emergency Wetlands Resource Act of 1986 are a five-year gradual increase in duck stamp prices to $15, an entry fee for
specified national wildlife refuges (70% would go to wetlands acquisition), and transfer of duties on imported sporting arms and ammunition from the general treasury into funds for wetland acquisition.

EFFECTS OF HABITAT MANIPULATIONS ON RALLIDS

Waterfowl management.—A substantial proportion of wetlands used by rallids, especially during migration and in winter, occurs on national wildlife refuges (NWR). Wetlands of greatest importance to rallids (other than Common Moorhens, Purple Gallinules, and American Coots) are shallower and have greater coverage by emergent vegetation than those typically managed for waterfowl (Shaw and Fredine 1956, Fredrickson and Taylor 1982). Waterfowl management on wetlands used for breeding by inland rail species, however, can be compatible with maintenance of rail habitat (Johnson and Dinsmore 1986). Dewatering in northern breeding areas should occur before 15 April to avoid disrupting nest initiation by rails (Andrews 1973, Johnson and Dinsmore 1986). Gradual dewatering (and presumably presence of topographic diversity) provides a maximum edge between moist soil and marsh; this edge is preferred by foraging rails. Wetland management should also strive to maximize coverage by emergent perennial vegetation which serves as nesting habitat. Habitat for rails within a wetland complex can be provided every year by flooding different impoundments in different years (Andrews 1973).

During migration, management for rails differs from waterfowl management in the timing of flooding and drawdowns (Rundle and Fredrickson 1981). For the autumn migration, shallow flooding should commence in late summer in middle latitudes (vs late autumn or winter for waterfowl); migrating rails require a variety of shallow water depths, robust cover, and short-stemmed seed-producing plants (Rundle and Fredrickson 1981, Rundle and Sayre 1983). Flooding impoundments too deeply and too early results in early macrophyte senescence and loss of robust plant structure needed for cover. A result of deep winter flooding is that foraging ducks and ice and wave action eliminate robust cover (Fredrickson and Reid 1986).

Spring management for migrating rails includes flooding areas that have annual grasses and smartweeds (Polygonum spp.) or herbaceous perennial plants (Rundle and Fredrickson 1981). Flooding should be shallow (<15 cm), but some habitat is provided at greater depths up to 50 cm. Rail response is best when partial drawdowns concentrate invertebrate prey. This hydrologic regime also is excellent for late spring migrating dabbling ducks such as Blue-winged Teal (Anas discors) and Northern Shovelers.
Land-leveling, whereby wetland management units are graded to allow easier irrigation, flooding, and drainage, has been practiced on some NWRs. This management practice should be eliminated because it minimizes the topographic diversity that provides the maximum amount of vegetation/water interface preferred by foraging rails.

**Agriculture.**—Agricultural rowcrops other than rice are often planted for waterfowl but have little value for rails (Rundle and Sayre 1983). Rice fields can be one component in the complex of wetland types for nesting King Rails (Meanley 1969), Common Moorhens, and Purple Gallinules (Helm et al. 1987). Wild rice in northern wetlands and middle-southern Atlantic coastal wetlands also provides habitat for migrating Soras (Fannucchi et al. 1986). Pesticides are a primary hazard to rails in this agricultural habitat. King Rails were formerly abundant in rice fields in the Arkansas Grand Prairie, but they have nearly disappeared from sites where pesticides (see below) have probably reduced the prey base of burrowing crayfish (*Procambarus* spp.) of this rail.

Harvest of wild and planted rice results in nest destruction and excessive disturbance to rails (Helm 1982, Fannucchi et al. 1986). Suggested solutions for this disturbance include planting later-maturing rice varieties (doubtful given economic constraints on farmers), leaving naturally vegetated areas fallow in association with planted fields, and establishing unharvested areas in wild rice beds. Damage to rice by nesting Common Moorhens and Purple Gallinules has been a problem to farmers in Louisiana, but it usually results in an insignificant loss of yield (Helm 1982). A few depredation permits, which allow shooting of these species in rice fields, have been issued.

**Grazing.**—Livestock grazing is usually detrimental to marsh habitat (especially for ground-nesting birds such as rails) unless it is extremely light (Todd 1977). Grazing reduces the height of emergent vegetation and has a greater effect on emergent vegetation near shore (Whyte and Cain 1979). Effects on Black Rail and Yellow Rail winter habitat, therefore, might be expected to be most severe because of their occupation of drier sites. Excessive grazing leads to loss of emergent cover, trampling, and disturbance of nesting pairs, and can have profound negative effects on rail use of wetlands (Whyte and Cain 1979). The effects of this practice on rails needs further study, especially in wintering areas.

**Fire.**—Fire has varied effects on rail habitats, depending on the species and wetland type under consideration. Fire can devastate habitats of some rallids, especially resident species, and may result in replacement of more desirable vegetation species by common reed (*Phragmites communis*) (Todd 1980). Fire is sometimes suggested as necessary to open marshes...
choked by excessive dead vegetation. In marshes where a residual mat is required by nesting rails (e.g., Yuma Clapper Rails—Eddleman, unpubl. data), fire may destroy suitable habitat, the effects lasting for several years.

Seral stages required by nesting Yellow Rails must be maintained by fire, or these areas succeed to forest (Stenzel 1982). These sedge meadow communities are maintained by periodic fire. Areas not burned periodically recover from the infrequent fire slowly, because a greater mat of dead vegetation creates a hotter fire which destroys root structure.

**Pesticides and contaminants.**—Lead shot is a major contaminant that can potentially affect rails. Ingested lead shot was found in the gizzards of 7.4%–12.3% of Soras in Maryland and 1.8% of those collected in Missouri (Artmann and Martin 1975, Stendell et al. 1980). The highest incidences occurred in marshes with tidal action (which exposes lead shot in the substrate), refuge areas for waterfowl, and traditional hunting areas. This threat, possibly severe in local areas, will diminish as the FWS phases out the use of lead shot in favor of steel shot for waterfowl hunting by 1991.

The effects of most pesticides and contaminants on rails are poorly known. Clapper Rails have shown a high tolerance to DDT and DDD (LC$_{50}$ in diet = 1612 ppm for males and 1896 ppm in females) (Van Velzen and Kreitzer 1975); sublethal effects were not studied. In Louisiana ricefields, nesting Common Moorhens and Purple Gallinules with high (2–13 ppm) residues of dieldrin showed no decrease in clutch size or hatchability of eggs (Causey et al. 1968). The effects of these levels of dieldrin on chick survival were not examined. Most potential pesticide/contaminant problems involving rallids have been localized in the East (Meanley 1985). The occurrence of selenium and other contaminants is of increasing concern in western wetlands. Selenium levels at Kesterson NWR are sufficient to cause severe hatching defects in coots, but heavy metal contamination has not been examined in detail at other wetland areas (U.S. Fish and Wildlife Service 1986).

Endangered and threatened rallid taxa may occur in areas of high contaminant levels. Potential problems with contaminants have been identified (U.S. Fish and Wildlife Service 1986) in a significant portion of the U.S. habitat for Light-footed Clapper Rails (*R. l. levipes*) (Tijuana Slough NWR), California Clapper Rail (*R. l. obsoletus*) (San Francisco Bay NWR and San Pablo Bay NWR), Yuma Clapper Rail (*R. l. yumanensis*) (Havasu, Cibola, Imperial, and Salton Sea NWRs) and California Black Rail (*Laterallus jamaicensis coturniculus*) (most of the mentioned refuges). Monitoring of contaminant levels in other wildlife and in Yuma Clapper Rails is being evaluated by FWS at present.

Seven eggs of Light-footed Clapper Rails were analyzed in 1983 and...
DDE levels of 9.6 and 6.8 ppm were found in two; DDE concentrations of 8.0 ppm in Black-crowned Night Heron (*Nycticorax nycticorax*) eggs and 3.0 ppm in Brown Pelican (*Pelecanus occidentalis*) eggs have been associated with poor reproduction (H. M. Ohlendorf, pers. comm.). In the typical Light-footed Clapper Rail nest, one or two eggs disappear, and one or two others do not hatch with the rest, which may or may not be contaminant-related.

### EFFECTS OF HUNTING AND TRAPPING ON RAIL POPULATIONS

Interest in hunting rails is low according to most resource managers (Zimmerman 1977). Most hunting pressure on rails has been on American Coots, Soras, Common Moorhens, and Clapper Rails (Ripley 1977, Martin 1979). Hunting seasons occur from early September through mid-December, depending on state regulations. Bag limits in recent years generally are 10–15 daily (Meanley 1985), depending on the species and the state. Coots are often covered under the waterfowl point system, being valued at 10–20 points, depending on the state. Black Rails have not been hunted since 1967, and the harvest was probably small when they were legally taken (Martin 1979). The season on Yellow Rails has been closed since 1968. Purple Gallinules have not been hunted in Florida since 1972. Clapper and King rails are hunted in most of the eastern and Gulf coastal states. The Common Moorhen is hunted in 43 states, and coots are hunted in 48 states. Sora hunting is an old tradition in coastal marshes in Connecticut, New Jersey, Maryland, and Virginia, but a drastic decline in birds, and consequently hunters, has occurred in recent years (Ripley 1977).

Trends in rail hunting by waterfowl hunters during the period 1964–1975 were summarized by Martin (1979). Numbers of hunters taking Soras and average number bagged showed no trend, although the number of hunters did decline in the Atlantic Flyway. Percentage of hunters who hunted other rails (mainly Clapper Rails) was up nationwide and in the Atlantic and Mississippi flyways; the average number of birds shot increased nationwide and in the Atlantic Flyway. During the same period, the proportion of waterfowl hunters that also hunted gallinules (mostly Common Moorhens) rose in the Atlantic, Mississippi, and Central flyways, and the average number of birds shot increased in the Mississippi Flyway. The proportion of waterfowl hunters that hunted coots rose in the Central and Pacific Flyways.

The average annual harvest of rallids by waterfowl hunters varied considerably in the years 1964–75 (Martin 1979). These figures underestimated total harvest of rails, because only 50% of Soras, 60% of other rails, and 75% of gallinules were taken by waterfowl hunters in the 1964–69...
hunting seasons (Banks 1979). The remainder were harvested by non-
waterfowl hunters. From 13,400 to 47,200 Soras were shot during 1964-
75 by waterfowl hunters (Martin 1979). Common Moorhen harvest ranged
from 10,100 to 63,500, coots from 765,700 to 1,659,800, and other rails
(mostly Clapper rails, but also King and Virginia rails) ranged from
24,100 to 175,200. Five states (New Jersey, Louisiana, Florida, Virginia,
and Iowa) harvested >2000 Soras. Fifty percent of the annual harvest of
gallinules (including Common Moorhens) and other rails occurs in Lou-
isiana, as does 25% of the coot harvest. The only other states reporting
substantial numbers of rallids harvested are California and Wisconsin,
which together account for 25% of the annual coot harvest.

Effects of the annual harvest on rail populations are unknown, although
timing of hunting seasons after the peak of migration (Eddleman et al.
1985), the low interest of hunters, the difficulty of hunting rails, and the
tendency for rails to run rather than fly (Holliman 1977) probably combine
to keep the annual take well within sustainable levels. The effects of
hunting on rare or endangered taxa are also unknown but probably have
minimal impact on populations. Waterfowl hunting is allowed on several
areas containing populations of Yuma Clapper Rails and California Black
Rails, but hunting pressure is low on these areas, and both races are so
seldom observed that such activity is probably of little danger to the rails.

Interest in hunting rallids may increase if waterfowl populations con-
tinue to decline (Holliman 1977). Research programs will be needed to
monitor the harvest and obtain data on species composition and age and
sex composition by population. Such procedures are available for other
migratory game birds, especially waterfowl, but are currently nonexistent
for rallids.

Banding data are scarce for rails, and only some eastern races of Clapper
Rail have been banded in any numbers. The recovery rate of 1028 clappers
banded in Virginia was 4.5% (Stewart 1954). The only significant infor-
mation provided by these data was the location of wintering areas for
migratory individuals.

A principal recommendation of the committee on rails and gallinules
of the International Association of Fish and Wildlife Agencies was the
institution of a hunting stamp for migratory game birds other than wa-
terfowl, which would provide revenues for research and habitat acquisi-
tion, and a source of information on composition of harvested popu-
lations (Holliman 1977). This recommendation has not been implemented
by the FWS or any state wildlife agency in the 10 years since it was
suggested. If interest in hunting of rallids increases, this recommendation
should be reconsidered because the FWS Accelerated Research Program
for Migratory Shore and Upland Game Birds was eliminated by the budget
cuts of 1982.
Trapping of furbearers is allowed on many NWRs. This activity sometimes results in mortalities of King, Clapper, and Virginia rails and Soras because the birds often use runways constructed by muskrats (Meanley 1969). On nine areas of Louisiana coastal marsh, 221 trappers took 127 birds, of which 61% were rails, 19% coots, 5% miscellaneous, including Purple Gallinules, and 15% ducks (Linscomb 1976). No significant difference was noted in catch of birds between #2 leghold traps and 220 conibear traps used in freshwater marsh, but conibear traps caught significantly more birds in brackish marshes, probably because of higher bird density in brackish marshes. Density of rails, water depth, and type of trap set were factors that affected catches of rails. Water depth may be the most important of these factors. Conibear traps set in runways at shallow sites where rails cannot avoid them, and leghold traps set at deeper sites where birds can’t see them cause the greatest mortality (G. Linscomb, pers. comm.). Mortality of rails might be reduced by using conibear traps for deepwater sets and leghold traps for shallow water sets. Nonetheless, losses appear small overall (Parker 1983, Stocek and Cartwright 1985).

CONSERVATION OF ENDANGERED AND THREATENED POPULATIONS

Five taxa of North American rallids warrant special concern. Four of these, the Light-footed Clapper Rail, the California Clapper Rail, the Yuma Clapper Rail, and the California Black Rail are found on or near the West Coast. The three Clapper Rail races are on the federal endangered species list (U.S. Bureau of Sport Fisheries and Wildlife 1973). The California Black Rail is on the state endangered species lists of California and Arizona (Wilbur 1974, Arizona Game and Fish Commission 1978). The King Rail is also considered endangered or threatened by several eastern and midwestern states.

Light-footed Clapper Rail.—The Light-footed Clapper Rail formerly occurred in coastal salt marshes from Santa Barbara County, California, to San Quintin Bay, Baja California, Mexico. This rail has declined mainly because of habitat loss to development and other effects of urbanization (U.S. Fish and Wildlife Service 1985). The estimated amount of habitat in the U.S. formerly available to this race was 10,256 ha. Currently, <3500 ha remain, and some of the better areas have been lost. The current U.S. population is estimated at 143 pairs, and a drastic, partly unexplained decline occurred in 1985 (Zembal and Massey 1986). In the two major habitat tracts remaining in Mexico, at least 64 pairs are present at El Estero near Ensenada, and 179 pairs remain at Bahia de San Quintin. The biology of the subspecies has recently undergone extensive study, making it one of the best known of the races of Clapper Rail. Nonetheless, the recent declines and continuing severe threats to the remaining habitat make this the most endangered rallid in the U.S. Actions recommended
in the recently revised recovery plan for this race include restoration of tidal action in some marshes, nest-hummock construction, development and enhancement of high and low marsh habitats where they presently do not occur, minimizing human disturbance, and minimizing losses to native and introduced predators. Of these, the most critical need is to expand the area of potential habitat available to maintain several self-sustaining populations. As of the spring of 1986, 99 pairs (about 70% of the population) were concentrated in Upper Newport Bay; the next largest concentration comprised only 12 pairs. Agency cooperation is needed for managing marshes where populations currently occur. For example, the mouth of Tijuana Estuary silted shut in 1984–85, preventing tidal fluctuations necessary to maintain marsh vegetation. An emergency request by the FWS to dredge open the mouth of the estuary was denied by the U.S. Army Corps of Engineers. By the time the necessary permits were obtained, marsh edges had dried out, and water had stagnated. The known population was reduced to two birds before dredging re-opened the estuary.

**California Clapper Rail.**—Historically, the California Clapper Rail occurred from Humboldt County (possibly) to San Luis Obispo County in California (U.S. Fish and Wildlife Service 1984). The largest populations occurred within San Francisco Bay. The initial threat to this race was overharvest, but industry, agriculture, salt-evaporation-pond construction, and urbanization began to reduce the habitat in the early 1900s (U.S. Fish and Wildlife Service 1984). About 80% of the 73,500 ha of original habitat has been diked or destroyed. The threat of urban development to potentially restorable habitat, such as salt evaporation ponds, poses a major threat. Eighty percent of the total population occurs in south San Francisco Bay where development pressure is greatest (T. Harvey, pers. comm.). The race occurs in pickelweed and cordgrass marshes, and high marsh is required during winter flood tides. The race is under study by personnel of the San Francisco Bay NWR, and current estimates of the population range from 1000 to 1500 individuals. Actions to address the habitat needs of this race include preserving present marsh habitat, restoring tidal action to diked areas, increasing emergent plant coverage, securing adjacent upland habitat, and eliminating pollution (U.S. Fish and Wildlife Service 1984). Information needs include general biology of the subspecies, specific habitat requirements, and the effects of introduced predators, waterfowl management, flood control activities, and mosquito abatement programs on rail habitats. The major problems in the recovery of this subspecies are lack of personnel and money to institute management actions.

**Yuma Clapper Rail.**—This race differs from the other endangered races
of Clapper Rail in that it breeds in fresh and brackish water marshes on the lower Colorado River of western Arizona and southeastern California, the Colorado River Delta, the lower Gila River, the Salton Sea, and other scattered sites in southern Arizona (Todd 1986). Some taxonomists consider that the two races of Clapper Rails nesting on the west coast of Mexico (R. l. rhizophorae and R. l. nayaritensis, Banks and Tomlinson 1974) are also of this race (Ripley 1977). The subspecies breeds mainly in cattail (Typha domingensis) and bulrush (Scirpus californicus) marshes, but it also breeds in other mixed vegetation types (Anderson and Ohmart 1985). Originally, the race occurred in the Colorado River Delta in Mexico and possibly in marshes along the Colorado River (Cooke 1914, U.S. Fish and Wildlife Service 1983, Todd 1986). The present marsh habitat has developed mainly on silt deposits formed behind U.S. Bureau of Reclamation dams. The U.S. population of this race was thought to migrate into Mexico on the coasts of Sonora, Sinaloa, and Nayarit, but a substantial portion of the population (>70%) is resident (Eddleman, unpubl. data). An annual call-count survey is conducted, but coverage is sporadic and routes are not standardized. The latest population estimates are 548 (minimum) in the U.S. (Powell 1985) and 205 in the Colorado River Delta in northern Sonora and Baja California (Anonymous 1981). Most U.S. habitat is in NWRs and state wildlife management areas that are subject to water management practices of the U.S. Bureau of Reclamation. Habitat loss caused by dredging, rip-rapping of stream banks, and high water flows on the Colorado River is the principal threat to this race (Todd 1986). Mitigation projects have caused negative impacts on some marsh habitats used by the birds. Havasu, Cibola, and Imperial NWRs offer potential management opportunities for this race. Actions needed to improve the status of this subspecies include protection and enhancement of current habitat; clarification and evaluation of its population status, including standardization of the call-count survey; clarification of its migratory status; development and implementation of management plans for federal and state lands on which the race occurs; clarification of the taxonomic status of birds occurring along the west coast of Mexico; and cooperative efforts with Mexico to protect habitat in the Colorado River Delta and possible wintering areas along the west coasts of Sonora, Sinaloa, and Nayarit.

**Black Rail.** — The California Black Rail occurs in a variety of habitats, from high marsh (mainly pickelweed and bulrush marshes) along the California coast from San Francisco Bay into northern Baja California to freshwater marshes along the lower Colorado River, at Salton Sea, and on some canal banks in three-square bulrush (Scirpus olneyi) stands (Wilibur 1974, Repking and Ohmart 1977). Threats to the race include marsh
subsidence caused by groundwater removal, diking of salt marshes, water level fluctuation, and wildfires (Todd 1980, Manolis 1978). The current population size in California is unknown; the estimate for Arizona is 100-150 birds. Information needs for this race include a clarification of population status throughout its range and studies of its general biology. Enhancement of habitat of the three western Clapper Rail races would likely also benefit the California Black Rail. The status of the midwestern population of inland breeding Black Rails is unknown, but sightings and calls have been alarmingly low in the last 40 years in breeding areas and in Gulf Coast wintering areas.

King Rail.—King Rail populations have declined alarmingly in several areas of former abundance in the last 30 years (Ripley 1977). Population declines in the Arkansas rice belt were mentioned above. King Rails also have declined in the Smyrna River marshes in Delaware (because of replacement of cordgrass and bulrush by common reed), have disappeared from the vicinity of the Patuxent Wildlife Research Center in Maryland, and have declined in the Ruthven marshes of northwestern Iowa (Weller 1979). Such declines, although often directly tied to habitat degradation, are sometimes unexplained. A comprehensive survey of status and distribution may be needed to ascertain if range-wide declines have occurred. The Blue List, published in American Birds and based on reports of interested observers nation-wide (Tate 1986), has included the King Rail as a species of special concern since 1976. Outside Louisiana and Florida, the King Rail probably warrants threatened status.

RESEARCH NEEDS

Many of the current research needs remain the same as those identified a decade ago (Holliman 1977). A major need in conservation of rallids is additional research on several aspects of general biology and population dynamics. Additional information on gains or losses in wetland habitats of importance to rallids is needed. Experimental studies on the effects of various land management practices are needed, especially as they relate to waterfowl management, because most management for rallids would be in conjunction with these programs. Refinement of census techniques for breeding rails (especially use of playbacks of vocalizations) has occurred in several studies, but most suffer from lack of an independent index to actual breeding numbers. Telemetry or transect methods (Bart et al. 1984) show promise in this area. If interest in hunting rallids increases, information on migration routes, wintering areas and winter habitat needs, harvest trends and composition, and population trends will be needed to manage the harvest intelligently. The effects of pesticides and other contaminants on rallids need additional evaluation, particularly
SUMMARY AND RECOMMENDATIONS

Current programs and needs for conservation of the nine North American rallids were considered. These species generally require wetlands and occur along a cline of increasing substrate moisture level, from Black Rails (driest) to American Coots (most aquatic). Wetland loss is the primary threat to all the species, and recent legislation could potentially aid in conserving wetlands in the United States. Waterfowl management can be compatible with management for rails, but careful alternation of different manipulations within complexes of wetlands is needed to accommodate both groups. Agricultural rowcrops have little benefit for rails. Grazing and fire have variable effects on rallid habitat, depending on the species under consideration and the intensity and frequency of the disturbance. The effects of most pesticides and contaminants on rallids are poorly known, and further study is essential. At present levels, hunting and incidental trapping probably have little effect on most rail populations, but improved methods of monitoring the harvest are needed. Research needs for rallids are extensive and mostly involve basic biology.

We offer the following recommendations:

1. The 1985 Farm Act should be enforced to protect a maximum acreage of wetlands from further agricultural drainage. The U.S. Congress should implement additional legislation to allow accelerated wetland acquisition by the FWS. The FWS, in turn, should emphasize acquisition of natural wetlands that have elevational diversity and a high percent coverage by emergent vegetation.

2. The U.S. Congress should resume funding of the Accelerated Research Program for Migratory Shore and Upland Game Birds as the best way to fund research on habitat management for rallids.

3. The FWS should institute a hunting stamp requirement for hunting of rails and other migratory game birds other than waterfowl. This program would provide a source for contacting the harvesting public for data, and the funds should be used for wetland preservation and acquisition.

4. In cooperation with state wildlife agencies and interested individuals, the FWS should undertake reviews of the status and distribution of the King Rail and Black Rail.

5. Mitigation or habitat enhancement work involving dredging operations in or near marshes inhabited by the Light-footed Clapper Rail, California Clapper Rail, Yuma Clapper Rail, and California Black Rail should be closely monitored by both agency biologists and independent
biologists to avoid excessive disturbance or marsh destruction. Habitat acquisition or enhancement for rallids should emphasize marshes in coastal California as a top priority for the Light-footed and California Clapper Rails and California Black Rail, because all of these taxa have a critical need for an expanded habitat base. NWRs which can provide habitat for the western Clapper Rails (including, but not limited to, Tijuana Slough, San Francisco Bay, San Pablo Bay, Salton Sea, Havasu, Cibola, and Imperial NWRs) should consider these birds as a top management priority. Experimental manipulation of water levels on diked marsh units should be examined as a possible management tool for the Yuma Clapper Rail.

(6) National wildlife refuges that provide potential habitat for substantial numbers of rails should strive to balance management strategies to maximize available habitat for rails and other waterbirds, where such management can be integrated into waterfowl management programs. (Some of these strategies, or references to them, may be found in this report.)

(7) Coastal wetlands operate as settling basins for the great variety of chemicals that are used or discarded in the watersheds feeding into them. Information about the presence of toxic chemicals in foods of rails and effects of various concentrations on reproduction and survival is needed for all rallids, and it is essential for the several endangered races of Clapper Rails.

(8) Whereas the use of lead shot by rail hunters is relatively minor when compared to that of waterfowl hunters, ballistics have now been developed for small, non-toxic shot, and it is suggested that federal guidelines include all wetland bird hunting in lead shot restrictions.

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LITERATURE CITED


Eddleman et al. • CONSERVATION OF RALLIDS


CALL FOR PAPERS

A Symposium is planned for February 9-11, 1989 titled “Kirtland’s Warbler at the Crossroads—Extinction or Survival” to be held in Lansing, Michigan. Topics for the symposium are open, but may include such things as Winter and Summer habitat requirements, Population dynamics, Economics of Kirtland’s Warbler management techniques, and benefits to other species by Kirtland’s Warbler management practices.

Persons interested in presenting a paper should respond by Sept. 1, 1988. Please submit your response to:

Kenneth R. Ennis
USDA-Forest Service
Huron-Manistee National Forests
421 S. Mitchell St.
Cadillac, MI 49601
616-779-8715

Notification of acceptance will be made by Sept. 15, 1988. Requests for final abstracts will be made after final acceptance of papers.
Fledging success of experimentally enlarged broods of the Glaucous-winged Gull.—Lack's (1947, 1948) hypothesis that the most common clutch size in a population reflects the maximum number of young that can be adequately fed by the parents has stimulated much research. Several experimental studies have supported this hypothesis (see Klomp 1970, Crossner 1977, Högstedt 1980); however, numerous exceptions exist in which the most productive brood size is larger than the most common brood size (e.g., see Klomp 1970, Haartman 1971, Bryant 1975, Schifferli 1978). Stimulated in part by these exceptions, Charnov and Krebs (1974) modified Lack's hypothesis to incorporate the "cost of reproduction" (see also Bryant 1979, Ricklefs, 1983, Nur 1984). Charnov and Krebs (1974) argued that the most common clutch size may be smaller than the most productive clutch size if the survival or future fecundity of adults rearing larger clutches is reduced. Several species in the genus Larus are capable of rearing broods larger than the most common clutch size. Gulls generally lay 2-3 eggs; however, in at least four species, adults are capable of rearing more than three young (Herring Gull [Larus argentatus, Haymes and Morris 1977]; Glaucous-winged Gull [L. glaucescens, Vermeer 1963, Ward 1973]; Lesser Black-backed Gull [L. fuscus, Harris and Plumb 1965], Western Gull [L. occidentalis, Coulter 1973]). However, in none of these studies has both the breeding success and survival of adults rearing enlarged broods been monitored. Thus it is not possible to distinguish between two hypotheses accounting for the ability of gulls to raise extra chicks: (1) because of a surplus of food the potential productivity of gulls is now greater than it was during the period when the three-egg clutch evolved (Lack 1966); or, (2) although gulls can raise more than three chicks, the cost to the adult resulting from decreased adult survival exceeds the benefit of more young fledged (Ward 1973). To address these hypotheses, I examined factors influencing clutch size in the Glaucous-winged Gull, and I report here on the ability of Glaucous-winged Gulls to raise enlarged broods. I assess chick growth rate, condition, and fledging success in broods of different size. I also examine the relationship between parental investment and chick growth.

Methods.—Glaucous-winged Gulls were studied on Protection Island, Washington (48°07'N, 122°55'W) between May and August of 1983-1985. Each year I manipulated the brood size of approximately 200 nests to create broods of 1-7 chicks (normal range 1-3). Chicks less than two days old were added to, or removed from, nests within two days of the hatching of the eggs in the nest. In each year, I established broods of 1, 2, 3, 5, and 7 chicks at approximately 31 nests (range 18-55) each. In 1984, I also established broods of 4 and 6 chicks.

I monitored fledging success at 172 nests in 1983, 176 nests in 1984, and 156 nests in 1985. I considered a chick to be fledged if it survived to at least day 30. Chicks alive at day 30 and subsequently found dead were counted as not-fledged. Glaucous-winged Gulls do not actually fledge until day 37-57 (Vermeer 1963); however, most chick mortality occurs in the first four weeks of life (Vermeer 1963, Reid 1987). Although fledging age increased with brood size (see below), this did not bias the determination of fledging success. Chicks from all brood sizes that survived to day 30 were large (>800 g) and were readily found if they died prior to fledging. Statistical analyses of fledging success were performed on log-transformed data (log[number fledged + 1]) to meet the assumption of homoscedasticity of variance.

I weighed and measured chicks at 136 nests in 1983, 176 nests in 1984, and 200 nests in 1985. All weights and measurements were log-transformed prior to analysis. I examined the size of chicks at two ages: during the intervals of 18-24 days (9-15 in 1983) and 31-
Table 1
Principal Component Loadings of Body Size Measurements at Three Chick Ages at Experimentally Synchronized Nests in 1985. The Magnitude of the Loading Reflects the Correlation between a Given Variable and the First Principal Component

<table>
<thead>
<tr>
<th>Chick age</th>
<th>Day 1</th>
<th>Day 20</th>
<th>Day 31</th>
</tr>
</thead>
<tbody>
<tr>
<td>Culmen</td>
<td>0.358</td>
<td>0.767</td>
<td>0.644</td>
</tr>
<tr>
<td>Tarsus</td>
<td>0.847</td>
<td>0.865</td>
<td>0.800</td>
</tr>
<tr>
<td>Wing</td>
<td>—</td>
<td>0.732</td>
<td>0.473</td>
</tr>
<tr>
<td>Weight</td>
<td>0.921</td>
<td>0.813</td>
<td>0.837</td>
</tr>
</tbody>
</table>

41. I adjusted the weights and wing lengths of chicks to the mid-point of these intervals using the slopes of regressions of weight and wing length on age. The growth analysis was performed on the mean adjusted chick weight and wing length for each nest. Neither weight nor wing length differed from a normal distribution in either chick age-group in any year (Kolmogorov-Smirnov Test, all groups: $P > 0.05$). I performed the analysis on two subsets of the data, first using all chicks measured during these two periods (N = 783 chicks) and second, excluding chicks that were known to die prior to fledging (resulting sample N = 593 chicks). The first method of analysis reflects the growth of the entire brood; the second method is a better indication of the condition of chicks that actually fledge.

I examined the influence of time allocation by the adults on the growth rate of chicks among experimentally synchronized broods of two chicks established in 1985. To control for effects of brood size and hatching date, I manipulated the brood size and phenology of 52 nests visible from three elevated blinds. I replaced the chicks present at each nest with two newly hatched chicks over a three-day period (July 7–9). All of the nests visible from a given blind were given the two chicks on the same day so that by watching nests from the three blinds on three successive days, I observed adults feeding chicks of identical age that had hatched over a three-day interval. Some chicks died during the course of the season; to avoid the confounding effect of differences in brood size, I analyzed only nests that had two chicks on the day of observation.

Observations of the nests were made at chick ages 17, 28, and 43. Each period of observation was 10 h and began between 06:00 and 06:20 (total observation time 90 h; 1560 nest-h). The nests were scanned every 10 min and the presence or absence of each adult was recorded. I analyzed the percent of total observation time that each adult was absent from the territory, averaged for the members of the pair. Arcsine square-root transformed values of the percent time absent from the territory did not deviate significantly from a normal distribution and were analyzed by Pearson correlation.

On days, 1, 20, and 31, the chicks at the experimentally synchronized nests were weighed, and the culmen, tarsus, and wing chord (only on day 20 and 31) were measured. The measurements on days 20 and 31 were made three days after the pattern of time allocation at these nests was measured. All chick measurements were log-transformed. Using only nests that had two chicks on the day of measurement, I used principal components analysis to create a “body size” factor for the chicks at each age (Table 1). Chick size on day 20 and day 31 was significantly correlated with size on day 1 (day 20: $r = 0.36, P < 0.001$, N = 74; day 31: $r = 0.33, P < 0.01$, N = 68). I removed the effect of initial size by regressing
Lig.

1. Fledging success as a function of brood size in 1983–1985. The top of each bar is the mean, and the vertical line represents one SE.

To measure the effect of brood size on the length of the nestling period, I scored the stage of plumage development of chicks older than 25 days at 63 nests in 1984. The last portion of the body to molt to juvenal plumage is the neck and head. I scored the percent of the head that had molted to juvenal plumage to the nearest 25%. This measure provides an index of the stage of development as the chicks approached fledging; no chicks were observed flying with more than 25% natal plumage on the neck and head. I calculated the mean molt score for chicks at each nest for each day of observation.

Results.—In each year, the fledging success among nests with artificially enlarged broods exceeded the success of nests with normal brood sizes (Fig. 1; correlation of number fledged with brood size, 1983: $r_s = 0.74$, $P = 0.001$, $N = 172$ nests; 1984: $r_s = 0.52$, $P = 0.001$, $N = 176$; 1985: $r_s = 0.46$, $P = 0.001$, $N = 156$). Highest fledging success was found in broods of seven chicks ($x = 3.29 \pm 1.76$ SD, $N = 79$ nests). Fledging success of the most common brood size, three chicks, was $2.05 \pm 0.92$ chicks ($N = 109$).
### Table 2
The Effect of Brood Size and Hatching Date on Chick Growth. Stepwise Linear Regression with Brood Size Entered on Step 1. Sample Size Refers to the Number of Nests (Measurements for Chicks at Each Nest Were Averaged). The Regression Coefficient Is the Standardized Coefficient in the Complete Model.

<table>
<thead>
<tr>
<th>Year</th>
<th>Weight</th>
<th>Young chicks</th>
<th>Hatch date</th>
<th>R²</th>
<th>N</th>
<th>Old chicks</th>
<th>Hatch date</th>
<th>R²</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Brood size</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Brood size</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td></td>
<td>-0.194</td>
<td>-0.076</td>
<td>0.050</td>
<td>80</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1984</td>
<td></td>
<td>-0.464</td>
<td>-0.075</td>
<td>0.223</td>
<td>141</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1985</td>
<td></td>
<td>-0.261</td>
<td>0.050</td>
<td>0.065</td>
<td>85</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Wing length</th>
<th>Young chicks</th>
<th>Hatch date</th>
<th>R²</th>
<th>N</th>
<th>Old chicks</th>
<th>Hatch date</th>
<th>R²</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Brood size</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Brood size</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>1983</td>
<td></td>
<td>-0.169</td>
<td>-0.085</td>
<td>0.042</td>
<td>80</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1984</td>
<td></td>
<td>-0.462</td>
<td>-0.183</td>
<td>0.254</td>
<td>141</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1985</td>
<td></td>
<td>-0.275</td>
<td>-0.165</td>
<td>0.122</td>
<td>85</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*P < 0.05.

*P < 0.01.

*P < 0.001.

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**Fig. 2.** Chick weight on day 37 as a function of brood size. Original analysis on log-transformed data. Sample size: 1983, N = 63; 1984, N = 73; 1985, N = 69.
Fig. 3. Chick development as a function of brood size. Stage of development scored as the percent of head and neck molted to juvenal plumage.

Average weight and wing length decreased significantly with brood size in all years and at both chick ages (Table 2, Fig. 2). Among older chicks in 1984, brood size alone explained 31% of the variation in the weight of chicks and 37% of the variation in wing length. In 1983 and 1985, brood size accounted for less than 16% of the variation in any measurement. The analysis of growth rate as a function of brood size (Table 2, Fig. 2) includes chicks that were known to die prior to fledging. I repeated the analysis, excluding chicks that did not fledge to obtain a more accurate measurement of the influence of brood size on the condition of chicks that fledge. The resulting pattern of correlations differed only slightly from the entire sample.

I examined the growth of broods of potentially high-quality adults by restricting the sample to only those pairs that fledged within one chick of the initial brood size. Among these pairs, the correlations between chick growth and brood size are reduced. In this restricted sample, initial brood size accounts for a maximum of only 17% (x = 8.0%) of variation in size and the relationship is significant among old chicks in 1984 (weight: r = -0.35, P < 0.05, N = 40; wing: r = -0.39, P < 0.01, N = 40). Nevertheless, all correlations (at both chick ages) were negative; thus, even among those adults that were capable of rearing large broods, the chicks fledged in poorer condition.

At experimentally synchronized nests in 1985, chick size increased significantly with the percent of time each adult was off territory at both day 20 (r = 0.33, P = 0.024, N = 37) and day 31 (r = 0.33, P = 0.026, N = 35).
The stage of plumage development (percent head molt) was negatively correlated with brood size after adjusting for chick age (Fig. 3; $B = -0.244$, partial $r = -0.201$, $P < 0.001$, $N = 94$; effect of chick age removed in step 1 of stepwise regression, slope of regression of percent head molt with chick age: $B = 0.697$, partial $r = 0.70$, $P < 0.001$). By day 40 the development of chicks in enlarged broods was roughly five days behind the development of chicks in normal broods (Fig. 3).

Discussion.—Four species of gulls are capable of increasing parental effort sufficiently to allow more than three chicks to be fledged (Vermeer 1963, Harris and Plumb 1965, Ward 1973, Coulter 1973, Haymes and Morris 1977). It is unlikely that the ability to raise more than three chicks is solely a result of the presence of artificial food sources (cf., Lack 1966, Haymes and Morris 1977), given the consistency of the pattern among species and habitats. Moreover, Ward (1973) found that experimentally enlarged broods of Glaucous-winged Gulls could be reared at colonies at which the birds did not have access to artificial food sources.

In this study, fledging success increased with brood size up to broods of seven chicks. However, chick weight and wing length decreased and the nestling period increased with brood size. The most pronounced decline in chick condition occurred among broods of 4-7 chicks; there was relatively little variation in chick condition among broods of 1-3 chicks (Fig. 2). Even among small broods (two chicks), chick growth rate varied as a function of time spent foraging by the adults. Thus, the growth rate of chicks at all brood sizes seems to represent the optimal growth rate from the perspective of the parents rather than the maximal growth rate of the chick.

Because of the decline in chick condition among chicks in enlarged broods, postfledging survival, rather than fledging success, most directly addresses Lack’s (1947, 1948) hypothesis. Based on postfledging survival, the most productive clutch size of the Glaucous-winged Gull has been found to differ between locations and years. Vermeer (1963) found that postfledging survival of chicks in artificially enlarged broods was higher than that of chicks in control broods, based on off-colony sightings. However, Ward (1973) reanalyzed Vermeer’s data including later sightings and found that the number of chicks surviving after fledging was maximal in broods of three, although broods of five were only slightly less productive. In three other experimental manipulations of the brood size of the Glaucous-winged Gull, Ward (1973) found that in two years (in two different colonies) broods of six chicks had the highest number of chicks surviving after fledging and, in one year, broods of three had the highest success. Fledging weights of chicks in artificially enlarged broods show equally inconsistent results. Haymes and Morris (1977) found no difference in the fledging weights of chicks in control broods and artificially enlarged broods (up to five chicks) of Herring Gulls. In the Glaucous-winged Gull, Ward (1973) found no difference in fledging weights in broods of 1-6 chicks at one study site but found a decline in fledging weight with brood size at another site. Coulter (1973) found a decline in weight with brood size (up to six chicks) in the Western Gull.

Acknowledgments.—I thank D. Boersma, G. Orians, and S. Rohwer for help throughout this study. Support was provided by Sigma Xi, The Chapman Fund, and National Science Foundation grant BSR-00236.

LITERATURE CITED


Fall migration of Ruby-throated Hummingbirds in the northeastern United States.—The Ruby-throated Hummingbird (Archilochus colubris) migrates long distances between its breeding range in eastern North America and its winter range in the southern United States and Middle America (Bertin 1982, A.O.U. 1983). Most references to the overland migration of Ruby-throated Hummingbirds concern their regional status or report large numbers of fall migrants, while behavioral, ecological, and energetic aspects of their migration have received little attention. The ridges of the Appalachian Mountains are major routes for southbound migrants, and in this study we describe the seasonal and daily timing of migrating Ruby-throated Hummingbirds and the influence of wind direction and velocity at one such Appalachian lookout, Hawk Mountain Sanctuary, Pennsylvania. We also present data from...
### Table 1

**Summary of Ruby-throated Hummingbird Counts in Northeastern United States: 1985 Data Only**

<table>
<thead>
<tr>
<th>Site</th>
<th>A Quaker Ridge, CT</th>
<th>B Lighthouse Point, CT</th>
<th>C Mt. Peter, NY</th>
<th>D Montclair, NJ</th>
<th>E Hawk Mountain, PA</th>
<th>F Waggoner’s Gap, PA</th>
<th>G Tuscarora Summit, PA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Count period (mo/day)</td>
<td>9/7–9/30</td>
<td>8/29–9/30</td>
<td>9/1–9/29</td>
<td>8/31–9/29</td>
<td>8/1–9/30</td>
<td>8/17–9/30</td>
<td>9/1–9/30</td>
</tr>
<tr>
<td>Days</td>
<td>20</td>
<td>32</td>
<td>27</td>
<td>29</td>
<td>46</td>
<td>24</td>
<td>27</td>
</tr>
<tr>
<td>Season summary:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hours</td>
<td>243.00</td>
<td>213.50</td>
<td>178.00</td>
<td>191.50</td>
<td>304.50</td>
<td>94.25</td>
<td>165.25</td>
</tr>
<tr>
<td>Total birds</td>
<td>21</td>
<td>113</td>
<td>9</td>
<td>20</td>
<td>120</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>Birds per hour</td>
<td>0.13</td>
<td>0.58</td>
<td>0.05</td>
<td>0.11</td>
<td>0.39</td>
<td>0.10</td>
<td>0.10</td>
</tr>
<tr>
<td>Peak flight:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date (mo/day)</td>
<td>9/14</td>
<td>9/12</td>
<td>9/2</td>
<td>9/1</td>
<td>8/28</td>
<td>8/23</td>
<td>9/7</td>
</tr>
<tr>
<td>Single-day total</td>
<td>9</td>
<td>17</td>
<td>3</td>
<td>6</td>
<td>20</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>Birds per hour</td>
<td>0.95</td>
<td>2.13</td>
<td>0.42</td>
<td>0.10</td>
<td>3.16</td>
<td>1.80</td>
<td>1.50</td>
</tr>
<tr>
<td>Date (mo/day) on which last migrant seen</td>
<td>9/20</td>
<td>9/23</td>
<td>9/23</td>
<td>9/21</td>
<td>9/25</td>
<td>9/21</td>
<td>9/20</td>
</tr>
</tbody>
</table>

* Sites are ordered from northeast to southwest; coordinates (N and °W) for each site: A = 41°05' 73°35'; B = 41°10' 72°50'; C = 41°10' 74°10'; D = 40°45' 74°10'; E = 40°35' 75°55'; F = 40°30' 77°25'; G = 39°40' 77°50'.

* Excluding August data, there were two peak flights at Hawk Mountain: 1.53 birds/h on 6 September and 1.40 birds/h on 11 September.
other sites in the northeastern U.S. and consider evidence for differences in the seasonal timing of different age-sex classes.

Study area and methods.—Hummingbirds were counted on 44 days from 1 August–29 September 1985 at the North Lookout (elevation = 463.6 m), Hawk Mountain Sanctuary (HMS), on the Kittatinny Ridge on the Schuylkill-Berks county line in southeastern Pennsylvania. Broun (1939) describes the physical setting with respect to the migration of raptors and other birds. Observations were made on 29 of 30 days in September, but only on 15 of 31 days in August. Because northwest winds are conducive to good flights of migrants, all days in August with such winds were covered. Observations were typically made between 8:00–18:00 h, Eastern Standard Time, for a total of 304.45 h. Observations were made by a single person from a central location overlooking the ridge to the northeast and the broad valleys to the north and the southeast. It was not possible to record the age and sex of individual migrants. Number of hummingbirds, air temperature, wind speed and direction, and cloud cover were recorded hourly.
### Table 2

**Daily Timing of Migrating Hummingbirds at Hawk Mountain Sanctuary and Two Sites (Combined) in Connecticut**

<table>
<thead>
<tr>
<th>Time period (EST)</th>
<th>Hawk Mountain*</th>
<th>Connecticut*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total coverage (h)</td>
<td>Total number of birds</td>
</tr>
<tr>
<td>06:00–09:59</td>
<td>57.0</td>
<td>12</td>
</tr>
<tr>
<td>10:00–13:59</td>
<td>73.0</td>
<td>77</td>
</tr>
<tr>
<td>14:00–17:59</td>
<td>39.0</td>
<td>20</td>
</tr>
<tr>
<td>Total</td>
<td>169.0</td>
<td>109</td>
</tr>
</tbody>
</table>

* Distribution of birds/h significantly different from uniform: $G = 66.197$, df = 2, $P < 0.001$.

b Distribution of birds/h significantly different from uniform: $G = 13.455$, df = 2, $P < 0.005$.

Daily counts of migrant hummingbirds at Hawk Mountain from 1979–1984 were summarized by adding all hummingbirds recorded for a given date over the 5-year period and dividing by the total hours of effort. Other observations are available from the journals of the first HMS curator, the late Maurice Broun (years 1942 and 1946–1960, archived at the Dept. of Biology, Muhlenberg College, Allentown, Pennsylvania).

Data gathered in 1985 at six other northeastern U.S. sites were used to supplement observations from HMS. Four of the sites are north of HMS; two are south (Table 1). Unlike HMS, counts of hummingbirds at these sites were incidental to counts of migrating raptors.

We examined specimens of Ruby-throated Hummingbirds at the Academy of Natural Sciences of Philadelphia and the American Museum of Natural History in New York to explore whether there are differences in the seasonal timing of migrants from different age and sex classes. Immature birds were distinguished from adult birds by the presence of serrations on the bills of the immatures (Ortiz-Crespo 1972). We did not distinguish the sexes of immature hummingbirds.

**Seasonal timing.** — The migration of Ruby-throated Hummingbirds at HMS in 1985 spanned 8 August through 25 September; we counted a total of 120 hummingbirds. The migration peaked from 26–30 August (highest count was 20 = 3.16 birds/h on 28 August) and remained high from 31 August–12 September (Fig. 1). More than 90% of all hummingbirds had been counted through 14 September. During 1979–1984, most hummingbirds at HMS were counted from 21 August–15 September (Fig. 1). The average date on which at least 90% of

### Table 3

**Numbers of Migrating Hummingbirds at Different Wind Speeds**

<table>
<thead>
<tr>
<th>Wind speed (km/h)</th>
<th>Birds observed</th>
<th>Birds per hour*</th>
<th>% Total birds</th>
</tr>
</thead>
<tbody>
<tr>
<td>1–5</td>
<td>9</td>
<td>0.23</td>
<td>16</td>
</tr>
<tr>
<td>6–11</td>
<td>21</td>
<td>0.72</td>
<td>38</td>
</tr>
<tr>
<td>12–19</td>
<td>26</td>
<td>0.83</td>
<td>46</td>
</tr>
</tbody>
</table>

* Only days with NW or W winds and >6 h coverage.

b Distribution significantly different from uniform: $G = 39.99$, df = 2, $P < 0.001$. 

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**SHORT COMMUNICATIONS**

**Table 2**

**Daily Timing of Migrating Hummingbirds at Hawk Mountain Sanctuary and Two Sites (Combined) in Connecticut**

**Table 3**

**Numbers of Migrating Hummingbirds at Different Wind Speeds**

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all migrants had been recorded was 11 September (SE = ±2.2 days, range = 1-17 September). The highest single-day count of migrating hummingbirds at HMS, 45, was on 3 September 1975. The earliest migrant was on 2 August 1983; the latest were recorded by Broun on 29 September in 1953 and again in 1956.

At the supplementary sites in the northeast in 1985, based primarily on September coverage, single-day peak flights ranged from 3-17 hummingbirds on 1-14 September (Table 1). The last date on which hummingbirds were recorded in 1985, including those at HMS, ranged from 20-25 September (Table 1).

**Daily timing.**—At HMS and a combination of the Lighthouse Point and Quaker Ridge, Connecticut sites, 109 and 103 hummingbirds, respectively, were recorded on days with >7 h coverage. We pooled these data within 4-h periods and found that the distributions of hummingbirds among the 4-h time periods were significantly different from being uniform both at HMS and in Connecticut (Goodness of Fit test, Sokal and Rohlf 1981; Table 2). The greatest proportion of hummingbirds and the highest number of birds/h at HMS and in Connecticut were during mid-day hours, 10:00-14:00 h.

**Wind direction and velocity.**—In 1985, the days with the highest counts of hummingbirds at HMS (28 August and 11 September) coincided with the arrival of strong cold fronts and northwest winds. More hummingbirds were recorded with northerly winds (0.55 birds/h) than with southerly winds (0.39 birds/h), but this difference was not statistically significant (G = 2.74, df = 1, P > 0.05). Our counting periods were biased toward days with northwest or west winds; more data need to be collected on winds from other directions. The relation between wind velocity and numbers of hummingbirds was clearer. For days with >6 h coverage and with northwest or west winds, the number of hummingbirds counted increased significantly with wind speed (Table 3).

**Differences between age and sex classes.**—We examined 102 museum specimens of Ruby-throated Hummingbirds, including 16 adult males, 35 adult females, and 51 immatures. No adult males had been collected in the U.S. after 30 August. Adult females or immatures collected in the U.S. were taken before 24 September. We could not detect a difference in the schedules of adult females and immatures of either sex. Broun’s journals indicate that at HMS locally breeding male hummingbirds depart before the females. For example, in 1955 he noted that the males had departed by 27 August, but that females were at his feeders until 11 September. Similarly, in 1957 he noted that females were present until 16 September, long after the departure of local males.

**Seasonality and differential migration.**—Differences in the migrations of sex- and age-classes have been noted in several species of hummingbirds in the western U.S. (e.g., Phillips 1975). Bent (1958) and others (e.g., Sprunt and Chamberlain 1949, Johnsgard 1983) reported that adult male Ruby-throated Hummingbirds precede adult females and immatures during fall migration. Of 32 hummingbirds captured or collected in Aiken County, South Carolina, 6-24 September 1955 (Norris et al. 1957), all but two were immature.

The fact that there are age- and sex-specific differences in the migration schedules of Ruby-throated Hummingbirds is a confounding variable when considering data recorded or reported without regard to age and sex classes. Nonetheless, our results, especially the closely grouped dates for “last migrants” (Table 1), and reports in the literature suggest that the migration of Ruby-throated Hummingbirds is temporally compressed compared to that of such western species as the Allen’s Hummingbird (*Selasphorus sasin*) and the Rufous Hummingbird (*S. rufus*) (Phillips 1975). For example, average departure dates reported by Oberholser (1924) and others (e.g., Poole 1964) for all age-sex classes of hummingbirds from Maine to North Carolina and west to Indiana and Michigan occur within a single month—September. North to south—from Maine to Louisiana—the period covering all average departure dates spans less than two months: 3 September–25 October (Oberholser 1924).
Various investigators have suggested that the phenology and availability of food resources along migration paths or at stopovers influence the timing of bird migrations (e.g., Schneider and Harrington 1981), and dependency on ephemeral food supplies could result in contracted migrations. Grant and Grant (1967) link movements of various hummingbird species to the flowering phenology of hummingbird-pollinated plants. Bertin (1982) specifically hypothesizes that the peak fall migration of Ruby-throated Hummingbirds is nearly synchronous with peak flowering of a major food source, jewelweed (Impatiens biflora). The timing and progression of their migration in the northeast are consistent with Bertin’s (1982) hypothesis, although he apparently does not consider the differences in the timing of migrations of the age-sex classes or the timing of the flowering of other plant species.

**Daily timing.**—Hummingbirds are diurnal, and they fast through the night (Calder 1974). The onset of morning activity is correlated with the intensity of light needed for successful foraging, and their time budget should allow maximum use of daylight feeding. We do not know whether Ruby-throated Hummingbirds fly at night during their overland migration. Even if they do not, the first hours of daylight must be used to replenish their energy reserves after a night’s fast. At the end of the day, they must refuel before fasting for the night. The mid-day hours, in effect, may be the only time available for protracted migration flights, and it is during these hours that we counted the most migrants (Table 2). Migrant hummingbirds on the Allegheny Front in West Virginia are usually seen in mid-day or afternoon, in contrast to nocturnal-migrant songbirds which are mostly recorded early in the day (Hall and Bell 1981).

**Wind direction and velocity.**—In the northeastern U.S., the passage of a cold front typically brings strong northwest winds and large flights of raptors and songbirds (Broun 1939, Hall and Bell 1981) and hummingbirds (e.g., Heintzelman and MacClay 1972). Hummingbirds may benefit energetically from the lift provided by higher wind velocities or other phenomena associated with the passage of low-pressure systems. We saw more hummingbirds at higher wind velocities (Table 3), but it is not known whether more hummingbirds are actually flying under such conditions or whether they are simply more visible from mountain lookouts.

Ruby-throated Hummingbirds concentrated in autumn at a site in South Carolina defended “vague territories,” and, near the time of their departure, had sufficient reserves to allow nonstop flights from South Carolina across the Gulf of Mexico (Norris et al. 1957). However, the basic pattern of Ruby-throated Hummingbird migration over land has not been established. Mid-day flights in the context of a temporally compressed migration suggest a strategy that is based on daily “short-hop” flights southward, rather than extended stops during a prolonged migration that is typical of such western species as the Rufous Hummingbird and Allen’s Hummingbird (Phillips 1975). More than likely, some combination of both is employed, depending on such variables as weather and food supply.

**Acknowledgments.**—We thank A. Bihun, Jr., S. Coleman, N. Currie, C. Elwell, C. Garner, J. George, M. Harwood, A. Martin, A. Rosengren, E. Shove, A. Siegle, and G. Smith for providing hummingbird count data. G. A. Hall, P. Kerlinger, F. Gill, B. Murray, Jr., C. Leck, and L. Wolf reviewed drafts of this manuscript. We thank the Academy of Natural Sciences of Philadelphia and the American Museum of Natural History for access to their skin collections. The Hawk Mountain Sanctuary Association provided support for the first author during a Research Internship at HMS.

**LITERATURE CITED**


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Fulvous Whistling-Duck abundance and habitat use in southwestern Louisiana.—The Fulvous Whistling-Duck (Dendrocygna bicolor) is a locally common breeding bird of the rice (Oryza sativa) belt of southwestern Louisiana, which had nesting densities of 13-20 pairs within a 12.95-km² area in the mid-1950s (Meanley and Meanley 1959). This species declined rapidly in the 1960s, apparently from exposure to pesticides applied to rice (Flickinger and King 1972). The population increased in the 1970s with the discontinued use of aldrin-treated rice seed and the conversion from aerial seeding to drill planting, and by late
summer 1975, there were an estimated 10,000 Fulvous Whistling-Ducks in Louisiana (Flickinger et al. 1977). The present paper provides estimates of Fulvous Whistling-Duck abundance and habitat use in the rice belt of southwestern Louisiana during 1984-1985.

Monthly aerial surveys were conducted to estimate Fulvous Whistling-Duck abundance and habitat use. This species was observed on transects only during April-August surveys, so only those five monthly surveys were included in analyses. Surveys consisted of 14 transects equally spaced at 3.75-min intervals (Fig. 1). Transects extended from longitude 93°10.00'W to 92°17.71'W. The Intracoastal Waterway was the southern terminus for all lines. The northern terminus varied among lines; some lines ended at US 190; others were terminated when large contiguous areas of woods, residences, or soybean (*Glycine max*) fields were encountered (Fig. 1). The total length of each survey was about 1300 km. Surveys were conducted from a Partenavia twin-engine aircraft (use of brand names does not imply endorsement by the U.S. Government) flown at approximately 165 km/h. The plane was modified to include a transect-width-estimation harness under each wing (Norton-Griffiths 1978). Harness markers corresponded to an approximate 250-m transect width at 46-m flight altitude. A computerized LORAN-C directional system was used to locate starting and ending coordinates and keep the plane on course. The first transect of each survey was alternated between the most westerly and the most easterly, with the beginning point always on the southern terminus. Surveys were conducted between 0800 and 1600 h with a 1 h break at midday. During each survey, two observers recorded on magnetic tape the numbers of Fulvous Whistling-Ducks and habitats encountered within their respective transects on opposite sides of the aircraft. When two different habitats fell within the transect width, the habitat representing the greatest percentage was recorded. Starting and ending times for each transect also were recorded. Results for each observer were summed for each transect; thus,
Table 1
ABUNDANCE (km$^2$) OF HABITATS WITHIN TRANSECTS DURING FIVE MONTHLY AERIAL SURVEYS IN SOUTHWESTERN LOUISIANA, MAY 1984-APRIL 1985

<table>
<thead>
<tr>
<th>Habitats</th>
<th>Apr.</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Aug.</th>
<th>± (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disked fields</td>
<td>120.5</td>
<td>125.5</td>
<td>118.6</td>
<td>14.0</td>
<td>11.5</td>
<td>78.0(59.6)</td>
</tr>
<tr>
<td>Ditches/canals</td>
<td>6.7</td>
<td>6.7</td>
<td>6.0</td>
<td>5.9</td>
<td>6.4</td>
<td>6.3(0.4)</td>
</tr>
<tr>
<td>Flooded disked fields</td>
<td>25.1</td>
<td>na</td>
<td>0.1</td>
<td>0.4</td>
<td>1.0</td>
<td>5.3(1.1)</td>
</tr>
<tr>
<td>Flooded harvested rice fields</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>20.7</td>
<td></td>
</tr>
<tr>
<td>Flooded pastures</td>
<td>1.3</td>
<td>0.5</td>
<td>2.8</td>
<td>4.0</td>
<td>1.8</td>
<td>2.1(1.3)</td>
</tr>
<tr>
<td>Flooded soybeans</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>0.5</td>
<td>3.1</td>
<td></td>
</tr>
<tr>
<td>Fresh marsh</td>
<td>25.1</td>
<td>26.4</td>
<td>24.4</td>
<td>23.0</td>
<td>27.4</td>
<td>25.3(1.7)</td>
</tr>
<tr>
<td>Harvested rice fields</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>34.7</td>
<td></td>
</tr>
<tr>
<td>Pastures/fallow fields</td>
<td>73.8</td>
<td>57.0</td>
<td>46.6</td>
<td>49.5</td>
<td>58.0</td>
<td>57.0(10.6)</td>
</tr>
<tr>
<td>Ponds/open water</td>
<td>7.2</td>
<td>6.0</td>
<td>9.2</td>
<td>4.9</td>
<td>3.8</td>
<td>6.2(2.1)</td>
</tr>
<tr>
<td>Residential/industrial</td>
<td>19.1</td>
<td>18.6</td>
<td>17.6</td>
<td>16.7</td>
<td>18.8</td>
<td>18.1(1.0)</td>
</tr>
<tr>
<td>Rice</td>
<td>13.6</td>
<td>66.8</td>
<td>74.8</td>
<td>78.6</td>
<td>21.1</td>
<td>51.0(31.1)</td>
</tr>
<tr>
<td>Sorghum/corn</td>
<td>13.4</td>
<td>3.8</td>
<td>2.7</td>
<td>4.6</td>
<td>2.9</td>
<td>5.5(4.5)</td>
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<tr>
<td>Soybeans</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>106.1</td>
<td>102.5</td>
<td></td>
</tr>
<tr>
<td>Woods</td>
<td>15.6</td>
<td>18.6</td>
<td>18.1</td>
<td>19.6</td>
<td>18.8</td>
<td>18.0(1.5)</td>
</tr>
</tbody>
</table>

* na = not available.

The results represent a 500-m wide transect. Amount of time in seconds over each habitat type was determined from recordings. This time was summed for each habitat type for each transect. Transect times for all surveys were corrected to a mean time to compensate for ground speed differences.

Population estimates, densities, and sampling variances were computed assuming a simple random sample (Cochran 1977) of transects from the survey area. Due to the small number of nonzero observations per habitat per transect per month, use of a ratio estimator was not feasible. Additionally, because our data set contained a few extreme values, mean numbers of ducks per month and standard errors were based on a logarithmic transformation. We obtained estimates of the Fulvous Whistling-Duck in the agricultural areas of southwestern Louisiana by multiplying the mean number of ducks per month per km$^2$ by the total area as delineated by Meanley and Meanley (1959). No adjustments for visibility bias were made.

Fifteen habitat types were identified in the rice belt of southwestern Louisiana during spring and summer months (Table 1). More than 75% of the area surveyed was in agricultural production throughout the period. Amount of nonagricultural land (ditches/canals, freshwater marsh, ponds/open water, residential/industrial, and woods) varied little among surveys. Conversely, abundance of soybeans, rice, disked fields, and flooded disked fields changed substantially between consecutive surveys. Disked fields were the most abundant habitat sampled during April, May, and June; soybeans were most abundant in July and August. Pastures/fallow fields were the second most abundant habitat sampled in April, but rice was second most abundant in all other months. Ten habitat types were available in all surveys. Flooded pastures were the least abundant habitat of those available in all surveys. Soybeans and flooded soybeans were observed only during July and August; harvested rice fields and flooded harvested rice fields were recorded only during August.
Fulvous Whistling-Ducks were most abundant in April; fewest birds were seen in June (Table 2). Numbers of flocks (i.e., groups of two or more birds) were largest in August and least in July. Mean flock size decreased from April through June, but was greatest in July (Table 2). Greatest numbers of Fulvous Whistling-Ducks were in flooded disked fields but this habitat type was only used in April. The most flocks per habitat were recorded in flooded harvested rice fields during August, the only month this habitat type was available (Table 2). Fulvous Whistling-Ducks were never observed in freshwater marsh, flooded pastures, woods, or the sorghum (*Sorghum bicolor*)/corn (*Zea mays*) habitat type. Numbers of habitats used by ducks varied from six in April to two in May.

Densities of Fulvous Whistling-Ducks in the rice belt of southwestern Louisiana were greatest in flooded soybeans in July (150.0/km²), but little of this habitat type (0.5 km²) was available during that month. Mean densities in rice, the only type used all months, were 1.41 (SD = 1.4)/km². Monthly densities (ducks/km²) varied from 0.58 in April to 0.11 in June (Table 3). The month with the lowest density had the lowest variance associated with the estimate. Within the rice belt’s approximately 12,500 km² (Fig. 1), which is the breeding range of the Fulvous Whistling-Duck in Louisiana (Meanley and Meanley 1959), we estimated 7268 Fulvous Whistling-Ducks in April 1985 with an approximate 95% confidence interval of 2950 to 17,900.

Fulvous Whistling-Ducks were not observed during our March survey. Lowery (1974) reported that this species was recorded for Louisiana every month except February, and Meanley and Meanley (1959) stated that this duck concentrates in freshwater marshes of Vermilion and Cameron parishes before rice planting begins in March and April. Our transects terminated near the northern edge of the freshwater marsh, so we may have sampled insufficient freshwater marsh to record this duck, or else densities were so low along transects that the ducks were not detected within the transects. We did not conduct a survey in

**Table 2**

<table>
<thead>
<tr>
<th>Habitats</th>
<th>Apr.</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Aug.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disked fields</td>
<td>0 (0)</td>
<td>20 (3)</td>
<td>1 (1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Ditches/canals</td>
<td>1 (1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Flooded disked fields</td>
<td>524 (16)</td>
<td>na²</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Flooded harvested rice fields</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>75 (1)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Flooded soybeans</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>8 (4)</td>
</tr>
<tr>
<td>Harvested rice fields</td>
<td>3 (1)</td>
<td>0 (0)</td>
<td>1 (1)</td>
<td>2 (1)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Pastures/fallow fields</td>
<td>14 (2)</td>
<td>0 (0)</td>
<td>1 (1)</td>
<td>30 (1)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Ponds/open water</td>
<td>18 (1)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Residential/industrial</td>
<td>45 (4)</td>
<td>159 (30)</td>
<td>36 (27)</td>
<td>57 (13)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Rice</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>5 (1)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Mean flock size</td>
<td>12.2</td>
<td>6.0</td>
<td>1.1</td>
<td>23.3</td>
<td>6.4</td>
</tr>
<tr>
<td>(SD)</td>
<td>(11.8)</td>
<td>(1.0)</td>
<td>(0.2)</td>
<td>(31.2)</td>
<td>(5.8)</td>
</tr>
</tbody>
</table>

² na = not available.
Table 3

ESTIMATES OF FULVOUS WHISTLING-DUCK DENSITY DURING FIVE AERIAL SURVEYS OVER THE RICE BELT OF SOUTHWESTERN LOUISIANA, MAY 1984-APRIL 1985

<table>
<thead>
<tr>
<th></th>
<th>Ducks/km²</th>
<th>Variance</th>
<th>95% confidence limit</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>0.58</td>
<td>2.95</td>
<td>0.32 1.43</td>
</tr>
<tr>
<td>May</td>
<td>0.18</td>
<td>2.41</td>
<td>0.11 0.41</td>
</tr>
<tr>
<td>June</td>
<td>0.11</td>
<td>0.83</td>
<td>0.82 0.18</td>
</tr>
<tr>
<td>July</td>
<td>0.13</td>
<td>1.54</td>
<td>0.87 0.25</td>
</tr>
<tr>
<td>August</td>
<td>0.16</td>
<td>3.14</td>
<td>0.86 0.40</td>
</tr>
</tbody>
</table>

September. In October, no Fulvous Whistling-Ducks were recorded on transects, suggesting that most had moved from the rice belt during September. McCartney (1963) reported that few Fulvous Whistling-Ducks were observed during aerial surveys in September and October. We found, as did Meanley and Meanley (1959) and Bolen and Rylander (1983), that Fulvous Whistling-Ducks are closely associated with rice culture. About 90% of individuals observed were in rice fields during all months except July, when 34% were in this habitat type. Largest concentrations were in flooded disked fields in April and in flooded harvested rice fields in August. This species feeds at night on rice seed in newly water-planted fields during spring and on weed seeds in harvested rice fields in the fall (Bolen and Rylander 1983). We suggest that food availability influenced habitat selection during the day also.

Availability of soybean seeds and/or weed seeds may have accounted for the high use of flooded soybeans during July when soybeans were being planted. Habitats with standing surface water appear to be preferred during the day by Fulvous Whistling-Ducks. During April, all use of disked fields was in those flooded, even though about five times as much of the nonflooded disked-fields habitat type was available. During July, only 0.5% of soybeans were flooded, yet over 90% of the ducks that used soybeans were in flooded soybeans. While similar amounts of flooded and nonflooded harvested rice fields were available in August, 90% of observed ducks was in the flooded habitat.

Differences among surveys in numbers of Fulvous Whistling-Ducks, numbers of flocks, and mean flock size appear to reflect breeding chronology, changes in cover, and observer visibility. Greatest numbers of this species and the second largest flock size were observed in flooded disked fields during April. McCartney (1963) reported that Fulvous Whistling-Ducks often congregate on the breeding grounds shortly after arriving in mid-April, but soon disperse in groups of 8-75 individuals. Similar behavior of whistling-ducks observed along our transects in April could account for the large flock sizes recorded. Also, ducks could be easily seen in flooded disked fields, which contributed to the large numbers recorded. Both numbers of ducks and mean flock size decreased during May and June. Pair formation and nesting activity during these months (Meanley and Meanley 1959) would explain reduced flock size. The reduction in numbers of ducks observed in May and June probably reflects visibility limitations of the survey due to increased vegetation height and density, rather than an actual reduction in duck numbers. A negative bias due to vegetation has been previously documented by Martinson and Kaczynski (1967).

The large mean flock size (23.1) recorded in July was influenced by the single flock of 75 birds in a flooded soybean field. Mean flock size of 4.4 in rice fields during the same month is probably more representative. Mean flock size was 6.4 in August, when Fulvous Whistling-
Ducks begin moving into large ponds, lakes, openings in rice fields and flooded rice stubble (Meanley and Meanley 1959). The large increase in numbers of ducks observed in August reflects recruitment and better visibility after the rice was harvested.

The only individuals seen in the residential/industrial habitat type (18) were airborne and probably were moving from one area to another. We estimated that approximately 7300 fulvous Whistling-Ducks were in the rice belt of Louisiana during April 1985. These numbers are 25% less than the 10,000 estimated in Louisiana for late summer 1975 by Flickinger et al. (1977). Meanley and Meanley (1959) reported that nesting densities of this species were greater in the northern part of the rice belt than in rice fields adjacent to the coastal marsh. Because we terminated our transects when we crossed US 90, or when we encountered large contiguous areas of woods, residences, or soybean fields, our transects did not extend to the northern limits of the rice belt. If nesting densities were higher in suitable habitat along the northern border of the rice belt as reported by Meanley and Meanley (1959), the mean number of ducks we calculated could have been higher, thus resulting in a higher estimate. Notwithstanding, our estimates suggest that the present population of the Fulvous Whistling-Duck in the rice belt of southwestern Louisiana has benefited from the elimination of aldrin as a pesticide. Because of the continued use of pesticides for rice production in this region, additional surveys could be useful in further monitoring the numbers of this unique waterfowl species.

Acknowledgments.—This paper was approved for publication by the Director of the Louisiana Agricultural Experiment Station as manuscript number 87-22-1498. The project was funded by the Louisiana Department of Wildlife and Fisheries to Louisiana State University. Research was conducted under the auspices of the Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana Department of Wildlife and Fisheries, U.S. Fish and Wildlife Service, Louisiana State University, and Wildlife Management Institute, cooperating. We thank J. Nassar and D. Hayden for assisting with aerial surveys. We thank G. Daigle, Louisiana Department of Wildlife and Fisheries, for piloting the survey aircraft.

LITERATURE CITED


Long-distance dispersal of an adult Red-cockaded Woodpecker.—The Red-cockaded Woodpecker (Picoides borealis) is an endangered species endemic to mature pine forests of the southeastern United States, and is especially characteristic of longleaf pine (Pinus palustris) and forest lacking in hardwood understory. Such habitat has grown increasingly sparse and fragmented in recent years, and the remaining populations of the bird are becoming increasingly isolated as a result (USFWS 1985, Ligon et al. 1986, Jackson 1987). As populations become isolated, the possibility of dispersal between them becomes an important issue, particularly in maintenance of genetic variability (Reed et al. 1988). In this note we describe a long-distance dispersal by an adult female Red-cockaded Woodpecker. She moved from an isolated group in the Piedmont of North Carolina to a group, 90 km away, within a large population in the Sandhills. The individual involved was banded with three color bands and a USFWS aluminum band as an adult in 1984. At that time she resided in an isolated group in the Piedmont, near the Shearon Harris nuclear power plant on land owned by Carolina Power and Light Company in southwestern Wake County. In 1984, the female was paired and fledged two young. The pair remained at the site in 1985 and nested again, but the nest failed. During the winter of 1985–1986, the male (banded) disappeared. The female was last observed there on 10 April, 1986, when she was involved in aggressive interaction with one of two unbanded birds that moved into the site. She was absent on 17 April, and from that date on, only the two new birds resided there.

The group at Shearon Harris to which the female belonged is part of a sparse, little known population. In 1981, only four groups could be found in the entire Piedmont of North Carolina, including two in Wake County, and only seven groups in the Coastal Plain counties adjacent to Wake County to the east (Carter et al. 1983a). In 1984–1986, the Shearon Harris group was 50 km from the next nearest known group. During this time, three unbanded Red-cockaded Woodpeckers were observed at Shearon Harris, suggesting that there were some unknown groups remaining in the area. After disappearing from Shearon Harris, the female was next seen 90 km to the southwest on Camp Mackall, a military base in Richmond and Scotland counties in the Sandhills. She was first seen in the Sandhills on 23 May 1986, 43 days after last being seen in Wake County, and was identified from her color-band combination. She was recaptured on 28 May, and her identity was confirmed from her aluminum band number. The minimum rate of movement of the female was 2 km/day, and the actual rate is presumably higher as it is unlikely that we observed her the first day she arrived in the Sandhills. Observers visited the site to which she moved every 9 days during the dispersal period, but no birds were contacted prior to 23 May.

The female was paired with an unbanded male when first observed at Camp Mackall. The pair failed to nest in 1986, and both birds had disappeared by the 1987 breeding season. The large Sandhills population (450 groups), including all the groups on Camp Mackall, has been studied intensively since 1979 (Carter et al. 1983b; Walters et al. 1988). Although not a certainty, it is likely that if the female moved within the Sandhills in 1986–1987, she would have been detected in her new group. Thus the female likely did not reproduce following her dispersal from the Piedmont to the Sandhills.
We suggest the distance of this particular movement was a result of the low density of Red-cockaded Woodpeckers in the vicinity of the female's original group. Within the Sandhills, dispersal distances average longer in areas of low population density (Walters et al. 1988). This female, traveling southwest out of Wake County, may not have encountered other birds until reaching the Sandhills population.

The habitat between Shearon Harris and Camp Mackall is not continuous pine forest. There are areas of pine, but also agricultural fields and hardwood stands. Possibly the bird followed U.S. Highway 1 between the two sites. Although not the shortest route between the two points, the highway is lined with pines much of the distance between Shearon Harris and Camp Mackall, with the notable exception of some sections in and around the city of Sanford. The cavity trees which the female used at Shearon Harris were within 200 m of Highway 1, and those she used in the Sandhills were less than 2 km from Highway 1. Jackson (1976) suggested that rights-of-way along highways in the Southeast be managed to provide habitat corridors for dispersal between isolated populations. Our observation indicates that long distance movements along corridors are possible.

This dispersal, and the additional dispersals of unbanded birds into Shearon Harris, suggest that isolated groups have some potential for persistence, and that genetic exchange between isolated populations via dispersal may be a more reasonable possibility than previously supposed.

Acknowledgments.—We thank C. Copeyon, M. LaBranche, J. Lape, M. Reed and P. Robinson for assistance in data collection. Research in the Sandhills has been funded by the National Science Foundation (BSR-8307090), the U.S. Fish and Wildlife Service via Section 6 of the Endangered Species Act of 1973 administered through the North Carolina Wildlife Resources Commission, the North Carolina Agricultural Research Service at North Carolina State University, and donations from individuals and conservation organizations. We thank personnel from Camp Mackall and Carolina Power and Light Company for allowing us to conduct research on their properties. D. Adams, M. Byrd, R. Conner, P. Doerr, J. Jackson, R. Lancia and D. Ligon provided constructive criticism of previous drafts of the manuscript. This is paper 11337 of the Journal Series of the North Carolina Agricultural Research Service.

LITERATURE CITED


Response of Least Bitterns to tape-recorded calls.—Tape-recorded calls have been used in the study of a variety of bird species. The technique is useful for estimating avian abundance, investigating habitat use or behavior, and in detecting elusive or secretive species (Johnson et al. 1981, Marion et al. 1981). Johnson et al. (1981) noted that the Least Bittern (Ixobrychus exilis) was responsive to playback recordings, but application of the technique for this species has not been documented. In the present study, we used tape-recorded calls of Least Bitterns to increase their detection in dense marsh vegetation. Although the study was not specifically designed to evaluate this technique, the data should be useful for planning further studies of this species, which is considered rare, uncertain, or declining, in many regions of the United States (Chandler 1985, Tate 1986, NYSDEC 1987.)

Methods.—Breeding bird censuses were conducted in six tidal freshwater marshes located along the Hudson River in New York State. All study areas included extensive stands of cattail (primarily Typha angustifolia) interspersed with varying amounts of river bulrush (Scirpus fluviatilis), purple loosestrife (Lythrum salicaria), reed (Phragmites australis), and tidal open water. In 1986 and 1987, we counted birds on 169, 0.28-ha plots (30-m radius) among the six areas. Only 50 of the plots were sampled in both years. Plot centers were located randomly within each study area and were separated by at least 60 m.

Breeding birds were counted four times in 1986 and five times in 1987. Counts were conducted by two observers during early morning (05:00-10:00 h DST) and evening periods (16:30-21:00 h), between 1 May and 20 June each year, at times with no measurable precipitation or strong winds (greater than approximately 25 km/h). Each plot visit consisted of an approximate 10-min observation period during which tape-recorded calls of Green-backed Heron (Butorides virescens), Least Bittern, American Bittern (Botaurus lentiginosus), Virginia Rail (Rallus limicola), Sora (Porzana carolina), and/or Common Moorhen (Gallinula chloropus) were broadcast from the center point using portable cassette recorders. Maximum sound pressure 1 m from the source was approximately 90 db. A standardized sequence of alternating calls and silent listening periods, including up to 5 min of Least Bittern calls, was used during each census round. For Least Bittern, we used the “cooing” call (Bent 1926) as recorded on the “Peterson Field Guide to Bird Songs” (Kellogg et al. 1975). This call is generally attributed to the male and may serve a function in courtship (Weller 1961, Palmer 1962). Estimated distance, movement, and time of observation were noted for all Least Bitterns seen or heard within 30 m of a plot center. Sex of individual birds was usually not confirmed. Additional information on study areas and census methods was reported previously (Swift 1987).

Results.—Least Bitterns were observed 73 times on 48 (28%) of the 169 plots. Approx-
Table 1

Number of Least Bitterns Observed (seen or heard) during 1986 and 1987

| Year | Counts per round | Census Round | OSL
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>1986</td>
<td>119</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>1987</td>
<td>100</td>
<td>0</td>
<td>4</td>
</tr>
</tbody>
</table>

*Census rounds corresponded to the following dates in 1986: 1—May 5–9; 2—May 11–21; 3—May 23–June 3; and 4—June 4–16. Census rounds in 1987 were as follows: 1—May 5–9; 2—May 11–19; 3—May 20–28; 4—June 1–11; and 5—June 15–18.

b Observed significance level for ANOVA between census rounds within years.

Imately 75% of these observations were based at least in part on vocalizations (47 “cooing” and 8 “cackling” birds), while the remainder (18 observations) were birds seen and not heard. Observation frequency was generally considered low, since repeat occurrences on a plot (within the same year) were noted only 8 times during the study. On plots where Least Bitterns were seen or heard, the mean number observed was 0.3 per plot visit. Use of tape-recorded calls appeared to increase substantially detection of Least Bitterns. Only 12 (16%) of all Least Bitterns seen or heard, and only 5 (9%) of those that were heard, were observed prior to playback of at least one Least Bittern call. In addition, over half of all Least Bitterns seen or heard moved towards the observer during the playback period.

Least Bitterns were first observed on 16 May in 1986 and on 4 May in 1987. Thereafter, frequency of observation increased significantly during the breeding season, to an apparent peak in early to mid-June (Table 1). This increase may have occurred as a result of behavioral changes, increased abundance over time, or greater responsiveness to the playback sequence. Our data suggested the latter, since in both years, highest response rates occurred during

Table 2

Number of Least Bitterns observed during one-hour intervals

<table>
<thead>
<tr>
<th>Count start time</th>
<th>Number of counts</th>
<th>Number of Least Bitterns observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>05:00–05:59 h</td>
<td>29</td>
<td>14</td>
</tr>
<tr>
<td>06:00–06:59 h</td>
<td>57</td>
<td>18</td>
</tr>
<tr>
<td>07:00–07:59 h</td>
<td>52</td>
<td>15</td>
</tr>
<tr>
<td>08:00–08:59 h</td>
<td>43</td>
<td>15</td>
</tr>
<tr>
<td>09:00–09:59 h</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Total AM</td>
<td>186</td>
<td>66</td>
</tr>
<tr>
<td>16:00–16:59 h</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>17:00–17:59 h</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>18:00–18:59 h</td>
<td>26</td>
<td>5</td>
</tr>
<tr>
<td>19:00–19:59 h</td>
<td>21</td>
<td>2</td>
</tr>
<tr>
<td>20:00–20:59 h</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Total PM</td>
<td>70</td>
<td>7</td>
</tr>
</tbody>
</table>

* Number of counts conducted among 48 plots where Least Bitterns were observed at least once during the year.
Table 3

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sum of squares</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>OSL²</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMPM</td>
<td>0.21</td>
<td>1</td>
<td>0.21</td>
<td>0.92</td>
<td>0.34</td>
</tr>
<tr>
<td>CENSRND</td>
<td>10.45</td>
<td>4</td>
<td>2.61</td>
<td>11.25</td>
<td>0.00</td>
</tr>
<tr>
<td>AMPM × CENSRND</td>
<td>1.34</td>
<td>4</td>
<td>0.34</td>
<td>1.45</td>
<td>0.22</td>
</tr>
<tr>
<td>Residual</td>
<td>57.09</td>
<td>246</td>
<td>0.23</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Total</td>
<td>72.18</td>
<td>255</td>
<td>0.28</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

² Includes data from only those plots where Least Bitterns were observed at least once during the year (N = 48).

³ Observed significance level.

census rounds with the greatest number of Least Bittern calls per sequence. Playback of other species' calls did not seem to influence the response of Least Bitterns.

Using data from only the 48 plots where Least Bitterns were observed (at least one time during the year), we analyzed possible effects of time of day and different observers. Observation rates were higher during morning visits (Table 2), but this was largely because most evening counts were conducted during the first three census rounds (Table 3). In 1986, differences between the two observers were significant (x = 0.4 vs 0.1; P < 0.01), suggesting possible differences in detection ability (Cyr 1981) and a need for additional observer training (Kepler and Scott 1981). In 1987, differences between observers were not significant (x = 0.3 for both; P < 0.6).

Subjective estimates of cloud cover (0-10, 11-50, 51-90, and 91-100%) and wind speed (0-17, and 17-25 km/h) were used to assess possible effects of weather conditions. No significant correlations were indicated from a chi-square test for goodness of fit among the 8 combinations of cloud cover and wind speed (x² = 4.91, df = 6, P < 0.5). Nonetheless, strong winds may decrease observation of Least Bitterns by reducing an observer's ability to hear their soft calls. Relationships to temperature were not analyzed, since site-specific data were not available.

Discussion.—Despite our relatively low observation rate, it appears that Least Bitterns are responsive to playback of tape-recorded calls. A number of factors seemed to influence response frequency, suggesting that there is considerable potential for developing a reliable survey method for this species. Despite obvious limitations of our study, we observed significant response to tape-recorded calls, both numerically, and in field observations of individual birds. Based on these observations, we offer the following conclusions and recommendations regarding application of the playback technique to the study of Least Bitterns:

1. under favorable circumstances, a relatively high response rate can be obtained from birds within 30 m; (2) relatively high response rates can be observed between mid-May and mid-June, during morning surveys, on relatively calm days, regardless of cloud cover; (3) a minimum of 3 visits, with at least 5 min playback of the “cooing” call each time, is recommended for survey of point locations; (4) observers must be trained to recognize calls and estimate distances to calling birds; and (5) basic research is needed to determine seasonal and sexual differences in response behavior.

Acknowledgments.—This study was financed in part through research grants from the Hudson River Foundation for Science and Environmental Research, Inc. Additional funding was provided by the New York State Division of Fish and Wildlife and the Hudson River
National Estuarine Research Reserve. The Laboratory of Ornithology at Cornell University provided tape recordings of bird calls used in this study. The authors appreciate the constructive comments and editorial reviews provided by C. Blem, J. Dinsmore, R. Johnson, and W. Marion. We also thank S. Sheridan for typing the manuscript.

LITERATURE CITED


The development of kleptoparasitic behavior in Red-billed Woodhoopoes.—In review of kleptoparasitism, Brockmann and Barnard (1979) state that birds from some orders are disproportionately likely to exhibit this behavior. Kleptoparasitism frequently has been recorded among passerines and predatory nonpasserines but seldom among insectivorous nonpasserines. In particular, only three instances have been documented in which members of the order Coraciiformes exhibited interspecific kleptoparasitic behavior, namely the Common Kingfisher (Alcedo atthis), Carmine Bee-eater (Merops nubicus), and Abyssinian Roller.
(Coracias abyssinica) (Grist 1934, Moncur 1946, Tye and Tye 1983). I report here on three observations of interspecific kleptoparasitism involving another member of this order, the Red-billed Woodhoopoe (Phoeniculus purpureus). Red-billed Woodhoopoes are long-billed, insectivorous, group-territorial birds, weighing about 75 g. They inhabit a wide variety of woodland types across a broad Afrotropical range (Ligon 1981). They live throughout the year in flocks of 2–12 birds, have a cooperative breeding system (Ligon and Ligon 1978), and a dispersal system involving both males and females.

The present observations were made during a study of woodhoopoe behavior in the eastern Cape Province, South Africa, involving more than 50 flocks observed for 500 days during a ten-year period. All records of kleptoparasitism relate to a single, resident, color-banded flock (BD) in the Queenstown district (31°47'S; 26°47'E), which was monitored from January 1976 until 1984 when the flock disappeared. During this period, more than 200 h of observation were made of the BD flock.

In December 1980, two Red-billed Woodhoopoes from flock BD interacted aggressively with a pair of Cardinal Woodpeckers (Dendropicos fuscescens) at the latter's nest cavity in a willow tree (Salix sp.). The woodpeckers were trying to feed their nestlings, but the woodhoopoes obstructed them and attempted to steal food intended for the young woodpeckers. On one occasion a woodpecker successfully evaded the woodhoopoes and fed a nestling, whereupon the woodhoopoe male (WW) hopped to the entrance of the nest hole, inserted its bill into the nestling's mouth, retrieved a small insect, and swallowed it. This successful retrieval of food from a nestling resulted in a change in the woodhoopoes' behavior, whereby the adult woodpeckers were now allowed to feed their young unharrassed, and the woodhoopoes would then take the food from the nestlings with little difficulty. A young woodhoopoe female (WB) took over WW's role whenever he carried food back to the breeding female (WY) 80 m away. In one hour, WW took four food items and WB three in the course of as many provisions of food by the woodpeckers.

In April 1981, the same two woodhoopoes, WW and WB, were observed molesting and kleptoparasitizing Acacia Pied Barbets (Lybius leucomelas) in a similar fashion. The woodhoopoes again waited for the barbets to feed their nestlings, but the woodhoopoes obstructed them and attempted to steal food intended for the young woodpeckers. On one occasion a woodpecker successfully evaded the woodhoopoes and fed a nestling, whereupon the woodhoopoe male (WW) hopped to the entrance of the nest hole, inserted its bill into the nestling's mouth, retrieved whatever was fed. In this instance, five food items were robbed in 22 min (four by WW and one by WB) before the woodhoopoe flock moved on.

In February 1983, when WW and WB were no longer present in the BD flock (presumably having died), members of the same flock were seen molesting a pair of Paradise Flycatchers (Terpsiphone viridis), feeding three downy chicks, in an identical manner. The nest was partially obscured and I did not see the actual retrieval of food from the chicks, but the woodhoopoes exhibited exactly the same behavior as previously observed.

Red-billed Woodhoopoes occasionally probe unoccupied nests of Masked Weavers (Ploceus velatus) (Spence 1974), occupied open-nest structures of Cape Sparrows (Passer melanurus) (Newman 1975), House Sparrows (P. domesticus) (Newman 1981), and Paradise Flycatchers (pers. obs.), and vacant nest cavities of Black-collared Barbets (Lybius torquatus), Knysna Woodpeckers (Campethera notata), Cardinal Woodpeckers, Bearded Woodpeckers (Thripis namaquas), and Olive Woodpeckers (Mesopicos griseocephalus) (pers. obs.). In these instances, they presumably are feeding on insect larvae which hatched in the nest cavities or structures. Although I have recorded such nest probing on 41 occasions in 13 different woodhoopoe flocks, only the BD flock indulged in kleptoparasitic behavior. Similarly, J. D. Ligon (pers. comm.) recorded woodhoopoes tearing dried cattle droppings apart and eating the small beetles inside, but in only one of his Kenyan study flocks. Here also, unusual foraging behavior persisted in the flock even when the original members had all disappeared and been replaced.

Where members of one species feed on the products, scraps, or parasites of another, the development of kleptoparasitic behavior is enhanced (Rand 1954). I suggest that the observed
woodhoopoe kleptoparasitism had its origins in this type of interspecific interaction. During the woodhoopoe-woodpecker interaction, the woodhoopoes were under considerable feeding pressure because they were providing food for the breeding female and three nestlings. This may have provided the stimulus for a change from simple nest probing to active attempts at food interception. The observed adjustment of the initial interception suggests that it was a new behavior for the woodhoopoes and that a process of tactical refinement or learning was involved. The woodhoopoe-barbet interaction observed a few months later, when the flock was under little feeding pressure, and the woodhoopoe-flycatcher interaction, when the initial kleptoparasites (WW and WB) were no longer present, point to the adoption of new, opportunistic, feeding behavior by the BD flock. This, together with J. D. Ligon’s observations of manure shredding, suggests that certain behaviors may develop by chance and then be culturally transmitted to younger flock members. The fact that dispersal in woodhoopoes takes place only very infrequently implies that any such new behavior pattern may either take many generations to spread through the population or never extend beyond the flock in which it was initiated, as was probably the case with the kleptoparasitic habits of the BD flock.

Acknowledgments.—The following people provided comments improving the manuscript: R. Siegfried, R. Prŷs-Jones, P. Hockey, P. Woodall, W. Ferguson, and R. Brooke. J. Ligon kindly provided unpublished information on his Kenyan Woodhoopoes.

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Moncur, G. 1946. Some further notes on Merops/Ardeotis perching associations. Ibis 88: 236-238.


Morné A. Du Plessis, Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa. Received 1 Sept. 1987, accepted 1 Feb. 1988.


Two Pied Flycatcher males feeding nestlings in the same nest.—The Pied Flycatcher (Ficedula hypoleuca) is a small (12 g), hole-nesting Old World flycatcher. In different studies, 3-30% of the males were polygynous (Askenmo 1977, Alatalo and Lundberg 1984, Winkel and Winkel 1984). Potentially polygynous males stay with the first female until she has
started laying before they start claiming another nesthole (Alatalo et al. 1987). If the male succeeds in attracting a second female (even trigyny is known; Askenmo 1977, Winkel and Winkel 1984), he usually returns to feed his first brood but he may also aid his second female to a varying degree. Extra-pair copulations (EPCs) are quite frequent in the Pied Flycatcher, at least in the high density conditions of nestbox studies (ca 30%; Alatalo et al. 1987). Despite this, no study seems to have reported more than one male feeding young at the same nest; this note reports one such case.

In 1987 we studied Pied Flycatchers breeding in nestboxes near Lund, southernmost Sweden. Almost all adults were caught in nestboxes when the nestlings were 6 days old, weighed and individually color banded, and their wing length measured. Most of them were captured again 7 days later. On the first day of capture at one of the boxes, on 24 June, two different males were caught in addition to the female. On the basis of plumage characters (Karlsson et al. 1986), both males were judged to be 1 year old; one of them a black morph, the other brownish. The adults' feeding visits to the nestbox were recorded from a blind for 2 h each on 29 and 30 June. Both males were present and each fed the four nestlings. The brownish male fed 19 times on 29 June and 21 times on 30 June, while the dark male fed 7 and 22 times, respectively. During the same periods, the female supplied food 13 and 9 times, respectively. Thus the males' joint share was 76%. Some agonistic interactions between the males were recorded. It was always the brownish male who chased the dark one; however, on 30 June, he was seen quietly looking on while the dark male fed the nestlings. On 1 July, all three birds were again captured while feeding the young.

That two males feed at the same nest has previously been reported in the Bluethroat (Luscinia svecica, Arheimer 1987), the Bobolink (Dolichonyx oryzivorus, Bollinger et al. 1986), and the Dunnock (Prunella modularis), whose variable mating system has been carefully documented (for a summary, see Houston and Davies 1985). In the last-mentioned species, trios consisting of a female and two males occurred regularly. Sometimes the dominant male monopolized the female; in other cases both males copulated with her, the alpha male more often. Interestingly, the feeding shares of the two males reflected their mating success; beta males who had not copulated with the female did not feed nestlings, whereas beta males who had, did so. Was our observation of two male Pied Flycatchers feeding the same brood a similar case? Alatalo et al. (1987) never saw a female Pied Flycatcher solicit copulation from a male other than her mate. However, experiments have shown that females react differently towards a dummy when their own mate is present and when he is absent (G. Smith, pers. comm.). EPCs could be advantageous to the female if they increased the chances that the non-mate would help feeding nestlings. Especially late in the breeding season, when the risk of being a secondary female, and thus of being deserted by the male, is great, EPCs might act as an insurance. EPCs might also increase total male aid, as in Dunnock trios. The observation that the subdominant male made fewer feeding visits to the nest than the dominant male agrees with Houston and Davies' (1985) results for the Dunnock.

LITERATURE CITED


Askenmo, C. 1977. Some aspects of the reproduction strategy of the Pied Flycatcher
Unusual agonistic behavior in a Green Honeycreeper.—I observed a Green Honeycreeper (Chlorophanes spiza) exhibiting unusual behavior in its interactions with Bananaquits (Coereba flaveola) at Asa Wright Nature Center, 12 km north of Arima, Trinidad. The nature center occupies a clearing, heavily planted with ornamental plants, in fairly dense tropical forest. On most days, an abundance of fruit (primarily bananas) and nectar (sugar water) is placed at a series of feeders at the center to attract small birds. While watching these birds at a fruit feeder on the morning of 26 February 1984, I saw a male Green Honeycreeper reach over, pick up a Bananaquit by the wing, and drop it off the side of the feeder. In about 2 min of further watching, I saw the same honeycreeper pick up Bananaquits (which constantly came and went from the feeder) three additional times, both by wing and tail, and drop them from the feeder in the same manner. The action was brief and without struggle. The honeycreeper fed several times, then left, not to be seen again while I watched for another 10 min.

In Trinidad, Green Honeycreepers forage primarily for fruit (63% of 267 observations), while Bananaquits are primarily nectar-feeders (76% of 570 observations) (Snow and Snow, Auk 88:291–322, 1971), but they were competing for the same resource in this instance. Bananaquits literally swarmed at the feeders at times, and the larger species (mean weight of Green Honeycreeper 18.2 g, of Bananaquit 10.6 g [Snow and Snow 1971]) disposed of its competitors quickly and effectively, although perhaps only momentarily, by this method. The action seemed to involve less energy expenditure than a threat display or displacement attempt would have.

Birds regularly make bodily contact with each other during agonistic encounters, but the unusual aspect of the presently described one was its calmness. Neither bird called, and perhaps the action was quick enough so the Bananaquit had no chance to struggle before it was dropped. The density of the vegetation precluded my observation of any of them after they were released.

I watched honeycreepers, tanagers and other birds coming to these feeders for a total of about 4 h during my brief stay. Although I saw Green Honeycreepers and Bananaquits feeding at the same feeder several other times, I saw this interaction only on this occasion. As the first bird observed was so persistent in this singular behavior, I expected to see it again, and the other birds I saw subsequently may have been different males, as there were...
several in the vicinity. I presume the honeycreeper chanced upon the behavior pattern and repeated it when it worked.—DENNIS R. PAULSON, Burke Museum DB-10, Univ. Washington, Seattle, Washington 98195. Received 11 Nov. 1987, accepted 15 Feb. 1988.

**Wilson Bull., 100(3), 1988, p. 504**

Osprey hunting on ground for small mammals.—Ospreys (*Pandion haliaetus*) are known hunting specialists that feed primarily on fish. Their hunting technique involves plunging feet first into water to capture prey. In contrast, here we report an Osprey successfully hunting on the ground for ground squirrels (*Citellus* sp.). The observation was made 27 June 1987 approximately 2 km south of Henry Lake, Idaho. The Osprey was observed walking along a dirt road for approximately 30–40 m. Every several meters it would turn its head to the right and either stop or continue to walk. Suddenly, it turned to the right, opened its wings and glided about 2 m, hitting the ground with its legs extended. The Osprey then hopped back toward the road with a ground squirrel in its talons, and flew off with its prey. The species of ground squirrel is unknown. However, ground squirrels were abundant in the area. Several Sandhill Cranes (*Grus canadensis*) also were seen feeding on ground squirrels. Therefore, we assume that the Osprey opportunistically adopted this particular hunting technique to utilize a locally abundant food resource. Although our assessment is subjective, the Osprey did appear to be accomplished in this hunting procedure, suggesting that the technique had been utilized previously. In addition to their regular diet of fish, Ospreys may feed on birds, frogs, crustaceans, and small mammals (Wiley and Loher, Wilson Bull. 85: 468–470, 1973). However, there are few actual sightings of Ospreys capturing mammals, and their hunting procedures are not well known. Proctor (Wilson Bull. 89:625, 1977) observed an Osprey capturing a small vole (*Microtus pennsylvanicus*) in a salt marsh. In that case the bird was observed to “hover in the same pattern it would in catching a fish and then plunge to the ground.” In contrast, we observed a rather unusual pattern (for Ospreys) of hunting by moving along the ground. Thus, at least two different hunting patterns may be used by Ospreys to catch small mammals. Since, in this instance, the observation was on hard ground rather than in a salt marsh, it is possible that the normal diving method of Ospreys precludes efficient swooping onto prey on hard ground, thus resulting in this particular bird’s adopting the walking hunting technique.—JOHN H. WERREN and C. JEANNE PETERSON, Dept. Biology, Dept. Pediatrics, Univ. Rochester, Rochester, New York 14627. Received 15 Dec. 1987, accepted 18 Feb. 1988.

**Wilson Bull., 100(3), 1988, pp. 504–506**

Unusual Greater Sandhill Crane egg.—Normally, the eggs of a given species of bird are uniform and fixed in coloration so that a species can be identified by its eggs (Welty 1975). Furthermore, individual birds ordinarily lay eggs of consistent color and pattern (Littlefield 1981, Harrison 1984). Although variations do occur within species, a contrary phenomenon occurs when a bird that normally lays pigmented eggs lays white eggs lacking in color (Welty 1975). This has been documented previously in at least 34 North American bird species (Gross 1968), but until now has not been observed in Sandhill Cranes (*Grus canadensis*). Here we describe the white egg of a Greater Sandhill Crane (*G. c. tabida*) found on Modoc National Wildlife Refuge (N.W.R.), Modoc County, California, during 1986. The 2543-ha Modoc N.W.R. surrounds the confluence of the north and south forks of
the Pit River, near the town of Alturas in extreme northeastern California. Geographically, the refuge is situated on the western edge of the Great Basin at an elevation of 1322 m. Sandhill Crane production receives high priority as a wildlife objective on the refuge, requiring collection of nest data for annual production estimates.

On 16 May 1986, I observed an adult Sandhill Crane on a nest in the southwest Sharkey Field of Modoc N.W.R. This field is an open, irrigated meadow with vegetation consisting of rushes (*Juncus* sp.), sedges (*Carex* spp.), grasses, and various forbs and is typical of the habitat type supporting the greatest number and highest density of crane nests on the refuge. On 23 May, I recorded nest data and photographed the nest which was composed of rushes, grasses, and bits of moss. It contained two long-oval eggs (Harrison 1979) of ca 20 to 24 days of age as determined by the float method (Westerkov 1950). No embryo movement was noted during flotation. One egg was light tan, marked with darker brown spots and blotches, and measured 100.0 mm x 58.0 mm. The other egg measured 98.4 mm x 57.3 mm, and was uniformly grayish white. Normal crane eggs are described as subelliptical to long oval, smooth with little or no gloss, pale to medium buff or olive in color, spotted and blotched with light to dark brown, and with pale purple or lavender spots (Udvardy 1977, Harrison 1979, Harrison 1984).

The white crane egg could not be confused with those of the Western Canada Goose (*Branta canadensis moffitti*) because of its size, color, and shape. Western Canada Geese, which have been documented as laying eggs in Sandhill Crane nests (Littlefield 1979), also nest on Modoc N.W.R., but lay eggs averaging 87.2 mm x 59.1 mm (Williams and Nelson 1943). Furthermore, Canada goose eggs are described as elliptical to subelliptical and white to creamy white (Harrison 1979).

I rechecked the nest on 6 June and found that the normally colored egg had hatched, as determined by the egg fragments and detached shell membrane. The white egg had a large hole in its side, evidence of avian predation, but was rotten and had not been consumed. Apparent lack of an embryo demonstrated that the egg was infertile or had died at an early stage. Predation of the white egg may have occurred after the normally colored egg had hatched and the cranes had left the immediate area.

Shadick (1985) described albino plumage in a Sandhill Crane, but albinism of the plumage is independent of albinism of the eggs (Gross 1968). Egg pigments are secreted by the walls of the oviduct, particularly in the region of the uterus. In albino eggs, the secretion of pigments is arrested either physiologically or by disturbance, or the egg did not remain in the uterus long enough to receive its full quota of pigment (Welty 1975). There is insufficient evidence to indicate that the trait of laying albino eggs has a genetic basis (Gross 1964, 1965, 1968).

**Acknowledgments** — We thank C. Littlefield, S. Derrickson, and C. Blem for reviewing this note. Observations were made while the senior author was employed by the U.S. Fish and Wildlife Service, which we thank for making information available for this paper.

**LITERATURE CITED**


Subadult intrusion and probable infanticide at a Cooper's Hawk nest.—We made the following observations from a tree blind 5 m from a Cooper's Hawk (Accipiter cooperii) nest in Portage County, Wisconsin. On 26 June 1987, a subadult female Cooper's Hawk in juvenile plumage landed within 3 m of the nest where an adult female was feeding her four young (12-14 days old). The adult looked at the subadult but resumed feeding the nestlings. The subadult called (“kek”) and leaned toward the nest as if she would fly to it, but the adult did not exhibit aggressive or defensive behavior. After about 18 min, the adult finished feeding the young and flew from view; almost immediately the yearling flew to within 0.5 m of the nest and landed on a nest support branch. The young moved away from the subadult as it walked toward them with its wings partially extended and crown feathers raised. It lunged and then flew to another nest support branch behind the young. There it resumed a threat posture and pushed itself through the young, knocking one from the nest. JMP immediately retrieved the fallen bird and returned it to the nest where it died less than 1 h later, apparently due to the fall. In the meantime, the fourth young hawk (a “runt”) disappeared from the nest. We believe the subadult removed it. On two other occasions later that day (while the adult female was not in view), and again on 27 June, a subadult female Cooper's Hawk landed within 2 m of the nest but flew from view within 1 min.

This observation is similar to one we made on 24 June 1984 at another Wisconsin nest. In that instance, we watched a subadult Cooper's Hawk which likewise elicited no detectable defensive behavior from an adult female, even though it approached to within 3 m of the nest and called for 3-4 min before departing. As in the other case, the adult female showed no defensive behavior. The lack of agonistic response from adults to a nearby subadult could be due to the adult and subadult being related, or to a tendency for nesting females not to attack subadults.

Acknowledgments.—We thank W. and P. Olson for allowing us access to their land, and J. Belefeldt, D. Evans, and G. Nuechterlein for their comments on this note. For financial support we thank C. and M. Nelson and the Lakeland, Madison, and Milwaukee Audubon Societies.—ROBERT N. ROSENFIELD, Zoology Dept., North Dakota State Univ., Fargo, North
American Dipper nestlings parasitized by blowfly larvae and the northern fowl mite.—Blowfly larvae of the genus Protocalliphora (Diptera: calliphoridae) and many mites of the genus Ornithonyssus (Acari: Dermanyssidae) are obligatory, bloodsucking parasites of birds. The former parasitizes nestlings of nidicolous birds (especially passerines) and the latter parasitizes all ages of birds (particularly poultry). Both genera have little host specificity and have been reported from a diverse variety of birds (Bennett 1957, Hall 1965, Baker et al. 1967, Whitworth 1976, Gold and Dahlsten 1983, Garrison et al. 1986). To the best of my knowledge, this note is the first published record of either the blowfly larvae (Protocalliphora aenea and P. braueri) or the fowl mite (Ornithonyssus sylviarum) on the American Dipper (Cinclus mexicanus). However, the fowl mite has been reported from the European Dipper (C. cinctus) (Spitznagel 1985).

Dipper nestlings and nests were examined manually for parasites during nesting or shortly after fledging along Dinkey Creek (a 10 m wide snowmelt stream in mixed conifer forest at 1067-1081 m elevation) and its tributaries, Fresno County, California. Fly larvae and pupae were removed from nestlings or nests, respectively, and reared to maturity.

In 1984, I found a single nestling and its nest (statant cupped or dome type nest) infested with approximately 400 O. sylviarum. Both nymphal and adult stages (about 1 mm in length) were collected from the feathers and skin of the nestling, but most mites were in the nest. From 1984 to 1987, I found 7 of 17, 3 of 19, 0 of 5, and 1 of 4 nests, respectively, parasitized by P. aenea or P. braueri. Specimens identified in 1984 and 1985 are P. aenea; 1987 specimens are P. braueri. Nests parasitized in 1985, 1986, and 1987 were parasitized in 1984. Two to six blowfly larvae (about 7 mm in length) per nestling were embedded subcutaneously on the head, wings, and legs. Ten to 40 puparia were found in some nests after fledging. In one case, only one of four nestlings was parasitized.

Additional unpublished records of P. aenea parasitizing the American Dipper include: two specimens from Utah (Whitworth 1976) and 89 males and 110 females from Gunnison County, Colorado collected by C. L. Remington in 1960 (C. W. Sabrosky, pers. comm.).

I attributed mortality of one nestling (14 days old) in 1987 to P. braueri parasitization. This nestling was infested with two larvae in a wing and five larvae in the head which caused limited movement of the mandible and probably impaired hearing and vision. However, other parasitized fledglings (as indicated by a swollen area with a round scab which covers the larva's emergence hole) did not appear to be seriously impeded.

The effects of Protocalliphora parasitism upon nestling survival range from no observed distress to death (Gold and Dahlsten 1983). Bennett (1957) and this paper attributed nestling mortality to Protocalliphora parasitism. Even when mortality is not observed in nestlings, the loss of blood may contribute to nestling stress and possibly reduce post-fledging survival (Bennett 1957, Whitworth 1976, Gold and Dahlsten 1983).

P. hirudo (a synonym of P. braueri; Sabrosky, pers. comm.) is reported as an obligatory, subcutaneous parasite, whereas other nearctic species are reported as intermittent ectoparasites (Bedard and McNeil 1979, Gold and Dahlsten 1983, Garrison et al. 1986). However, my observations indicate that P. aenea (and P. braueri), at least in the dipper, are subcutaneous parasites, and that they pupate in the dipper's nest.
Acknowledgments.—I thank C. Sabrosky for identifying *P. aenea* and *P. braueri* and for providing additional records, and T. Kono for identifying *O. sylvirum*. B. Garrison, J. Oldham, J. Single, B. Valentine, and C. Blem reviewed this note. L. Benjamin, S. Boland, and M. Stafford aided with field work. These observations were made while conducting American Dipper population ecology studies as part of the Kings River Conservation District's Dinkey Creek Hydroelectric Project.

LITERATURE CITED


Wilson Bull., 100(3), 1988, pp. 508-509

Ring-necked Pheasant parasitism of Wild Turkey nests.—Ring-necked Pheasants (*Phasianus colchicus*) are facultative nest parasites of several species including Greater Prairie-Chickens (*Tympanuchus cupido*) (Simpson and Westemeier 1987), Ruffed Grouse (*Bonasa umbellus*), Northern Bobwhite (*Colinus virginianus*) (Bent 1932), Blue-winged Teal (*Anas discors*), Mallard (*A. platyrhynchos*), Northern Shoveler (*A. clypeata*) (Bennett 1936), and other Ring-necked Pheasants (Baskett 1947). Nest parasitism of Wild Turkeys (*Meleagris gallopavo*) has not been conclusively documented. I here report three instances of pheasant nest parasitism of Rio Grande Wild Turkeys (*M. g. intermedia*).

Wild Turkey habitat use was studied in the South Platte River flood plain in northeast Colorado in 1986 and 1987. Thirty-three of 35 turkey nests were in the riverbottom community, with peak nest initiation in mid-April to early May. Ring-necked Pheasants occur throughout northeastern Colorado, including riverbottom habitats, with greatest pheasant abundance in dryland wheat areas. Pheasant nest initiation normally begins in late April and early May (W. D. Snyder, pers. commun.).
On 5 May 1987, an adult turkey hen was flushed from a nest containing nine turkey eggs and one pheasant egg. All eggs were present on 25 May, and on 29 May the hen was still incubating. Visual inspection of the nest on 31 May indicated all eggs had hatched. At a second turkey nest, 11 of 12 turkey eggs and one pheasant egg hatched. Brood evasive behavior, thick understory, and similarity of turkey and pheasant chicks prohibited determination of pheasant chick survival. On 19 May 1987, a third hen was flushed from a nest containing 15 turkey eggs and one pheasant egg. On 23 May, the nest was found depredated and contained intact eggs or eggshell remains of 16 turkey eggs and one pheasant egg. The other 32 turkey nests were also inspected soon after hatching or depredation and no evidence of pheasant parasitism was found.

Assuming a 28-day incubation period for turkeys (Bailey and Rinnell 1967) and a 23-day period for pheasants (Bent 1932), the first hen was parasitized either during late egg laying or the first three days of incubation. Therefore, this pheasant egg hatched after inspection on 25 May but before the hatch of the hen’s own eggs. The observation of a 16th turkey egg in the third hen’s nest indicates she was parasitized during egg laying. Studies of other facultative, precocial nest parasites, primarily anatids, indicate parasitism is most common and successful during the egg-laying period of the host (e.g., Weller 1959). Incubation periods for eggs of parasitic anatids and their hosts’ eggs are usually similar and result in synchronous hatching of host’s and parasite’s eggs. Pheasant parasitism of turkey nests during egg laying or early incubation, however, will result in asynchronous hatching due to differential incubation periods. Hatching asynchrony was observed for one nest and would have occurred in the depredated nest. Asynchronous hatching potentially is maladaptive for precocial species due to the chick’s probable inaccessibility to quality brood areas under the protection of the hen. None of the turkey hens left their nest site until their own eggs hatched. Simpson and Westemeier (1987), however, observed Greater Prairie-Chicken hens leaving nest sites after single pheasant eggs hatched but before their own eggs had hatched.

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LITERATURE CITED


First record of the Blue-throated Goldentail (Hylocharis eliciae) in Belize.—The Blue-throated Goldentail (Hylocharis eliciae) is resident from southern Mexico to western Panama (AOU 1983, Check-list of North American Birds, 6th ed. A.O.U., Washington, D.C.), but it has not been recorded previously from Belize (Wood, Leberman, and Weyer 1986, Check-list of the Birds of Belize. Carnegie Museum of Natural History Special Publication No. 12). The Blue-throated Goldentail has not been found in the Yucatan peninsula or in the Tikal area of northeastern Guatemala, and the nearest record to Belize is from the Caribbean lowlands of Guatemala (D. S. Wood, pers. comm.). A Blue-throated Goldentail was captured in a mist net in Belize on 19 April 1987 in a 4-ha orange orchard, and was released after being photographed (VIREO accession numbers V06/5/001, V06/5/002, V06/5/003). No other individuals were observed or captured during the nine months (25 Aug 1986–10 May 1987) of netting and observation in the citrus plantation. The Blue-throated Goldentail has a shiny gold tail, a red bill with a black tip, and a blue gorget. The underparts are mostly green, and the rump is copper (Peterson and Chalif, 1973, A Field Guide to Mexican Birds. Houghton Mifflin, Boston, Massachusetts). The identification of the bird was confirmed from our photographs by P. E. Scott and J. V. Remsen, Jr., Museum of Zoology, Louisiana State University. The study area (17°10'N, 88°40'W) is part of a 1400-ha citrus plantation owned by Belize Groves Management Company and is located 55 km west of Belize City on the Western Highway in the Cayo district. The plantation is situated in a transition zone from pine savannah to broadleaf hardwood forest. The vegetation surrounding the plantation predominantly is second growth, consisting mainly of Cecropia sp. trees, but also contains Castilla and Orbignya. There is a slender area of bamboo (Gramineae) where the plantation borders the Sibun River. The valencia orange trees (Citrus sinensis) were fairly uniform in height (x = 3.1 ± 0.45 [SD] m, N = 25) and diameter before branching (x = 12 ± 2 cm). The approximately 950 trees were spaced at 6 m x 6 m, and the ground was completely covered with grasses in the 6-yr-old orchard. The orchard is about 100 m from the Sibun River and is bordered by a dirt road, a 10 ha clearing, and a small housing compound.

Acknowledgments.—Work during 1986–87 in Belize was funded by the J. Nicholene Bishop Memorial Fund, the Latin American Studies Program, and a Student Government Association research grant, all from the University of Alabama. We are indebted to B. Sokolsky, V. Sokolsky, Y. Plasmann, B. Hasse, J. Van Der Vinne, D. Van Der Vinne, and Belize Groves Management Company Limited for aid in Belize. We thank C. Blem and D. Wood for their comments on an earlier draft of this manuscript, and P. Scott and J. V. Remsen, Jr. for confirming the identification of the hummingbird. EDWARD D. MILLS AND DAVID T. ROGERS, JR., Dept. Biology, Univ. Alabama, Tuscaloosa, Alabama 35487. Received 18 Aug. 1987, accepted 8 Feb. 1988.

A new record of the Streaked Bittern from northeastern Brazil.—In South America, the Streaked Bittern (Ixobrychus involucris) is known from disjunct populations in the north (Colombia, Venezuela, Trinidad, Guyana, and Surinam) and the south (southern Brazil, Paraguay, Uruguay south to Chile, and northern Patagonia) (Mayr and Cottrell 1979). In Brazil, the northernmost edge of the normal range is in the southeast region of Lago Feia, state of Rio de Janeiro (Meyer de Schauensee 1966). There are two previous records from
northeastern Brazil, one for São Bento, Maranhão (about 02°40'S, 44°50'W) and one from Propriá Sergipe (10°13'S, 36°50'W). There are no records from the semiarid hinterland of this area (Teixeira et al. 1986). On 1 December 1986, one adult female of this species was collected by our local guide on the Venezia ranch, municipality of São Raimundo Nonato, state of Piauí (approximately 09°40'S, 41°30'W). It was not in reproductive condition. The stomach contained four dragonflies (Odonata). The specimen is now in the collection of the Zoology Department of the Universidade Estadual de Campinas (UNICAMP, ZUEC 1495).

The bird was taken on the shore of a large artificial lake surrounded by xerophytic arboreal “caatinga” (dry deciduous forest) typical of the region, with very few natural pools and subject to periodic, irregular, and often prolonged droughts. This habitat is quite unlike the typical habitat of the species, namely marshy grasses and sedges (Hancock and Kushlan 1984).

This individual was far from the known range of the species. Although the movements of the Streaked Bittern are not well known, it has been suggested that southern birds may sometimes stray northward (Hancock and Elliot 1978) and that the records from northeastern Brazil are from stragglers (Blake 1977). As southeast Piauí has never been studied in detail by ornithologists (only Spix and Matius before us in the early nineteenth century), we cannot discount the possibility of the regular occurrence of the species there.

Acknowledgments.—Our research is supported by the Missão Franco Brasileira no Sudeste do Piauí. J. Vielliard has given us much helpful advice. K. Brown kindly revised this paper. We are indebted to N. Guidon for help with the beginning of the research and for introducing us to the Missão.

LITERATURE CITED


Fabio Olmos, Depto. Zoologia, Univ. Estadual de Campinas, CP 6109, Campinas SP, Brazil CEP 13081; and Maria Fatima Barbosa Souza, Pro Reitoria de Extensão, Univ. Estadual de Campinas, CP 1170, Campinas SP, Brazil CEP 13081. Received 24 Aug. 1987, accepted 20 Feb. 1988.
Helpers at Birds’ Nests. By Alexander F. Skutch, illust. by Dana Gardner. University of Iowa Press, Iowa City, 1987: 298 pp., many black-and-white sketches. $25.00.—Fifty years ago, Alexander Skutch (Auk 1935) launched the study of “Helpers at the Nest” with brief reports on three Central American birds—a jay, a wren, and a bushtit—in which nestlings were attended by individuals other than their parents. At that time only a very few other species were known to exhibit helping behavior. Twenty-five years later, Skutch (Condor 1961) surveyed the occurrence of “Helpers Among Birds” and found records for scores of additional species. No doubt Skutch’s earlier paper had triggered other naturalists to search for and report on birds with helpers.

What has been the growth of this field of study since 1961? The answer is “extremely rapid.” “Helpers at Birds’ Nests” lists about 400 titles. Despite an historical bent, 70 percent of the references postdate Skutch’s 1961 review. Why has this field of study grown so rapidly in recent years? In large part, I suggest, because in the early 1960s biologists came to realize that social behavior, like anatomy, is adaptive, and can be studied using modern methods of science. Following this realization, theoreticians, W. D. Hamilton (1964) for example, framed observations such as helping behavior into testable hypotheses. This state of affairs sent the field biologists back to nature to find, observe, and record the activities of bird species with helpers. The differences in approach between these observers and Skutch allow us to predict the design of Skutch’s new book on helpers among birds.

“Helpers at Birds’ Nests” is organized into 53 chapters, 49 of which describe the life histories of species in families of birds known to have helpers. Length of chapters varies many fold; those pertaining to families that include few species with helpers, or for which little information is available about helping, are as short as two pages. Many of the chapters include species Skutch himself has studied. The accounts for those he has not studied seem generally accurate. His bibliography includes ten references from 1984 and one from 1985. With the field growing so rapidly, overlooked references are to be expected. The most unfortunate omissions I found were to the important work done, and being done, on Campylorhynchus wrens by Wiley and Rabenold, some of which predate 1985. I found pleasing the black-and-white sketches, which represent more than 60 bird species and emphasize cooperative breeders.

Skutch is renowned for his life history accounts of many species of neotropical land birds. He writes with the familiar, easy style of the good 19th-century naturalists. For this reason, the book is enjoyable, and I can recommend it to students of cooperation in animals as an introduction into the lives of cooperative-breeding birds. However, beware the numerous anthropopathisms. Birds simply are not known to have the emotions Skutch assigns to them.

The 49 taxonomically arranged, descriptive chapters are followed by three short chapters that synthesize and analyze the information Skutch has presented. These chapters make up only 10% of the book; they include no tables and no figures. These facts foreshadow my criticisms of the book.

Chapter 52, “Characteristics of Cooperative Breeders,” discusses topics such as geography, habitat, diet, social structure, sex ratio, dispersal, group composition, number of helpers, and activities of helpers. While almost a necessity for a book of this kind, I find nothing discussed or concluded that has not appeared already elsewhere.

The subject of Chapter 51, “The Significance of Interspecific Helping,” is rarely treated more than casually by other authors. This subject accounts for many of the references in Skutch that do not appear in other books on cooperative birds. Interspecific helping seems relevant to the evolution of brood parasitism, to the proximate mechanisms that cause
helping, and to contemplating possible benefits to the doners in cooperative species. Skutch uses it to support his theory for helpers at birds' nests, which he develops in the last chapter.

The final chapter, "Benefits and Evolution of Cooperative Breeding," is written in the phraseology of natural selection. However, it is frustrating, if not impossible, to follow in detail Skutch's lines of reasoning. He never makes clear the subtle differences in various theories. His discussions wander in and out of individual selection, kin-group selection, intergroup selection, and selection for the good of the species. Even if he does hold the opinion that all these levels of selection operate on cooperative breeders (p. 269), Skutch should distinguish them more clearly.

Skutch outlines his theory on the origin of cooperative breeding in the final five pages of the book. The first two steps are those proposed by many investigators, namely, young birds remain at home for direct fitness benefits (individual selection), and feed close relatives for indirect fitness benefits (kin-group selection). Next he suggests that some species may not need the greater reproductive potential that early breeding by unaided parents might give them (intergroup and/or species selection perhaps?).

As a final step, Skutch proposes "that many birds breed cooperatively because they value the feeling of security that comrades give, enjoy companionship, and find this a satisfying way of life." Skutch freely admits that this step (for which I propose the phrase anthropopathic selection) includes "values that are not amenable to scientific investigation . . . ." The idea may stem from his philosophy of life, which he elucidates in the final paragraph. "If . . . evolution did not raise at least some of its creations to higher levels of awareness and enjoyment, it would be . . . producing nothing of worth." Interesting, but defendably outside the scope of a review for a journal of science.—GLEN E. WOOLFENDEN.

**Birds of the Pacific Slope.** With species accounts and field notes by Andrew Jackson Grayson, and with current ornithological identifications to accompany the 156 bird portraits, all his surviving paintings from the Bancroft Library, University of California, Berkeley, reproduced as plates in the companion portfolio. By Lois Chambers Stone. Arion Press, San Francisco, 1986:433 pp., illus., + portfolio of 156 colored and 1 uncolored prints, 19 x 25 in., in heavy cloth-covered box. Limited to 425 numbered copies. $4500.—Book reviews in The Wilson Bulletin and similar journals are intended in large part to present an informed opinion of the quality of the work under review, so as to help the reader decide whether to order a personal or institutional copy. This aspect of reviewing is obviously not pertinent for most readers when a $4500 limited edition work is under discussion.

Similarly, reviewers for most scientific journals, unlike those for newspapers and commercial magazines, are not paid for their manuscripts, their only tangible reward being retention of the review copy of the book. But publishers can hardly afford to donate copies of $4500 books to reviewers. For purposes of the present review, therefore, Arion Press provided me with a paperbound copy of the text, and loaned me a dozen of the prints. Subsequently I was able to examine a bound text and a full set of prints that had been presented to the library of Carnegie Museum of Natural History by a private donor.

The name of Andrew Jackson Grayson has been relatively unfamiliar to American ornithologists, but readers with access to a set of The Condor will find that 23 of Grayson's paintings were reproduced, much reduced, in volumes 51-59 (1949-1957). With the first of these appeared a brief biographical note on Grayson (Condor 51:49-51, 1949) by Lois Chambers Taylor, now Lois Chambers Stone. Of these 23 plates, 9 were reprinted in the "Distributional Check-list of the Birds of Mexico" (Pac. Coast Avifauna 29, 1950, and 33, 1957).

The present work was produced by Arion Press and designed by its Director, Andrew
Hoyem, generally regarded as one of America’s outstanding living book designers. The text is handsomely printed in a large and eminently readable Van Dijck font. S. Dillon Ripley provided a 2-page Preface, “Rediscovery of a pioneer naturalist”; in this account, the oceanic Isla Socorro is called “offshore” and is erroneously divorced from the “Revilla Gigedo Archipelago” [=Isla Revillagigedos]. Glenn R. Todd, who edited the text for Arion Press, wrote a 10-page Introduction, “Grayson’s place in ornithology,” with acknowledged input from George E. Watson on Grayson’s scientific contribution and Mary LeCroy on Grayson’s paintings in the context of 19th-century ornithological art. This Introduction is rather disorganized, especially in its chronological wanderings.

Part One of the text proper (pp. 23–151) consists of a thoroughly researched 10-chapter biography of Grayson by Mrs. Stone. Part Two is a series of notes on the 156 color plates and the uncolored plate of California Quail (Callipepla californica), the latter reproduced from the only full-scale print made from any of the art work of Grayson during his lifetime. The notes for each plate include the current A.O.U. English and scientific names; “Description,” a fine-print paragraph describing the contents of the picture (including scientific names of any identifiable plants); “Distribution” of the species, again in fine print; “Inscription,” the wording on the original painting, plus, if not included by Grayson, the date and place of its execution; and “Field Notes” in Grayson’s own words. For some species there are additional notes, including quotations from the correspondence of Grayson and Spencer Fullerton Baird, notes on the Grayson specimens in the Smithsonian Institution, etc.

Andrew Jackson Grayson (1818–1869) was a fascinating and, to some extent, a tragic figure in the history of North American ornithology. Born in Louisiana, he was attracted to nature as a boy, and enjoyed drawing, but his father, a wealthy planter, disapproved of such activities. Eventually Grayson, at the age of 28, emigrated to San Francisco with his wife and infant son; the frontispiece of the present work is “The Promised Land,” a painting by William S. Jewett commissioned by Grayson in 1850 to memorialize the family’s arrival in California. Although his success as a businessman fluctuated with the prevailing economy, he managed to support his family and still have time to study ornithology and practice his painting.

In 1853 Grayson saw a copy of Audubon’s “Birds of America,” an event that provided him with a lifetime inspiration. As Audubon had painted only a few Pacific Coast birds, from specimens sent to him by correspondents, Grayson was determined to complete Audubon’s work by painting the birds of the Pacific Slope. His first efforts were naturally of the birds of California, but on a visit to Tehuantepec, Mexico, he began the series of portraits of Mexican birds that are the principal feature of the present collection. Two years later he moved permanently to Mazatlán, as his business ventures in California were failing, and he hoped to do better in Mexico. Earlier he had formed a connection with the Smithsonian Institution, to which he had sent some of his specimens. In the early 1860s, Spencer Fullerton Baird, then Secretary of the Smithsonian, prevailed upon Grayson to collect bird specimens in some then unexplored areas of Mexico, beginning with the Islas Revillagigedos. During Grayson’s first visit to those islands in 1865, he discovered most of their endemic birds, several of which were named either by him or for him. Grayson continued his ornithological explorations of western Mexico and adjacent islands, adding constantly to his portfolio of paintings. An attempt to secure financial assistance from the government of Mexico failed with the overthrow of the Emperor Maximilian. He nevertheless continued to paint, although his health was deteriorating. During the last few years of his life he was shipwrecked on Isla Socorro in the Revillagigedos, his son Ned was murdered in San Blas at the age of 22, and his financial situation became more desperate. Grayson died in Mazatlan in 1869 from Yellow Fever.

Grayson’s widow, Frances Timmons Grayson, sought in vain for ten years to find a publisher for her husband’s paintings. She finally decided to donate them to the University.
of California at Berkeley, and at her death in 1909, all of her husband’s papers were added to the archives, now housed in the University’s Bancroft Library.

In reviewing the present edition, it is of course impossible to evaluate the color reproduction of the plates without comparison with the original paintings. Comparison with the much-reduced versions in *The Condor* shows the latter, as might be expected, to have lost some of the subtlety of coloring apparent in the Arion edition. The *Condor* plates are heavy on the yellows and reds, further emphasizing the subdued appearance of the Arion version. The reproduction of the Arion plates was accomplished with the use of the latest state-of-the-art techniques, including laser scanning. Mr. Hoyem informs me that the first copies were so literal that slight irregularities and discolorations in the original paper were faithfully reproduced, and had to be removed by hand retouching. In a sense, therefore, the plates are closer to Grayson’s original concept than to the paintings in their present condition.

And what of Grayson as an ornithological artist? Glenn Todd’s introduction is cautious on this score, but suggests that Grayson was “the preeminent bird painter of his generation, both for the fidelity of his renderings and for his consummate artistry.” Todd places Grayson’s “generation” among American bird artists as after Audubon and prior to Louis Agassiz Fuertes and “Allen” [=Allan] Brooks. It is true that Grayson had few competitors in North America during this period, but during his lifetime the great flowering of British bird illustrations was beginning; the magnificent Josef Wolf, for example, was only two years younger than Grayson.

Grayson emulated his predecessor Audubon in several ways. Most of his paintings include botanical and/or entomological materials, and several have recognizable background landscapes (such as Cerro Evermann on Isla Socorro). Like Audubon, Grayson often attempted to portray birds in livelier positions than was traditional in European bird paintings, but he painted many species in rather stiff upright poses. As George Sutton emphasized many times in correspondence and conversations with aspiring bird artists, the degree of “life” in a painting rests to a large extent on the rendition of the eyes. The eyes of Grayson’s birds are flat, with the traditional stereotyped wedge-shaped highlight. Audubon generally used the same kind of highlight, but was already beginning, through subtle shading of the iris color, to give the eyeballs of some of his birds a more rounded and thus lifelike appearance. Even Wolf broke away from the wedge highlight in only a few of his paintings; among his more successful renditions of rounded eyes is that in his Greenland Falcon plate for Gould’s “The Birds of Great Britain” (1863) (reproduced in A. Lysaght, “The Book of Birds,” 1975).

One major decision by the Arion Press editors is understandable, but I regret it nevertheless. The plates are arranged taxonomically, in the sequence of the 6th edition of the A.O.U. Check-list. This isn’t really a book about birds, but about Andrew Jackson Grayson. I was privileged to attend an illustrated talk about Grayson by Andrew Hoyem, in which the slides of the plates were presented in chronological sequence. This permitted me to appreciate for the first time the maturation of Grayson as a bird painter; leafing through the plates as presently arranged gives an unwarranted and unfair impression of inconsistency of style and accuracy, ranging from grotesque to charming.

Arion Press has done historians of bird art a major service in reproducing the Grayson paintings. Of fully equal importance is the text, which should revive interest in the life and accomplishments of an undeservedly forgotten pioneer in American ornithology. Let us hope that eventually a more modestly priced edition of the text will be made available for the general ornithological community.—KENNETH C. PARKES.
heading on the cover. In doing so, the authors have provided a primer, and reminder, for students interested in seabirds. There is a strong bias toward coastal marine systems of the northeast and southeast Atlantic, as well as gulls and terns, the areas of expertise of the authors. One must remember, however, that other oceans do exist and that larids may not be “typical” seabirds. The first 52 pages in four chapters deal with an exposition of seabird life styles and theories on ecology and population regulation with good short introductory and summary paragraphs. The following four chapters deal with interactions with fisheries (45 pp.), monitoring marine environments (25 pp.), seabirds as pests (10 pp.), and seabird conservation requirements (9 pp.). Twelve pages are devoted to the references, and most of the historical and pertinent primary literature through 1985 is included. The authors do cite heavily summary articles in the text, a method that probably is very useful to beginning students. Throughout the text, the sectional numbered divisions are useful, and alternate theories/hypotheses are presented.

I do have a few quibbles and illustrations of my own biases: on page 7, 5th line from the bottom, in discussing mate fidelity, the statement is made that “they will change mates” if a pair is unsuccessful at breeding. I would suggest may be a better verb, at least as demonstrated by the few studies of banded birds that have lasted long enough to show this phenomenon. On page 8, in discussing colonial breeding, a clear distinction between the “consequences” and “functions” of coloniality must be made in order to understand the differences in colonial habits. On page 9, the authors suggest only as an alternative that “sites . . . safe from predators . . . may be in short supply, birds collect together when they occur.” I would suggest that from a seabirds’ point of view, at least in tropical oceanic species, nesting islands are limited in number and distribution, and thus the social activities we observe in colonial species are the consequences of breeding together, not the “advantages” as noted in this text. On page 12, the authors set up the “r” and “K” selection dichotomy rather than present it as a continuum, although this is discussed in later chapters. For the beginning student, I believe the continuum is a more useful concept. On page 23, I suggest that bill shape and size are as important to feeding as is body size. On page 24, the authors give squid short shrift as a diet item, when in tropical oceans they certainly are equal in frequency and volume to fishes. Figure 3.2 on page 28 is an unfortunate oversimplification, especially since it emulates the excellent drawing by Jon Ahlquist in Ashmole (1971, p. 227, in Farner and King, Avian Biology, Vol. 1). On page 29, the authors cite Nelson (1967) to the effect that frigatebirds “have reduced the amount of oil in their feathers to such an extent that they can no longer enter the water.” This is clearly nonsense! The discussion on page 77 and following dealing with overharvesting by man in the Peru-Ecuador marine system does not relate the situation with ENSO events as being an important density independent population control mechanism. Several typos mar the text: p. 6 the reference (see section 2.3 last line) is meaningless; p. 15, the reference (see 2.5.4) does not exist in the text; p. 26, the reference to Murphy should be Murphy et al.; and in the references this reviewer’s citation title is misspelled as “Respectives” rather than “Perspectives.”

These points aside, I find this book a welcome addition to the seabird literature. It’s a valuable summary and a major exposition of the interactions among fisheries, man, and birds. The cost of this book seems excessive, but I guess publishers must make a profit. If only authors could also.—RALPH W. SCHREIBER.

AUKS. AN ORNITHOLOGIST’S GUIDE. By Ron Freethy, illus. by Carole Pugh. Facts on File Publications, New York and Oxford, 1987:208 pp., 12 color plates, 23 black-and-white photographs, 22 range maps, 6 tables. (Price not given.)—The auks are a family of 22 extant and one recently extinct species found in cool, northern waters, mainly in the Pacific. After
the penguins, they are the seabirds most highly adapted to life in the water. Ron Freethy's book is a general introduction to the group—a review of the existing literature rather than a presentation of original research. It's popularly written, but with nine pages of bibliography that provide an introduction to the literature. Unfortunately, this list does not include the latest symposium on the family: Nettleship and Birkhead's "The Atlantic Alcidae" (Academic Press 1985).

Freethy gives a section to each species, and finishes with "Auks in the Modern World," a chapter on the influence of man as a hunter, polluter, and rival fisherman. He discusses the birds' distributions, food, behavior, movements, and breeding biology. He has, however, two unfortunate biases. His perspective is land-based, with little to say about auks in their marine environments. He is also firmly anchored in the British Isles: the Atlantic west of Iceland gets short shrift, and his treatment of the Pacific species is perfunctory. These have led to some odd imbalances. For example, Freethy describes the storm-driven "wrecks" of Dovekies (Alle alle) along the coasts of western Europe at some length—yet the birds' principal "normal" wintering area, off Newfoundland, is not shown on the distribution map. The section on the food and feeding ecology of the Thick-billed Murre (Uria lomvia) takes no account of the Japanese work with birds drowned in gill-nets in the Pacific. Freethy cites the famous sketch of Great Auks (Pinguinus impennis) on the Grand Banks, from the 'English Pilot' of 1728, but only as a sketch—not for what it tells us about their pelagic ecology. The extinction of the last birds in Iceland is little more than a postscript to a long description of the species' former distribution in British waters. (To make matters worse, quite inexplicably, he doesn't even cite Alfred Newton's classic account [1861. Ibis 3:374-399] of the final execution, preferring instead to quote an abridged and unacknowledged version from a secondary source. The great man must be turning in his grave.)

"Auks," then, is not the last, or even the latest word on the group. But these are relatively minor faults. Despite its biases, the book makes a useful introduction to these odd little birds. The author is clearly, and rightly, fascinated by them, and his enthusiasm is infectious. The making of converts, I suspect, is one of the reasons he wrote "Auks" in the first place. I hope he succeeds.—RICHARD G. B. BROWN.

THE BIRDS OF AFRICA. Vol. II. By Emil K. Urban, C. Hilary Fry, and Stuart Keith (eds.), with line drawings by Ian Willis, plates by Martin Woodcock, and acoustic references by Claude Chappuis. Academic Press Inc. (London) Ltd., London, England, 1986:xvi + 552 pp., 28 color plates, 4 black-and-white plates, 2 figs. (maps), Bibliography, Errata of Vol. I and Indexes. £65.00 ($99.00).—The second volume of this ambitious undertaking (six volumes instead of four are now projected) is written by contributing ornithologists under a joint editorship. Treated are the Galliformes, Gruiformes, Charadriiformes, Pterocliformes, and Columbiformes.

"Encyclopaedia of African Birds" might be a more appropriate title of a work which undertakes to summarize the total knowledge of Africa's birds. As in Volume I, orders, suborders, families, subfamilies, and genera are briefly summarized as to diagnostic features, ranges, included taxa, and taxon affinities. Species treatments are compressed into several categories, usually: range and status, description, field characteristics, voice, general habits, food, and breeding habits. One to as many as five references follow each treatment. There is an "all Africa" bibliography and one for each family. With terse and stylized prose, enormous amounts of information are condensed into each page. Imagine, six such folio-sized volumes!

To an ongoing work of this scope, criticism and suggestions can be of particular importance.
This reviewer's comments are offered in expectation of even more noteworthy succeeding volumes.

The range maps for the species draw my special concern from standpoints of inadequate "landmarks," accuracy, and readability. "Landmark" inadequacy involves latitudes and longitudes as well as natural features for points of reference. In describing the range of one species (p. 483) the text employs: latitudes 18°N, 21°N, 15-16°N, 1°N and longitude 40°E. Readers can approximate the equator's position on the maps, but latitudinal distances north and south of this are not obvious. The range description can be compared with the maps themselves and from the maps approximation of latitude and longitude gained (but map accuracy can be open to question—see beyond). In the interests of precision, I suggest that the equator, as well as latitude both above and below it, be indicated along the margin of the map; and how about a longitude for orientation?

A point of reference such as the outline of Lake Victoria provides a useful addition to the range maps of Volume II. Some of the great lakes of Africa and their surroundings are hubs of species assemblages. I doubt that the outline of 150-mile long Lake Turkana, for example, would impart undue clutter to the maps. Interpretation of a good many ranges would be enhanced by indication of natural features large enough to allow inclusion in these very small range maps.

Accuracy is a more serious consideration. We are told (p. xiii) that "map and text are complimentary and in all cases should be considered together." However, drawn ranges and the descriptions of them do not always agree. On p. 7 a species is described as "Resident from extreme NE Uganda . . . north to S Ethiopia, Somalia, arid parts of N and E Kenya . . .". The shading of the accompanying map does not include any portion of Uganda although astride that country's northeast border are an "X" and question marks! Now note, the range was said to extend from NE Uganda "north to S Ethiopia." Ethiopia does not lie north of Uganda; the Sudan does but there is no mention of that country in the description of the range and no part of the Sudan is shaded on the range map. " . . . north of S Ethiopia, Somalia . . ." Can one arrive at Somalia by going north from Uganda? Yes, by going north-east (or east and then north-east) but only if you pass through north-west Kenya and that area is not shaded on the range map. Precision is lacking in the description of other ranges. A swamphen's range is described as including Lake Turkana. The map's small patch of shading for this portion of the species' range (p. 119) in no way represents the N-S length of this lake; the shading does not extend to the Ethiopian border where, in the marshes of the Omo River delta fringing the lake, the swamphen can be found. A coot (p. 129) is "common [at] Lake Turkana." Again shading does not cover the N-S extent of the lake, in particular, the Omo River delta marshes. A francolin (p. 43) is said to have a range extending "south through Kenya"; this should read south through eastern Kenya to be in accordance with the map which shows the species absent from central and north-west Kenya. These are samples of such inconsistencies.

Range maps should be easily and quickly read. With these maps I do not always find this so. Does every map, no matter how restricted a species' range, have to represent the entire continent? Africa's 11,700,000 square miles are herein reduced to about 6 square inches. If the range is limited, would it not be better displayed by enlarging that portion of Africa to fill the six square inches? Locations of some "isolated occurrences" are emphasized by arrows, but these arrows are small and not always immediately apparent (p. 65). Why not arrows of a size that attracts attention? Some maps have but a few "X" marks set within the continent (p. 383); to have these stand out why not color them? If a range narrowly parallels the marine littoral (p. 189) would this not be better set off by a colored rather than a thin, lightly shaded strip? Editors, scan the range maps in the Cramp et al. 1983 "Handbook of the Birds of Europe, the Middle East and North Africa," Vol. 3. Here versatility in illustration of range maps is noteworthy. The result is that the maps can be read with ease.
Illustrating the birds of a continent is a monumental undertaking. Almost 300 species are shown by the plates of Volume 2. These obviously merit careful consideration. This volume's jacket states that "the beauty of the plates will assure them pride of place on the shelves of ornithologists and bird-watchers everywhere." "Beauty" this reviewer considers too subjective for him to critique. There are aspects of Woodcock's plates which do elicit my comment.

The artist has, I would say, nicely captured the characteristic poses of bustards (plates 10 and 11). My feelings at watching live bustards are refreshed by these plates. I do not think that the artist "captured" shorebirds as nicely as bustards. The adult male Great Sand Plover (Charadrius leschenaultii) and some others of plate 15 are to me having balance problems; such stances in life would, I suspect, be unstable.

The plates of flying shorebirds are obviously designed to compare diagnostic features of the many species; they could serve for little else when as many as 43 individuals are crowded onto one plate (21). But compare the flying shorebirds by D.I.M. Wallace (e.g., plate 22) in Cramp et al. 1983, op. cit. All 13 of these figures have room in which to fly and are in realistic attitudes of flight. If figured birds can be life-like—why not!

The backgrounds of the plates are white (not so in Vol. I). Some birds with extensive areas of white plumage—the same shade of white as the background—are not well portrayed (plates 13 and 28). Pastel backgrounds would correct this. Moreover such backgrounds can bring figures into pleasing prominence. Compare Philip Burton's plovers (plates 11-14 in Cramp et al. 1983, op. cit.) with Woodcock's plates (14 and 15) of many of the same species.

The assemblage of guineafowls (plate 5) is a notable one. Some I consider very well executed. The vulturine Guineafowl (Acryllium vulturinum) disappoints me. The artist could have better "exploited" such an extravagantly plumaged subject. H. Gronvold's color plate (no. 21 in Mackworth-Praed and Grant, 1952. "Birds of Eastern and Northeastern Africa," effectively posed this bird to show the extent of the striking blue plumage of the breast, the spread of the hackles, and the pinkish-violet of the outer secondary. The latter can hardly be distinguished in Woodcock's plate. The short, dense feathers of the nape are redder in Woodcock's plate than I have observed in life. According to the text (p. 7) these are chestnut. The text describes the legs as black; they are gray in the color plate.

In summary, the plates are good. Some, I think, are better than good. A few, I believe, could have been much more effective. Important in my criteria of evaluation is how effectively the artist has posed the bird—is it lifelike and are the characteristics of the bird well displayed?

Here are some miscellaneous suggestions to the editors. Place the names of the orders covered either on the spines or boards of succeeding volumes. Although space consuming, it will be helpful to have the table of contents include the species. Where, oh where, is a glossary? Proofread the indexes more carefully; in the English Name Index (p. 547) alphabetical sequence is scrambled. Finally, when treating the Bee-eaters (Meropidae) make up for an omission re the Kori Bustard (Ardeotis kori). A. H. Neumann (1898, "Elephant-hunting in East Equatorial Africa") was among the first to describe the Northern Carmine Bee-eater (Merops nubicus) using these bustards as "animated perches" from which to hawk for insects. Why not include his quaint sketch as a line drawing and his comment that "they sit far back on the rump as a small boy rides a donkey.. . ."

Few avifaunal treatments have been marked by such thoroughness, detailed and, I suspect, devoted attention as the "Birds of Africa." At last the inventory of information about this avifauna is in one place and available to all. Despite my criticisms, which are in good measure subjective, this is an outstanding production! The amount of information the volume contains is awesome. Far into the future this will be the basic reference for African birds—and a model for such works. All plaudits and progress to the editors!—Oscar T. Owre.
THE TANAGERS. NATURAL HISTORY, DISTRIBUTION, AND IDENTIFICATION. By Morton L. Isler and Phyllis R. Isler. Illus. by Morton L. Isler. Smithsonian Institution Press, Washington, D.C., 1987:404 pp., 32 color plates. $70.00 (cloth), $49.95 (paper).—The tanagers are a high-profile family of birds of the New World Tropics, known even to many non-birdwatchers. How completely tropical the tanagers become is readily apparent when looking at the range maps in this book. Only four of the 242 species listed here consistently occur in North America—for only part of the year—and none occurs farther south than central Argentina.

“The Tanagers” treats all species of the family, and all are illustrated. It is not a coffee-table book, however, in the style of other single-family treatments such as “Parrots of the World” (Forshaw 1973, Lansdowne Press, Melbourne). For one thing, it is considerably smaller (23.5 x 15 x 3 cm). Rather, it is a tool for ornithologists or very serious birdwatchers, those with an interest in tropical birds.

The Islers have not attempted to make any revision of the systematics of the tanager family, but follow the order of Peters’ Check-list (Storer 1970, Check-list of Birds of the World. Vol. 13. R. A. Paynter, Jr., ed., Cambridge, Massachusetts, Mus. Comp. Zool.), with the addition of the five species of tanagers described since the Check-list was published. They do not include a synonymy. “The Tanagers” is mostly a secondary source, although it does contain new information on natural history and geographic ranges. Most of the new information comes from field notebooks of other workers and from museum collections, but the Islers themselves contribute considerable information from their own observations, especially on vocalizations, diet, and behavior. They introduce each genus, most by a single paragraph which describes the generic characters. Usually, they also discuss behavior, and they give some information on the relationships of species in the genus, including a table listing the species and possible species groups. The authors devote considerably more space to large, complex genera such as *Tangara* and *Euphonia*.

The species accounts are highly structured and well done. Each has an initial morphological section giving lengths and weights of the species, some subspecies information, and plumage description if not illustrated (usually subadult). Separate sections cover geographic range, elevational range, habitat and behavior, vocalizations, and breeding. The final section of each account is most useful. It conveniently gives the sources used, by section, for each section of the species account. Using these sources one can quickly find out more about, for example, the stomach contents of the Brassy-breasted Tanager (*Tangara desmaresti*).

The Islers give species with a particularly complex lifestyle or uncertain taxonomic position more than one species account. For example, they give two accounts for the North American migrant tanagers, one for summer and one for winter. They also provide separate accounts for possibly distinct forms in species with taxonomic uncertainties. A range map accompanies each species account, although often not on the same page. Many of the maps take up more than half of a page, and a few have a page to themselves. This gracious use of space allows detail not usually found in range maps. All of the maps are drawn to the same scale, with national boundaries and most large rivers drawn on each one. The features, however, are not labelled. While most people who study tanagers probably would know where Paraguay is without it being labelled, many people probably would have difficulty identifying the Marañón, Huallaga, and Ucayali rivers on a line map. Yet all three are important in distributions of tanagers. The Islers often refer to minor political divisions or to cities in the range descriptions, but these are not marked anywhere in the book. A single base map on the endpapers with the major features labelled would have enhanced the book a lot. It would keep readers from having to flip through their atlas while trying to use this book.

Mort Isler’s color plates are grouped in the center of the book. As many as six different plumage types in highly variable species, such as the Common Bush-Tanager (*Chlorospingus*
ophthalmicus) are illustrated. Both males and females are shown when their plumage is different. The plates are done adequately, although some of the shapes and positions seem a little off. Isler seems to have paid attention to eye and soft-part colors; he is correct for those I know. Some of the deep, saturated reds (Calothraetes) and blues (some Tangara) I'm sure are difficult to paint and print. The color of iridescent species, such as many in the genus Tangara, changes with the viewing angle, an effect impossible to render in a painting. Isler does reasonably well, certainly well enough to be useful. The quality of the color printing is fair, but not as high as two other recent books I compared it to (Hilty 1986, A Guide to the Birds of Colombia. Princeton Univ. Press, Princeton, New Jersey; Pratt, Bruner, and Berrett 1987, A Field Guide to the Birds of Hawaii and the Tropical Pacific. Princeton Univ. Press, Princeton, New Jersey). In fact, in both copies I have seen, Plate 15 (mainly Thraupis) seems to have been printed with the blue tint slightly out of register, giving the birds a watery, out-of-focus look.

The references at the end of the book seem to be complete. Two references for E. P. Edwards are duplicated, a minor editing lapse. The printing of the book is probably its greatest disappointment. Numerous places in the book show smudges as if the printing plates were over-inked or the pages put together before they were completely dry. One blob almost obliterates two entries in the index. Another page in the index has almost every a, e, g, and o filled in, giving it a cheap, mimeographed look. The two copies I have seen both have identical smears, so the fault lies with the printing plate.

On the whole, I think this book makes a very welcome contribution. Because the text is well-organized and sources carefully cited, it can be a useful tool to someone who is getting to know the tanagers, as well as a convenient reference book for someone who already knows them. The Islers present a great deal of natural history data. They provide a source that can give ornithologists a way to know a tropical family well and a good starting point when studying problems in tanager systematics, biogeography, and ecology. I recommend this book.—David A. Wiedenfeld.


While Harris’ book was intended for the professional ornithologist and serious amateur, this new puffin book is written for the beginning-level bird watcher, the kind of person who would travel to Skomer Island in Wales or Machias Seal Island off the Maine coast to obtain a first glimpse of puffins. In contrast to the graphs and tables which give Harris’s book an in-depth perspective, “The Atlantic Puffin” contains 70 color photos and summarizes in a popular way much of the information reported by Harris and other field researchers. David Boag has written the text based largely on his and Mike Alexander’s experiences at Skomer Island National Nature Reserve in West Wales where Alexander served as a wildlife warden.

In addition to a careful overview of puffin natural history condensed from the literature, the book contains some original observations by the authors. Boag and Alexander obtained unusual photos of puffins in the water by swimming with the birds and they have added to our understanding of chick behavior by excavating burrows in order to see puffins at home.
underground. These techniques provide some new insights about courtship and feeding behavior as well as the behavior of chicks in their burrows.

The book contains chapters about world distribution, life at sea, courtship and egg laying, chick development, mortality and kleptoparasitism, and conservation problems such as oil spills. It is surprising that the conservation chapter does not refer to the problems of entanglement in gill nets or concerns about overfishing of puffin food stocks. While the book has too many mediocre color portraits, there are also some very unusual photos such as views of puffins swimming at eye level, diving underwater, and young with parents in nest burrows.

The book creates some confusion about western North Atlantic puffin colonies by stating that “By 1887 there were no puffins on Machias Seal Island, which was the largest colony in Maine.” This statement actually refers to Matinicus Seal Island. Although puffin numbers declined to about 60 individuals during this period at Machias Seal Island, they were not eliminated. There is also confusion about the location of Gulf of Maine puffin colonies on a distribution map on page 124 which shows Eastern Egg Rock off the coast of New Hampshire and Matinicus Rock almost in the Bay of Fundy. Actually, both colonies are off mid-coast Maine.

The above details do not detract from my overall view that “The Atlantic Puffin” is a well-written and informative natural history about this appealing seabird. I recommend it as a very readable introduction for the beginning bird watcher. — Stephen W. Kress.

The Eagle’s Nest: Natural History and American Ideas, 1812–1842. By Charlotte M. Porter. Univ. Alabama Press, University, Alabama, 1986:251 pp. $24.95.—In this our centennial year, Charlotte Porter’s treatise on the early history of the Academy of Natural Sciences of Philadelphia offers an intriguing glimpse at the world of Alexander Wilson and his contemporaries. The book, which appears to be the published version of Porter’s Harvard University dissertation of 1976, offers much for those interested in the historical role of Alexander Wilson in American Ornithology, including the suggestions that Wilson’s “American Ornithology” (1808-1814) quickly became the benchmark “against which all other works of natural history would be judged,” and that its publication “inspired” the founding of the Academy of Natural Sciences.

Porter depicts the period of the late 18th and early 19th centuries as being a rather trying one for North American naturalists, especially those dealing with taxonomy. In 1766, Buffon had proclaimed in his widely read “Histoire naturelle, général et particulière” (1749-1767) that many supposed newly discovered New World species were, in fact, merely degenerate versions of Old World forms. Although North American authors spent considerable time and effort demonstrating otherwise, the lack of a viable evolutionary theory posed considerable problems for these early naturalists. Jefferson, for example, struggled with the “problem” of North American extinctions. Without Darwinian theory in hand to explain such events, he challenged Buffon’s claim that extinctions reflected the inferiority of the New World climate by proposing that mammoths, although extirpated in eastern North America, might still exist in the unexplored interior of the continent. Porter suggests that only with the publication of Wilson’s work could New World authors dispense with what was until then an obligatory introductory argument debunking Buffonian taxonomy. But it was not until much later, when Asa Gray championed Darwinian thought in North America, that naturalists possessed the theoretical framework needed to address the taxonomic problems their discoveries created; and even then, many refused to embrace the theory.

Porter has written a feisty book filled with strong personalities arguing what were then
important, and what are now seemingly inane questions of natural history and taxonomy, including numerous acrimonious clashes between Wilson's and Audubon's disciples. (I wonder whether our era of ornithology will offer similar grist for an historian's mill.) Written in a thesis style (end notes comprise 20% of the text), the book is interesting, but not easy reading. There are also a number of passages that lead me to suspect that Porter is not as well versed in evolutionary theory as one would hope. With these caveats in mind, I recommend the book to those whose interests in ornithology include its historical aspects.—Keith L. Bildstein.

BIRDS OF THE ROCKY MOUNTAINS. By Paul A. Johnsgard. Colorado Associated University Press, Boulder, Colorado, 1986:504 pp., 42 color plates, 15 numbered text figs. $39.50.—This book summarizes bird distribution and abundance information from 8 U.S. and Canadian Rocky Mountain national parks and one national monument in the north central Rocky Mountains. It also offers a brief compilation of notes on identification, habitats and ecology, and seasonality for 354 Rocky Mountains species from "latilong" studies, park checklists, and unpublished sources. "Birds of the Rocky Mountains" shares many similarities with Johnsgard's 1979 "Birds of the Great Plains" (BGP): the chosen boundaries do not encompass the entire region suggested by the title; the maps emphasize the distribution of breeding rather than migrating or wintering birds; and attractive photos and line drawings are interspersed throughout the text. Written for a nontechnical audience, the book is useful as a cursory overview of the distribution and natural history of Rocky Mountain birds. It may be of assistance to birders visiting the north-central Rockies for the first time, but as a reliable technical reference "Birds of the Rocky Mountains" is lacking.

The introduction provides an overview of the physiography and ecology of the region, with maps summarizing aspects of the climate, mountain ranges, drainages, vegetation communities, and land use. A useful synopsis of the areas with the greatest bird-watching potential in each of the parks and numerous other refuges is included. The author provides for each species a summary of the latilong status and a map showing the species breeding distribution within the study area, which consists of southern Alberta, Montana, Idaho, Wyoming, and northern Colorado. The latilong information and the map are difficult to cross-reference visually, but careful comparison often yields contradictions. Johnsgard notes that the range maps are "usually more 'generous' than is indicated by available data" reflecting the author's "belief that, based on its general distribution and habitat characteristics, the species may eventually be found there." The book was designed for use in the field and, therefore, the page size is smaller than in BGP. As a result, the quality of the identification and comments sections are compromised. Much space is devoted to 30 or more vagrant species that tell us little about the bird life in the Rockies.

An operating assumption of the book is that "the bird life of the Rocky Mountains is surprisingly uniform." The narrow scope of inquiry is such that this idea is not seriously challenged, and thus we come no closer to the many fascinating aspects of Rocky Mountain biogeography: the influences of fauna from the coastal Cascade Range, the Chihuahuan mountains, and the Great Basin on the Rockies. I wish that the author had included a discussion of geographic variation within the Rocky Mountain region and a biogeographic comparison to the Sierra Nevada, for example.

The greatest problem I have with the book is the contradiction between the apparent scope of the book, as suggested by the title, and the actual area analyzed. At most, 40% of the Rocky Mountains comprise his study area, and approximately 40% of this consists of habitats well within the Great Plains. Thus, when nesting periods are cited for the species,
one wonders whether these truly represent nest dates for birds from the Rockies or from other regions. I suspect the latter because for several species he cites egg records from North Dakota.

Two critical stages in the production of this book seem to be lacking: professional review and editing. Errors in the species accounts include Black-backed Woodpecker (*Picoides arcticus*), which does occur in central and southern Wyoming, but not in Colorado and Barred Owl (*Strix varia*), which has not yet been confirmed to nest in Colorado. Scott’s Oriole (*Icterus parisorum*) is omitted from the species accounts, but it breeds in several areas in western Colorado and southwestern Wyoming. Errors, omissions, and incorrect entries abound in the photo captions, the suggested reading list (referenced at the end of the text), and the appendix. I found 27 errors in citations alone. Codes used to designate categories in the species checklist are not defined.

This book is less of a well-coordinated synthesis than I had hoped for. A detailed, comprehensive study of Rocky Mountain avian biogeography still awaits us.—Mark A. Holmgren.

**Breeding Birds of Ontario: Nidiology and Distribution. Vol. 2: Passerines.** By George K. Peck and Ross D. James. Royal Ontario Museum Life Sciences Miscellaneous Publications, Toronto, Canada, 1987:xi, 387 pp., 2 maps of localities and regions, 140 range maps, 96 figures of habitats, birds and their nests. $36.00 (Canadian).—This volume is organized in a similar format to the first volume which covered the nonpasserines (see J. M. Speirs’ review, Wilson Bull. 96:510, 1984). After a brief introductory section, the main body of the work consists of 140 full species accounts, followed by brief accounts of 4 unconfirmed species. Each full account includes a distribution map showing the locations of definite breeding records, based on information in the Ontario Nest Records Scheme. A section headed Nidiology summarizes the number and distribution of records, describes breeding habitats, nest sites and structures, and gives information on numbers of eggs per nest, cowbird parasitism, incubation period, and egg dates. Finally, a section on Breeding Distribution briefly describes what is shown in the maps, sometimes drawing on additional information from other sources. Some of the accounts are illustrated with attractive drawings by James. The photographs of habitats, birds, and nests, mainly by Peck, are generally of good quality but are gathered together at the back of the book following appendixes, literature cited, and index. Appendix A gives corrections and additions to volume 1 and Appendix B is a chart of egg dates for species in both volumes.

This book has limited objectives which it achieves quite well. It provides the first detailed maps of the distribution of breeding records for Ontario and summarizes nest and habitat data from the Ontario Nest Records Scheme, but little attempt is made at interpretation of the observed patterns. This volume has benefited greatly from new records accumulated in the course of the intensive fieldwork conducted in 1981–85 for the recently published “Atlas of the Breeding Birds of Ontario,” but the two books tend to complement rather than duplicate each other. The maps in this book show only confirmed breeding records (nests or unfailed young), including both recent and historical data, whereas the Atlas maps are based on a wider range of breeding evidence collected over a five-year period. The texts here emphasize details of nesting sites, nest structures and habitats, in contrast to the Atlas which provides extensive commentary on breeding distributions and abundances.

My main criticisms concern the unconventional approach to clutch sizes and incubation periods adopted by the authors. The introduction to volume 1 says that each account lists all “clutch sizes” given on nest-record cards unless it was specifically indicated that the clutch was incomplete. Thus the frequency distributions given are of observed egg numbers
rather than of completed clutches. The authors recognize this by using bold face type for sizes of clutches that were known to be complete and incubated by one pair, but the frequency distribution of such clutches is not given. Therefore, it is not possible to calculate mean clutch size from the data presented, nor do the authors provide this statistic. Indeed, they justify its omission by saying that it often results in “an unrealistic number,” such as “an average clutch size of 3.5 eggs.” Instead they provide “the average-clutch range,” which is actually the size range of the middle 50% of egg counts.

Incubation periods are usually measured from the laying of the last egg to the hatching of the last egg, because this method provides the greatest certainty that the egg was actually incubated during the measured period. For most species, Peck and James use instead the interval between the laying of the last egg and the start of hatching—so their incubation periods will be reduced by an amount determined by the extent to which the onset of incubation preceded clutch completion, as the authors often note in explanation of unusually short periods. However, “for those species that commence incubation with the laying of the first egg (e.g., cuckoos and owls),” they defined the incubation period as the interval between laying of the first egg and first hatch. Therefore, it will be longer than the standard incubation period if, in fact, full incubation did not start with the first egg. Thus anyone wishing to use the clutch size and incubation period data for comparative purposes would be well advised to examine the original nest record cards rather than relying on the information presented here.

Nevertheless, the authors have done a valuable job of concisely summarizing the distributional and nesting data from over 67,000 passerine nest record cards. J. M. Speirs’ conclusion that the first volume was an important reference work on the distribution and nesting habits of birds applies equally to the second volume.—David J. T. Hussell.

The Atlas of Wintering Birds in Britain and Ireland. Compiled by Peter Lack. T. & A. D. Poyser, Ltd., Calton, Staffordshire, England, 1986:447 pp., 192 species illustrations, 202 distribution maps, 16 numbered text figures, 4 tables. $55.00 (distributed in the U.S. by Buteo Books, Vermillion, South Dakota 57069).—In 1976, the British Trust for Ornithology, in cooperation with the Irish Wildbird Conservancy, published “The Atlas of Breeding Birds in Britain and Ireland,” the first published atlas of breeding birds for a major land area. Following the lead of the United Kingdom, breeding bird atlas projects have become a global activity, with more than a dozen countries having produced breeding bird atlases by now. In North America, more than thirty states and seven Canadian provinces have fielded breeding bird atlas projects. Now, the appearance of “The Atlas of Wintering Birds in Britain and Ireland” marks yet another milestone of excellence in the fifty-year tradition of bird study of the British Trust for Ornithology.

The new winter bird atlas follows very closely the pattern of the earlier breeding bird atlas. There are 192 natural history accounts of wintering birds, each introduced with a handsome line drawing of the species. The species accounts were prepared by 101 authors. Twenty-three artists, coordinated by Robert Gillmor, are responsible for the illustrations of species, which are executed with clarity, accuracy, and imagination. I found the series of winter Paridae drawn by Norman Arlott especially endearing. Shorter accounts and smaller maps are printed near the end of the book for eight summer species of very rare winter occurrence. Those eight species are not illustrated. In general, the species accounts are well-written, carefully edited, and very readable. The accounts relate details of the species’ natural history during the winter season in Britain and Ireland. Particular attention is paid to how winter weather can affect species abundances. References for further reading are included at the end of each species account.
On the page facing each species account and its illustration appears an outline map of Britain and Ireland showing the winter distribution for the species, mapped for 3761 survey squares of $10 \times 10$ km each. The winter distribution maps employ an innovation over the earlier maps of breeding bird distributions, however. For each survey square from which a species was reported, a blue dot shows the species estimated relative abundance at either low, medium, or high levels. Although the actual numeric values for relative abundance can be different, depending upon the species mapped, the smallest colored dots always represent the lowest relative abundance, medium dots correspond to medium relative abundance, and the largest dots represent the greatest relative abundance. As a result, one very easily can ascertain at a glance not only where a species occurs in the United Kingdom during the winter, but also those regions where the species is likely to be most abundant. An introductory chapter presents a detailed discussion of the distribution maps and how they were derived and should preclude their misinterpretation by all but the most careless readers.

"The Atlas of Wintering Birds in Britain and Ireland" cross references "The Atlas of Breeding Birds in Britain and Ireland" extensively, and yet there is remarkably little duplication of information between the two atlases. At the end of each account for a wintering species which also breeds in the region, a page number indicates where a corresponding account for the species can be found in the breeding bird atlas. And for those winter species which also breed in Britain and Ireland, a small map of the species' breeding distribution is reproduced from the breeding bird atlas in the upper right corner of the winter distribution map for comparison. Information from other surveys of the British Trust for Ornithology (e.g., wading bird surveys, garden bird surveys, Common Birds Census, and Nest Record Scheme) also is skillfully integrated into species accounts.

Survey work for the winter atlas took place during the winters of 1981-1982, 1982-1983, and 1983-1984. An introductory chapter, The Weather in the Three Winters, helps the reader to place the survey in the context of winter weather patterns during the period of the survey. Another chapter, Birds in Winter: Patterns and Movements, is especially stimulating reading and a good illustration of the kinds of biogeographic patterns which can emerge from careful analysis of the extensive information which atlases provide. That chapter examines in detail the biogeography of groups of wintering birds in Britain and Ireland, based on habitat requirements or feeding habits (e.g., freshwater species, wader species, and seed-eating species). Patterns of winter distribution and abundance also are discussed in the context of body weights for wintering species. Irruptive species reported during the survey and the effects of cold weather on selected species also are given special attention. This broad analytical overview and synthesis of the biogeography of birds wintering in Britain and Ireland makes a fine introductory complement to the individual species accounts which follow.

If one is interested, a separate set of twelve transparent overlay maps, for use with both the winter atlas and the breeding bird atlas, can be ordered from the British Trust for Ornithology (available in the U.S. from Buteo Books for $10). The set of overlays maps rainfall patterns, winter and summer temperatures, elevations, river systems, plant associations, and other features. Combining the transparent overlays with the printed maps helps the user gain greater insight into factors relating to where birds are found in Britain and Ireland. It is unfortunate that the overlays are an option and are not automatically included with each copy of the atlas, even though it would increase the price. They can add a whole new dimension of fascination to the study of the distribution maps for either the winter atlas or the breeding bird atlas.

More than 10,000 volunteers contributed over 180,000 hours of observation to the field surveys which made "The Atlas of Wintering Birds in Britain and Ireland" possible. Not until substantial numbers of North American observers regularly commit themselves to large-scale cooperative efforts to collect basic information about birds with the same en-
thusiasm as shown for life lists, Christmas Bird Counts, or “ecological activism,” will there be any base of information about North American birds comparable to that for Britain and Ireland. And although a “North American Trust for Ornithology,” modeled after the British Trust for Ornithology, has been rumored in various quarters for more than a decade, there seems little hope for the emergence of such an organization in the foreseeable future. Large numbers of carefully trained and coordinated volunteers can make significant contributions to our knowledge and understanding of the distributions and abundances of birds, especially in cooperation with well-trained professionals who have a sound knowledge of avian ecology. The two published atlases of birds of Britain and Ireland show clearly what can be done. “The Atlas of Wintering Birds in Britain and Ireland” is yet another illustration of the exceptionally fine field studies pioneered by the British Trust for Ornithology over the past fifty years.—Charles R. Smith.

Birds of Britain and Europe. New Generation Guide. By Christopher Perrins. Univ. Texas Press, Austin, 1987:320 pp., over 1500 col. paintings, many range maps. $14.95.—There seems to be no limit to the number of British field guides, and this latest entrant is an American edition of a book originally published by Collins of Great Britain. This one is more than a field guide. Approximately 160 of the 320 pages are devoted to an introduction to bird biology. This is divided into three sections: The Evolution of Birds, The Life of Birds, and The Ecology of Birds. They are profusely illustrated with small sketches, graphs, and diagrams. These are written in authoritative but readable style and should serve to introduce the novice bird-watcher to bird study beyond the “ticking” stage. The emphasis on European species and examples will decrease the interest of American readers in these sections.

The remainder of the book is devoted to “The Directory of Species.” This is in standard modern field guide format with 6–8 species covered per page with illustrations opposite text. The text for each species occupies a space of 100 × 22 mm which includes 2 tiny range map as well as text. On the opposite page, the illustrations occupy a similar space with as many as 4 or 5 figures. Thus, as many as 4 plumages and one flying bird are illustrated. The illustrations, by Norman Arlott, are quite good and clear despite their small size. I am not currently up on the latest techniques for identification of European birds, but I would judge that the beginner can do well with this book, but that as with others, will have his troubles with such things as Phylloscopus and Acrocephalus as well as waders in the autumn. The small size may be a definite handicap in using the pictures, and it certainly is in studying the range maps.

Americans making their first trip to Europe might well consider this guide, but they will probably find one of the others more satisfactory.—George A. Hall.

ANNOUNCEMENTS

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANT AWARDS

The North American Bluebird Society is proud to announce the presentation of the fifth annual research grant awards. The 1988 recipients are:

Bluebird Grant

Dale L. Droge.—The effect of parent-offspring interactions on parental care in the Eastern Bluebird. $1000
Philip K. Gaddis. — Reproductive success of western and mountain bluebirds in areas sprayed for control of grasshoppers in eastern Oregon. $1725

General Grant

Daniel E. Varland. — Behavior and ecology of post-fledging American Kestrels. $1000

Timothy Brush. — Nesting ecology of Prothonotary Warblers in riparian vegetation. $600

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS

The North American Bluebird Society announces the sixth annual grants in aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus Sialia. Presently four grants of single or multiple awards totalling $11,000 are awarded and include:

Bluebird Research Grant. — Available to student, professional or individual researchers for a suitable research project focused on any of the three species of bluebird from the genus Sialia.

General Research Grant. — Available to student, professional and individual researchers for a suitable research project focused on a North American cavity nesting species.

Student Research Grant. — Available to full-time college or university students for a suitable research project focused on a North American cavity nesting species.

Bermuda Research Grant. — Available to a professionally qualified ornithologist, post-graduate or professor on sabbatical, for research specifically relating to the study of the conservation problems or taxonomy of breeding biology of the bluebird in Bermuda.

Further guidelines and application materials are available upon request from Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746. Completed applications must be received by December 1, 1988; decisions will be announced by January 15, 1989.

This issue of The Wilson Bulletin was published on 13 September 1988.
SUGGESTIONS TO AUTHORS


Manuscripts intended for publication in The Wilson Bulletin should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Abstracts of major papers should be brief but quotable. In both Major Papers and Short Communications, where fewer than 5 papers are cited, the citations may be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the “CBE Style Manual” (AIBS, 1983). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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Membership inquiries should be sent to Dr. Richard Stiehl, Department of Biology, Southeast Missouri State Univ., Cape Girardeau, Missouri 63701.
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The Wilson Bulletin (ISSN 0043-5643)

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This publication is printed on acid-free paper.
Antioquia Bristle-tyrant (*Phylloscartes lanyoni* sp. nov., upper left), and its two sister species, Venezuelan Bristle-tyrant (*P venezuelanus*, upper-right) of coastal Venezuela and Spectacled Bristle-tyrant (*P orbitalis*, lower) of the eastern Andean foothills south of Colombia. Watercolor by John W. Fitzpatrick.
PHYLLOSCARTES LANYONI, A NEW SPECIES OF 
BRISTLE-TYRANT (TYRANNIDAE) FROM THE 
LOWER CAUCA VALLEY OF COLOMBIA

GARY R. GRAVES

ABSTRACT.—A new species of bristle-tyrant, Phylloscartes lanyoni, from the lower Cauca Valley of Colombia is described. P. lanyoni is morphologically similar to the small Andean bristle-tyrants formerly placed in the genus Pogonotriccus (venezuelanus, orbitalis, guala-quizae) and may be a trans-Andean allospecies of P. orbitalis. Received 17 Nov. 1986, accepted 11 Feb. 1987.

From 1941 to 1952, the National Museum of Natural History (USNM) obtained 23,258 skins, 478 skeletons and alcohol-preserved specimens, and 44 nests and eggs of Colombian birds from Melbourne A. Carriker, Jr. (Appendix 1). Although little publicized, this collection, which is still under systematic study, has proved to be one of the most significant from that country. Several new species were described from this material by Alexander Wetmore (e.g., Crypturellus saltuarius, Coeligena orina, Metallura iracunda). Here I describe a new species of bristle-tyrant from the foothills of the Central Cordillera above the lower Cauca Valley in northern Colombia.

Phylloscartes lanyoni, sp. nov.

ANTIOQUIA BRISTLE-TYRANT

HOLOTYPE.—National Museum of Natural History, USNM 402716; adult male from El Pescado, 12 km below Pto. Valdivia on the Río Cauca, ca 1500–1700 ft [457–518 m],

Table 1

Means and Ranges (mm) of Selected Measurements of *Phylloscartes lanyoni*, *P. orbitalis*, *P. gualaquizae*, and *P. venezuelanus*

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Wing</th>
<th>Tail</th>
<th>Tarsus</th>
<th>Culmen</th>
<th>Bill width</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>lanyoni</em></td>
<td>1 (type) δ</td>
<td>56.6</td>
<td>48.9a</td>
<td>13.7</td>
<td>6.4</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>1 (USNM 402715) γ</td>
<td>50.4</td>
<td>42.2</td>
<td>12.8</td>
<td>5.4b</td>
<td>3.4</td>
</tr>
<tr>
<td><em>orbitalis</em></td>
<td>15 δ</td>
<td>54.0 (51.8–59.1)</td>
<td>45.2 (43.2–47.5)</td>
<td>13.6 (12.5–15.0)</td>
<td>6.8 (6.4–7.2)</td>
<td>3.3 (3.0–3.6)</td>
</tr>
<tr>
<td></td>
<td>9 γ</td>
<td>50.4 (46.9–54.5)</td>
<td>40.4 (38.2–45.9)</td>
<td>13.0 (12.4–14.1)</td>
<td>6.6 (6.1–7.2)</td>
<td>3.3 (3.1–3.4)</td>
</tr>
<tr>
<td><em>gualaquizae</em></td>
<td>3 δ</td>
<td>51.9 (50.2–53.8)</td>
<td>47.3 (45.8–48.5)</td>
<td>13.9 (13.5–14.3)</td>
<td>6.6 (6.1–7.0)</td>
<td>3.3 (3.2–3.4)</td>
</tr>
<tr>
<td></td>
<td>2 γ</td>
<td>(45.1–47.3)</td>
<td>(41.8–42.4)</td>
<td>(12.5–12.8)</td>
<td>6.0</td>
<td>(3.1–3.7)</td>
</tr>
<tr>
<td><em>venezuelanus</em></td>
<td>3 δ</td>
<td>51.4 (47.7–53.7)</td>
<td>46.2 (42.2–48.7)</td>
<td>13.4 (13.1–13.5)</td>
<td>6.7 (6.1–7.4)</td>
<td>3.1 (2.8–3.3)</td>
</tr>
<tr>
<td></td>
<td>1 γ</td>
<td>49.5</td>
<td>44.9</td>
<td>12.7</td>
<td>6.3</td>
<td>—</td>
</tr>
</tbody>
</table>

*a* Significant difference (two-tailed *t*-test) between *lanyoni* and *orbitalis* at *P* < 0.05.

*b* Significant difference (two-tailed *t*-test) between *lanyoni* and *orbitalis* at *P* < 0.01.

*c* Sample of *P. orbitalis* includes specimens from Ecuador, Peru, and Bolivia.
Graves • NEW BRISTLE-TYRANT FROM COLOMBIA

Department of Antioquia, Colombia; collected 15 May 1948 by M. A. Carriker, Jr.; original number 13482.

DIAGNOSIS.—Distinguished as a Phylloscartes (Pogonotriccus) by small size, contrasting auriculars, two well-developed wing bars, greenish back, small thin bill, and by lacking a crown patch. *P. lanyoni* is most similar to *P. orbitalis* but differs as follows: (1) *lanyoni* has much yellower breast, belly, undertail coverts, and wing bars; (2) yellow outer margins of middle and greater wing coverts more extensive; (3) incomplete eyering as opposed to a complete eyering; (4) whitish instead of yellowish feathers above bill; and (5) a greenish-gray crown blending into the greenish back, rather than a clear gray crown contrasting with the back (see frontispiece). Differs from *P. ophthalmicus* in being smaller and lacking distinct black auricular spot and grizzled throat; from *P. gualaquizae* and *P. venezuelanus* in having much yellower plumage throughout and lacking a well-developed black auricular patch; and from *P. poecilotis* and *P. flaviventris*, in lacking ochraceous wing bars and rufous lores, respectively.

DESCRIPTION OF HOLOTYPE.—All color comparisons were made under Examolites® (Macbeth Corp.). Crown neutral gray suffused with greenish and blending posteriorly with bright olivaceous green back. Back and rump bright olivaceous green. Upper tail coverts bright olivaceous yellow. Wings and tail dark brownish gray; remiges and primaries and outer secondaries edged on outer webs with bright olivaceous green. Outer web of inner secondaries, especially innermost, with broader pale olivaceous yellow margins. Outer webs of middle and greater wing coverts edged with bright yellow bar. Lesser wing coverts bright olivaceous green tipped with dull yellow. Feathers above nostrils and lores to the anterior margin of the eyering grizzled gray and white. A few scattered grizzled feathers around the orbits form a faint incomplete eyering and trailing superciliary. Auriculars yellow with light gray tips which form a faint gray “auricular spot.” Chin, throat, breast, abdomen, flanks, and undertail coverts bright yellow, palest on chin and becoming more intense caudally, approaching Strontian Yellow (capitalized color name from Ridgway 1912) on abdomen. Soft part colors in dried specimen: upper mandible brownish black; lower mandible pale, horn-colored (probably flesh-colored in life), with a dusky tip; feet and tarsi dark brown.

MEASUREMENTS.—See Table 1.

DISTRIBUTION.—Known only from the type locality. May occur in the foothills at the northern ends of the Central and Western Cordillera in the drainage of the Rio Cauca.

ETYMOLOGY.—I am pleased to name this new species for Wesley E. Lanyon in recognition of his research on tyrannid systematics over the past three decades.

SPECIMENS EXAMINED.—*Phylloscartes lanyoni*: (USNM holotype, USNM 402715 9) from type locality. *P. gualaquizae*: Ecuador: Prov. Napo, San José Abajo (AMNH 1 8); Prov. Morona-Santiago, Cordillera Cuitucú (ANSP 1 3); Prov. Zamora-Chinchipe, Zamora (AMNH 1 8, 1 2); Peru: Dpto. San Martín, Moyobamba (ANSP 1 3). *P. venezuelanus*: Venezuela: Aragua, Maracay (ANSP 1 4, 1 9); Aragua, Cerro Golfo Triste (ANSP 1 4); Carabobo, Hcda. Sta. Clara (USNM 1 8). *P. orbitalis*: Ecuador: Prov. Napo, Cordillera de Galeras (AMNH 1 8, 2 9); San José Abajo (AMNH 3 22, 3 9); Río Suyo above Avila (AMNH 3 22, 1 9; ANSP 1 3); Peru: Dpto. San Martín, Moyobamba (ANSP 1 3); Dpto. Cuzco, Cordillera Vilcabamba (AMNH 1 3); Dpto. Puno, La Pampa (AMNH 1 8, 2 9; ANSP 2 9); Huacamayo (ANSP 1 3, 1 9). Bolivia: Dpto. Cochabamba: Palmar (ANSP 1 2).

I also examined large series (>50 of each species) of *P. ophthalmicus*, *P. poecilotis*, *P. ventralis*, *P. eximius*, and *P. (Capsiempis) flaveola* and smaller numbers of *P. nigrifrons*, *P. chapmani*, *P. flaviventris*, *P. flavivirens*, *P. superciliaris*, *P. oustaleti*, *P. difficilis*, *P. paulistus*, and *P. syvius*.

REMARKS.—There appear to be no sexual differences in plumage color or pattern.
DISCUSSION

Ecology.—The only ecological information on *P. lanyoni* is contained in Carriker's field catalog deposited in the National Museum of Natural History. From 10 to 17 May 1948, Carriker and an assistant were engaged in general collecting from a base camp at El Pescado, a cattle ranch on the highway along the Río Cauca, 12 km below Puerto Valdivia. They collected a total of 166 specimens (91 species) (Appendix 1) in a mixture of pasture edge, second growth, and virgin forest on the ridges and hills east of the river from 180 to 600 m elevation (mostly from 335–520 m). This sample of species is typical of the lowland avifauna of northwestern Colombia (Haffer 1975); no strictly montane species are represented.

Carriker noted that the specimens of *P. lanyoni*, which he misidentified as "*Capsiempis flaveola leucophrys*,” were collected in “an area of second-growth” on 15 May. Carriker apparently used the term “second-growth” to refer to rather tall regenerating forest as distinguished from “brush.” Carriker noted that the testes of the male were greatly enlarged. Other species taken during the same morning (450–520 m) (*Xenops minutus, Sclerurus mexicanus, Gymnopithys bicolor, Pipra coronata, Manacus vitellinus, Schiffornis turdinus, Ramphocacenus melanurus, Heterospingus xanthopygius*) were taken in “more or less virgin forest.”

Systematic relationships.—Based on the similarity of body plumage and reduced auricular spot, *P. lanyoni* appears to be a trans-Andean relative of *P. orbitalis*, although a close relationship to *P. venezuelanus* and *P. gualaquizae* is possible. Measurements of these species overlap extensively (Table 1). All four species inhabit Andean foothills and satellite ranges at elevations of 300–1100 m. *P. lanyoni* and *P. venezuelanus* have allopatric distributions; *P. gualaquizae* and *P. orbitalis* are sympatric from northern Ecuador south to northern Peru. *P. poecilotis*, which has been collected above Valdivia at 7000 ft (ca 2135 m), is sympatric with *P. lanyoni*, although there probably is a large elevational gap between their distributions. *P. ophthalmicus* occurs in the Central Cordillera as far north as Hacienda Sofia, Department of Caldas (USNM 436619, 436620, 436621). These specimens are nearly identical in plumage pattern and color with those from southern Colombia (Bélen, Department of Huila) and the eastern slope of Ecuador and show no trend toward *P. lanyoni*.

Commentary on generic relationships.—The small, greenish tyrannulets in the subfamily Elaeniinae (Traylor 1977) present some of the most challenging problems in avian systematics. Characters used to discriminate generic limits consist primarily of external proportions (bill, tarsus, and wing), tarsal scutellation, and plumage color. Traylor (1977) discussed the extensive overlap and intergradation of these characters among the
genera recognized by Hellmayr (1927), and synonymized more than one-third of them in his classification.

Of particular interest in this paper is the expanded genus “Phylloscartes” (Traylor 1977), which includes species formerly placed in Pogonotriccus, Leptotriccus, and Capsiempis. P. lanyoni is clearly related to the nominal species of Pogonotriccus. The aggregate “Phylloscartes,” comprising 20 species, is rather heterogeneous in plumage pattern and color with no distinctive characteristics that unite the taxa to the exclusion of other species. Unfortunately, the available anatomical data also fail to permit the critical discrimination of “Phylloscartes” within the Elaeniinae. For example, Ames (1971) considered the syringes of the aforementioned genera to be different from one another and from all other genera. On the other hand, Warter (1965) found cranial characters to be similar throughout his subfamily Euscarthminae, comprising 13 genera of small flycatchers; the range of cranial character states (e.g., nasal septum) in the expanded “Phylloscartes” includes nearly all the variation found within the subfamily. Recently, Lanyon (1988) found that the syringeal structure of five species of Pogonotriccus and Leptotriccus sylviolus did not differ significantly from two species of Phylloscartes (ventralis and chapmani). However, cranial and syringeal morphology suggested that Capsiempis was most closely related to Phaeomyias and Nesotriccus. These incongruent character sets and the apparent lack of plumage synapomorphies prevent an explicit generic diagnosis of “Phylloscartes” (sensu Traylor) from being formulated, and in an operational sense, suggest that the expanded genus is not strictly monophyletic. Additional analyses are needed to resolve the generic limits within this group.

ACKNOWLEDGMENTS

I thank J. Fitzpatrick, K. Parkes, and T. Schulenberg for comments on the manuscript, and W. Lanyon for sending me his unpublished manuscript. I thank the curators and staff of the Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), and the University of São Paulo, Museum of Zoology for permission to examine specimens. Part of this work was supported by a grant from the Research Opportunities Fund, Smithsonian Institution. I thank J. Fitzpatrick for preparing the artistic and accurate frontispiece.

LITERATURE CITED


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**APPENDIX 1**

**SPECIES COLLECTED BY M. A. CARRIKER AT EL PESCADO (180-600 m ELEVATION), DEPARTMENT OF ANTIOQUIA, COLOMBIA, FROM 10 TO 17 MAY 1948**


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**COLOR PLATE**

The Frontispiece painting by John W. Fitzpatrick has been made possible by an endowment established by George Miksch Sutton.
VARIATION IN THE JUVENAL PLUMAGE OF THE RED-LEGGED SHAG (PHALACROCORAX GAIMARDI) AND NOTES ON BEHAVIOR OF JUVENILES

PAMELA C. RASMUSSEN

Abstract.—The juvenal plumage of the Red-legged Shag (Phalacrocorax gaimardi) was found to be highly variable individually and geographically, based on examination of 16 specimens, 23 birds in photographs, and observations of 48 living birds. Juveniles from the Pacific coast of South America ranged from very dark to pale-plumaged, while juveniles from the Atlantic coast were very pale in plumage color. Gular pouch color, foot color, and extent of filoplumes of the neck patch varied as well among juveniles. This variation supports recognition of the race P. g. cirriger for the Atlantic population, and may facilitate parental recognition in the Pacific population. Fledged juvenile Red-legged Shags creche below nest cliffs where their parents locate them for feeding; this behavior may be correlated with obligate cliff-nesting in small colonies. Received 24 Feb. 1988, accepted 20 May 1988.

The Red-legged Shag (Phalacrocorax gaimardi) is a distinctive, gray cormorant that nests on narrow ledges of sheer cliffs and caves of coastal Peru, Chile, and Santa Cruz Province, Argentina (Doello-Jurado 1917, Murphy 1936, Johnson 1965, Meyer de Schauensee 1966, Zapata 1967, Humphrey and Bridge 1970, Brown et al. 1975, Siegel-Causey 1987). The juvenal plumage has been described as: "paler [than subadults]... whitish throats and a conspicuous sprinkling of white plumules on the center of the throat and the sides of the neck" (Murphy 1936:p. 874). Other descriptions (Alexander 1928, Blake 1977, Tuck and Heinzel 1978, Harrison 1983, Araya and Millie 1986) did not differentiate recently fledged juveniles from subadults (undergoing the prolonged first prebasic molt; Rasmussen, unpubl. data). Figures in Tuck and Heinzel (1978) and in Harrison (1983) depict subadults; although these figures and associated descriptions are essentially correct, as is the illustration of a juvenile in Murphy (1936: facing p. 1144), they do not acknowledge the great variability in the juvenal plumage. Two subspecies have been recognized: P. g. gaimardi on the Pacific coast, and P. g. cirriger in Santa Cruz Province, Argentina; adults of the Atlantic subspecies are slightly smaller and paler than are Pacific birds (Humphrey and Bridge 1970, Blake 1977), but no information is available concerning differences in juvenal plumages of the two subspecies.

Juvenile cormorants are dependent on their parents for a variable period
after fledging. Parental recognition of chicks is known in several cormorant species (Serventy 1952, Palmer 1962, Snow 1963, Derenne et al. 1976, Urban 1979), and is at least partially visual (Snow 1963, Derenne et al. 1976). In some species, fledglings are fed in creches (Serventy 1952; Snow 1960, 1963, 1966; Fenwick and Bourne 1975; Carter and Hobson 1988), while in others fledglings return to the nest to be fed (Palmer 1962; Morrison 1977; Urban 1979; Bernstein and Maxson 1984, 1985; Brothers 1985). These aspects of behavior have not been described previously in Red-legged Shags.

In this paper, variation in the juvenal plumage of this species is described, and frequencies and geographic origin of juvenal plumage types are presented. These data are examined in relation to the hypothesis that Atlantic and Pacific populations of P. gaimardi have diverged evolutionarily. The hypothesis that variability in the juvenal plumage facilitates recognition of fledglings by their parents is discussed, and location of parental feeding of fledglings is compared with that in other cormorant species.

METHODS

Specimens and characters examined.—Sixteen juvenal-plumaged study skins of Red-legged Shags were examined in this study (12 from the Pacific coast, 4 from the Atlantic coast). P. S. Humphrey collected four of the specimens (KUMNH 83594-83597, for abbreviations see Acknowledgments) at Punta Guapacho (41°45'S, 73°53'W), Peninsula Lacuy, Chiloé Island, Chile on 12 January 1987, and 1 (KUMNH 81201) at Puerto Deseado, (47°45'S, 66°40'W), Santa Cruz Province, Argentina, on 29 January 1985. I recorded soft part colors immediately after the death of these specimens. Other skin specimens examined were from Peru (AMNH 443220, 443225, 443235, 73019; ANSP 104124; NMNH 212036), other localities in Chile (AMNH 113431, CMNH 120832), and Rio Gallegos, Santa Cruz Province, Argentina (DMNH 16288, 16289, 16297). The four plumage classes into which I categorized each specimen were (Fig. 1A-D): (A) dark—very few (as in Fig. 2A) or no pale feathers in throat and neck, crown blackish gray, underparts medium gray, general coloration very dark; (B) intermediate—throat pale but blotchy and streaked (as in Fig. 2B-D), crown blackish gray, underparts pale, upperparts dark gray; (C) light—throat white or nearly so, crown medium gray (as in Fig. 2E), underparts pale, upperparts medium dark gray; (D) very pale—throat white (as in Fig. 2F), ventral neck very pale, no dark pectoral band, very pale gray underparts, and crown and back paler than in 2C. In the few cases in which a specimen did not fit exactly into a category, decisions were based on throat and crown color. Specimens undergoing the first prebasic molt (which appears to begin at about one year of age; Rasmussen, unpubl. data) were excluded, as were those that showed noticeable wear of feathers (other than rectrices), because wear is usually accompanied by bleaching of feathers. Rectrices, however, may be appreciably worn prior to fledging, as shown by some specimens with remnant nestling down and worn rectrix tips (e.g., AMNH 443220).

I recorded whether the gular pouch color was blackish (mostly or totally) or orange (mostly or totally) on these museum skins; this appears to be justified because, while there was some color change after preservation, soft part colors of specimens of P. gaimardi collected in 1985 were still clearly assignable to the original category in 1988. Older museum specimens appeared comparable (but duller) in gular pouch color.
Fig. 1: The four general plumage patterns of juvenal *P. gaimardi* into which birds examined in this study were grouped. (A) Dark (AMNH 443225); (B) intermediate; (C) light; (D) very light (KUMNH 81201). The light-colored gular pouch in Fig. 1D is orange.
Although foot color varied among juveniles, most museum specimens lacked adequate color notes, so few data on foot color were available. Juveniles were classed as to whether the feet were slightly dusky orange, dark dusky orange, or reddish-black. The color of webs, toes between joints, and tarsi was recorded; the skin of the joints and the soles tended to be darker.

The white neck patches of adults were composed of wide filoplumes which grew among and covered the gray contour feathers of the patch area. Juveniles showed variable development of these filoplumes at fledging; specimens were grouped in the following four classes of presence of filoplumes in the presumptive neck patch: (1) very few; (2) few; (3) moderate numbers; and (4) sufficient filoplumes to form a sparse neck patch.

Living juveniles and photographs examined.—At the cormorant nesting colony at Punta Guapacho I examined fledged juvenile-plumaged birds through a 45× scope in good light on 16 January 1987, and repeated this on 18 January. I classified each juvenile into one of the four plumage categories, and one of the two gular pouch colors. I did not judge foot color or filoplume development for these birds. The birds were determined to be recently fledged juveniles by their food-begging behavior and/or their fresh plumage. Subadults were easily distinguished from juveniles, because the former have a mottled appearance to the back, wings, and underparts due to bleached, brownish, worn juvenal feathers mixed with fresh gray basic feathers; they also have well-developed neck patches, bright orange to red facial skin and feet, and yellow sides to the bill (Rasmussen, unpubl. data).

Juveniles photographed at Punta Guapacho on 16 January 1987 were classified as to plumage color, gular pouch color, and (when possible) foot color and neck patch development (each photograph was taken on different sections of the loafing rocks. During photography, no juveniles were seen to move between sections, so probably no individuals occurred in more than one photograph. These photographs were taken in a different section of the colony from where observations of living juveniles were made). Plumage and gular pouch data were also taken from juveniles in other color slides (one by D. Siegel-Causey, February 1985, Puerto Deseado, Argentina; one by T. A. Parker III, Peru), and black and white photos (one from Santa Cruz Province, Argentina [J. Heinrich]; one photo from Cabo Blanco, Santa Cruz Province, Argentina [Daciuk 1977]; in this photo only 1 juvenile was in good light so was classified, and 3 others were in class C or D, but were not classified).

Behavioral observations.—On 18 (09:30-14:00) and 19 (08:30-12:30) January 1987 at Punta Guapacho, I observed interactions between fledgling P. gaimardi in creches at the base of the colony and adults returning there from foraging. During my observations the group continually comprised 25–40 juvenile P. gaimardi and 10–15 adults, as well as similar numbers of fledgling and adult Blue-eyed Shags (P. atriceps) which nested in different portions of the colony.

RESULTS

Plumage, gular pouch, foot color, and filoplume development class frequencies.—Plumage class B was the most common (61%) of the three classes occurring at Punta Guapacho, and class A the least (13%; Table 1). Plumage class D did not occur among juveniles from the Pacific coast, but all six Atlantic coast juveniles were in plumage class D. Of 20–30 juveniles I observed at Puerto Deseado in February 1985, none differed noticeably in plumage from the class D juvenile collected there (KUMNH 81201). Most (77%) of the Pacific coast juveniles had black gular pouches; all 6 Atlantic coast juveniles had orange gular pouches. Based on variation
Fig. 2. Gular pouch, throat, and neck patterns of six juvenile P. gaimardi specimens. (A) AMNH 443225; (B) KUMNH 83597; (C) KUMNH 83596; (D) KUMNH 83585; (E) KUMNH 83594; (F) KUMNH 81201. The light-colored gular pouches in Fig. 2C and F are orange.

evident in these two characters, most specimens I examined were easily recognizable (Fig. 2).

Five juveniles from the Pacific coast had slightly dusky orange feet; three had very dusky orange feet; and four had reddish-black feet. The single Atlantic coast specimen examined had reddish-black feet.

Filoplume development was highly variable in juveniles. Twenty-five (73%) of the Pacific juveniles had very few filoplumes in the neck patch area; six (18%) had few filoplumes; two (6%) had moderate numbers of filoplumes; and one (3%) had a sparse neck patch. Of five Atlantic juveniles, two had very few and two had moderate numbers of filoplumes; one had a sparse neck patch. No obvious pattern was found, but the specimens with few filoplumes had filoplumes outlining the neck patch area and a very few scattered through the contour feathers of the neck. In all juveniles examined, contour feathers in the area of the presumptive neck patch tended to be shorter and downier than the surrounding contour feathers. No juveniles had well-developed white neck patches.

Behavior. — Juveniles in the creches at Punta Guapacho were frequently threatened by adults and the larger juvenile and adult Blue-eyed Shags, from which they retreated every time without contest. Upon the return of each adult Red-legged Shag from foraging at sea to the creches, a few
Table 1
NUMBERS OF JUVENAL P. GAIMARDI RECORDED WITH EACH PLUMAGE TYPE AND GULAR POUCH TYPE FOR EACH REGION AND TYPE OF OBSERVATION

<table>
<thead>
<tr>
<th>Locality</th>
<th>Plumage type</th>
<th>Gular pouch type</th>
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<th></th>
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<tbody>
<tr>
<td></td>
<td>A  B  C  D</td>
<td>Black  Orange</td>
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<td>Live juveniles</td>
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<td></td>
<td></td>
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<tr>
<td>Punta Guapacho, Chile, 16 Jan 1987</td>
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<td>29  6</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>5  13  10  0</td>
<td>22  4</td>
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<td></td>
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<tr>
<td>Specimens</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Punta Guapacho, Chile, 12 Jan 1987</td>
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<td>3  1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other Chile</td>
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<td>1  0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peru</td>
<td>1  5  0  0</td>
<td>4  1</td>
<td></td>
<td></td>
</tr>
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<td>0  4</td>
<td></td>
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<tr>
<td>Photographs</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Punta Guapacho, Chile, 16 Jan 1987</td>
<td>1  14  5  0</td>
<td>5  5</td>
<td></td>
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</tr>
<tr>
<td>Peru</td>
<td>0  1  0  0</td>
<td>1  0</td>
<td></td>
<td></td>
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<tr>
<td>Santa Cruz Province, Argentina</td>
<td>0  0  0  2</td>
<td>0  2</td>
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<tr>
<td>Totals</td>
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</tr>
<tr>
<td>Pacific</td>
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</tr>
<tr>
<td>Atlantic</td>
<td>0  0  0  6</td>
<td>0  6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Recount of same area counted 16 Jan; not included in totals.

(2–5) juveniles usually walked up to the adult (one after another) and begged, giving shrill cries, spreading and waving the wings, and extending the gular pouch by depressing the hyoid, while jabbing at the adult’s bill. Adults usually rejected and chased some chicks that begged before accepting and feeding a begging chick. Two juveniles of different plumage types (one pale and the other intermediate) begged from and were accepted by the same adult, suggesting plumage variation among siblings.

No fledgling Red-legged Shags attempted to return to the nesting ledges from the creches, although some (if not all) of the fledglings in the creches were flighted, and while begging they sometimes pursued adults on the wing to sea. At Isla Mazorca, Peru, juveniles were fed by adults in creches (D. C. Duffy, in litt.), as at Punta Guapacho. Fledgling Blue-eyed Shags, however, routinely flew up to their nesting colony from the creches below. Juvenile Blue-eyed Shags did not beg at the creches, even though they were continually present there with adults; the fledglings were fed only in the vicinity of the nests.

DISCUSSION

In Chile and Peru, the juvenile plumage of Red-legged Shags, while variable, appears to be consistently darker than that of juveniles from the
Argentine coast. In addition, while only 23% of the Pacific coast birds examined had largely or completely orange gular pouches, all six Atlantic birds examined had largely orange gular pouches. These data demonstrate a greater differentiation between Atlantic and Pacific populations in the juvenal plumage than in definitive plumage, and therefore support Humphrey and Bridge’s (1970) treatment of the Atlantic population as subspecifically distinct (P. g. cirriger) from nominate P. g. gaimardi of the Pacific. Although more specimens are needed, particularly from the Atlantic coast, the Pacific population seems to be much more variable in juvenal plumage. The six Atlantic juveniles examined were all very similar, differing mainly in development of the white neck patch. Red-legged Shags probably colonized Santa Cruz Province, Argentina, after arriving by overland flight from the Chilean coast (Devillers and Terschuren 1978). The low variability of the juvenal plumage of the Atlantic population could be due to the bottleneck effect, while the pale plumage may reflect the action of the founder effect.

In the juvenile’s begging posture, the hyoid is depressed (as in other cormorants), so gular pouch markings are displayed. These markings and plumage characters could facilitate recognition of offspring by parents, at least in the Pacific population of the Red-legged Shag. Parental recognition of older chicks is known in several cormorants (Serventy 1952; Snow 1960, 1963; Palmer 1962; Berry 1976; Derenne et al. 1976; Brown et al. 1982). Some cormorants recognize their fledglings by sight, without aid of vocalizations (Derenne et al. 1976). European Shags (P. aristotelis) apparently recognize each other by facial characteristics (Snow 1960). In these species, some variability is present in the juvenal plumage (Paulian 1953, Voisin 1970, Cramp and Simmons 1977, Derenne et al. 1976). Not all cormorant species, however, have variable juvenal plumages, and parental recognition abilities are unknown for most species. Present data are not sufficient to establish whether plumage variability evolved to facilitate parental recognition.

Red-legged Shag adults feed fledged juveniles in creches, probably because of the hazards of landing on the narrow nesting ledges (even adults often have difficulty landing; McNicholl and Hogan 1979, pers. obs.), and because of the lack of space there for both adults and fully grown young. In other cliff-nesting species for which this behavior is recorded, fledged juveniles abandon their nesting areas for creches, where they are fed (Snow 1960, 1963; Fenwick and Bourne 1975), as is also the case with some species that nest on flat areas (Serventy 1952, Snow 1966, Berry 1976, Carter and Hobson 1988). In tree-nesting cormorants, fledglings usually wait in the nest tree for feeding (Harley 1946, Oliver 1955, Palmer 1962, Morrison 1977, Olver and Kuyper 1978, Urban 1979, Olver 1984). The P. atriceps nesting colony had many suitable landing places, so juvenal
P. atriceps could land there to be fed. Their colonies are usually on flat areas (Murphy 1936, Johnson 1965, pers. obs.), and although fledged juveniles creche away from nests (Bernstein and Maxson 1984, 1985; Malacalza 1984; Shaw 1984), they usually (but not always; V. E. Malacalza, in litt.) return to their nests to be fed (Bernstein and Maxson 1984, 1985; Brothers 1985; G. F. van Tets, in litt.), as do fledged Guanay Cormorants (P. bougainvillii, Vogt 1942; D. C. Duffy, in litt.). In these shags, generally adapted to nesting in large colonies on flat ground, it appears advantageous for fledglings to return to the nest where parents can easily find them. In contrast, several (but not all; Berry 1976, Carter and Hobson 1988) of the species in which fledglings creche, nest in small colonies (Snow 1963, 1966; Fenwick and Bourne 1975), so fledglings do not form large groups and parents can easily find their offspring. Further comparative study of post-fledging behavior in cormorants is needed to determine whether these behavior patterns are constant within each species and are primarily determined by phylogeny or by nest-site and colony characteristics.

ACKNOWLEDGMENTS

I thank P. Humphrey and D. Siegel-Causey for the opportunity to visit the field site and for help in many ways during this study. D. Duffy, G. van Tets, and V. Malacalza generously provided information on fledgling behavior, and J. Chebez provided data on a photograph. Curators and staff of the following museums provided access to and loan of specimens: Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CMNH), Denver Museum of Natural History (DMNH), Louisiana State University Museum of Zoology (LSUMZ), National Museum of Natural History (NMNH). VIREO supplied a photograph by T. Parker III. M. Gottfried, H. Carter, and N. Bernstein improved the manuscript. Logistics and other assistance were provided in Argentina by J. Vinuesa, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET); R. Wilson, Puerto Deseado, Santa Cruz Province; and R. Clarke, Conservación de la Fauna, Santa Cruz, Argentina; in Chile by the Dirección Nacional de Fronteras y Límites del Estado; the Servicio Nacional de Pesca; the División de Protección de los Recursos Renovables, Servicio Agrícola y Ganadero; M. Salaberry A., A. Veloso, T. Iriarte, Universidad de Chile; N. López, Asunción, Paraguay; J. Llaiquén, Pargua, Chile; O. de Soto, Ancud, Chile. Import permits were granted by U.S. Fish and Wildlife Service and APHIS, Department of Agriculture. Field and museum work was funded by grants to the author from the Frank M. Chapman Memorial Fund and the American Museum of Natural History Collections Study Program; the Humphrey family; the Museum of Natural History, Department of Systematics and Ecology, and Endowment Association, the University of Kansas; and National Science Foundation grant no. BSR 84-07365 to Humphrey and Siegel-Causey.

LITERATURE CITED


NEST-SITE TENACITY AND MATE RETENTION OF THE PIPING PLOVER

TERRY P. WIENS AND FRANCESCA J. CUTHBERT

Abstract. — Piping Plovers (Charadrius melodus) were studied for three breeding seasons (1982–1984) at Lake of the Woods, Minnesota, to determine the effects of previous breeding success on nest-site tenacity and mate retention. The population consisted of approximately 47 adults that nested at four breeding localities within the study area. Nest-site tenacity was strong; 84% of all breeding birds nested within 200 m of their nest site of the previous year. No significant relationship was found between previous breeding success and nest-site tenacity. Moderate mate retention was observed; of all pairs for which both members returned to the study area the subsequent season, 45% reunited. No significant relationship was found between previous breeding success and mate retention. This study demonstrates the importance of protecting traditional breeding sites used by threatened and endangered populations of Piping Plovers. Received 3 Nov. 1987, accepted 25 Mar. 1988.

Interest in the mating systems of higher vertebrates has increased in recent years (e.g., Orians 1969, Emlen and Oring 1977, Greenwood 1980, Oring 1982). Research has focused not only on overall strategies (e.g., monogamy) but also on specific aspects of reproductive behavior such as nest-site tenacity and mate retention. Numerous studies have demonstrated that the tendency to return to the same breeding site in consecutive years is widespread among temperate-zone birds (see review in Greenwood 1980). The tendency to reunite with the same mate from year to year has been documented to a lesser extent (see Rowley 1983). Within populations, the degree of nest-site tenacity and mate retention varies. It has been shown that either or both may be affected by age (Austin 1949, Ryder 1980), sex (Nice 1937, Wilcox 1959, Lenington and Mace 1975, Darley et al. 1977), site stability (McNicholl 1975, Southern 1977), or previous breeding success (Coulson 1966, Nolan 1978, Oring and Lank 1982).

The objectives of this research were to determine: (1) extent of nest-site tenacity and mate retention, and (2) the effect of previous breeding success on site and mate fidelity of Piping Plovers (Charadrius melodus) nesting in northern Minnesota. We hypothesized that birds producing offspring in a given year would be more likely to exhibit nest-site tenacity and to retain mates in the next season than birds that failed to breed successfully.
STUDY AREA AND METHODS

This study was conducted along the southern shoreline of the Lake of the Woods (LOTW), Lake of the Woods County, Minnesota. Within the study area, Piping Plovers bred at four specific locations referred to as breeding localities: Pine and Curry Island (48°52'N, 94°45'W), Morris Point (48°51'N, 94°46'W), Zippel Bay (48°53'N, 94°52'W), and Rocky Point (48°58'N, 95°02'W). Pine and Curry Island is a long (7 km), narrow, sand barrier island located at the mouth of the Rainy River. The remaining localities are sand spits less than 1 km in length. All nest sites were located on sandy beaches and low dunes formed by extensive wave action and current movement. Habitat consisted of open beach and beach community, characterized by relatively sparse vegetation that rarely exceeded 1 m in height. The dominant vegetation was sandbar willow (Salix interior), tail-wormwood (Artemisia caudata), and beach pea (Lathyrus japonicus).

Observations were continuous throughout the plover breeding season, from late April/early May to late July/early August, 1982–1984. Most observation time was spent at Pine and Curry Island and Morris Point, where 96% of all LOTW plover nesting occurred. Zippel Bay and Rocky Point were checked approximately once a week and three times a season, respectively. In 1982 and 1983, additional surveys were conducted throughout the Minnesota portion of LOTW to document additional or potential nesting habitat.

Fieldwork involved observation of plovers to determine reproductive success and the identity and location of individuals. Most observations were made from a boat anchored 5 to 100 m from beaches where plovers were present. In 1982 additional observations were made from a portable land-based blind. Checks to determine nest status and location were conducted on foot. To identify individual plovers, we banded 47 adults and 91 juveniles each with a U.S. Fish and Wildlife Service aluminum leg band and a unique combination of colored plastic leg bands. An additional 15 juveniles received only an aluminum band. Most adults (31) were captured with mist nets placed on open beach and/or near nests. The remaining 16 adults were captured on the nest with a wire mesh drop trap (Wilcox 1959). Trapping was restricted to nests a week or more into incubation and attempts were discontinued if the adults did not return to incubate within 15 minutes. All juvenile plovers were captured by hand.

Nests were checked approximately every other day (except Zippel Bay and Rocky Point) and chicks were monitored until fledging age. Chicks were considered to be fledged if they reached 10 or more days of age (after Cairns 1977, 1982). Pairs were considered to be successful if they raised one or more chicks to fledging.

Some authors have defined nest-site tenacity as the return of birds to their former territories (Lenington and Mace 1975, Darley et al. 1977, Holland et al. 1982, Petrinovich and Patterson 1982). Others consider nest-site tenacity to be the tendency of birds to return to a specific nest location (MacDonald 1977, Howe 1982, Fiedler and Grewe 1983, Morse and Kress 1984, Shields 1984, Gratton et al. 1985). The latter interpretation is used in this study, with nest site being defined as the precise location of a nest within a breeding locality.

Nest-site tenacity was determined by measuring the distance between nests in successive years for each breeding pair. To determine this distance, we marked all nest sites after nesting with permanent stakes to facilitate locating them in subsequent years. Measurements of the distances between nests were made to the nearest meter using a tape measure. For birds moving more than 500 m, the distance between nests was estimated from a map.

In 1983 and 1984 we classified each breeding pair from the previous year into one of four categories: reunite (both birds remate with each other), separate (both birds present but at least one mating with a different bird), discontinue (one bird absent and the other mating with a different bird), and status unknown. Only pairs that reunited or separated were considered in determining mate fidelity.
To compare the nest-site fidelity of successful breeders to that of unsuccessful individuals, a Mann-Whitney U-test was used (Siegel 1956). Comparisons of mate changes based on reproductive success were made using Fisher’s exact test of independence (Sachs 1982). For all analyses data from more than one year were combined. As a result, some individuals (14–23%) may have been represented more than once in a sample.

RESULTS

Population size and distribution. — The LOTW Piping Plover population had a mean size of 47 adults per year, with little variation (Table 1). Breeding adults represented 68% to 94% of the total population for any given year. Breeding attempts were limited to four localities within LOTW: Pine and Curry Island (74% of all nests), Morris Point (22%), Rocky Point (3%), and Zippel Bay (1%). These four localities represented most of the suitable nesting habitat present within the Minnesota portion of LOTW.

Nest-site tenacity. — Distances between nests in successive years were not normally distributed with extremes of 0 to over 15,000 m; the median was 41 m (N = 31). Most (84%) of the movements were less than 200 m and occurred within one breeding locality (e.g., Morris Point). Large extremes occurred when birds nested at different localities in successive years.

Comparing nest-site tenacity for birds that bred successfully to those that failed, the median year-to-year movement was 24 m and 297 m, respectively. These results suggest a correlation between nest-site tenacity and previous breeding success. However, there was no significant difference in nest-site tenacity between birds that succeeded and those that failed (U = 35, P = 0.12 for analysis excluding all birds that reunited [variables not independent]; U = 48, P = 0.10 for analysis including only one member of each reuniting pair; U = 61, P = 0.08 for analysis including all members of reuniting pairs). Therefore the hypothesis that nest-site

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**Table 1**

<table>
<thead>
<tr>
<th>Breeding adults</th>
<th>1982</th>
<th>1983</th>
<th>1984</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pine and Curry Island</td>
<td>24</td>
<td>32</td>
<td>36</td>
</tr>
<tr>
<td>Morris Point</td>
<td>4</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>Zippel Bay</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Rocky Point</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Non-breeding adults</td>
<td>14</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>44</td>
<td>49</td>
<td>47</td>
</tr>
</tbody>
</table>
Table 2.
Fates of Breeding Piping Plover Pairs in Consecutive Seasons in Lake of the Woods

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of pairs</th>
<th>Reunite</th>
<th>Separate</th>
<th>Discontinue</th>
<th>Status unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td>1982</td>
<td>15</td>
<td>3</td>
<td>3</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>1983</td>
<td>21</td>
<td>2</td>
<td>3</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td>36</td>
<td>5</td>
<td>6</td>
<td>16</td>
<td>9</td>
</tr>
</tbody>
</table>

tenacity is positively influenced by previous breeding success is rejected at the 95% confidence level.

Mate retention.—Combining data from 1982 and 1983, a total of 36 pairs was present (Table 2). For 11 pairs (31%) both male and female were present the next season. Five (45%) of those 11 reunited. Two pairs nested together for all three years, accounting for 4 of the 5 pairs reuniting per year.

The effect of previous breeding success on mate retention was inconclusive. Five (63%) of 8 successful pairs reunited the next season, whereas none of 3 pairs that failed reunited (Table 3). The results suggest a tendency for previous breeding success to influence mate retention. However, there was no significant difference in mate retention between the two groups ($P = 0.12$).

DISCUSSION

Nest-site tenacity.—Although the criteria for comparing nest-site tenacity are not well defined in the literature we conclude that Piping Plover site tenacity was strong during this study. The results of this study are consistent with those obtained from similar studies of plovers and related species. Nest-site tenacity has been reported in other populations of Piping Plovers (Wilcox 1959, Cairns 1982), and in Mountain Plovers (C. montanus, Graul 1973), Killdeers (C. vociferus, Lenington and Mace 1975), Spotted Sandpipers (Actitis macularia, Oring and Lank 1982), Common Sandpipers (A. hypoleucos, Holland et al. 1982), and Stilt Sandpipers (Micropalama himantopus, Jehl 1973). Nest-site tenacity is hypothesized to be adaptive because familiarity with a site facilitates food exploitation, territorial defense, and predator avoidance. Superimposed on these benefits is the fact that Piping Plover nesting habitat is limited in LOTW; very few localities possess the relatively narrow ecological requirements that Piping Plovers appear to prefer. Therefore, plovers that choose to breed in LOTW have very limited nest-site choices.
Wiens and Cuthbert • PLOVER FIDELITY TO SITE AND MATE

Table 3

<table>
<thead>
<tr>
<th>Reproductive success in original season</th>
<th>Number of pairs</th>
<th>Reunite</th>
<th>Separate</th>
<th>Discontinue</th>
<th>Status unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td>Succeeded</td>
<td>27</td>
<td>5</td>
<td>3</td>
<td>12</td>
<td>7</td>
</tr>
<tr>
<td>Failed</td>
<td>9</td>
<td>0</td>
<td>3</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

Data from our study do not provide statistically significant support for the hypothesis that nest-site tenacity is influenced by previous breeding success. Lack of a significant relationship between previous breeding success and nest-site tenacity has also been observed in studies of Semipalmated Sandpipers (Calidris pusilla, Gratto et al. 1985) and Savannah Sparrows (Passerculus sandwichensis, Bedard and LaPointe 1984). Yet these results contrast with those from many other studies of philopatric birds. Breeding success was found to increase nest-site tenacity in Yellow-eyed Penguins (Megadyptes antipodes, Richdale 1957), Gray Catbirds (Dumetella carolinensis, Darley et al. 1977), Northern Fulmars (Fulmarus glacialis, MacDonald 1977), Prairie Warblers (Dendroica discolor, Nolan 1978), Bank Swallows (Riparia riparia, Freer 1979), Great Tits (Parus major, Harvey et al. 1979), and Spotted Sandpipers (Oring and Lank 1982).

It is possible that breeding success may have little effect on nest-site tenacity if suitable nesting habitat is limited, as it appears to be in LOTW. Competition for territories may be intense, and as a result any individual that has established a territory may be better off retaining it despite failure in the previous season.

Mate retention.—The degree of mate retention by Piping Plovers observed in this study was not extensive. Wilcox (1959) also reported mate retention in less than half the birds he retrapped during his 20-year study of Piping Plovers on the east coast.

Results of our study indicate that Piping Plovers may retain mates less frequently than other shorebirds with similar mating systems. Studies have shown that of all breeding pairs for which both members returned in consecutive seasons, 62% reunited in Western Sandpipers (Calidris mauri, Holmes 1971), 72% in Dunlins (C. alpina, Soikkeli 1967), 81% in Semipalmated Sandpipers (Gratto et al. 1985), 95% in Willets (Catoptrrophorus semipalmatus) (Howe 1982), and 100% in Stilt Sandpipers (Jehl 1973). If Piping Plovers retain mates less frequently than shorebirds in general, the explanation for this difference is not immediately apparent.
Rowley (1983) has argued that the extent of mate retention found in monogamous, migrant species depends largely on longevity; a greater survival rate leading to greater mate fidelity. There is no evidence, however, to indicate that Piping Plover longevity is low relative to other shorebirds.

It is possible that mate fidelity of Piping Plovers is related to site stability. The nesting habitat at LOTW can be considered to be of intermediate stability; it is altered to some extent each year by beach erosion, sand deposition, and changes in vegetation. During years of higher than average water levels significant plover habitat is submerged or periodically inundated by storm driven waves. In contrast, shorebirds such as Dunlins, Semipalmated Sandpipers, Stilt Sandpipers, and Western Sandpipers nest in the arctic tundra where changes in habitat from year to year are comparatively slight. Cuthbert (1985) presents evidence that the degree of mate fidelity in Caspian Terns (*Sterna caspia*) may be positively correlated with site stability. The relatively weak mate fidelity observed in Piping Plovers at LOTW may be related to the lack of long-term site stability at this location. For example, following several years of very high water levels a plover banded during our study was sighted in a subsequent season in southern Manitoba (R. Johnston, pers. comm.).

Data from this study do not provide statistically significant support for the hypothesis that mate retention is influenced by previous breeding success. Few other shorebird species have been studied to determine if any relationship exists between breeding success and mate retention. What little is known supports the conclusions of this study. Howe (1982) found that breeding failure did not diminish the strong mate fidelity of Willets. In addition, studies of Stilt Sandpipers (Jehl 1973) and Semipalmated Sandpipers (Gratto et al. 1985) revealed no significant difference in previous breeding success between individuals that reunited and those that separated.

There may be no relationship between previous breeding success and mate retention in Piping Plovers if selection favors reuniting despite breeding failure in the previous year. It has been argued by Rowley (1983) that there are distinct advantages to reuniting with the same mate; established pairs may obtain better breeding sites, pair members will be familiar with each other, and there is certainty that both individuals will have at least some experience. It is possible that these factors are more important for LOTW plovers than previous breeding success. It is also possible that competition for mates is very intense at LOTW. Although there was no direct evidence for this (e.g., skewed sex ratio), the small size of the population limits the number of choices available to an individual. The importance of obtaining a mate may outweigh any tendency to avoid a particular individual following breeding failure.
It is difficult to separate the effects of mate retention from nest-site tenacity. Rowley (1983) argued that nest-site tenacity may function to reunite pairs that are split during the non-breeding season. Jehl (1973) believed that for older pairs of Stilt Sandpipers, mate retention appeared to be largely a consequence of territorial fidelity. Morse and Kress (1984) artificially removed nest sites within a colony of Leach's Storm-Petrels (Oceanodroma leucorhoa) to assess the roles of mate fidelity and site tenacity in retaining mates. Their results indicated mate retention was strongly site-dependent. Thus, it appears that for at least some territorial species nest-site tenacity is of primary importance and mate retention may be a secondary benefit of returning to the same nest territory used the previous year. Because they show strong nest-site tenacity and a lower frequency of mate retention, Piping Plovers at LOTW fit this pattern.

Conservation implications.—In 1986 the Piping Plover was listed as threatened and endangered under the provisions of the federal 1973 Endangered Species Act; LOTW plovers are considered part of the threatened northern Great Plains population. One of the reasons for the decline of this species appears to be loss of breeding habitat to shoreline development or river channel modification for commercial or recreational purposes (Sidle 1985). Our study found that a significant portion of the breeding population returned in consecutive years to nest at limited localities in northern Minnesota. These results demonstrate the importance of preserving important traditional plover breeding sites and, if necessary, managing these sites to minimize impacts of naturally occurring ecological processes (e.g., predators, fluctuating water levels) that may cause individuals to move to other breeding localities.

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LITERATURE CITED


HABITAT USE BY BREEDING AND MIGRATING SHOREBIRDS IN SOUTHCENTRAL SASKATCHEWAN

MARK A. COLWELL AND LEWIS W. ORING1.

Abstract.—Habitat use by breeding and migrating shorebirds was studied at three sites in southcentral Saskatchewan from May through August 1984, a year of extreme drought conditions. Habitat use among species was examined using ordination and classification analyses. At each site, analyses identified four major species groups in different zones of a terrestrial–aquatic habitat gradient. Patterns of habitat use differed between breeders and migrants at the one site with large numbers of nesting individuals; the average seasonal shift in habitat use was greater for breeders than for migrants. Overall, habitat use differed among taxonomic groups at two of three sites, but this pattern was reduced to only one site when seasonal patterns were examined. There was no significant difference among taxa in seasonal changes of habitat use. Interspecific differences in habitat use are discussed with regard to morphology, annual cycles, and migration chronology. Received 7 Jan. 1988, accepted 6 June 1988.

Habitat use by assemblages of migrating (Recher 1966, Recher and Recher 1969, Burger et al. 1977, Burger 1984), breeding (Holmes and Pitelka 1968, Baker 1979, Connors et al. 1979a), and wintering shorebirds (Baker and Baker 1973, Baker 1979, Myers and Myers 1979) has received considerable attention, particularly in marine habitats (Pitelka 1979, Evans et al. 1984, Davidson and Pienkowski 1987). However, habitat use has been studied less often in mixed groups of breeding and migrating species, and relatively few studies have examined shorebird habitat use at inland, freshwater sites in North America. As a result, an understanding of habitat requirements of many shorebird species that use wetlands of the continental interior of North America, either as breeding sites or migratory staging areas, is negligible. Such a dearth of knowledge may compromise management endeavors that seek to maintain viable populations.

Although management schemes for prairie wetlands are founded on a mixed-species, multi-use approach, waterfowl have been the focus of most such efforts (Peek 1986). Since shorebirds as a group are more terrestrial than waterfowl, waterfowl management practices that maximize availability of deep-water areas in close proximity to nesting habitat may benefit some shorebird species. However, patterns of habitat use of most

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migrant shorebirds may run counter to common waterfowl management efforts that seek to restrict some terrestrial habitats.

We studied shorebirds in southcentral Saskatchewan, Canada during 1984, a year of extreme drought conditions when approximately 90% of local wetlands were dry. As a result, shorebirds were concentrated at a limited number of wetlands, and locally breeding species may have experienced restricted breeding opportunities (Colwell 1986). This paper presents data on habitat use by breeding and migrating shorebirds at three prairie wetlands and makes suggestions for shorebird management practices in the prairies.

**METHODS**

**Study areas.**—Shorebirds were censused in northern prairie habitat at Last Mountain Lake National Wildlife Area (51°10'N, 110°2'W) in southcentral Saskatchewan, Canada. For comparative purposes, three wetland sites (Colwell 1987) were chosen that differed in substrate, vegetation, and open-water features. Additionally, census data from 1982 and 1983 (Colwell, unpubl. data) indicated that, together, these sites included habitat that enabled a complete survey of both migrating and breeding shorebirds in the area (Colwell 1987).

Shorebirds were censused from 30 April to 30 August 1984 at Lanigan Creek, a 100-ha site with a permanent wetland and surrounding pasture that was grazed by 45–50 cattle from late May to autumn. The study area was divided by a steep-banked, deep-water creek that was dammed on its northern half by a man-made structure. Dense bulrush (*Scirpus paludosus*) stands bordered open-water areas. During spring, wet meadow dominated the study area, and mudflats constituted a small amount of available habitat. However, as summer progressed, mudflats became increasingly available to shorebirds. Salt-tolerant grasses (*Distichlis stricta*, *Puccinellia nuttalliana*) and forbs (*Plantago eriopoda*, *Salicornia rubra*, *Glaux maritima*) bordered the creek and wet meadow. During spring, flooded grasses (*Hordeum jubatum*, *Koeleria gracilis*, *Poa spp.*) and sedges (*Carex spp.*) rimmed deep-water areas. In upland habitat, over-grazed grasses (*Poa spp.*) and forbs (*Anemone canadensis*, *Achillea millefolium*) separated patches of buckbrush (*Symphoricarpos occidentalis*) and rose (*Rosa acicularis*). Shorebirds also were observed from 8 May to 28 August 1984, 1.5 km south of Lanigan Creek at Basin A, a 10-ha shallow-water site typified by expansive mudflats under varying moisture conditions. Bulrush and foxtail barley dominated the vegetation. Drought conditions combined with gently sloping terrain to expose extensive mudflats during July and August. Shorebirds also were censused from 3 May to 20 August 1984 at Perry's Beach, a 1.5-km stretch of sandy and rocky beach on the shore of Last Mountain Lake. Beach width varied from approximately 5 to 30 m; areas of the beach used by shorebirds were unvegetated. Lake water levels changed little at Perry's Beach during the study.

**Sampling methods.**—At Lanigan Creek and Basin A, one to three observers censused shorebirds from 3-m towers using 20–25× spotting scopes and 7× binoculars. At Perry's Beach, one observer walked the beach and recorded data at vantage points that maximized observations of shorebirds. A stratified random sampling scheme was used to schedule Lanigan Creek censuses (*N* = 222); during each successive week, observations were made during random sampling periods that included all daylight hours (05:00–21:00 h). Most Basin A censuses (*N* = 53) were paired with a Lanigan Creek survey. Perry's Beach was sampled less frequently (*N* = 23), particularly in the spring.

Observers scan-sampled (Altmann 1974) a site and recorded each bird's habitat and
Table 1
HABITATS USED BY SHOREBIRDS

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>UG</td>
<td>Upland grasses (Agropyron, Koeleria, Stipa, Distichlis, Poa), forbs (Anemone, Antennaria, Galium, Plantago, Glaux), and shrubs (Symphoricarpos, Rosa)</td>
</tr>
<tr>
<td>HR</td>
<td>Wetland margins of foxtail barley (Hordeum jubatum)</td>
</tr>
<tr>
<td>GS</td>
<td>Unflooded grasses and sedges (Triglochin maritima, Carex)</td>
</tr>
<tr>
<td>WM</td>
<td>Wet meadows of flooded grasses, sedges (Carex), and forbs</td>
</tr>
<tr>
<td>MV</td>
<td>Compressed mats of aquatic vegetation resulting from standing water of early spring runoff</td>
</tr>
<tr>
<td>BR</td>
<td>Dense stands of thickstem bulrush (Scirpus paludosus)</td>
</tr>
<tr>
<td>SR</td>
<td>Unvegetated lakeshore substrate of rocks and sand</td>
</tr>
<tr>
<td>AD</td>
<td>Dried mud substrate occasionally sparsely vegetated (Salicornia)</td>
</tr>
<tr>
<td>AW</td>
<td>Unvegetated, wet mud substrate, dampened by proximity to standing water</td>
</tr>
<tr>
<td>AF</td>
<td>Unvegetated, mud substrate covered by a thin film of water</td>
</tr>
<tr>
<td>WL</td>
<td>Mud or sand substrate with water level less than the birds' upper tarso-metatarsal joint</td>
</tr>
<tr>
<td>WG</td>
<td>Mud or sand substrate with water level equal to or greater than the birds' upper tarso-metatarsal joint</td>
</tr>
<tr>
<td>OW</td>
<td>Unvegetated aquatic habitat with bird floating on surface</td>
</tr>
<tr>
<td>RK</td>
<td>Large rock elevated above substrate or vegetation</td>
</tr>
</tbody>
</table>

* Habitat acronyms are given for reference to figures.

behavior (Table 1). Wading shorebirds were assigned to habitats following Baker's (1979) scale relating water level to an individual's upper tarso-metatarsal joint. Distance to wetland edge was estimated on a logarithmic scale (1 = 0-10 cm, 2 = 11-100 cm, 3 = 1-10 m, 4 = 10-100 m, and 5 = greater than 100 m) and involved a bird's position relative to the aquatic-vegetative or aquatic-terrestrial interface.

Statistical methods.—For each site, data were summarized as the percent of total observations for a species in each habitat x distance category. Five distance categories and 9-14 habitats described 45-70 possible habitat classes. The number of habitat classes tallied was much less owing to unrepresented combinations of some habitat and distance measures (e.g., UG less than 10 cm from the wetland edge, AF greater than 100 m from the edge). Site differences resulted from the types of available habitat. Distances were not used for birds occupying some habitats (Table 1; GS, WM, and HR) because of difficulty in determining where edges occurred. Species were excluded from ordination (see below) if they were observed less than 10 times, and habitats were eliminated if they were used by one species exclusively. We did this to minimize distortion of analyses owing to rare occurrences.

The matrix consisting of species percent total observations in each habitat class was analyzed using detrended correspondence analysis (DCA, Hill 1979a). DCA, an improved ordination technique (Gauch 1982), has as its fundamental criterion the rescaling of second and higher axes resulting in no systematic relation to lower axes. This feature caused expansion and contraction of small segments along the species ordination, with the result that species turnover occurred at a uniform rate along ordination axes. Consequently, equal ordination distances among species corresponded to equal differences in sample composition (Gauch 1982).

Using shorebirds (species) and habitat classes (samples), DCA organized shorebirds based
on similarities in habitat use. Shorebirds with similar patterns of habitat use were assigned similar axis scores. When species differed widely in the types of habitat they occupied, differences in axis scores were correspondingly greater. Thus, a species' axis score represents a composite of habitat use based on all habitats frequented by that species in relation to habitat use by all other species.

Indicator species analysis (ISA, Hill et al. 1975, Hill 1979b), a polythetic, divisive classification method, was used to categorize shorebird species based on similarities in habitat use. ISA used the same species x habitat matrix as DCA (percent total observations of a species in each habitat). Based on the ordination method of reciprocal averaging, ISA first ordinated the data and then used those habitats that characterized the extremes of ordination axes to polarize the species (Gauch 1982). Species were divided into two clusters by breaking the ordination axis at its middle, and the process continued with each subset of species until a minimum number of members was included (Gauch 1982). Gauch (1982) presents a thorough discussion of DCA and ISA.

Seasonal habitat use was examined by a combined ordination of spring and summer observations, based on the chronology of migration and breeding at Last Mountain Lake. A mid-June decline in the number of migrants followed by a July increase represented the hiatus between north and south migratory periods (Colwell et al., 1988a). Observations of shorebirds before and after 1 July were placed into spring and summer totals, respectively. Observations of breeding individuals, based on behavioral data, were placed into spring totals, regardless of date. Otherwise seasonal status of individuals of locally breeding species was judged by the same date criterion as migrants. Seasonal analyses were restricted to fewer species (see above) owing to diminution of sample sizes caused by the restricted sampling periods.

Patterns of habitat use were examined using nonparametric statistical tests (Siegel 1956, Sokal and Rohlf 1981) of DCA axis scores, and $P < 0.05$ was used for determining statistical significance. Species were divided into breeders and migrants based on the presence of locally breeding individuals in the area. Analyses of taxonomic correlates of habitat use were made at the level of the tribe or subfamily (AOU 1983).

**RESULTS**

Patterns of habitat use. — Shorebirds varied in their patterns of habitat use at each site. At Lanigan Creek, DCA portrayed a terrestrial–aquatic habitat gradient (Fig. 1); and ISA distinguished several groups (Table 2). Wilson's Phalaropes (*Phalaropus tricolor*) and Red-necked Phalaropes (*P. lobatus*) were conspicuous in their use of open-water areas. Wilson's Phalarope, which bred in large numbers at Lanigan Creek (Colwell and Oring, 1988), was less aquatic and frequented a greater range of habitats than Red-necked Phalarope. Lesser Golden Plover (*Pluvialis dominica*), Killdeer (*Charadrius vociferus*), American Avocet (*Recurvirostra americana*), Spotted Sandpiper (*Actitis macularia*), and Upland Sandpiper (*Bartramia longicauda*) occurred in terrestrial habitats. Marbled Godwits (*Limosa fedoa*) also used upland areas, but were grouped with most calidridine sandpipers (Sanderling, *Calidris alba*; Red Knot, *C. canutus*; Semipalated Sandpiper, *C. pusilla*; Least Sandpiper, *C. minutilla*; Baird's Sandpiper, *C. bairdii*; Stilt Sandpiper, *C. himantopus*; Pectoral Sandpiper, *C.
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melanotus), tringine sandpipers (Willet, Catoptrophorus semipalmatus; Lesser Yellowlegs, Tringa flavipes; Greater Yellowlegs, T. melanoleuca), Hudsonian Godwit (L. haemastica), and Common Snipe (Gallinago gallowago), based on use of wet meadow and mudflats in close proximity to the wetland edge.

At Basin A, DCA portrayed a habitat continuum spanning open-water and mudflat habitats (Fig. 1). Four discrete groups were identified by the classification (Table 2). Phalaropes and American Avocet used open-water areas nearly exclusively. Dowitchers (Limnodromus spp.), Marbled Godwit, and Stilt Sandpiper waded in deep-water areas, greater than 10 m from shore. Shallow-water areas within 10 m of the wetland edge were frequented by tringine sandpipers and a group of calidridine sandpipers, including Dunlin (Calidris alpina). Mudflats were used by Semipalmated Plover (Charadrius semipalmatus), Killdeer, and several calidridine sandpipers.

At Perry’s Beach, DCA depicted species across habitats from rocky shore to deep-water (Fig. 1); ISA identified four species assemblages (Table 2). Baird’s Sandpiper was grouped with Spotted Sandpiper, Solitary Sandpiper (T. solitaria), and small plovers that frequented rocky shore zones greater than 10 m from the wetland edge. Closer to the lakeshore, but still using rocky shore habitat, were Black-bellied Plover (P. squatarola), Lesser Golden-Plover, Wilson’s Phalarope, and several calidridine sandpipers. Lesser Yellowlegs and Willet also used the immediate lakeshore habitat, but were slightly more aquatic. American Avocet, godwits, dowitchers, Red Knot, tringines, and Stilt Sandpiper occupied aquatic habitats.

As a group, local breeders did not use different habitats than migrants, based on axis 1 scores (Mann-Whitney U-test: Lanigan Creek, $P = 0.58$;

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Fig. 1. Habitat use by shorebird assemblages at Lanigan Creek, Basin A, and Perry’s Beach, portrayed by species axis scores of detrended correspondence analysis. Species’ habitat use (right side of each figure) can be viewed as the mirror image of habitats (left side of figure). Habitats are a combination of habitat acronyms (Table 1) and distance estimates (see text). Species acronyms: LGP, Lesser Golden-Plover; SPV, Semipalmated Plover; PPV, Piping Plover; KLL, Killdeer; AAV, American Avocet; GYL, Greater Yellowlegs; LYL, Lesser Yellowlegs; WWTL, Willet; SSP, Spotted Sandpiper; USP, Upland Sandpiper; HGD, Hudsonian Godwit; MGD, Marbled Godwit; KNT, Red Knot; SAN, Sanderling; SEM, Semipalmated Sandpiper; LEA, Least Sandpiper; WRS, White-rumped Sandpiper; BSP, Baird’s Sandpiper; PEC, Pectoral Sandpiper; DUN, Dunlin; STL, Stilt Sandpiper; PEP, unidentified small calidridine sandpiper, either SEM, LEA, WRS, or BSP; PPL, unidentified calidridine sandpiper, either WRS or BSP; PPS, unidentified calidridine sandpiper, either SEM or LEA; DOW, dowitcher spp.; CSN, Common Snipe; WPH, Wilson’s Phalarope; RPH, Red-necked Phalarope.
### TABLE 2

**Classification of Shorebirds at Three Wetlands, Based on Indicator Species Analysis of % Observations in Various Habitats**

<table>
<thead>
<tr>
<th>Species</th>
<th>Lanigan Creek</th>
<th>Basin A</th>
<th>Perry's Beach</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lesser Golden-Plover</td>
<td>III</td>
<td>III</td>
<td>II</td>
</tr>
<tr>
<td>Black-bellied Plover</td>
<td>III</td>
<td>IV</td>
<td>II</td>
</tr>
<tr>
<td>Semipalmated Plover</td>
<td>IV</td>
<td>IV</td>
<td>IV</td>
</tr>
<tr>
<td>Killdeer</td>
<td>III</td>
<td>IV</td>
<td>IV</td>
</tr>
<tr>
<td>American Avocet</td>
<td>III</td>
<td>I</td>
<td>I</td>
</tr>
<tr>
<td>Greater Yellowlegs</td>
<td>II</td>
<td>III</td>
<td>I</td>
</tr>
<tr>
<td>Lesser Yellowlegs</td>
<td>II</td>
<td>IV</td>
<td>III</td>
</tr>
<tr>
<td>Willet</td>
<td>II</td>
<td>IV</td>
<td>III</td>
</tr>
<tr>
<td>Solitary Sandpiper</td>
<td>III</td>
<td>IV</td>
<td>IV</td>
</tr>
<tr>
<td>Spotted Sandpiper</td>
<td>III</td>
<td>IV</td>
<td>IV</td>
</tr>
<tr>
<td>Upland Sandpiper</td>
<td>III</td>
<td>IV</td>
<td>IV</td>
</tr>
<tr>
<td>Hudsonian Godwit</td>
<td>IV</td>
<td>III</td>
<td>I</td>
</tr>
<tr>
<td>Marbled Godwit</td>
<td>II</td>
<td>II</td>
<td>I</td>
</tr>
<tr>
<td>Red Knot</td>
<td>IV</td>
<td>IV</td>
<td>I</td>
</tr>
<tr>
<td>Sanderling</td>
<td>IV</td>
<td>IV</td>
<td>II</td>
</tr>
<tr>
<td>Semipalmated Sandpiper</td>
<td>IV</td>
<td>IV</td>
<td>II</td>
</tr>
<tr>
<td>Least Sandpiper</td>
<td>IV</td>
<td>IV</td>
<td>II</td>
</tr>
<tr>
<td>Baird's Sandpiper</td>
<td>IV</td>
<td>IV</td>
<td>IV</td>
</tr>
<tr>
<td>White-rumped Sandpiper</td>
<td>III</td>
<td>III</td>
<td>I</td>
</tr>
<tr>
<td>Pectoral Sandpiper</td>
<td>IV</td>
<td>IV</td>
<td>II</td>
</tr>
<tr>
<td>Stilt Sandpiper</td>
<td>IV</td>
<td>II</td>
<td>I</td>
</tr>
<tr>
<td>Dunlin</td>
<td>III</td>
<td>IV</td>
<td>I</td>
</tr>
<tr>
<td>Common Snipe</td>
<td>IV</td>
<td>II</td>
<td>I</td>
</tr>
<tr>
<td>Dowitcher spp.</td>
<td>IV</td>
<td>II</td>
<td>I</td>
</tr>
<tr>
<td>Wilson's Phalarope</td>
<td>I</td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>Red-necked Phalarope</td>
<td>I</td>
<td>I</td>
<td>I</td>
</tr>
</tbody>
</table>

Within each site, species sharing Roman numerals occupied similar habitats (see text and Fig. 1).

Basin A, $P = 0.19$; Perry's Beach, $P = 0.54$). However, axis 2 scores of breeders were significantly greater than migrants at Lanigan Creek ($P = 0.005$), but not at Basin A ($P = 0.75$) or Perry's Beach ($P = 0.47$), reflecting a greater use of terrestrial habitats.

Patterns of habitat use differed among taxonomic groups, based on axis 1 (Kruskal-Wallis test: Lanigan Creek, $df = 7$, $P = 0.12$; Basin A, $df = 6$, $P = 0.05$; Perry's Beach, $df = 4$, $P = 0.03$), but not axis 2 (Lanigan Creek, $P = 0.44$; Basin A, $P = 0.41$; Perry's Beach, $P = 0.98$).

*Seasonal patterns.*—Seasonal habitat use and the magnitude of shift in habitat use differed among species (Table 3). Overall, breeders used significantly different habitats than migrants during spring and summer at Lanigan Creek; there was no difference in habitat use between these two
Table 3
Seasonal Patterns of Habitat Use among Shorebirds, Expressed as Probability Level Associated with Nonparametric Analyses

<table>
<thead>
<tr>
<th>Study site and comparison</th>
<th>Group averages</th>
<th>Magnitude of seasonal habitat use shift</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring</td>
<td>Summer</td>
</tr>
<tr>
<td></td>
<td>Axis 1</td>
<td>Axis 2</td>
</tr>
<tr>
<td>Lanigan Creek</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breeders/migrants</td>
<td>0.19</td>
<td>0.03</td>
</tr>
<tr>
<td>Taxonomic group</td>
<td>0.07</td>
<td>0.06</td>
</tr>
<tr>
<td>Basin A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breeders/migrants</td>
<td>0.46</td>
<td>0.30</td>
</tr>
<tr>
<td>Taxonomic group</td>
<td>0.15</td>
<td>0.06</td>
</tr>
<tr>
<td>Perry's Beach</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breeders/migrants</td>
<td>0.44</td>
<td>0.12</td>
</tr>
<tr>
<td>Taxonomic group</td>
<td>0.41</td>
<td>0.26</td>
</tr>
</tbody>
</table>

Axis scores of breeders and migrants were compared using Mann-Whitney U-test, scores of taxa were analyzed with Kruskal-Wallis test, and seasonal shifts were analyzed using Wilcoxon matched-pairs signed-rank test.

Species were classified according to the presence of breeding individuals at Last Mountain Lake National Wildlife Area (Colwell 1987).

Analyses were conducted at the level of tribe or next highest level of classification if no tribe was available (AOU 1983).

DISCUSSION

Habitat use patterns. Migrating and breeding shorebirds differed in their use of habitats at Last Mountain Lake. Interspecific differences in habitat use reflect coadapted morphological and behavioral traits that may be influenced by proximate factors affecting habitat availability. Baker (1979) examined habitat use in assemblages of breeding and wintering shorebirds and noted relationships between a species' morphology and feeding microhabitat: culmen and tarsus length were positively correlated...
with vegetation height and water depth, respectively. While we did not quantify microhabitats used by shorebirds at Last Mountain Lake, qualitative relationships between morphology and habitat use were suggested by differences in habitat use among taxa. Aquatic habitats were frequented by taxa with long culmens and tarsi (e.g., godwits, dowitchers, and avocet), or species with specialized aquatic adaptations (e.g., lobe-toed phalaropes). Wetland edges and terrestrial habitats were used by smaller species such as plovers and calidridine sandpipers.

Interspecific variation in habitat use also reflects fundamental behavioral differences associated with feeding and reproduction, which may operate on a daily or seasonal basis. In marine environs, daily tidal rhythms affect shorebird habitat use by inundating preferred habitat (Burger et al. 1977, Connors et al. 1979b). Although shorebirds at inland sites may not be confronted by regular diurnal changes in habitat, habitat use may be altered over short periods by climatic conditions. Wind-related “tides,” drought, and cold temperatures may restrict habitat availability.

Habitat use also varies over longer intervals associated with periods of a species’ annual cycle. Of several factors influencing seasonal habitat use by Arctic shorebirds at Barrow, Alaska, Connors et al. (1979a) stressed the importance of whether use occurred during periods of breeding, post-breeding, or migration. During the Arctic breeding season, most shorebirds used tundra, with a subsequent shift to coastal littoral habitat during post-breeding and migratory periods (Connors et al. 1979a).

Differences in habitat use between breeders and migrants at Lanigan Creek stemmed from the greater use of terrestrial habitats by breeding individuals that were defending territories, courting, nest building, incubating, or brooding. In contrast, nearly exclusive use of wetland habitats by most migrants was related to a predominance of foraging activities. At Lanigan Creek, breeders showed a larger seasonal shift toward aquatic habitats than did migrants, which reflected a shift from reproductive behavior to foraging activities. A similar pattern did not hold for assemblages at Basin A and Perry’s Beach, and the magnitude of seasonal change in habitat use was not different between breeders and migrants. Although local breeders were present at these sites, few individuals nested there owing to unsuitable habitat.

Differences among species in migration chronology may account for differences in habitat use. Recher (1966) noted that the distribution of migratory shorebird species differed temporally and spatially, perhaps reflecting the effects of interspecific interactions. Regardless of underlying mechanisms, interspecific differences in habitat use may result from the timing of migratory movements in relation to habitat availability (Connors et al. 1979a). Peak migration periods for shorebirds at Last Mountain
Lake vary among species (Colwell et al., 1988a), especially during summer. As a result, species that exhibit disjunct migration peaks may experience differences in habitat availability at the times of their presence.

Our data represent a coarse view of habitat use by an assemblage of shorebirds during a year of extreme drought. Nevertheless, seasonal shifts in habitat use were discernible. However, we suspect that seasonal patterns may be evident on a much finer temporal scale owing to interspecific differences in migration chronology. Moreover, within species, habitat use may vary with age (a variable we did not record) and sex of individuals. On a larger geographic scale, van der Have et al. (1984) showed that differences in habitat use by adult and juvenile Dunlin in the Dutch Wadden Sea were related to density of individuals; they suggested that age-related dominance behavior may cause habitat segregation. Juveniles occurred in secondary habitat where densities were lower. Numbers of shorebirds at Lanigan Creek, Basin A, and Perry's Beach changed dramatically during the study (Colwell et al., 1988a). If intraspecific habitat segregation occurs at prairie wetlands, one might predict the pattern to be most prevalent during drought episodes, when high densities of birds are coupled with resource limitation. In nondrought years, greater habitat availability and lower bird densities likely result in less dramatic habitat shifts within and among species.

Although drought conditions may offer an atypical view of habitat use by shorebirds in the northern prairies, it is at times of resource limitation that natural selection may operate most strongly (Wiens 1977). Much attention has been paid to the seasonal changes in resource abundance that affect numbers of wintering and migrating shorebirds in marine environments (Evans and Dugan 1984), where habitats and their food resources are influenced strongly by daily tidal cycles. Few studies have examined the relationship between prey availability and shorebird numbers at inland sites. We suspect that there may be marked differences between marine and interior subpopulations of nearctic shorebird species with regard to fidelity to staging and breeding sites and tenure of stay at these areas; these differences are probably habitat- and resource-related. Specifically, unpredictable and seasonally diminishing resources at ephemeral prairie wetlands likely are correlated with low annual fidelity of species to migratory staging areas and breeding sites (Colwell et al., in press) and to short stays. By contrast, species using permanent wetlands or predictable habitats, such as lakeshore sites, probably exhibit greater site-faithfulness.

Management implications.—At Last Mountain Lake, shorebird habitat use occurred across a broad habitat gradient, spanning terrestrial and aquatic zones; some species were restricted in their use of habitats, whereas other species used a variety of habitats (Colwell 1987, Colwell et al.,
The importance of maintaining habitat diversity for shorebird populations is particularly striking in the northern prairie, where a large shorebird assemblage can be strongly affected by extreme climatic conditions (Colwell 1986). Topographically simple wetlands with uniform habitat, such as Basin A, may be inundated during wet years, resulting in a predominance of deep-water habitats of limited value for calidridine sandpipers and small plovers. Moreover, simple shallow wetlands may be left entirely dry during drought, affording little use by breeding (Colwell 1986) or migrating species. By contrast, complex wetlands, such as Lanigan Creek, that offer a mix of habitats and topography, ensure the availability of a variety of habitats under extreme conditions.

Areas managed for waterfowl could benefit other avian taxa by employing manipulations other than the common practice of inundating large areas. Additional habitats could be created by relatively minor habitat alterations prior to impoundment construction. For instance, construction of sparsely vegetated nesting islands with gently sloping beaches surrounded by deep-water zones would benefit colonial-breeding Avocets and migrant shorebirds, as well as providing waterfowl with loafing areas.

Like many waterfowl species (Peek 1986), breeding shorebirds appear most strongly influenced by the proximity of nesting areas to wetlands. Extensive upland and wet meadow habitat at Lanigan Creek supported nesting individuals of most (8 of 9) local breeders (Colwell 1986), whereas unsuitable nesting habitat at Basin A and Perry’s Beach restricted nesting opportunities of most breeders (Colwell, unpubl. data). By maintaining flooded meadows adjacent to deep-water basins, especially during brood-rearing periods, a benefit would accrue to both upland nesting shorebirds and waterfowl. In the absence of such a wetland complex, adults may be forced to move broods long distances to rearing areas (Colwell and Oring 1988).

The shorebird assemblage in the northern prairie constitutes a large proportion of nearctic-breeding shorebirds (Colwell 1987). With loss of wetland acreage to human development (Peek 1986), some populations of prairie-breeding shorebirds are threatened (Haig and Oring 1985). Populations of Arctic-breeding shorebirds that use prairie wetlands as migratory staging sites also may be at risk. Remaining habitats, essential to the maintenance of populations of many avian taxa, must be managed according to more than the needs of waterfowl alone.

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LITERATURE CITED


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NORTH AMERICAN LOON FUND GRANTS

The North American Loon Fund is now accepting grant proposals concerning loons for the 1989 field season. Last year over $20,000.00 in aid was distributed to individuals and management organizations to study the loon.

The deadline for submitting proposals is January 31, 1989, and guidelines are available from:

- North American Loon Fund
  Grants Committee
  RR #4 Box 240C
  Meredith, NH 03253
  (603) 279-6163
BREEDING BIOLOGY OF WILSON’S PHALAROPE IN SOUTHCENTRAL SASKATCHEWAN

MARK A. COLWELL AND LEWIS W. ORING

ABSTRACT.—The breeding biology of Wilson’s Phalarope (Phalaropus tricolor), a sex-role reversed shorebird, was studied from 1982-1987 at Last Mountain Lake National Wildlife Area in southcentral Saskatchewan, Canada. Female mating tactics involved direct competition for mates, rather than competition via territories. Unpaired, competing females ranged more widely than paired or laying females. By contrast, males were more restricted in their movements, particularly during incubation and brooding periods. Modal clutch size was four; and clutches weighed an average of 55% of the body weight of a nonlaying female. Females laid 0-4 clutches in a breeding season. Male reproductive patterns were characterized by nearly exclusive care of eggs and chicks. Weight of incubating males decreased during incubation. Nesting success varied significantly among years, primarily owing to the effects of predation. Approximately 25% of males that lost clutches during the nesting season renested. Among the three species of phalaropes, ecological factors favor higher incidences of polyandry in Wilson’s Phalarope, but estimates may be complicated by wide-ranging movements of females during the breeding season. Received 7 Jan. 1988, accepted 12 May 1988.

The sex-role reversed, nonterritorial mating system of phalaropes (Phalaropus spp.) is unusual among birds (Oring 1982, 1986). Females contest access to mates in “scramble competitions” (Reynolds 1987, Colwell and Oring 1988a), and males perform virtually all parental care. The low incidence of sequential polyandry in all three species (Hildén and Vuolanto 1972, Raner 1972, Schamel and Tracy 1977, Colwell 1986a, Reynolds 1987, Colwell and Oring 1988b) indicates that the ability of females to become polyandrous is limited (Reynolds 1987). Females do not appear to be constrained energetically or by the amount of time available to obtain mates, but rather by the availability of unmated males (Reynolds et al. 1986; Reynolds 1987; Colwell and Oring 1988a, b).

Recent studies have contributed greatly to our understanding of the breeding biology of Red-necked Phalarope (P. lobatus; e.g., Hildén and Vuolanto 1972, Reynolds et al. 1986, Reynolds 1987) and Red Phalarope (P. fulicaria; e.g., Schamel and Tracy 1977, Mayfield 1979, Schamel and Tracy 1987, Tracy and Schamel 1988). Although published accounts of the reproductive biology of Wilson’s Phalarope (P. tricolor) are numerous (e.g., Colwell 1986a, b; Colwell and Oring 1988a, b), few studies have spanned more than a breeding season and most have dealt with populations of unmarked individuals. Thus, in many instances, behavioral...
interpretation was limited by lack of knowledge of individual reproductive patterns. In this paper, we present data on Wilson's Phalarope breeding biology, emphasizing factors that may contribute to variability in phalarope mating systems in general. We deal only superficially with behavioral aspects of sex-role reversal, because Howe (1975a, b) treated this topic in depth.

METHODS

We studied Wilson's Phalarope from 1982-1987 at Last Mountain Lake National Wildlife Area in southcentral Saskatchewan, Canada (51°10'N, 110°2'W). During 1982 and 1983, phalaropes were observed at East Alkaline Lake, a 40-ha ephemeral wetland and surrounding prairie, separated at its southern third by a road. During the breeding season, cattle grazed around the wetland north of the road in 1982, but not in 1983; otherwise the site was undisturbed. Approximately 45 and 20 males nested at East Alkaline Lake during 1982 and 1983, respectively.

In 1984, phalaropes did not breed at East Alkaline Lake owing to extreme drought conditions (Colwell 1986b). As a result, the study shifted to Lanigan Creek, one of the few remaining areas with sufficient water to support breeding shorebirds; work continued there in 1985-1987. Lanigan Creek was a permanent wetland amid approximately 100 ha of pasture that was heavily grazed by 40 to 65 cattle from late May to autumn in all years. Phalarope numbers at Lanigan Creek were higher than at East Alkaline Lake, totalling approximately 55, 80, 100+, and 100+ nesting males during 1984-1987, respectively.

Colwell and Oring (1988a) described the study areas. Phalaropes were caught with mist nets, walk-in traps, decoy traps, and nest traps, and each bird was banded with a unique combination of three colored leg bands and one metal band. During 1984-1987, phalaropes were marked with a patagial tag (Curtis et al. 1983), and in 1986 and 1987, 28 females were fitted with a 3.5-g radio transmitter (Raim 1978) to investigate reproductive tactics during the breeding season (Colwell and Oring 1988b). Birds were weighed to the nearest g with a 100-g Pesola scale. The length of the flattened wing, tarsus, and culmen (from the tip of the bill to the proximal margin of the nares) were measured with calipers to the nearest 0.1 mm. During 1982-1984, the weight of eggs was measured to the nearest g with a 10-g Pesola scale. Analyses included only those clutches measured immediately after clutch completion, to eliminate error caused by desiccation of eggs over time.

Each year, the study began prior to the arrival of phalaropes (1983-1986) or initiation of nesting (1982 and 1987) and continued until most or all clutches had hatched. Ad lib observations (Altmann 1974) were conducted regularly during mornings (sunrise: ca 05:00) and evenings (sunset: ca 21:00) mostly from 3-m towers and a field vehicle. During 1986 and 1987, daily movements and behaviors of individuals were recorded on maps of the study site. Nests were located either by watching a pair of birds as they visited nest scrapes during courtship or laying, or by observing males returning to incubate clutches. Occasionally, a clutch was found when an incubating male was flushed from the nest. Most clutches, however, were found during the egg-laying stage (1982, 29% [14/49]; 1983, 72% [18/25]; 1984, 59% [35/59]; 1985, 75% [59/79]; 1986, 84% [52/62]; 1987, 81% [88/108]). Throughout the breeding season, nests were checked regularly, and the fate of clutches (hatched, lost to predators, deserted, crushed by cattle, human-induced loss, or unknown) was recorded. Statistical analyses follow procedures in Siegel (1956) and Sokal and Rohlf (1981).
Table 1

MORPHOLOGICAL COMPARISON (X ± SD) OF FEMALE AND MALE WILSON’S PHALAROPES

<table>
<thead>
<tr>
<th></th>
<th>Female</th>
<th>Male</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Culmen (mm)</td>
<td>32.8 (1.6)</td>
<td>29.6 (1.1)</td>
<td>8.81a</td>
</tr>
<tr>
<td>N = 45</td>
<td></td>
<td>N = 139</td>
<td></td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>38.5 (1.6)</td>
<td>36.5 (1.0)</td>
<td>7.35a</td>
</tr>
<tr>
<td>N = 47</td>
<td></td>
<td>N = 140</td>
<td></td>
</tr>
<tr>
<td>Wing (mm)</td>
<td>137.7 (3.2)</td>
<td>127.1 (2.9)</td>
<td>9.93a</td>
</tr>
<tr>
<td>N = 47</td>
<td></td>
<td>N = 127</td>
<td></td>
</tr>
<tr>
<td>Weight (g)</td>
<td>68.1 (7.1)</td>
<td>51.8 (4.1)</td>
<td>10.12a</td>
</tr>
<tr>
<td>N = 48</td>
<td></td>
<td>N = 155</td>
<td></td>
</tr>
<tr>
<td>79.0 (4.9)b</td>
<td></td>
<td>N = 31</td>
<td></td>
</tr>
</tbody>
</table>

*Mann-Whitney U-test, P < 0.05.
*b Laying females with formed eggs in oviduct.

RESULTS

Sexual dimorphism.—Female Wilson’s Phalaropes had brighter plumage and were significantly larger than males in all morphological features (Table 1). Males averaged 92% of the size of females based on tarsus, culmen, and wing measurements, and mass was 76% of that of nonlaying females. Females with at least one egg in their oviduct averaged approximately 11-g heavier than nonlaying females; the average weight of nonlaying females may be biased by the inclusion of “heavy” females of unknown status. One female lost 8 g (74 g - 66 g) in the two days between the laying of her second and fourth egg; she still had not laid the fourth egg when weighed the second time.

Breeding chronology.—Phalaropes arrived at Last Mountain Lake in late April or early May. Female-biased sex ratios early in the season indicate that most females preceded males to breeding areas (Reynolds et al. 1986; Colwell and Oring 1988a, b).

The nesting period (interval between dates of first and last initiated clutch) for the population ranged from 21 days (1983) to 45 days (1982 and 1987) (Fig. 1). There was considerable annual variability in the onset and cessation of nesting resulting in significant differences in the seasonal distribution of clutch initiations (Kolmogorov-Smirnov two sample test, P < 0.05), especially in comparison with 1983. The first clutch for the population was initiated between 8 May (1987) and 20 May (1983). In 1983, a spring snowstorm was responsible for delayed onset of nesting,
and drought conditions (Colwell 1986b) truncated late-season nesting. Although drought conditions abbreviated nesting during 1983, this was a local phenomenon. Breeding continued during mid-June at neighboring wetlands with favorable water conditions. On average, 73% of clutch initiations occurred between 22 May and 11 June. Annual duration of the period of hatching varied from 14 (1983) to 38 (1982) days (Fig. 2).

The sexes differed markedly in dates of departure from breeding areas (Fig. 3), which was correlated with differences in the sex roles of males


Fig. 2. Seasonal distribution of hatching dates for 1982–1987. Field seasons ended before all clutches had hatched in 1986 and 1987.

and females (see below). Females left nesting areas during mid- to late June. Few females remained when the last clutches were initiated, and females were seldom seen after 1 July. Large saline lakes in southern Saskatchewan supported large numbers of females in early July (W. Harris, pers. comm.). Males that failed to hatch chicks began to leave the study area in mid-June, otherwise care of chicks kept males in the area into July.
Mating system and space use.—Mate acquisition was mediated directly in scramble competition among females; neither sex was territorial. Both sexes of phalaropes frequently fed together in tight flocks with no apparent aggression related to food resources (primarily *Daphnia* spp., and dipteran larvae and adults). Aggression was observed regularly, but it was always related to competition for mates (Colwell and Oring 1988a). Typically, females assumed the active role in courtship and competition for mates (Colwell and Oring 1988a). On several occasions, however, intrasexual competition among males occurred briefly when local sex ratios were male-biased. Aerial chases of males by females marked the early stages of competition for mates. Throughout the breeding season, however, unpaired females pursued males about the wetland (Colwell and Oring, in press). Male breeding status was significantly associated with the tendency for females to pursue them ($G = 19.9$, df = 2, $P < 0.001$). On nearly all occasions (28/29) when males departed an area and females followed, males were either unpaired (N = 8) or on incubation recess (N = 20). Either sex was equally likely to follow the other among pairs (N = 37). During courtship, females remained close to prospective mates, and defended them by posturing toward contesting females or fighting (see Höhn 1969, Howe 1975a, Colwell and Oring 1988a).
Once paired, females led males on circling flights (Howe 1975b) about upland areas. Nest scraping behavior usually followed flights. Pairs that nested in close proximity to the wetland walked into the vegetation to scrape. In 1982 and 1983, nests around the wetland were hyperdispersed. At the time of clutch initiation for each nest, the average distance to the nearest active conspecific nest deviated significantly from the expected mean distance based on a random dispersion (nearest neighbor technique: 1982, $\bar{x} = 57$ m, $z = 3.07$, $P < 0.05$; 1983, $\bar{x} = 105$ m, $z = 4.02$, $P < 0.05$).

Most females (75%, $N = 36$) laid eggs between 05:00 and 11:00. Males accompanied mates on 34% (18/53) of occasions when females were observed laying. During 1986 and 1987, 30% (7/23) of females that were captured while they were laying were caught simultaneously with their mates. When their mate was laying an egg, an accompanying male remained alert within several m of the nest.

The interval between laying of successive eggs in a clutch averaged approximately 26 h (range: 24—27 h, $N = 5$). Occasionally, females skipped a day during laying, especially if they were disturbed early in the nesting season. Ninety-one percent of clutches ($N = 158$) that were followed from laying of first to last egg were completed in four days, and 9% required more than four days. Inclement weather occasionally interrupted normal laying patterns with the subsequent desertion of an incomplete clutch. Human disturbance sometimes had a similar effect on laying patterns. During 1986, a female that was captured as she laid her second egg skipped three days before laying two additional eggs. Her mate subsequently deserted this clutch and the pair renested.

During the six years of the study, we observed four instances of sequential polyandry (Colwell 1986a, Colwell and Oring 1988b). Females that had completed a clutch occasionally paired with second mates but left the study area shortly thereafter (Colwell 1986a, Colwell and Oring 1988b). Most females obtained at least one mate; a small proportion may not have bred.

Males and females differed in their use of space during various reproductive stages (Fig. 4). During prelaying and laying stages, both sexes (males: $N = 16$; females: $N = 28$) exhibited localized movements at foraging sites near nests. Unpaired, competing females ranged widely owing to intrasexual competition and mate-locating tactics. Groups of females frequently pursued individual males for more than 1 km during aerial chases related to mate acquisition. Competing females frequently traversed the wetland, vocalizing to other phalaropes, and engaging in chases of males (Colwell and Oring, in press).

Males on incubation recess were regularly observed foraging at the same
Fig. 4. Space use by male (A) and female (B) Wilson's Phalaropes during the reproductive cycle. Individuals were assigned to a distance class based on the largest observed movement during a reproductive stage. Distances were estimated on a logarithmic scale, where ■ = 0–10 m, □ = 10–100 m, △ = 100–1000 m, and □ = greater than 1 km.

site, suggesting advantages of site familiarity despite a nonterritorial mating system. Although most males foraged at wet meadow sites closest to their nests, some males repeatedly moved >1 km to forage at a given site. Brooding males sometimes moved chicks >1 km during the first days after hatch, but, in general, daily movements of brooding males were restricted to a small area of wet meadow. Males usually moved chicks away from nests to the nearest area of dense, wet vegetation. Brooding males foraged with their chicks and seldom left broods unattended. In 1983, wetland desiccation forced males that hatched chicks in mid-June to move them over 1 km of upland to the nearest wetland.
Table 2


<table>
<thead>
<tr>
<th>Year</th>
<th>Banded males</th>
<th>Total clutches</th>
<th>Total eggs</th>
<th>Average clutch size</th>
<th>% Males successful</th>
<th>% Clutches successful*</th>
<th>% Chicks hatched</th>
<th>% Eggs hatched</th>
<th>Total chicks</th>
</tr>
</thead>
<tbody>
<tr>
<td>1982</td>
<td>37</td>
<td>49</td>
<td>189</td>
<td>3.9 (0.2)</td>
<td>62.2</td>
<td>56.0</td>
<td>3.5 (0.9)</td>
<td>49.7</td>
<td>94</td>
</tr>
<tr>
<td>1983</td>
<td>21</td>
<td>25</td>
<td>95</td>
<td>3.8 (0.4)</td>
<td>28.6</td>
<td>28.0</td>
<td>3.1 (1.1)</td>
<td>23.2</td>
<td>22</td>
</tr>
<tr>
<td>1984</td>
<td>38</td>
<td>60</td>
<td>216</td>
<td>3.7 (0.6)</td>
<td>31.6</td>
<td>18.3</td>
<td>3.2 (1.0)</td>
<td>16.2</td>
<td>35</td>
</tr>
<tr>
<td>1985</td>
<td>78</td>
<td>82</td>
<td>310</td>
<td>3.9 (0.4)</td>
<td>50.0</td>
<td>43.2</td>
<td>3.4 (0.7)</td>
<td>43.9</td>
<td>136</td>
</tr>
<tr>
<td>1986</td>
<td>49</td>
<td>62</td>
<td>227</td>
<td>3.9 (0.4)</td>
<td>42.9</td>
<td>33.9</td>
<td>2.9 (1.0)</td>
<td>27.3</td>
<td>62</td>
</tr>
<tr>
<td>1987</td>
<td>75</td>
<td>108</td>
<td>382</td>
<td>3.5 (0.8)</td>
<td>21.3</td>
<td>16.7</td>
<td>2.9 (1.1)</td>
<td>12.0</td>
<td>46</td>
</tr>
</tbody>
</table>

*Clutch success was significantly different among years ($G = 40.1$, df = 5, $P < 0.001$). A clutch was successful if it hatched at least one chick. The proportion of males that were successful in hatching chicks is conservative in that it includes males of unknown reproductive fate. Average ($±$SD) chicks hatched deals only with successful clutches.

Clutch size, nesting success, and renesting.—Clutch size averaged 3.8 eggs (Table 2); modal clutch size was four. Although three-egg clutches were recorded on occasion, partial predation or disturbance during laying probably resulted in these seemingly smaller clutches. For instance, on two occasions in 1987 we witnessed partial clutch loss during laying, resulting in a smaller clutch size. We observed three five-egg clutches and one seven-egg clutch. The latter resulted when two females laid eggs in the same nest (Colwell 1986b). On one occasion, a four-egg clutch lost an egg eight days into incubation and gained an egg three days later; we did not know the identity of the female that laid the single egg during incubation. At hatch, clutch size averaged 3.7 eggs. Most successful clutches produced four chicks, but one male hatched five (Table 3).

Total clutch weight (four-egg clutches only) averaged 38 g, approximately 55% of the average weight of a nonlaying female. Total clutch weight was positively correlated with initiation date in 1984, but not in 1982 or 1983 (Kendall’s correlation: 1982, $t = -0.17$, $N = 9$, $P > 0.05$; 1983, $t = -0.06$, $N = 15$, $P > 0.05$; 1984, $t = 0.41$, $N = 15$, $P < 0.05$).

Nesting success varied among years (Table 2). Significantly more clutches hatched during 1982 and 1985; success was especially low in 1984 and 1987. In all years, however, the breeding success of individual males was slightly higher than nesting success owing to renesting (see below). Predators took 12–60% of clutches annually (Table 3). Predation (59%), desertion (21%), and cattle (10%) accounted for the greatest proportion of nest loss. During 1987, 10% of clutches lost one or more eggs during incubation, but the male continued to incubate. We observed three American Crows (Corvus brachyrhynchos) and one Ring-billed Gull (Larus
Table 3

FATE OF WILSON’S PHALAROPE CLutches EXPRESSED AS PERCENT OF TOTAL CLutches

<table>
<thead>
<tr>
<th>Year</th>
<th>Total clutches</th>
<th>Number of chicks at hatch</th>
<th>Unknown</th>
<th>Depredated</th>
<th>Cattle</th>
<th>Abandoned</th>
<th>Human</th>
<th>In fertile</th>
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<tr>
<td></td>
<td></td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1</td>
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<tr>
<td>1982</td>
<td>49</td>
<td>34.7</td>
<td>8.2</td>
<td>8.2</td>
<td>4.1</td>
<td>4.1</td>
<td>12.2</td>
<td>10.2</td>
</tr>
<tr>
<td>1983</td>
<td>25</td>
<td>16.0</td>
<td>0.0</td>
<td>12.0</td>
<td>0.0</td>
<td>0.0</td>
<td>60.0</td>
<td>0.0</td>
</tr>
<tr>
<td>1984</td>
<td>60</td>
<td>8.3</td>
<td>6.6</td>
<td>1.7</td>
<td>1.7</td>
<td>0.0</td>
<td>60.0</td>
<td>5.0</td>
</tr>
<tr>
<td>1985</td>
<td>82</td>
<td>25.0</td>
<td>19.5</td>
<td>3.7</td>
<td>0.0</td>
<td>4.9</td>
<td>20.7</td>
<td>17.1</td>
</tr>
<tr>
<td>1986</td>
<td>62</td>
<td>11.3</td>
<td>16.1</td>
<td>1.6</td>
<td>4.8</td>
<td>9.7</td>
<td>46.8</td>
<td>0.0</td>
</tr>
<tr>
<td>1987</td>
<td>108</td>
<td>5.5</td>
<td>4.6</td>
<td>1.9</td>
<td>2.8</td>
<td>6.5</td>
<td>50.0</td>
<td>2.8</td>
</tr>
<tr>
<td>Average</td>
<td>16.3</td>
<td>9.2</td>
<td>4.9</td>
<td>2.2</td>
<td>2.2</td>
<td>4.2</td>
<td>41.6</td>
<td>7.0</td>
</tr>
</tbody>
</table>

* Abandonment was often caused by partial clutch loss to predators.
* Cattle were not present on the study site this field season.
* Includes one clutch that hatched five chicks.

*delawarensis*) as they consumed phalarope eggs. During 1984, a striped skunk (*Mephitis mephitis*) denned under an observation tower and probably was responsible for the loss of some clutches (one direct observation) and one incubating male. Unknown predators killed four males as they incubated, about 1% of marked males (*N* = 275).

Daily risk of clutch loss (Table 4) varied within and among years. Overall, clutches experienced less risk of failure in 1985, and were especially vulnerable in 1984. Average weekly risk was greatest early in the season. Males often renested following clutch loss (Table 5). On average, 27% (range: 23–36%) of marked males that lost a clutch before the end of the nesting season (prior to 24 June) obtained a replacement clutch on the study site. The average interclutch interval (period between clutch failure and occurrence of the first egg of the renest) was six days (*N* = 21). Four males nested three times in a season. In 1985, a male obtained three clutches in 19 days; the identity of the laying female(s) was unknown. In 1986, a male nested three times in approximately 21 days, each time with a different female. In 1987, two males nested three times in 25 and 34 days, respectively, each changing mates once between attempts.

Renesting intervals did not differ for males renesting with the same mate and a new mate (Mann-Whitney *U*-test, *P* > 0.05). However, polyandrous females (*N* = 4) laid second clutches after significantly longer intervals than females laying replacement clutches for their initial mate (*N* = 5) (Mann-Whitney *U*-test, *P* < 0.05). In 1987, two females laid at least 11 eggs, one in three nests (clutch sizes: 4, 4, and 3) and the other in four attempts (clutch sizes: 3, 3, 3, and 3). Small clutch sizes (<4) resulted from clutch loss to predators or desertion during laying. The
### Table 4

**Seasonal Changes in the Daily Risk of Clutch Loss for Wilson’s Phalarope during 1983–1987**

<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>2</td>
<td>—</td>
<td>—</td>
<td>0(1)</td>
<td>0(1)</td>
<td>0(19)</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>0(5)</td>
<td>21(29)</td>
<td>0(38)</td>
<td>0(1)</td>
<td>0(1)</td>
<td>0(19)</td>
</tr>
<tr>
<td>4</td>
<td>8(53)</td>
<td>6(70)</td>
<td>1(102)</td>
<td>3(99)</td>
<td>0(19)</td>
<td>0(19)</td>
</tr>
<tr>
<td>5</td>
<td>9(88)</td>
<td>5(121)</td>
<td>4(208)</td>
<td>2(229)</td>
<td>0(19)</td>
<td>0(19)</td>
</tr>
<tr>
<td>6</td>
<td>3(66)</td>
<td>2(193)</td>
<td>2(302)</td>
<td>3(264)</td>
<td>0(19)</td>
<td>0(19)</td>
</tr>
<tr>
<td>7</td>
<td>3(60)</td>
<td>8(153)</td>
<td>3(341)</td>
<td>2(211)</td>
<td>0(19)</td>
<td>0(19)</td>
</tr>
<tr>
<td>8</td>
<td>0(39)</td>
<td>9(86)</td>
<td>2(312)</td>
<td>4(120)</td>
<td>0(19)</td>
<td>0(19)</td>
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<tr>
<td>9</td>
<td>6(17)</td>
<td>6(16)</td>
<td>1(206)</td>
<td>6(35)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>10</td>
<td>—</td>
<td>0(2)</td>
<td>9(59)</td>
<td>—</td>
<td>—</td>
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<td>4</td>
<td>10</td>
<td>3</td>
<td>5</td>
<td>6</td>
<td>4</td>
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</tbody>
</table>

**Average**

<table>
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<tr>
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<td>4</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

*Daily risk was calculated by dividing the total number of clutches lost each week by the number of nest-days that week (× 100). The two weekly entries represent calculations based on all nest failures and those lost to predators, respectively. Week 1 = 1–7 May, etc.*

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minimum interclutch interval (3 days) for these interrupted attempts indicates that subsequent clutches were probably not an extension of laying of the destroyed clutch.

**Parental care.**—In nearly all cases, males were solely responsible for care of eggs and chicks. Exceptions involved females that continued to associate with their incubating mates, circled the nest site when a human observer approached, or defended the nest site (when male was absent) from other females (Colwell and Oring 1988b). Banded females did not tend chicks, and most were absent at the time their clutches hatched. During 1986, one female was within 100 m of her hatching chicks, but she failed to aid her mate in mobbing when an observer approached the nest. Most females deserted males immediately following clutch completion, especially if surplus males were available (Colwell and Oring 1988b).
Table 5

ANNUAL COMPARISON OF RENESTING BY WILSON’S PHALAROPES

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Nesting period (days)</td>
<td>45</td>
<td>21</td>
<td>42</td>
<td>42</td>
<td>38</td>
<td>45</td>
</tr>
<tr>
<td>% Males renestinga (N failed)</td>
<td>25 (8)</td>
<td>23 (13)</td>
<td>24 (21)</td>
<td>30 (20)</td>
<td>36 (14)</td>
<td>24 (45)</td>
</tr>
<tr>
<td>Average male interclutch interval (N)</td>
<td>7 (2)</td>
<td>5 (1)</td>
<td>2 (1)</td>
<td>4 (4)</td>
<td>2 (4)</td>
<td>8 (9)</td>
</tr>
<tr>
<td>Average female interclutch interval (N)b</td>
<td>—</td>
<td>—</td>
<td>10 (1)</td>
<td>2 (2)</td>
<td>5 (9)</td>
<td>—</td>
</tr>
</tbody>
</table>

a Includes only clutch failures of marked males.
b Includes second clutches of polyandrous females (1985, N = 1; 1987, N = 3).

However, some females continued to defend their mates when the males were on incubation recess (Colwell 1986a, Colwell and Oring 1988b). Females were never observed incubating eggs or mobbing predators (other than humans) in defense of broods. In defense of clutches and broods, males mobbed potential predators such as mink (Mustela vison), Franklin’s ground squirrel (Spermophilus franklini), and Richardson’s ground squirrel (S. richardsoni).

Incubation (interval between laying of the fourth egg and hatch) averaged 23 days (range: 18–27 days) and was inversely correlated with date of clutch initiation (1982–1987 combined, \( r = -0.47, N = 39, P < 0.01 \)); clutches that were initiated at the end of the season required approximately five days less incubation than early clutches. During 1984, one male incubated a clutch of addled eggs for 34 days before he was collected as part of the endocrinology study.

Weight of males (N = 73) decreased significantly during the breeding season. Overall, 78% of males lost an average of 0.5 g per day, 14% maintained weight, and 8% gained an average of 0.3 g per day. One male lost 12 g in 25 days. Although there was no relationship between the weight of a male and date of capture (Kendall’s correlation: 1982–1987 combined, \( t = -0.174, N = 66, P > 0.05 \)), repeated captures of individuals revealed that weight declined steadily during the breeding season, especially in incubating birds. Male weight dropped significantly from early (first five days) to late (more than 17 days) incubation (paired t-test: \( t = 6.3, df = 27, P < 0.0001 \)), representing a loss of approximately 6% of male body weight. The few males for which we have weights during late incubation and early brooding continued to show a significant decline in weight (paired t-test: \( t = 8.9, df = 4, P < 0.003 \)). We noted nothing unusual about the reproductive histories of males that gained weight.
Discussion

Polyandry in phalaropes. — Phalaropes are unusual among birds in exhibiting extreme sex-role reversal (Oring 1982, 1986; Erckmann 1983). Variable mating tactics (Colwell and Oring 1988b) and correlations between seasonal changes in mate availability and intensity of intrasexual competition in Wilson’s Phalarope (Colwell and Oring 1988a) indicate that female phalaropes may experience strong sexual selection.

Despite evidence of intense intrasexual competition among females (Colwell and Oring 1988a) and the opportunity for sexual selection, the incidence of polyandry in all three species of phalaropes appears to be low (Hilden and Vuolanto 1972, Raner 1972, Schamel and Tracy 1977, Colwell 1986a, Reynolds 1987, Colwell and Oring 1988b). Differences in the incidence of polyandry and renesting among phalarope populations may be related to any number of proximate factors, including: (1) duration of breeding season, (2) breeding synchrony of males and females, and (3) levels of clutch failure (Emlen and Oring 1977).

Asynchronous arrival of males over a long breeding season favors polyandry by enhancing opportunities for acquiring multiple mates and producing multiple clutches (Emlen and Oring 1977, Erckmann 1983, Reynolds 1987). The opportunity for obtaining multiple mates is constrained by the interaction between the length of breeding season and period required to complete a nesting attempt. Because female Wilson’s Phalaropes require 7-10 days to complete a nesting attempt (Colwell and Oring 1988b), or approximately one sixth of the nesting period, considerable time remains for many early-nesting females to pursue additional mates.

Nesting periods vary considerably among the three phalarope species. The duration of nesting for Wilson’s Phalarope is nearly twice that reported for most populations of Red and Red-necked phalaropes (see Erckmann 1983), providing more time for second nesting attempts and replacement clutches. Multiple renesting, observed in Wilson’s Phalarope, has not been recorded for either Red or Red-necked phalaropes.

Frequent clutch failure may provide additional breeding opportunities for females by reintroducing males into the breeding population, but it also may result in renesting by a pair, depending on the timing of clutch loss with respect to pairbond and clutch completion (Oring et al. 1983, Colwell and Oring 1988b). Levels of clutch failure vary greatly among phalarope species, ranging from 0–100% losses (Table 2, see Erckmann 1983, Reynolds 1987).

The incidence of polyandry may also be constrained by factors influencing competitive abilities of females. Reynolds (1987) argued that the ability of female Red-necked Phalaropes to obtain multiple mates was not energetically constrained by egg production. Similarly, female Wil-
son's Phalaropes do not appear to be energetically limited by egg laying, but are capable of rapid, multiple clutch production.

Overall, the relationship between proximate and ultimate factors affecting levels of polyandry in phalarope species remains poorly understood. Estimates of incidence of polyandry may be complicated by a number of factors related to the species' unusual mating system. In particular, the lack of territoriality and wide-ranging movements of individuals, particularly females, affects arrival and departure dates and tenure at a given site. Many females that complete a clutch early in the breeding season depart the study area and presumably compete for second mates (Colwell 1986a). On several occasions, females have paired with second mates on the study site, and disappeared shortly thereafter (Colwell and Oring 1988b). Similarly, females that arrive late may have nested elsewhere. In short, estimates of the incidence of polyandry in phalaropes may be premature. Ideally, estimates require an isolated population with very restricted movement of individuals. To date, only the study by Hilden and Vuolanto (1972) of an insular population of Red-necked Phalaropes in Finland meets these standards, and even there arrival patterns of females may influence estimates of polyandry.

Male reproductive patterns.—In contrast to variable female mating patterns (Colwell and Oring 1988b), reproductive tactics of smaller, dull-plumaged male phalaropes are less diverse, characterized by exclusive care of eggs and chicks. Males, however, occasionally compete for mates when local sex ratios are male-biased (Colwell and Oring 1988a, Tracy and Schamel 1988), indicating plasticity to some behavioral aspects of sex-role reversal.

Uniparental care by male phalaropes may impose costs in terms of increased predation and energetic stress during incubation. Comparative details are not available for incubation-related predation in Red or Red-necked phalaropes. Weight loss by incubating males, however, is not typical of all phalarope species. Erckmann (1981) reported that, based on repeated captures of individuals, male Red and Red-necked phalaropes at Wales, Alaska, did not lose weight during incubation. Additional weight change estimates (Erckmann 1981, Schamel and Tracy 1987), based on regression of bird weight vs number of days into incubation, indicate that incubating males in some populations of Arctic breeding phalaropes do lose weight. Such conclusions, however, may be premature because a similar relationship may obtain owing to a correlation between bird weight and clutch initiation date.

Interspecific differences in weight loss may be related to variability in resources available to incubating males at Arctic and temperate latitudes.
A thorough understanding of the energetic costs of male incubation, however, requires a rigorous experimental approach.

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LITERATURE CITED


KIRTLAND'S WARBLER SYMPOSIUM

The Huron-Manistee National Forests are co-sponsoring a nationwide symposium on the endangered Kirtland's Warbler February 9-11, 1989, in Lansing, Michigan. The symposium, entitled, "Kirtland's Warbler at the crossroads—extinction or survival" is designed to provide information to wildlife biologists, researchers, special interest groups, and the public. For additional information telephone 1-800-999-7677 or 1-616-779-8715 and ask for Kenneth R. Ennis. Written inquiries can be made to Mr. Ennis, USDA—Forest Service, Huron-Manistee National Forests, 421 South Mitchell Street, Cadillac, MI 49601.
SONG REPERTOIRES AND THE SINGING BEHAVIOR OF MALE NORTHERN CARDINALS

GARY RITCHISON

Abstract.—The singing behavior of male Northern Cardinals (Cardinalis cardinalis) was examined to determine how singing is used in communication between individuals and, specifically, to determine if different song types convey different information. The mean number of songs per observation period, mean number of songs per bout, and mean number of notes per song were all highest during the pre-nesting and nest-building periods. The higher singing rates and longer songs observed during these periods may play a role in mate attraction/stimulation, and reduce trespassing by conspecific males. Both the mean number of songs per bout and the mean number of notes per song varied significantly among males, perhaps reflecting differences in male quality. During interactions with conspecific males, the mean number of songs per bout decreased while the mean number of notes per song increased. Males tended to utter songs with a greater number of different note types during interactions with conspecific males and females. Thus, variation in several song parameters apparently was used to convey information concerning motivation. Although some significant associations between song types and contexts were observed, all such associations were imperfect. Thus, some song types may be used in a graded form of communication, correlated with, but not restricted to, particular contexts. Most song types, however, appeared to be used randomly with respect to context. Received 16 Nov. 1987, accepted 15 May 1988.

Passerine song may advertise specific and individual identity (Becker 1982, Falls 1982) and may also provide information concerning motivation (Catchpole 1973) and male quality (Lambrechts and Dhondt 1986, 1987). As noted by Becker (1982), information may also be conveyed through changes in song length, amplitude, frequency, or complexity. Additional information may be conveyed through the use of different themes or song types. For example, diverse repertoires might reduce habituation, misrepresent territorial density, confuse territorial neighbors, attract or stimulate mates, or indicate the singer’s capabilities for defending their territories (Schroeder and Wiley 1983). It is also possible that certain themes or song types might convey more specific information. Baptista (1978), for example, noted that Cuban Grassquits (Tiaris canora) use one song type for aggressive interactions and another for intersexual interactions. Different song types have been reported to be associated with certain contexts in other species as well (Smith 1959, Smith et al. 1978, Gaddis 1983, Schroeder and Wiley 1983, Johnson 1987).

Several aspects of the singing behavior of Northern Cardinals (Cardinalis cardinalis) have been examined. The songs of Northern Cardinals

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have been found to vary geographically (Lemon 1966) and males respond differently to playback of songs from different areas (Lemon 1967). Male cardinals generally have song repertoires of 8 to 12 song types, many of which are shared with neighboring males (Lemon 1968). When singing, male cardinals utter a series or bout of one song type, followed by a series of another type. When neighboring males sing simultaneously, they often use the same song type (Lemon 1968). Such matching may permit a male to direct a “message” to a particular individual, and both song length and bout length may provide additional information concerning the motivation of a singing cardinal (Lemon 1968, Gottfried and Gottfried 1978). Conner et al. (1986) reported a possible relationship between song length and nesting success in Northern Cardinals, with more successful males using songs that were less complex and shorter. Although these studies have provided much information about the singing behavior of Northern Cardinals, questions still remain concerning the significance of song repertoires in this species. The objective of this study was to examine how singing is used in communication between male Northern Cardinals and, specifically, to determine if different song types convey different types of information.

MATERIALS AND METHODS

Observations of five male Northern Cardinals located on contiguous territories were made from 26 February through 6 September 1985 at the Central Kentucky Wildlife Management Area, located 17 km SSE of Richmond, Madison County, Kentucky. Each male was observed approximately once every 9 days, thus averaging about 20 times throughout the study. All males under observation were captured in mist nets and marked with colored leg bands and colored plastic tape attached to the rectrices (Ritchison 1984). Observation periods were two h in duration and began at or shortly after sunrise. I attempted to record on tape all bouts of song. Whether recorded or not, for each bout uttered by the focal male I noted the date and nesting stage. The nesting period was divided into six stages: pre-nesting, nest building, incubating, brooding (female spending most of her time at the nest and male feeding female and young), and late post-fledging (male feeding fledged young and female beginning another nesting attempt). I also recorded song types (Figs. 1, 2), the number of songs per bout and the number of notes per song. These data were generally obtained by reviewing field recordings. Although each song type consisted of unique note types, the number of such notes per song was variable. For example, song type I consisted of repetitions of the same note type. Although type I songs sometimes consisted of seven such notes (as in Fig. 2), the number of notes in type I songs (and other types of songs) was variable.

Bouts were defined as a series of songs of the same type. Although such bouts were often separated in time from each other by intervals that were significantly longer than the intervals between songs within a bout, males sometimes uttered bouts in rapid succession. In such cases, the length of time between successive bouts was similar to the length of time between songs in a bout. I further noted whether or not the focal male was within 25 m of the territory boundary, and any interaction with other males. There were four categories of interactions: spontaneous
advertising (no other males singing), distant exchange (countersinging with another male at a distance of more than 25 m), distant exchange and matching (countersinging and both males using the same song type), and close exchange (countersinging with another male at a distance of less than 25 m). I also noted the location of females and categorized them as: very close (within 5 m), close (within 25 m), or distant (not within 25 m). Finally, I noted whether or not the focal male was within 10 m of the nest or young.

Each of the five males under observation used the same nine song types. Although males exhibited some interindividual variation (Fig. 3), all song types were easily identified in each male’s repertoire. With practice, each song type could be recognized by ear in the field. A Kay Elemetric Sonagraph (Model 6061A) at wide-band settings was used to verify identification of song types made in the field. Recordings were made with a Uher 4000 Report...
Monitor tape recorder with a Dan Gibson parabolic reflector and microphone. All analyses were performed using procedures found in the Statistical Analysis Systems Guides (SAS Institute 1985). Differences in number of notes per song and number of songs per bout were analyzed for variance (GLM procedure) and post hoc comparisons were made using the Student-Newman-Keuls (SNK) test. Contingency tables were constructed by tallying each song type's occurrence in song bouts associated with specific behavioral contexts. Chi-square tests were used to test for non-random distributions. Sample sizes for individual males were sometimes too small to permit statistical testing and, therefore, data concerning song types and context for all males were pooled. In such cases, it was necessary to assume that all males in the population used song types similarly with respect to context.

RESULTS

Singing rates.—Five male Northern Cardinals were observed for a total of 206 h (103 days) from 26 February through 6 September and these males uttered an average of 140.8 ± 10.3 [SE] songs per two hour observation period. Although not significant, the mean number of songs per
observation period did vary by month \( (F = 2.15, P = 0.0545) \), with singing rates highest from February through April (Fig. 4). Singing rates did vary significantly by nesting stage \( (F = 2.54, P = 0.0332) \), with rates highest during the pre-nesting and nest-building periods. Although singing rates declined during the brooding and post-brooding/early post-fledging periods, singing increased again during the late post-fledging period as females initiated new nests (Fig. 5).

Number of notes per song, all song types combined.—The mean number of notes per song was 6.74 ± 0.14 (N = 14,629 songs). A significant
difference was observed in the mean number of notes per song by month 
\( (F = 16.11, P < 0.001) \), with more notes per song in February, March, 
April, and August \( (P < 0.05, \text{SNK test}) \; \text{Fig. 6} \). The mean number of
notes per song also varied significantly with nesting stage \( (F = 9.34, P < 0.001) \), with a greater number of notes per song during the pre-nesting 
and nest-building periods \( (P < 0.05, \text{SNK test}) \; \text{Fig. 7} \).

Although each song type exhibited some variation in number of notes 
per song, each type was usually composed of the same type(s) of notes 
(Figs. 1, 2). However, males sometimes uttered songs with extra notes at
the end, usually a low frequency trill. Bouts that included songs with these
extra notes were more common in February, March, and April \( (\chi^2 = 
28.26, \text{df} = 6, P < 0.001) \). Such songs were also uttered more often during
the pre-nesting and nest-building periods \( (\chi^2 = 23.74, \text{df} = 5, P < 0.001) \).

**Number of notes per song, individual song types.** The nine song types
differed significantly in mean number of notes per song \( (F = 38.49, P <
0.001) \), with song type C consisting of significantly more notes and song
types D, E, and F of significantly fewer notes \( (P < 0.05, \text{SNK test}) \). Song
types C \( (F = 4.38, P = 0.009) \), D \( (F = 6.71, P < 0.001) \) and I \( (F = 9.67, 
P < 0.001) \) differed significantly in mean number of notes by month, with
each consisting of significantly more notes per song in February \( (P < 
0.05, \text{SNK test}) \). Song type F also differed significantly by month \( (F = 
4.10, P = 0.012) \), with more notes per song in April than July \( (P < 0.05, 
\text{SNK test}) \). Four of the nine song types exhibited significant differences in
mean notes per song by nesting stage, F ($F = 2.42, P = 0.0419$), G ($F = 2.98, P = 0.0156$), H ($F = 2.40, P = 0.0456$), and I ($F = 3.07, P = 0.0142$). For each of these four song types, the mean number of notes per song increased during the late post-fledging period after declining to a low during the preceding period(s) (Fig. 8).

**Number of bouts and songs per bout.**—The mean number of bouts per observation period was $5.64 \pm 0.27$. No significant differences were observed in mean number of bouts per observation period on a weekly ($F = 0.73, P = 0.818$), biweekly ($F = 1.17, P = 0.315$), or monthly ($F = 1.94, P = 0.082$) basis. No significant differences were noted in mean number of bouts per observation period during the different stages of the nesting cycle ($F = 1.19, P = 0.319$). The mean number of songs per bout was $18.49 \pm 0.68$ ($N = 790$ bouts), with no significant differences among the nine song types ($F = 0.52, P = 0.844$). Significant differences were observed in the number of songs per bout by month ($F = 4.71, P < 0.001$), with bouts typically consisting of more songs in March and April ($P < 0.05$, SNK test; Fig. 6). The mean number of songs per bout also varied with nesting stage ($F = 3.66, P < 0.003$), with significantly fewer songs per bout during the brooding and post-brooding/early post-fledging periods ($P < 0.05$, SNK test; Fig. 7).

**Number of song types.**—The mean number of different song types used...
Fig. 6. Mean [±SE] number of notes per song and songs per bout by month.

by the males per observation period was 4.41 ± 0.18. No significant differences were observed in the mean number of song types used per observation period on a weekly ($F = 0.81, P = 0.719$), biweekly ($F = 1.22, P = 0.281$), or monthly ($F = 1.66, P = 0.139$) basis. Similarly, no significant relationship was noted between the mean number of song types used per observation period and nesting stage ($F = 1.50, P = 0.197$).

**Individual variation, songs and bouts.**—Individual males differed significantly both in mean number of songs ($F = 5.05, P < 0.001$) and mean number of bouts ($F = 3.45, P < 0.05$) per observation period. Males also differed significantly in the mean number of notes per song ($F = 26.62, P < 0.001$; Fig. 9) and the mean number of songs per bout ($F = 6.88, P < 0.001$), with one male uttering significantly fewer songs per bout than the other four males ($P < 0.05$, SNK test; Fig. 9). Males also differed in the extent to which they uttered songs with extra notes ($\chi^2 = 24.76, df = 4, P < 0.0001$), with the percentage of bouts including such songs ranging from 2.8 to 16.8%. Finally, males differed significantly in the mean number of song types used per observation period ($F = 5.34, P < 0.0006$), ranging from 3.5 to 5.6.

**Notes per song, variation with context.**—As the level of interaction with other males increased, the number of notes per song also increased ($F = 18.42, P < 0.0001$; Fig. 10). Although songs consisted of the greatest number of notes during close exchanges with other males ($P < 0.05$), males used songs with more notes when matching than during sponta-
neous advertising ($P < 0.05$, SNK tests). The number of notes per song also differed with location of the young ($F = 8.43, P < 0.005$) and location of the nest ($F = 12.84, P < 0.0005$). Males uttered songs with fewer notes when within 10 m of the young or the nest ($P < 0.05$ in both cases, SNK

![Graph showing mean number of notes per song and songs per bout by nest stage](image)

**Fig. 7.** Mean [$±SE$] number of notes per song and songs per bout by nest stage (see Fig. 4 for meaning of letters).

![Graph showing mean number of notes per song during different nest stages for song types F, G, H, and I](image)

**Fig. 8.** Mean number of notes per song during different nest stages for song types F, G, H, and I (see Fig. 5 for explanation of nest stage categories).
No significant relationship was noted between mean number of notes per song and either the location of the male in the territory ($F = 1.11, P = 0.290$) or the location of the female ($F = 2.45, P = 0.087$).

Songs with extra notes were almost always uttered during close exchanges with either males ($\chi^2 = 180.33, df = 3, P < 0.0001$) or females ($\chi^2 = 119.49, df = 2, P < 0.0001$). Such songs were uttered significantly less often when males were within 10 m of the nest ($\chi^2 = 3.94, df = 1, P < 0.05$). No significant relationship was observed between the use of songs with extra notes and either location in the territory ($\chi^2 = 0.04, df = 1, P = 0.838$) or location of the young ($\chi^2 = 0.01, df = 1, P = 0.991$).

**Notes per song, variation with context among song types.**—Most song types exhibited an increase in mean number of notes per song with increasing level of interaction with other males (Fig. 11). However, differences were significant only for song types C ($F = 5.86, P = 0.0013$), F ($F = 3.72, P = 0.0281$), G ($F = 6.72, P = 0.0004$), and I ($F = 5.37, P = 0.0021$). Only song types F ($F = 7.93, P = 0.0082$), and G ($F = 4.78, P = 0.0408$) differed significantly with location of the young, with both consisting of fewer notes per song when uttered within 10 m of the young. Although all song types consisted of fewer notes per song when uttered within 10 m of the nest, only song types E ($F = 6.89, P = 0.0127$) and G ($F = 7.24, P = 0.0096$) consisted of significantly fewer notes per song. No song type differed significantly in mean number of notes per song with either location in territory or location of mate.
The mean number of songs per bout varied with the level of interaction with conspecific males \((F = 7.16, P < 0.001)\), with males uttering fewer songs per bout during close exchanges \((P < 0.05, \text{SNK test}; \text{Fig. 10})\). No significant relationships were observed between the number of songs per bout and location in the territory \((F = 0.01, P = 0.981)\), location of females \((F = 1.83, P = 0.161)\), location of the young \((F = 0.88, P = 0.351)\), or location of the nest \((F = 1.30, P = 0.254)\).

**Songs per bout, variation with context.** — The mean number of songs per bout varied with the level of interaction with conspecific males \((F = 7.16, P < 0.001)\), with males uttering fewer songs per bout during close exchanges \((P < 0.05, \text{SNK test}; \text{Fig. 10})\). No significant relationships were observed between the number of songs per bout and location in the territory \((F = 0.01, P = 0.981)\), location of females \((F = 1.83, P = 0.161)\), location of the young \((F = 0.88, P = 0.351)\), or location of the nest \((F = 1.30, P = 0.254)\).

**Song types.** — Individual males differed significantly in use of the nine song types \((\chi^2 = 54.97, \text{df} = 32, P = 0.007)\). One male uttered more bouts of song type B than expected \((37 \text{ vs } 23.7)\) and fewer bouts of song type H \((5 \text{ vs } 16.2)\). A second male uttered more bouts of song type G than expected \((33 \text{ vs } 21.4)\), while a third uttered more bouts of song type H than expected \((31 \text{ vs } 20.6)\). For all males combined, significant nonrandom use by month was observed \((\chi^2 = 70.93, \text{df} = 48, P = 0.017)\) for only two song types. Song type A was used less than expected in May while song type G was used less than expected in April and July and more than expected in May and June. No significant relationship was noted between song type and nesting stage \((\chi^2 = 38.94, \text{df} = 40, P = 0.518)\).

**Song types and behavioral context, all males combined.** — Although the nine song types were used in a nonrandom manner during interactions
with other males ($\chi^2 = 36.56$, df = 24, $P = 0.048$), further analysis revealed significant nonrandom associations for only three song types. Bouts of song type B were used more than expected (58 vs 48.6) while bouts of song types C and I were uttered less than expected during spontaneous advertising (26 vs 32.4 and 26 vs 35, respectively). Further, nine of 16 bouts of song uttered during close exchanges with other males consisted of either song type C or I (4 and 5 bouts, respectively). Nonrandom use of song types was also noted during interactions with females ($\chi^2 = 32.09$, df = 16, $P = 0.01$), with males using song type H more than expected (14 vs 5.6) when females were within 5 m.

**Song types and behavioral context, individual males.**—Sample sizes for individual males were large enough to permit statistical testing for nonrandom use of song types with respect to location in the territory, location of fledged young, and location relative to the nest, respectively. In each of these contexts the use of different song types was found to be random.

Although sample sizes for individuals were too small to test for significance, all males exhibited a similar pattern during interactions with other males. That is, all five males used song type B more than expected and song types C and I less than expected during spontaneous advertising. Further, four males uttered bouts of song during close interactions with other males and all used either song type C or I during such encounters. Two of these males were each involved in two such encounters and song type I was used in each case. The other two males also used either song
type C or I during close interactions with other males, although not exclusively (3 of 7 bouts for one male and 2 of 5 for the other).

Sample sizes for individual males were also too small to test for possible associations between song types and interactions with females. As noted above, song type H was significantly associated with very close interactions with females for all males combined. However, one male accounted for seven of the 14 bouts of this song type uttered during such interactions. Two additional males used several song types during such interactions, including song type H (4 of 9 and 3 of 11 bouts, respectively). The two remaining males uttered a total of 26 bouts during such interactions (10 and 16, respectively) and never used song type H.

Order of and intervals between bouts.—Male cardinals sometimes uttered a series of bouts in rapid succession and the nine song types differed significantly in the order in which they were used in such series ($F = 4.07$, $P = 0.001$). Males often used either song type F (mean order = 1.16 ± 0.06) or A (mean order = 1.27 ± 0.10) initially while song types D (mean order = 2.18 ± 0.26) and C (mean order = 2.22 ± 0.33) were typically used later in such series.

Position changes.—The five male Northern Cardinals changed perches while singing on 387 occasions. In most cases (300 or 77.5%) males switched to a different song type after changing positions. This tendency to switch song types after a position change was noted throughout the study, with no differences noted on a monthly basis ($\chi^2 = 8.35$, df = 6, $P > 0.1$).

DISCUSSION

Singing behavior, variation over time.—Singing rates of males have been found to vary during the breeding season in many passerine species (Catchpole 1982), and male Northern Cardinals are no exception. Although male cardinals sang throughout the present study, singing rates declined somewhat after April. Kinser (1973) observed that singing by male cardinals was uncommon in July and August in southern Indiana. Much of the variation in singing rates noted in the present study appeared to be related to nesting stage, with rates highest during the pre-nesting, nesting, and incubation periods, much lower during the brooding and post-brooding/early post-fledging periods, and higher during the last post-fledging period.

Cardinals are multibrooded, with one pair sometimes raising three or four broods per year (Laskey 1944, pers. obs.). In addition, cardinals frequently lose nests to predators (pers. obs.). Thus, female cardinals initiate several nesting attempts during a breeding season. The singing
rates of male cardinals in the present study typically increased after a nest was lost to predators or when a female was beginning another nesting attempt after young from the previous nest had fledged. Kinser (1973:76) also reported that singing rates of male cardinals increased “following the departure of a brood or the loss of a nest.” Such song cyclicity has been reported in other species, particularly multibrooded species (Slagsvold 1977, Logan 1983). Logan (1983) suggested that a mechanism for resetting the complicated endocrine interactions essential for a normal nesting cycle would be adaptive in multibrooded species subject to considerable predation or nest loss. Thus, the increased singing rates of male cardinals during the period when a female is beginning another nesting attempt may be a means by which the female’s reproductive system is reset. It is also possible that higher rates of singing are directed toward conspecific males. When females initiate another nest, other males may seek extra-pair copulations (Birkhead et al. 1987). If so, increased levels of territorial defense (increased rates of singing) by the female’s mate may reduce trespassing by conspecific males and help to insure paternity.

Other changes in the singing behavior of male cardinals were also observed. During the pre-nesting period, bouts consisted of significantly more songs, songs typically consisted of a greater number of notes (significantly greater for 4 of 9 song types), and songs with extra notes were more common. Conner et al. (1986) suggested that young male cardinals may use longer, highly complex songs when first establishing a territory. Perhaps all male cardinals use a similar strategy on an annual basis, using longer bouts and longer, more complex songs during the period of territory establishment (pre-nesting period). Once boundaries are established they may put “less effort” into song, resulting in shorter, less complex songs. It is also possible, however, that changes in singing behavior are related to other factors. For example, males may continue to use longer bouts and songs even after territories have been established if, as noted above, trespassing neighbors or other males might attempt to copulate with their mate. The chance of such extra-pair copulations may lead males to maintain high levels of territory defense, including continued “complex” singing. The longer bouts and longer, more complex songs may also play a role in mate attraction (or “stimulation” as just described). Once paired (or once nesting has begun), males may again put less effort into song. The breeding chronology of cardinals suggests that either (or both) the mate guarding or mate attraction/stimulation hypothesis may be correct. Territory boundaries are well established by mid-March or even earlier (Ritchison 1986), yet males in the present study continued to utter more songs per bout, more notes per song, and more songs with extra notes through April. The increased number of songs per bout and number of
notes per song noted during the late post-fledging period when females were initiating new nests further suggests that the “complex” singing of male cardinals may be more important for either (or both) mate attraction/stimulation or mate guarding than in the establishment of territories.

_Singing behavior, motivational information._ Changes in singing behavior have been found to convey motivational information in a variety of passerine species (Becker 1982) and this also appeared to be true for male Northern Cardinals in the present study. As the intensity of interaction with other males increased, so did the mean number of notes per song, with a mean of six notes per song during spontaneous advertising and nearly 12 notes per song during close interactions with other males. Similar increases in song length during conflict situations in cardinals have been reported previously. Gottfried and Gottfried (1978) performed playback experiments with male Northern Cardinals and found that the number of notes per song decreased significantly during playback but increased significantly during the post-playback period, with a mean of over 16 notes per song. Similar increases in song length either during conflict situations or after exposure to playback have been reported in the Indigo Bunting (_Passerina cyanea_, Emlen 1972), Black-headed Grosbeak (_Pheucticus melanocephalus_, Ritchison 1983), and Willow Warbler (_Phylloscopus trochilus_, Helb 1973).

As noted above, male cardinals sometimes uttered songs with extra notes at the end. Males often uttered these songs during situations suggesting a high level of excitement, either when other males were within 25 m or females were within 5 m. The extra notes were often harsh, wide-band in structure, and low in frequency and usually included a trill or “growl.” It has been suggested that harsh sounds are generally aggressive in nature (Morton 1977, 1982). However, these notes were used in the presence of both males and females, suggesting that they were not purely aggressive in nature. Other authors have reported the use of more complex songs, often in aggressive contexts. For example, Bremond (1968) reported that European Robins (_Erithacus rubecula_) utter songs of greater complexity when they are likely to attack. Lein (1978) observed that Chestnut-sided Warblers (_Dendroica pensylvanica_) use a highly variable song (“jumbled song”) only during territorial encounters. Groschupf (1985), on the other hand, reported that male Five-striped Sparrows (_Amphispiza quinquestriata_) used more complex songs in intrasexual contexts. The complex songs of cardinals may simply communicate increased excitement or likelihood of interacting, regardless of sex.

Male Northern Cardinals also appeared to use changes in bout length to provide motivational information. When counter-singing and, especially, when matching neighboring males the mean number of songs per
bout generally increased. Lemon (1968) suggested that matching may permit male cardinals to direct a “message” to a particular individual. An increased number of songs per bout during such interactions may help insure reception of the message by that individual. On the other hand, during close exchanges with males the mean number of songs per bout decreased significantly, with males switching song types more rapidly as the probability of confrontation increased. Lemon (1968) noted similar behavior by male Northern Cardinals. Increased rates of switching during intense territorial encounters have been reported in many other species, including the Plain Titmouse (Parus inornatus, Dixon 1969), Chestnut-sided Warbler (Lein 1978), Red-winged Blackbird (Agelaius phoeniceus, Smith and Reid 1979), Song Sparrow (Melospiza melodia, Kramer and Lemon 1983), and Carolina Wren (Thryothorus ludovicianus, Simpson 1985).

Singing behavior, individual variation.—All five male Northern Cardinals used the same nine song types. Extensive sharing of song types by male cardinals has been reported previously (Lemon 1965, 1966). Such sharing means there is little or no variation among male cardinals in the size of their song-type repertoires, providing females with little information about the relative quality of males. However, other characteristics of song could be correlated with male quality. As noted previously, Conner et al. (1986) found that male cardinals exhibited differences in song complexity, and males with less complex songs appeared to hold better quality territories. Female cardinals might perceive these differences in song and use this information to choose a male with a better quality territory. In the present study, the five male cardinals exhibited significant differences in both mean number of songs per bout and mean number of notes per song. As noted previously, variation in these measures appears to provide information concerning motivation, with shorter bouts and longer songs apparently indicating increased excitement or likelihood of interacting. Variation in these measures could also provide information about male quality. A similar correlation has been reported in the Great Tit (Parus major). Lambrechts and Dhoodt (1986) reported a significant correlation between winter dominance position (a measure of male quality) of male Great Tits and mean song length (number of phrases per song). In the present study, the mean number of notes per song was significantly lower than the population mean for one male cardinal (4.5 vs 6.7). Interestingly, this male was also the last of the five males in the present study to pair with a female. Although these results and those of Conner et al. (1986) are suggestive, studies with additional males are needed to determine if there is a correlation between various measures of song quality and male mating success.
Song types and context. — Few significant associations between song type and context were observed in the present study, and all such associations were imperfect. In other words, all song types were used in several contexts and each context involved the use of most or all song types. Song type B was found to be significantly associated with spontaneous advertising. Further, the mean order of use of this song type in a series of bouts was relatively low, indicating early use in such series. In addition, although not significant, the mean period of silence before bouts of song type B was the longest of any song type. Such spontaneity is a characteristic feature of vocalizations that serve in territorial advertisement (Marler 1968). Although song types C and I were found to be associated with close exchanges between males, only sixteen such exchanges were observed. Further, two of the four males that sang during such exchanges used other song types in addition to song types C and I. For all males combined, song type H was significantly associated with very close interactions with females. However, one male accounted for seven of the 14 bouts of this song type used in such interactions and, further, two of the five males in the present study were not observed to use this song type during very close interactions with females. The use of song types by male cardinals was random with respect to nesting stage, location in the territory, location of fledged young, and location relative to the nest.

Investigators have reported clear contextual associations for different song types in Chestnut-sided Warblers (Lein 1978) and Bridled Titmice (Parus wollweberi, Gaddis 1983). However, the association between song types and contexts has proven to be imperfect in most species (Smith et al. 1978, Gaddis 1983, Kramer and Lemon 1983, Derrickson 1987, Johnson 1987). Kramer and Lemon (1983) proposed three possible explanations for such findings: (1) The contexts chosen by an investigator may only approximate the circumstances relevant to the birds in their differential production of song types. (2) Each song type may contain a probability of less than one of encoding a particular message, implying that song types are used in a graded form of communication. (3) The associations may simply be a by-product of other patterns of singing.

Kramer and Lemon (1983) suggested that the observed association between song type and context in Song Sparrows may have been a by-product of the correlation between bout length and context. Lending further support to their conclusion that the observed associations probably had little or no meaning to the birds was the finding that neighboring Song Sparrows shared few song types. Clear associations between certain song types and certain messages would be more likely in species where neighboring individuals share most or all song types (Smith et al. 1978). I found no significant differences among cardinal song types in number
of songs per bout in different contexts. In other words, the mean number of songs per bout changed with certain contexts but such changes were observed for all song types. Thus, the associations between song types and context in cardinals do not appear to be the by-product of cardinal singing patterns. Further, neighboring cardinals share most or all song types (Lemon 1968, this study). Thus, if the contexts I have chosen are in fact relevant to the birds, then perhaps certain cardinal song types (e.g., B, C, and I) are used in a graded form of communication. In other words, these song types may be correlated with, although certainly not restricted to, certain contexts or behaviors. However, most song types in the present study were not significantly associated with particular contexts. This may be the result of inadequate sampling (and thus having to pool data for all males), an imperfect choice of contexts, or, perhaps, some song types simply exhibit no associations. Song types not associated with specific contexts or behaviors could serve other functions, e.g., facilitating vocal interactions with neighbors (Kroodsma 1979), avoiding monotony (Hartshorne 1956, Kroodsma 1978), permitting males to accurately judge the distance of conspecifics that use the same song types (Morton 1982, 1986), or preventing exhaustion that might result from repeating the same song type (Lambrechts and Dhondt 1988). In addition, Johnson (1987) suggested that all or part of an individual's song repertoire may serve no function, being created or maintained simply as a by-product of the song learning process.

**Song repertoires and the Beau Geste hypothesis.** — The Beau Geste hypothesis (Krebs 1977) provides a mechanism by which repertoires of song types can function in territorial defense, with the use of multiple song types creating the impression of a densely populated area. Such deception would be enhanced if singers would change positions between bouts of different song types. Further, deception should be most pronounced during the period of territory establishment (Schroeder and Wiley 1983). In support of this hypothesis, male Northern Cardinals did exhibit a significant tendency to change perches in conjunction with changes in song type. Simultaneous song and perch changes have been noted in a variety of other species, including Dark-eyed Juncos (*Junco hyemalis*, Williams and MacRoberts 1977), Great Tits (Krebs et al. 1978), Red-winged Blackbirds (Smith and Reid 1979, Yasukawa 1981), and Song Sparrows (Krämer and Lemon 1983). The tendency of male cardinals to switch perches in conjunction with changes in song type was noted throughout the study, with no increase in such behavior during the period of territory establishment. Further, males did not use a greater number of different song types per observation period during the period of territory establishment than during the rest of the breeding season. Thus, the Beau Geste effect
does not appear to provide a complete explanation for the use of song repertoires in the Northern Cardinal. A similar conclusion has been drawn for the Carolina Wren (Morton 1982), Tufted Titmouse (Parus bicolor, Schroeder and Wiley 1983), Song Sparrow (Kramer and Lemon 1983), and Red-winged Blackbird (Yasukawa and Searcy 1985).

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VOCALIZATIONS, FOOD HABITS, AND NESTING BIOLOGY OF THE SLENDER-BILLED KITE WITH COMPARISONS TO THE SNAIL KITE

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Abstract.—We studied the vocalizations, food habits, and nesting biology of the Slender-billed Kite (Rostrhamus hamatus) in the llanos of Venezuela and made comparisons with its sympatric congener, the Snail Kite (R. sociabilis). Two types of structurally simple vocalizations were identified, and both occasionally were given as duets. Slender-billed Kites fed mostly on Pomacea dolioides snails (91.9%), captured by still-hunting, but they also ate aquatic crabs (Dilocarcinus dentatus). Although Slender-billed Kite diet composition was similar to that of the Snail Kite, Snail Kites fed on significantly larger snails. Slender-billed Kites extracted snails in the same manner as Snail Kites. Slender-billed Kite aerial displays, courtship feeding, and copulation sequences are described and resemble those of Snail Kites (R. sociabilis). Ten Slender-billed Kite nests were found and they usually were built in the crotches of slanting limbs in large trees in the flooded gallery forest. Nest height averaged 14 m above ground, and some sites were reused in subsequent years. Minimum distances between known active pairs ranged from 1.0–1.2 km. Both sexes incubated, brooded, and fed the young. Slender-billed Kites delivered food to nestlings at a significantly higher rate than did Snail Kites. No mate desertion was observed at a Slender-billed Kite nest of two young monitored for this behavior, although desertion occurred at one-third of the Snail Kite nests fledging two young. Slender-billed Kite nestlings stood by two weeks of age, swallowed whole snails by 17 days, fledged by 35 days, and were capable of sustained flight by 40 days. Nesting occurred in the wet season (July–October) and the duration of a nesting cycle was estimated to be 98–112 days. Only 37.5% of the nests found before hatching were successful, fledging 1 or 2 young. Differences between Slender-billed and Snail kite behavioral ecology are related to differences in habitat utilization and the potential effects of hydroperiod on snail size and abundance. Received 3 Dec. 1987, accepted 30 Mar. 1988.

The Slender-billed Kite (Rostrhamus hamatus) is a South American hawk with plumage coloration and bill morphology superficially resembling its congener, the Snail Kite (R. sociabilis). However, Slender-billed Kites are broader winged and about 15% heavier, and the sexes lack plumage dimorphism (Bangs and Penard 1918, Haverschmidt 1959, Brown and Amadon 1968). Another striking difference between these two raptors is that Slender-billed Kites frequent flooded forests or wooded plantations (Haverschmidt 1959, Thomas 1979a), while Snail Kites are usually found...

Little else is known about the ecology and behavior of the Slender-billed Kite. Few nests and only one set of eggs have ever been described (Haverschmidt 1959, Mader 1981). Like the Snail Kite (Haverschmidt 1962, Snyder and Snyder 1969, Beissinger 1988), Slender-billed Kites are thought to feed almost entirely on freshwater snails (Haverschmidt 1959, Voous 1969), but little information on their food habits and no description of their methods of snail capture or extraction exist. Although it is patchily distributed and sometimes locally abundant (Haverschmidt 1959, Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986), the Slender-billed Kite is uncommon throughout much of its range. Phelps and Phelps (1957) suggested that this kite had only recently extended its range northward into Venezuela.

This paper presents new information on the vocalizations, food habits, and nesting biology of the Slender-billed Kite in the llanos of Venezuela. We also compare the behavior and ecology of this species to a concurrently studied Snail Kite population (Beissinger unpubl. data).

STUDY AREA AND METHODS

We studied Slender-billed Kites on the ranch "Fundo Pequario Masaguaral" 45 km south of Calabozo in Guarico, Venezuela (8°34'N, 67°35'W). The ranch is composed of nearly 7000 ha of natural savanna and gallery forest (Troth 1979) that are lightly grazed by cattle. The nearly flat terrain is 60 to 75 m above sea level. Many parts of the gallery forest and savannah are flooded during the wet season (May–November) but dry out completely during the dry season (December–April). A few areas remain wet throughout the dry season, including two small lagoons that are flooded by pumping. The vegetation is intermediate between the well-drained high llanos, about 60 km to the north, and the lower, more flooded low llanos, about 60 km to the south (Troth 1979, Sarmiento 1984).

We conducted field work as part of other projects (Thomas 1979b, 1986; Strahl 1985, m press; Beissinger unpubl. data) in all months from 1975–1985 (Thomas); from July–August 1981, May–October 1982, and May–December 1983 (Strahl); and from July through November 1985 and 1986 (Beissinger). Observations of Slender-billed Kites were made with binoculars and spotting scopes from 13–15 m tall towers placed at canopy level in the gallery forest or from the ground. Because of the difficult placement of the nests, they were inaccessible by climbing and were too high to reach with our extension ladder. However, nest contents could often be inferred by adult behaviors or, after hatching, by direct observations. Mader (1981) reported on two of the ten nests that we describe here but we give additional details.

Data were gathered incidentally from 1975–1985. But from August–October 1986 one nesting pair was observed approximately one or two mornings a week for periods of 2–5 h (usually 3 h) from mid-incubation through fledging (for a total of 25 h) from a blind constructed 50 m from the nest site. The behavior of the adults and nestlings, and the types of food fed to the young were noted. Usually the adults at this nest could be differentiated by the size of the orange cere extending upwards from the bill toward the eye, which was much more extensive in one bird than in the other. However, their sexes were not determined.
Empty snail shells were collected from beneath the nest or nearby feeding perches, and standard shell length was measured with calipers. A Marantz tape recorder and Gibson sound parabola were used to record vocalizations which were analysed on a Kay Elemetrics Corporation Sona-Graph 7800 in the National Zoological Park’s sound laboratory.

RESULTS

Vocalizations.—Two distinctive adult vocalizations were recognized. Type I (Fig. 1A) is richly harmonic and tonal in quality. It increases rapidly in frequency followed by a slow decrease, and then a sudden downward shift in frequency leading to a slow decline and another sudden downward shift near the end. We paraphrase this call as “KE-EE-AAY-AAY-AAY.” This is probably Haverschmidt’s (1959) “mewing” call. It was the most frequently used call and was given by birds flying or soaring, approaching the nest, or responding to potential predators or intruders. Type II (Fig. 1B) was often given by one member of the pair as it approached its mate near the nest. It is a frequency-modulated whistle, with abrupt ups and downs followed by a slow up and down frequency modulation at the beginning of the last half of the call. We paraphrase this as “KER-AH.” It is usually given three or four times in succession, sometimes repeating the “AH-AH” phrase several times.

Both calls were sometimes given as duets (sensu Farabaugh 1982). One member of the mated pair called in a syncopated manner usually just after but rarely during the other’s vocalization. Sometimes the mate joining in the duetted type II call would syncopate the “AH-AH-AH” syllables with the same part of its mate’s call. This was particularly striking because (in at least two pairs) one member of the pair had a much lower pitched voice than the other.

Nestlings rarely vocalized, even when their parents returned with food. Once a nestling directed a soft “peeping” call toward a nearby adult after its sibling had been fed. The only true call uttered by a young Slender-billed Kite was given by a fledgling about seven weeks of age in answer to a type I call given by its nearby parent. The call sounded like the type I adult call but was much higher and more whistle-like in quality.

Food and feeding behavior.—We saw adult Slender-billed Kites eat or feed to their chicks 77 food items and all but three prey items (4%) were identified. Aquatic Pomacea dolioide snails comprised 91.9% of the food items identified (68) while freshwater crabs (Dilocarcinus dentatus) composed the remainder (6). All unidentified food items appeared to be either snails or crabs. In September and October 1986, parents fed nestlings (N = 57) a diet of 89.5% snails and 10.5% crabs. Watches at Snail Kite nests during the same period also revealed that crabs composed 10% of the diet and snails the remainder (Beissinger unpubl. data). However, Slender-
billed Kites ate significantly ($t = 7.2, \text{df} = 210, P < 0.001$) smaller snails ($\bar{x} = 43.9 \pm 5.0 [\text{SD}] \text{mm}, N = 21$) than did Snail Kites ($\bar{x} = 55.8 \pm 7.4 \text{mm}, N = 191$). This difference in snail size selection represents a 1.5 times greater caloric intake per snail for Snail Kites than Slender-billed Kites (Beissinger unpubl. data).

On seven occasions we saw Slender-billed Kites extract snails from their shells in a manner similar to Snail Kites (Snyder and Snyder 1969,
Snyder and Kale 1983). Grasping the snail in one or both talon(s) against a limb, the kite inserted its bill, presumably between the shell and operculum, and twisted its neck back and forth to pull off the operculum. We were unable to see the initial orientation of the mollusk but after the operculum was removed, the snail was positioned with the aperture facing up and the spire sideways. Then placing its upper mandible inside the shell and the lower one outside, the kite cut the columellar muscle with a few strokes of the bill. The body mass was freed from the shell, which fell to the ground. The kite discarded the digestive tract before tearing pieces from the body and eating the snail, or delivering it to a nestling. We were unable to see if albumen glands were discarded, which Snail Kites usually do when eating gravid female snails (Snyder and Snyder 1971). Extracting a snail from its shell required less than a minute.

On three occasions we saw Slender-billed Kites capture snails. The kites had been still-hunting (Snyder and Snyder 1969, Beissinger 1983) and flew down to the water's surface from overhanging branches to pluck the snail from the water with their talons.

We did not observe Slender-billed Kites capturing or dismembering crabs. But when feeding nestlings, adults tore pieces of meat from crabs and passed them bill-to-bill to the chicks. Apparently the adults had removed the crabs' carapaces before arriving at the nest.

Group movements and displays.—Slender-billed Kites were often observed soaring in groups of two to five birds. Typically, the group circled about 100-300 m in the air but sometimes as high as 500 m. Usually one or two members of the group gave the type I call. Group soaring occurred during the nesting season, from July through October.

Often at least one member of the group, and sometimes two, displayed while circling. The displays, lasting up to 40 min, consisted of a series of repeated swooping dives in which the bird would fold its wings and plummet about 5 m before opening them again and rising. When two members of a soaring group displayed, they sometimes chased each other. On one occasion we saw a lone adult give an undulating flight display about 5 m above the ground while returning toward its nest site. While soaring in groups or alone, Slender-billed Kites joined or were joined by Turkey Vultures (Cathartes aura), Black Vultures (Coragyps atratus), and King Vultures (Sarcoramphus papa).

Courtship.—We observed courtship and copulation behavior of two pairs of Slender-billed Kites. The sequence of events appeared very similar to that of the Snail Kite (Beissinger 1987a, 1988). In one pair, the presumed male brought snails to a female perched on a dead snag along an old drainage canal at the edge of the gallery forest. However, no known
nest site was within 300–400 m of the pair. The female remained perched in the same vicinity throughout most of the observation period (1.75 h) while the male left, presumably to hunt, and returned with a snail five times. As the female begged vociferously giving rapid type I calls, the male extracted the snail on a perch 1–2 m away. Often the female began calling when the male was first seen approaching with food. The male would pass the snail to the female bill-to-bill after she had shuffled along the branch to within 0.5 m of him. Twice the male fed the female pieces of the snail instead of relinquishing the whole mollusk to her.

Four copulation sequences were observed. Two occurred just after or while the female ate a snail recently delivered by the male. In the typical copulation sequence, the female crouched, opened and quivered her wings (quarter open at the wrist), lowered her head, and arched her back. The male mounted the female, with wings spread two-thirds to full, and pushed his tail around to the left and beneath the female’s to make cloacal contact. Using a pumping motion, the male copulated for 5–6 sec. Sometimes during mounting, the female arched her back forward and held her head back, looking at the male with her mouth open, and softly made a high nasal call or a low pitched rattle-like “BRAH.” At the conclusion the male remained on the female’s back for 3–4 sec, and then hopped off and perched 0.5 m away. Twice type I calls were uttered by the female before and after copulation.

Nest sites.—We discovered 10 nests, eight in gallery forest and two in shrub woodland bajio (terminology of Troth 1979). All nests were in habitat that flooded during the wet season, with standing water 5–60 cm in depth, but dried nearly completely during the dry season. Most nests were positioned over heavy brush, although sometimes nests were located over open water (pools or borrow-pit pools).

Nest sites were situated 9–20 m above the ground ($x = 14$ m) in large trees (up to 25 m in height) usually in the middle of long, horizontal, or gently sloping limbs. Nests were found in the following trees: Albizia aff. polycephala (2), Pterocarpus acapulcensis (3), Bombacopsis sp., Spondias mombin (2), and unidentified (2). All nests were small platforms approximately 50–60 cm in diameter, constructed of bulky dead twigs, and most were placed in bifurcating crotches. Often nests were surrounded by green leafy twigs that stuck into the air at an angle. At least some leafy twigs were gathered and stuck into the side of the nest by the birds, perhaps to assist in camouflage. Nests were usually well-shaded by the tree canopy but easily visible from the ground.

Slender-billed Kite nests were well dispersed and some were traditional sites. Distances between pairs of simultaneously active nests in 1976 and
1978 were approximately 1–1.2 km. In two instances, the same nest sites were used by kites in successive years, and in one case evidence suggested two years of prior occupancy of the site (Ernest Stevens pers. comm.).

**Parental behavior and mate desertion.**—Both sexes incubated as do Snail Kites (Beissinger 1987b). When relieving its mate during incubation, the approaching bird often gave the type I call. Unlike Snail Kites which fly directly onto the nest or hop on from a nearby perch but never walk, Slender-billed Kites usually landed a few m away from the nest, and shuffled or slid along the tree limbs to the nest site.

At the 1986 nest, both parents fed and brooded the two young. Snails or crabs were torn into small pieces and passed bill-to-bill from parent to chick. The food delivery rate increased through the first three weeks (Fig. 2). From weeks three through six, delivery rates averaged 3.92 ± 1.50 (N = 4) per h for Slender-billed Kites, significantly higher (t = 2.09, df = 32, P < 0.05) than the rate at which concurrently active Snail Kite nests with two chicks were being fed by both parents (x̄ = 2.51 ± 1.25 [SD], N = 32). Neither Slender-billed Kite parent in 1986 deserted its mate and both fed the fledglings until at least 7 weeks of age.

**Nestling development and behavior.**—The young hatched approximately 2–4 days apart at all three nests that we could observe. Haverschmidt’s (1959) plate 2 depicts a light grey, downy nestling that resembled our chicks at about 7–10 days of age. At this stage, the nestlings strongly resembled those of Snail Kites (see Bent 1937 for a photograph). By four weeks of age, however, nestling plumage became a dark grey and looked similar to the immature in Haverschmidt’s plate 1. In this plumage, a standing nestling resembled the adult except that its iris was dark brown instead of yellow and its cere was bright yellow (resembling *R. sociabilis* young) instead of orange.

The young were nearly always tranquil and quiet in the nest. When the adults landed near the nest with food, the chicks remained quiet and did not give begging screams. We never observed any fighting between the two nestlings, except once (1.5% of the feedings) when the young engaged in a tug of war over snail meat.

Nestling development appeared to be rapid. By two weeks of age the parents no longer brooded. Nestlings stood frequently during the second week after hatching and by the third week stood consistently. Nestlings were capable of taking extracted snails from adults and swallowing them whole by 17 days after hatching. Fledging occurred at 35 days of age, but the young were not capable of sustained flight until 40 days of age and remained perched in trees adjacent to the nest site.

**Nesting phenology and success.**—In Venezuela, the nesting season extended from July through October. The earliest nest records were on 22
July 1983, when a pair was found but the nest contents were unknown, and on 29 July 1982 when a pair was located with a half-built nest. While Slender-billed Kites have been sighted occasionally in our study area as late in the year as December, we have not seen this bird from January through April, the height of the dry season.

We could not determine the exact length of a nesting cycle. Our best data are from the intensively studied nest in 1986. If we assume that egg laying had begun (as judged by adult defensive behaviors) when the nest was found on 30 July and that the young were about 4 days old when discovered on 5 September, the incubation period would be about 30 days. The nestling period at this nest was about 35 days, but the fledglings were still receiving food from their parents in the nest area a week later. This suggests that the nesting cycle of the Slender-billed Kite has a minimum length of 72 days. Assuming an estimate of two weeks for nest-building and another 2-4 weeks of parental care before the young become independent (no observations but see Beissinger [1987b] and Beissinger and Snyder [1987] for R. sociabilis), a nesting cycle would be closer to 98-112 days.

We were able to determine the fates of nine of ten nests found during
this study. Four (44.4%) successfully fledged young. If, however, we ex-clude one nest found after the young had hatched, nesting success was 37.5%. In three nests we were sure of the number of young fledged; two fledged two young and one fledged a single young. In the other nest, one young fledged but we could not be certain whether the second nestling had fledged successfully.

Interspecific interactions.—On two occasions we saw R. hamatus defend a nest site. Once a family unit of red howler monkeys (Alouatta seniculus) was foraging on leaves in the nest tree about 3–20 m from the nest. After a trip to feed the young, a Slender-billed Kite parent perched near the monkeys and began vocalizing type I calls towards the group. Then after diving once at the monkey group, the kite departed and the monkeys moved to another tree. Red howler monkeys are folivorous and are not known to eat vertebrates (Crockett and Eisenberg 1987).

Nest-site defense also occurred when a pair of Laughing Falcons (Herpetotheres cachinnans) called about 50 m from a Slender-billed Kite nest. The kite parent, perched nearby, flew to the top of the nest tree and gave type I calls. Then it gave chase in the direction of the Laughing Falcons.

DISCUSSION

One of the most interesting discoveries in this study was that Slender-billed Kite pairs can give calls as duets. To our knowledge, the Slender-billed Kite is the only falconiform for which duetting has been documented (Thorpe 1972, Farabaugh 1982). Duets were given when the pair was perched on the territory, when a member of the pair approached its mate near the nest or in response to human intruders. Although the function of these duets is not known, they may be used as a broadcast call for territorial defense, directed toward nearby nesting pairs, and/or in pair-bond maintenance. Voices of mates differed in pitch and this may be a sexually dimorphic characteristic.

Slender-billed Kites were thought to have a specialized diet solely of freshwater snails (Haverschmidt 1959). In this study they fed mostly (about 90%) on Pomacea snails but the remainder of their diet was comprised of crabs, which were also taken by a nearby population of Snail Kites at a similar rate. Neither species (Beissinger 1988) should be considered solely snail eaters but clearly they are snail specialists.

Slender-billed Kites extracted and ate snails in the same manner as R. sociabilis (Snyder and Snyder 1969, Vouw and van Dijk 1973, Snyder and Kale 1983). However, Slender-billed Kites were observed on three occasions catching snails by still-hunting and have not been seen coursing for food as Snail Kites frequently do (Snyder and Snyder 1969, Beissinger 1983). This could be due to the paucity of observations on this species.
but is more likely a constraint imposed by the closed forest habitat hunted by Slender-billed Kites. Here many perches are suitable for still-hunting but it is probably difficult for kites to maneuver in flight through the dense forest while searching for snails. Also, still-hunting may be more profitably employed in the forest if snail availability is higher there than in open marshes (Beissinger 1983). There is some evidence supporting this hypothesis since Slender-billed Kites fed their nestlings at a higher rate than did Snail Kites.

Alternatively, a higher rate of food delivery by Slender-billed Kites to their nestlings may have compensated for feeding smaller snails to their young than did Snail Kites. Differences in the sizes of snails captured by these two hawks probably reflected a different distribution of snail sizes in the two habitats that they hunted (see Bourne and Berlin 1982 for an example). Rice fields in Venezuela hunted by Snail Kites can be artificially flooded year round, even during the dry season, and may permit increased growth and survival by snails. The snail populations of the gallery forest, however, must aestivate throughout the dry season when the water disappears.

The Slender-billed Kite and the Snail Kite (Beissinger 1987a, b, 1988) have very similar nesting behaviors. Copulation and courtship feeding sequences appear identical. Aerial displays are also similar but Slender-billed Kites usually perform them high above the tree canopy while male Snail Kites nesting in open habitat give them most frequently at low elevations and near nest sites. In both species, the sexes share the duties of incubation and feeding the young. The duration of incubation, nestling, and fledgling periods of the two kites appears similar, although Slender-billed Kites apparently have a shorter breeding season (July–October) than Snail Kites (May–December).

One aspect of the nesting behavior of the Slender-billed Kite that may differ from the Snail Kite is territorial defense. Snail Kites usually defend only a small area near the nest site (see Snyder and Snyder 1970 for an exception). Our study did not determine whether Slender-billed Kites do the same or defend larger parts of their home ranges. We witnessed few aggressive interactions and, because Slender-billed Kites are not plumage dimorphic, the context of displays often could not be clearly understood. Territoriality is suggested by the large distance between nests. The frequency with which we saw Slender-billed Kites soaring over the forest suggests that this activity might have been territorial patrolling. However, we sometimes saw Slender-billed Kites soaring in groups and it may be that the large home ranges of *R. hamatus* pairs overlap.

In Florida, most Snail Kite nests are deserted by a parent, if food is abundant, when the young are between three and six weeks of age (Beis-
singer and Snyder 1987). At the only Slender-billed Kite nest checked for mate desertion, neither parent deserted their brood of two. In Venezuela, Snail Kite broods of two young were deserted only about a third of the time, whereas broods of one young were nearly always deserted (Beissinger unpubl. data). Therefore, we do not have enough evidence to determine if Slender-billed Kites ever desert their mates. Comparisons of food delivery rates to young suggest that the food base of *R. hamatus* might be large enough for mate desertion to occur: Slender-billed Kites fed their young 1.5 times more frequently than did Snail Kites. However, this difference was offset by a difference in size and total caloric value of the snails fed, which was 1.5 times greater for Snail than Slender-billed kites. However, the smaller-sized snails fed by Slender-billed Kites and the larger body size of their nestlings could necessitate biparental care because two parents are needed to make additional trips to the nest with food to yield nestling food intake equivalent to *R. sociabilis*.

Other evidence suggests that mate desertion might not be expected for Slender-billed Kites. Mate desertion would be surprising in this species if it is territorial or does not raise more than one brood in a breeding season (suggested by the relatively short breeding season compared to the length of the nesting cycle). Thus, it would be difficult for potential deserters to secure new mates and nest sites or have enough time to attempt to nest again, perhaps the most important benefit of mate desertion (Beissinger and Snyder 1987). That exact nest sites can be used several years in succession suggests that pairs may mate more permanently.

Slender-billed Kite young sit quietly in the nest and rarely fight over food delivered by the parents. In contrast, Snail Kite young scream loudly at parents approaching with food and may continue screaming at the parent, even after the food has been eaten, until the parent departs from the nest area. The silence of Slender-billed Kite nestlings, and the semi-camouflaged nest of this species probably help to prevent detection from predators, which are common in the gallery forest (Strahl, in press). Young of both kite species were rarely observed fighting. Nestling fights are uncommon in medium-sized raptors, occurring only during times of obvious food shortage (Newton 1979).

Slender-billed Kite populations appear to be highly localized and restricted to flooded gallery forest or semiforest habitats. The species has been designated as rare or uncommon (Haverschmidt 1959, Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986). Although Slender-billed Kites are easily detected because their calls are unique and because they vocalize frequently, we believe that it is unlikely that this hawk recently expanded its range into Venezuela (Phelps and Phelps 1957). Instead, it probably was overlooked due to its irregular and seasonal
distribution. In the llanos of Venezuela, gallery forests are rapidly being destroyed and replaced by rice agriculture or human settlements. Because of its strong dependence on one prey species and its needs for a large forested territory for foraging and nesting, the Slender-billed Kite may be especially sensitive to tropical deforestation. Further study of its population biology is needed.

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WILSON SOCIETY ANNUAL MEETINGS

The 1989 annual meeting of the Wilson Ornithological Society will be held 25-28 May, at St. Mary's College, Notre Dame, Indiana. Doris J. Watt will chair the Committee on Arrangements. Richard C. Banks will chair the Scientific Program Committee.
A HISTORY OF THE FIRST ONE HUNDRED YEARS OF THE WILSON ORNITHOLOGICAL SOCIETY

JEROME A. JACKSON,¹ HAROLD MAYFIELD,² AND GEORGE A. HALL³

Preparing a history of an organization such as the Wilson Ornithological Society is a challenging task. For the first few years the Society was held together as much by personal correspondence as by its fledgling journal, and most of that is not available. The journal provided a means of recording the Society’s activities, although more often it was just an organ for disseminating the results of members’ studies. When annual meetings were held, the formal Minutes generally were published, but we all know that the Minutes tell only a fragment of the story. Fortunately others have prepared sketches of our history before us, foremost of which is a history prepared for our fiftieth anniversary by R. M. Strong. Far from dull, the history of the Wilson Ornithological Society has all the elements of a good novel: heroes and villains, tribulations and celebrations. By studying it we have learned about ourselves. We hope this review will better prepare the Wilson Society for the challenges of the next century.

In preparing this history of the Wilson Ornithological Society we have relied on the earlier efforts, the archives at the Josselyn Van Tyne Memorial Library at the University of Michigan Museum of Zoology, the published records of the Society in *The Wilson Bulletin* and elsewhere, and our own recollections spanning nearly half of the Society’s existence. We have all served as President and in other capacities on the Wilson Council, two of us (Hall and Jackson) as Editor of *The Wilson Bulletin*. We thus feel that we can offer a special insight into the past and present character of the organization, its activities, membership, and journal. Our efforts have been substantially improved by conversations and correspondence with other members, by the materials ferreted from the Wilson Society archives by Janet Hinshaw, and by careful critiques of the manuscript by current Council members and by Richard Banks, Charles Blem, Abbot Gaunt, Bette Jackson, Kim Smith, Peter Stettenheim, and Elliot Tramer.

Some portions of the history presented here are more detailed than others because of the extent of available details. Perhaps on reading this, others will recall additional details or be able to provide copies of cor-

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respondence and other materials relevant to the history for the Society’s archives and for the use of future historians. We hope so.

Our approach to the history was to divide the effort among ourselves: Mayfield covered the first third, Hall the middle third, and Jackson the final third of our first one hundred years. Our writing styles and perspectives vary, and although we have collated our manuscripts and made an effort to avoid discrepancies and redundancies, we each assume the responsibility for our individual sections. Lists of the officers who have served the Society and of the sites of our annual meetings are included in appendices. The literature citations are summarized at the end of the third section.
Every society, like every human being, has a personality of its own. The Wilson Ornithological Society is no exception. From its very beginning right up to the present we can see the imprint of the founders and early leaders, who were drawn together by their interest in the birds about them. Over the decades the concerns of the Society and its members have expanded, but the traces of the origins are still discernible.

The founders did not appear to be historic figures. They were not famous scientists at prestigious institutions, museum curators leading expeditions to exotic lands, nor university professors with established reputations. They were boys, some as young as 15, living mostly in small towns from Maine to Texas, reaching out by mail for kindred spirits with whom they could share their ideas and their collections.

The birth of this Society, however, was not an isolated event. The three decades after the Civil War brought a ferment of enthusiasm for nature study, with clubs springing up in many specialties—wildflowers, butterflies, rocks, shells, birds, and others. From 1873, when the Nuttall Ornithological Club started in Boston, until 1893, when the Cooper Ornithological Club began in California, at least 17 bird study societies appeared in various regions of the country, and many of them are still in existence.

These had been stimulated by a general rise in literacy and interest in cultural subjects, manifest in the Chautauqua movement, bringing lecturers on thoughtful topics to the remotest villages, and by the publication of many books and magazines on natural history, including notably Elliott Coue's "Key to North American Birds" in 1872 and many popular books and magazines appealing to naturalists and sportsmen. During the period 1884–1888 many small magazines, often not associated with any society, sprang up to reach the new audience. In *The Auk* for April, 1885, editor J. A. Allen noted: "Juvenile and amateur publications in Natural History appear in different parts of the country with bewildering frequency, not less than twelve or fifteen such publications having started within the last twelvemonth."

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The early history of the Wilson Society was intertwined with the bibliographic maze of its publications. Two were particularly significant. *The Young Ornithologist*, an eight-page magazine, appeared in Boston in 1885 under the editorship of A. A. Child. In its December issue, L. O. Pindar of Hickman, Kentucky, suggested that subscribers should form a corresponding association. The magazine lasted only long enough to give its name to the group. Then Pindar wrote Frank W. Lattin, publisher of *The Oologist*, for permission for these young men to publish reports in his journal. The first of these appeared in the July-August issue of 1886, consisting of a constitution drawn up by Pindar with the help of John B. Richards of Fall River, Massachusetts. It named the Society, “The Young Ornithologists’ Association,” and *The Oologist* the “official organ of communication” among the members. Lattin appointed Pindar as President and Richards as Secretary (Bagg 1968).

*The Oologist* also had a faltering life. Lattin started it as *The Young Oologist* in 1884 in Gaines, New York, and continued it later in Albion, New York. In 1885 he merged it with *The Agassiz Journal*, published in Lynn, Massachusetts, but in 1886 he resumed publishing it as the bi-monthly *The Oologist*. In this era the hobby of egg collecting was at its height, particularly among young men. Published notices included offers to trade not only bird eggs and skins, but also books, magazines, and bicycles.

Although the Society set down its roots in 1886, it acquired the Wilson name and a new constitution in 1888, causing this year to be recognized as the year of its founding in the annals. The 1888 constitution specified the purpose of the association to be “the study of birds, their nests, and eggs.” The elimination of the word “collect,” which had appeared in the 1886 constitution, may seem small, but it signified a conscious intention to move away from the postage-stamp style of collecting that had become the vogue, by some commercialized, at the time. Seriousness of purpose was demonstrated also by Richards as early as 1888, when he suggested that the association be divided into local divisions to encourage cooperative research. A little later, in 1891, Lynds Jones set up committees to concentrate on melology (song), oology, and general research (Strong 1939:4).

The organization took another crucial step when, affiliating with The Agassiz Association, a national federation of natural history groups, it took a new name: The Wilson Ornithological Chapter of The Agassiz Association, in honor of Alexander Wilson, pioneer ornithologist in
America. A charter was granted on December 3, 1888, by Harlan H. Ballard, President of The Agassiz Association. The Agassiz Association had been inspired by the writings and public lectures of Louis Agassiz, celebrated zoologist and authority on glacial geology at Harvard. By 1888 The Agassiz Association had grown into a national network of clubs devoted to various aspects of nature, numbering 15,000 members in 800 chapters.

Early in 1888 O. P. Hauger of Orleans, Indiana, had offered to publish a monthly magazine for the group, *The Curlew*, and accordingly, this was adopted as the official journal. The first issue appeared in October 1888, under the editorship of J. P. Richards. The March 1889 issue listed 35 members—8 from Massachusetts, 5 from Iowa, 4 from Wisconsin, 3 from New York, 2 each from Maine, Kentucky, and Texas, and 1 each from Connecticut, Illinois, Indiana, Kansas, Michigan, Minnesota, Nebraska, Ohio, and Pennsylvania (Bagg 1968). In 1890 the list had grown to 85 names (Strong 1939:5).

*The Curlew* lasted only from October 1888 to April 1889, providing a medium of communication during the transition from the Young Ornithologists’ Association to the Wilson Chapter. After the demise of *The Curlew*, the Society turned briefly in 1890 to the *Ornithologists’ and Oologists’ Semi-Annual* published by W. H. Foote of Pittsfield, Massachusetts. Then after the *Semi-Annual* was suspended in April 1892, the Chapter used the pages of the *Taxidermist*, published by E. W. Martin and C. F. Mignin of Akron, Ohio, until May 1892. Lynds Jones and R. M. Strong put out one issue of *The Wilson Quarterly* at Oberlin, Ohio, in April 1892, and one issue of *The Journal* in January 1893, but did not continue for lack of funds.

In 1893, communication among members was maintained by mimeographed sheets printed by Jones at Oberlin College, and in the same year W. N. Clute secured space in *Popular Science News* for the Agassiz Association, which carried Chapter news and a committee report on owls compiled by Jones (Jones 1914:25).

*The Wilson Bulletin* under this name began in February 1894, consisting of postcard-size reports on specific birds mailed by W. B. Caulk, secretary of the Chapter, and financed by the authors. The reception of these was unexpectedly enthusiastic, encouraging Jones to continue *The Wilson Bulletin* as a small-format bi-monthly, beginning in January 1896. The future of this publication did not show promise until 1900 when new life was infused into it with two studies more ambitious than any heretofore in this series: one on the flicker by Frank L. Burns, and one on the songs of the warblers by Jones. With new vigor *The Wilson Bulletin* changed
to a quarterly in approximately its present page size. In 1901 the editorship was taken over by Burns at Berwyn, Pennsylvania, but from 1902 to 1924 *The Wilson Bulletin* was edited by Jones at Oberlin, Ohio.

There seems to have been little interaction between the Wilson group and its parent association, if we may judge from the published record. As early as 1890 some dissatisfaction was voiced about this affiliation and a shorter name was desired, but the struggling group felt the relationship gave them prestige and help in reaching prospective members. As the chapter and its leaders became more mature, these advantages seemed less important, and in 1902 the ornithological group cast loose from the Agassiz Association and adopted its own name under a new constitution.

The boyish trivia of the earliest years soon disappeared, and after the turn of the century *The Wilson Bulletin* was attracting contributions from distinguished American ornithologists. By 1915 the list also included prominent Canadians, P. A. Taverner and W. W. Saunders, along with such well-known Americans as Ira Gabrielson, Aretas Saunders, Althea Sherman, R. W. Shufeldt, B. H. Swales, and Otto Widmann. By 1920 it included F. C. Lincoln, W. L. McAtee, E. A. Preble, and Alexander Wetmore. The emphasis remained on field ornithology, however, and *The Wilson Bulletin* printed life histories, local bird lists, unusual occurrences, nesting records, and reports from travelers far from familiar haunts. It included little on anatomy, taxonomy, and other specialties of museum workers. A proposal to change the name from Club to Society was voted down at the annual meeting in 1916 (Strong 1939:4) and came up again in 1919 without result (Ganier 1920:29). Before this time for several years the Bulletin proclaimed itself “an illustrated quarterly magazine” on the cover and carried out its promise with many photographs. If World War I had any impact on the Society, it was not reported except for a paper in 1920 on the birds of France and Germany by a member serving in the army.

**THE EARLY LEADERSHIP**

Although the Wilson Ornithological Club had roots in New England as well as westward, the long-continued leadership of a few men tended to give the society a midwestern flavor (Kastner 1986:132–144). This regional character was reinforced by the affiliation of the Nebraska Ornithologists’ Union in 1916, the Iowa Ornithologists’ Union in 1923 (Strong 1939:5), and the Kentucky Ornithological Society, and Tennessee Ornithological Society in 1924 (Wilson 1924:61). In 1917 excerpts from the diary of E. I. Shores of Connecticut added an explanation that *The Auk* was the “bird journal of the Atlantic Coast” (Henninger 1917:2).

Many of the earliest leaders dropped from view in ornithology when
they went on to adult careers in other fields. For example, J. B. Richards of Fall River, Massachusetts, was 15 years old in 1885 when he promoted the beginnings of the society. He dropped out a few years later when he went into business. L. O. Pindar of Hickman, Kentucky, was also 15 and a ringleader in 1885, but gave up this activity when he took up medicine (Bagg 1968).

A pillar of the organization for decades was Lynds Jones of Oberlin, Ohio. He learned taxidermy and egg collecting in childhood from an older neighbor boy (Taylor 1938:228). Jones started higher education at the academy and college at Grinnell, Iowa, but transferred to Oberlin College, where he could get a wider variety of science courses. Later he went on to a doctorate at the University of Chicago and returned to teach throughout a long life at Oberlin.

Jones was a burly, energetic man who brought not only ornithology to Oberlin, but also football. He played tennis until late in life, and he was famous for strenuous cross-country field trips to the Pacific Northwest with his classes (Taylor 1938:236). At Oberlin he instituted the first ornithological course in an American college in 1895, and in 1910 offered a course in the new science of ecology (Kendeigh 1952:259). His contributions to the Wilson Club were incalculable. In addition to being one of the founders, he held offices in the society for 39 years—Secretary, Treasurer, President for 11 years, and Editor for 36 years.

Only a little less influential was Reuben M. Strong, also a founder, whose friendship with Jones in the Club led him to attend Oberlin, first in the preparatory school, and then in the college from which he graduated. He shared with Jones the financial and editorial duties in the early years, and he served as Treasurer in 1892–1893, and as President from 1894 to 1901, and again from 1920 to 1921. In his professional career Strong moved through a series of professorships in anatomy at several colleges and universities, finishing his work at Loyola (Chicago) Medical School. He continued to attend the annual meetings until near the time of his death at age 90 (Rand 1966).

Another memorable founder was Franklin L. Burns, who served as Secretary in 1906 and as President from 1909–1911. Perhaps more importantly, he gave dignity to the early publications by monographs on the American Crow (*Corvus brachyrhynchos*), Northern Flicker (*Colaptes auratus*), and Broad-winged Hawk (*Buteo platypterus*), and by a series of biographical papers on Alexander Wilson (Van Tyne 1946:187, Palmer 1954:105).

A Midwesterner who played a prominent role was T. C. Stephens of Sioux City, Iowa. Although not one of the original founders, he was President at the time of the first two meetings in 1914, and was editor of
The Wilson Bulletin from 1925 until 1938 (Palmer 1954:543–544). Another was Albert F. Ganier of Nashville, Tennessee, a member from 1915, Secretary and President, who remained active in Society affairs for more than 50 years.

MEETINGS

From the earliest days the founders recognized the desirability of regular meetings. Several of them were already mingling with other ornithologists as early as 1890 at the sessions of the American Association for the Advancement of Science that were often held in the Midwest. Jones had prepared an announcement of a meeting to be held at Oberlin in December 1891, including titles of papers to be presented, but there is no record that the meeting ever occurred. The first recorded meetings were held in February and December 1914, both at Chicago. In 1915 the Wilson Club became affiliated with the American Association for the Advancement of Science and, from 1916 through 1937, met fairly regularly in concert with that organization.

For its own meetings the Wilson Club often chose sites in part for their natural attractions, where people could walk afield from the doors of their lodgings. The meetings contributed greatly to the organization’s strength and stature, and they came to be remembered among ornithologists for their friendly, informal spirit.
1922-1932

The Wilson Ornithological Club continued to grow during these years and a concerted membership drive brought on by a financial crisis enlisted 162 new members in 1921. After much debate at the 1921 meeting, the dues were raised to $2.50 for Active Members and $1.50 for Associate Members (Ganier 1922). The different classes of membership were apparently “distinguished” simply by the amount of dues a member was willing to pay. By the end of this period membership held steady at about 700, with a rather high annual turnover. While numerous professional ornithologists appear on the membership list, most of the members appear to have been amateur bird students. The leaders of the Club, such as Lynds Jones, Reuben M. Strong, T. C. Stephens, and others, were biologists, usually college professors, although the professional ornithologist H. C. Oberholser was a Vice President in 1921 and George M. Sutton was Vice President in 1929-1930.

A new constitution was presented in 1930. At that time six Honorary Members were nominated: Founders Leon Pindar, Reuben M. Strong, Lynds Jones, and Franklin L. Burns, as well as Althea Sherman and Otto Widmann. In this year an agreement was reached with the University of Michigan to establish a library. The University was to provide housing for what was called the W.O.C. Research Library. The rules established at that time are essentially those that pertain today for this library, now known as the Josselyn Van Tyne Memorial Library.

The contents of The Wilson Bulletin continued to be dominated by faunal lists and life histories. However, except for the lack of technical papers on taxonomy or anatomy, the contents differed little from those of The Auk at the same period. In 1924 Editor Jones commented that he believed that simple local lists no longer merited publication, but there was little change in the Bulletin as a result of this.

Secretaries Ganier and Gordon Wilson contributed a lengthy section to each issue on “Personal Notes,” outlining activities and affairs of members gleaned from their official correspondence. These tended to cement
the “clubbiness” of the organization. Albert F. Ganier (President, 1924–1926), a southern gentleman of the old school, was an important part of the Club at that time. He was a civil engineer by profession who became a major figure in the development of ornithology in Tennessee, Kentucky, and Mississippi. He lived into the 1970s and was an outspoken critic of the drift of the Wilson Society away from field ornithology. This scorn for “new fangled” ideas was the subject for an Auklet sketch (Bandwagon 1965).

In 1922 a “Department of Bird-Banding” under W. I. Lyon (1922) became a feature of The Wilson Bulletin and was continued for several years. This section of the journal included notes submitted by banders that were similar to those now published in North American Bird Bander. A paper in 1922 by Leon Cole traced the history of bird banding in North America. That year also saw the first paper published in The Wilson Bulletin by George Sutton (1922).

An event of major importance was Lynds Jones’ retirement as Editor of The Wilson Bulletin after having served for 36 years. The new editor was T. C. Stephens, a biology professor at Morningside College in Sioux City, Iowa. In his editorials over the years Stephens expressed a number of views that, while then out of step with the time, are now widely accepted. For instance, in 1929 he suggested that holders of collecting permits be required ultimately to turn their specimens over to museums, the practice today. In 1934a he presented a discussion of English names for subspecies that prefigures our present ideas.

The year 1926 saw two major milestones in Wilson Bulletin history. In the first issue the classic figure of Wilson’s Warbler (Wilsonia pusilla) by George Sutton made its debut on the cover, and in the June issue a Sutton painting of American Avocets (Recurvirostra americana) became the first colorplate to be published in the journal. Four other colorplates appeared before 1930. Gradually new kinds of papers began to appear. In 1925 Althea Sherman published her famous paper denouncing the House Wren (Troglodytes aedon), starting a lively controversy. In 1929 an important paper on Harris’ Sparrows (Zonotrichia querula) by M. H. Swenk and O. A. Stevens was illustrated by another Sutton colorplate. The June issue of 1931 included one of Margaret Nice’s first papers on the Song Sparrow (Melospiza melodia). In 1932 papers by S. C. Kendeigh and V. E. Shelford were important analyses of the Merriam Temperature Laws and their failure.

Annual meetings were held each year, almost always in conjunction with some other meeting. If the American Association for the Advancement of Science was meeting in the Midwest, the Club met jointly with that large organization. Such meetings were, traditionally during the Christmas-New Year’s holiday break. In years when the A.A.A.S. was
not available, meetings were held jointly with such organizations as the
Inland Bird Banding Association, The Ecological Society of America, and,
indeed, once (1922) jointly with the American Ornithologists’ Union at
Chicago. These meetings were usually on the Thanksgiving weekend. The
timing of the meetings reflects the predominantly academic character of
the leaders of the Club, as well as a prevailing negative attitude of colleges
and universities towards faculty members taking time off to attend meet-

ings. Attendance at these meetings was usually around 100 people, but
at Des Moines in 1929, 202 people attended. The attendance in 1927 at
Nashville was small enough that the whole group could attend a reception
at the home of Past President Albert Ganier. The group photographs of
these meetings reveal that most of the people attending were middle-aged
or older, and young people were not really evident until about 1931. The
people attending the meetings, like the leaders of the Club, were generally
not professional ornithologists, but were either professional biologists,
usually educators, or interested amateurs. In 1932 for the first time the
Club held a meeting independently of any large national organization,
but for a few more years the earlier practice prevailed. The papers given
at the meetings were similar to those published in the *Bulletin*.

1933–1943

The Great Depression finally caught up with the Club and it was decided
that no meeting should be held in 1933. In 1934 the Editor commented
that Treasurer W. M. Rosene was president of one of the very few banks
in his county which did not fail during the bank crisis, and hence the
Club’s funds were intact (Stephens 1934b). Membership at this time,
however, decreased only slightly.

A questionnaire issued in 1938 resulted in an analysis of membership
by Secretary O. S. Pettingill in 1939. This breakdown revealed that 24.8%'
of the members were teachers, 16% were businessmen, 13.5% were stu-
dents, and the remainder was distributed among various professions
(Pettingill 1939). Many of the early leaders of the Wilson Society were
men who earned their livelihoods outside the field of biology. In 1938
Margaret Nice became the first woman to head a major American orni-
thological organization. Membership slowly began to increase, with in-
tensive membership campaigns carried out by Secretaries L. E. Hicks and
O. S. Pettingill, Jr. By 1941 membership had topped 1000.

Olin Sewall Pettingill, Jr. (President, 1948–50) is a professional orni-
thologist and photographer, who was a college professor at the time he
was elected Secretary. His service to the Society dates from 1937 and his
contributions, which continue to this day, have been many. Lawrence E.
Hicks (President, 1940–41) of Ohio was also a professional ornithologist
and a prodigious worker, both in the field and for the Club. A flamboyant
character, he sometimes let his enthusiasm overcome his scientific caution and thus many of his records are suspect at the present time.

In 1934 the Annual Meetings were revived and the Club met in Pittsburgh together with the A.A.A.S. Attendance at the meetings had slowly increased until at Minneapolis in 1940, 353 people attended (273 from Minnesota). In 1941 at Champaign-Urbana, Illinois, 174 (a record high) people attended the annual banquet. The increased attendance at meetings came about with the increased attendance of younger people and with the increased participation of professionals. This in turn reflected the gradual evolution of the subject matter of the papers away from simple faunistics to the newer phases of ornithology.

The 50th Anniversary meeting was held at Ann Arbor, Michigan in 1938 and there was no co-host society. From this time until recent years, meetings were held independent of other major organizations. The time of meetings was still the weekend after Thanksgiving. In 1939 this led to some difficulty. The meeting was scheduled for December 1 and 2 in Louisville, Kentucky. In the late summer President Franklin D. Roosevelt announced that Thanksgiving would be moved from November 30 to November 23. In September the Club officials hastily advanced the date of the meeting, which was then held in Louisville on November 24-25, although the host state was one of the few which did not go along with the President’s change. In conjunction with the 50th anniversary, a history of the Club was written by one of the founders, R. M. Strong (1939).

With the coming of World War II, the 1941 meeting was the last one held for several years. The officers and Council conducted necessary business by mail during the interval.

*The Wilson Bulletin* also showed growth and change during this period. The content of the papers, as with those given at the meetings, was evolving as scientific ornithology evolved. Emphasis was still on field studies, but such noteworthy papers as H. W. Hann’s life history of the Ovenbird (*Seiurus aurocapillus*) (1937), which occupied a whole issue, reached new dimensions in importance. Faunal lists still appeared, but now they were reports from little-known areas, such as the paper by Sutton and Thomas Burleigh on the birds of Tamazunchale, San Luis Potosi (1940). The first of a series of color field sketches of Mexican birds by Sutton accompanied this paper. In 1938 the Sutton drawing on the cover of *The Wilson Bulletin* was removed. A storm of protests came from the membership and the drawing returned the next year.

A watershed for *The Wilson Bulletin* was reached in 1939 when Josselyn Van Tyne of the University of Michigan, a scientist of exceedingly high standards, became editor. Under his leadership the caliber of papers in *The Wilson Bulletin* increased. Van Tyne was a prodigious worker who
insisted that authors meet his own high standards. His austere and somewhat stern appearance, coupled with his six-foot-eight-inch height, may have frightened some people, but he was a man with a penetrating sense of humor. If he approved of your work (and if you did things his way), he could be a fast friend. Many authors owed a part of their reputation as writers to his stern editing. On the other hand there were confrontations with such strong-minded authors as A. W. Schorger and Margaret Nice. Once Van Tyne had the temerity to eliminate two paragraphs from one of Mrs. Nice’s papers. Incensed, she promptly published the paragraphs in question in *The Auk* (M. Brooks, pers. comm.).

1944–1955

This period started in the heart of World War II. Travel was too limited to hold meetings and none was held during 1942, 1943, 1944, or 1945. The Articles of Incorporation required annual meetings, and so abortive attempts were made to gather a quorum of the Executive Council for such meetings. Finally in the summer of 1944 a quorum gathered at the Franz Theodore Stone Laboratory at Put-in-Bay, Ohio, and then again in the fall of 1945 another meeting was held in Columbus, Ohio. President George Sutton had resigned in mid-1943 to enter the Army and was succeeded by Vice-President S. C. Kendeigh. Many other members were also in the military and these people were stationed all over the world. Secretary Maurice Brooks was the middleman in a communications network that put servicemen members in touch with like-minded people wherever they might be stationed. Maurice Brooks (President 1950–52) of West Virginia, a professional biologist and ecologist, has served on the Council since 1942 and continues to make contributions.

Membership held constant or slightly increased during this period and in 1946 the Club boasted 1300 members. With the end of hostilities, the absent members returned home, including President Sutton who resumed office in 1946. When the plight of many foreign ornithologists came to the attention of Americans, an organized campaign led by Margaret Nice, Frances Hamerstrom, Theodora Melone, and Joseph Hickey sent clothing and books to needy families abroad. At the banquet of the 1947 meeting, an auction of bird paintings raised money for this project. Over 3000 packages were sent. A revised Constitution was adopted in 1946 and the Club entered a prosperous period of growth.

Annual meetings were resumed in the fall of 1946 at Omaha. The guest speaker at this meeting was Niko Tinbergen, Nobel-Laureate-to-be, who not only spoke of his basic ethological research, but also told of the plight of the Dutch ornithologists during the war. At the 1947 meeting in Columbus, a new award, the Louis Agassiz Fuertes Award, to support the
research of a young bird student, was made for the first time. The recipient was L. R. Mewaldt. This award has continued to the present time as the most prestigious award the Society has to give to students.

At the 1947 meeting the momentous decision to hold future meetings in the spring was taken. As a result, no meeting was held during the calendar year of 1948, but the University of Wisconsin, as part of its Centennial Celebration, hosted a meeting in April 1949. All further meetings have been held in the spring or in early June. The 1950 meeting also departed from precedent when, at the urging of Vice-President Maurice Brooks, it was held in informal surroundings at a 4-H camp, Jackson's Mill, West Virginia. This innovation proved popular and many other meetings have been held in rural settings.

The papers given at the meetings continued to improve in caliber. Immediately after the war many returned servicemen reported on the birds of distant places. Such reports included Fred Hall's report of the rediscovery of the Cahow (Pterodroma cahow). In this period two papers given at meetings of the Club have had more than casual importance. At Madison in 1949 Robert McCabe and Harold Deutsch (a chemist) gave a paper on the difference in the electrophoretic patterns of the egg albumins of different species of birds. In the audience that day was C. G. Sibley, who went on to develop the chemical-based taxonomy which has occupied him for so many years. At the 1953 meeting at Douglas Lake, Michigan, Donald Borror and Carl Reese gave the first paper on the analysis of bird song recordings by the sound spectrograph. Neither author could attend the meeting, and the paper was presented on tape!

Editor Van Tyne was able to keep The Wilson Bulletin going during the war years, although both the declining number of papers submitted and the restrictions of wartime publication limited the size. In the immediate post-war years two important papers were published. Ernst Mayr's "History of North American Bird Fauna" (1946) may be the most cited paper ever published in The Wilson Bulletin. Niko Tinbergen's "Social Releasers and the Experimental Method Required for Their Study" (1948) was a seminal paper for avian ethology in this country. By the time Van Tyne retired from the editorship in 1948, The Wilson Bulletin was a journal of the highest standards. According to Ernst Mayr (1975), during this period it was the leading bird journal in the country.

In 1949 the new editor, David E. Davis, made his debut in a storm of protest. By custom, The Wilson Bulletin was printed in the home city of the editor. Because of the nature of his equipment, the new printer reduced the height and width of The Wilson Bulletin by a half inch each. The membership reacted in a highly negative fashion and in 1950 the journal returned to its former size. Davis found it necessary to give up the edi-
torship in mid-1950 and in this emergency George Sutton volunteered to be interim editor. Sutton's successor was H. B. Tordoff, then at the University of Kansas. Following custom he took the printing of *The Wilson Bulletin* to a small local printer, Harold Allen. From this beginning grew a major enterprise, The Allen Press of Lawrence, Kansas, which is now one of the foremost printers of biological and other scientific journals in the country.

By the end of this period the organization was gradually changing to more of a professional society. Growth continued to be steady. By 1954, 1700 members were on the rolls. *The Wilson Bulletin* remained a journal of the highest quality, and the papers published were at the leading edge of the science. More and more professionals joined the Club, although serious amateurs still constituted the majority of members. This trend was recognized in 1955 when it was voted to change the name of the Wilson Ornithological Club to the Wilson Ornithological Society. The name change was largely a matter of form and, despite the growth of the membership and the increased number attending the annual meeting, the atmosphere of friendliness still prevailed. The annual meetings were as much times of fun and comradeship as they were times of learning.

JEROME A. JACKSON

The transition from the mid-years of the Wilson Ornithological Club to the present Wilson Ornithological Society has involved much more than a name change in 1955. And after all, President Myron Swenk had appointed a committee in 1919 (Ganier 1920) to look into the possibility of changing our name to Wilson Ornithological Society! It was time. On the other hand, the name change perhaps symbolizes many of the other “sophistications” that the “Society” fell heir to. The world was changing rapidly in 1956 and WOS was swept along with it.

I have chosen to interject a more personal style to this portion of our history, relating many events as my colleagues in the Wilson Society have related them to me or as I saw them. No doubt I will slight the contributions of some individuals or the significance of some events. To the individuals I apologize. I have tried to be reasonably brief and yet to impart the “flavor” of the Wilson Ornithological Society in these years. This section has been tempered by the judgment of accuracy and propriety of the current Council and Centennial Committee members of the WOS who have reviewed the manuscript. To them I am most grateful. I hope the characterizations I include here will shed some light on the “real” people who made the Wilson Society go and grow in the last third of its first century.

Rather than a purely chronological approach, I have chosen to divide the account into four sections: People and Events, The Wilson Bulletin, Grants and Prizes, and The Josselyn Van Tyne Memorial Library. My purpose in making such a division is to single out the three tangible products/assets of the Society with the idea that perhaps such emphasis will result in more members availing themselves of the opportunities they provide.

PEOPLE AND EVENTS

Sites of annual meetings spanned eastern North America during this last third of our first hundred years. Indeed, new ground was broken when the Society held its first Canadian meetings at Huntsville, Ontario (1961) and Sackville, New Brunswick (1981), and “Deep South” meetings at Dauphin Island, Alabama (1971) and Mississippi State University near...
Starkville, Mississippi (1977). A push westward was also accomplished by establishment of a “tradition” to hold joint meetings with the Cooper Ornithological Society at five-year intervals.

A few individuals stand out for their lasting and exceptional contributions to the Wilson Society during this period. Foremost among these are George Miksch Sutton, Olin Sewall Pettingill, Jr., and Phillips B. Street. Each has served the Society as President. In addition, each continued involvement and very dedicated support of the Society, providing guidance and raising funds for our general support and special endeavors during nearly the entire period. Their contributions deserve special recognition, but so too do the efforts of many others. I will comment on some—mostly those with whom I am most acquainted—but hasten to add that space does not permit acknowledgment of the efforts of numerous others. We are a strong organization because of the generous commitment of many members.

George Miksch Sutton (President 1942–43, 1946–47) was in many ways the “Patriarch” of the WOS, and although he rarely attended annual meetings, he was always ready to help the Society. One of his dreams was to have a color plate in each issue of *The Wilson Bulletin*, a dream which he ultimately made possible by his establishment of the Sutton Color Plate Fund. The stature of Sutton the man has been made clear by George Hall’s account of Sutton during the middle period of the Society’s history. It was brought home to me during my first year as editor of *The Wilson Bulletin*. One of the first manuscripts submitted to me was a short note on Northern Mockingbird (*Mimus polyglottos*) behavior written by “Doc.” Both reviewers felt that it should not be published, and, although I can’t remember why, I agreed with them. How was I to tell the man who had just established the fund to assure a color plate in each issue that his manuscript was not worthy of being published in *The Wilson Bulletin*? As a neophyte editor, and one who stood in awe of Doc Sutton, I agonized over the manuscript and the decision I knew I had to make. In the end I rejected it, but feared the response I might get. By return mail I got the most wonderful letter from Doc, thanking me for keeping him from making a fool of himself!

Olin Sewall Pettingill, Jr. (President 1948–50) has always had a gift for bridging the gap between the professional and amateur, and has been one of the driving forces that has helped WOS keep the blend of amateurs and professionals that characterize the Society.

One of the key figures in this period of our history—an individual who remains intimately active with the Society today—is Phillips B. Street (President 1962–64). Although Phil studied ornithology as an undergraduate at Cornell University, he is professionally an investment broker. In
recent years Phil has very successfully managed the Society's investments. He is one of the many "amateur" members who have given the WOS its unique character.

Phil attended his first Wilson meeting at Jackson's Mill, West Virginia, in 1950, and his talents were quickly put to use by the Wilson Council. In 1951 he was elected Secretary of the Club, serving in that capacity until 1956, when he was elected Second Vice-President. In 1962 he became President.

Others have also passed on the ideals of the Wilson Society through their tenure as WOS officers. John Emlen (President 1956–58), a professional ornithologist and educator, as most Presidents have been in recent years, recognized the contributions of amateurs and fostered the development of their ornithological skills. His banquet address at the 1958 annual meeting, on "The Art of Making Field Notes," described the changes in ornithological note-taking from the 19th century to the mid-20th century, and provided clear guidance as to the need and approach to making detailed and accurate field notes. Fortunately for those not present and for students in years to come, his address was published in *The Jack-Pine Warbler* (Emlen 1958). Kenneth C. Parkes (President 1973–75) has been a regular attendee at Wilson Council meetings in recent years, and has constantly strived to maintain the amateur/professional balance in the Society and to bring recognition to the amateurs who have contributed significantly to ornithology.

The Society was privileged to have Reuben M. Strong, one of its Founders, present at our 75th anniversary meeting in 1963 in Charleston, South Carolina. This last of the Society's Founders died 11 August 1964.

At the 1965 meeting, the Council voted to discontinue affiliation with the American Association for the Advancement of Science, an affiliation that had begun in the early years of the Wilson Ornithological Club and which had for many years been marked by the annual meeting of the Club being held in conjunction with the A.A.A.S. meeting.

A special symposium on Regional Bird Books dominated the 1968 annual meeting. It is interesting to note that several of the symposium speakers have since published or revised regional bird books (e.g., J. Bull, B. Monroe, G. Hall, T. Imhof, D. James, A. Phillips, N. Whitney).

In 1968 the Society also officially acquired a permanent address—\% The Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104—the home of our library.

One of the important roles of the Wilson Ornithological Society has been as an official voice for our members on conservation matters. Conservation committees have almost always been appointed by Council and have produced numerous reviews and reports which have been published
in *The Wilson Bulletin*. Conservation-related resolutions passed by the Society have been timely and often strongly worded. To some extent it might be said that we have been jumping on the "environmental bandwagon." Often we have led the way. Collectively, the wishes of our members and those of other organizations have undoubtedly influenced the political process by which positive environmental changes have come about. For example, a resolution was passed at the 1963 annual meeting commending Rachel Carson for her leadership in awakening Americans to "what may be a disastrous misuse of pesticides." Another was passed at the 1969 annual meeting strongly urging "the immediate banning of persistent, broad-spectrum, toxic pesticides." One feature of the 1973 annual meeting was a symposium on "Progress in Rare and Endangered Species Programs." Several conservation-oriented resolutions were passed at that meeting.

Perhaps it was largely by coincidence that our 1969 Federal Tax return was audited by the Internal Revenue Service. Although there were undoubtedly some tense moments for Treasurer William Klamm, our tax-exempt status was maintained.

The 1975 annual meeting was the 2nd joint meeting with the Cooper Ornithological Society. At that meeting several proposed changes in the Constitution and Bylaws of the Wilson Society were approved by Council. These were largely "housekeeping" changes, bringing them into agreement with established practice. One notable (?) change was deletion of the phrase "... of good moral character ..." from the stipulations for membership. It was jokingly noted that some Council members might otherwise not qualify as members. All proposed changes were approved at the 1976 annual meeting.

In 1977, President Douglas James appointed a committee chaired by Kim Smith to study recruitment and to evaluate student membership. The committee reported that of the 2074 members, about 10% had been members for only one year, and only 72 had been members for 40 years or more. The average member had belonged to the Society for 14.4 years, although the data were obviously skewed.

My own association with the WOS as an officer came about in part because of an attempt by the Wilson Council to involve more members with the affairs of the Society. In 1969 they circulated a questionnaire to all members, asking, among other things, how members might be interested in serving the WOS. As an ambitious graduate student, I checked many of the blanks (perhaps all of them!)—I wanted to be involved and no task seemed too great.

The year 1972 was one of great transition in that George Hall stepped down after having been editor of *The Wilson Bulletin* for ten years. The
length of his tenure was reminiscent of earlier decades, but not even approached in recent years—no doubt a result of the tremendous increase in volume of manuscripts, but I feel also a result of lesser commitments by individuals to single organizations today, less support from editors’ institutions, and increasing complexity of subject matter. *The Wilson Bulletin* had become a major scientific journal, and the pressures of finding reviewers, critically evaluating manuscripts, and maintaining the high quality of the journal leave a modern editor little time for anything else.

My first encounter with George Hall was when I was a graduate student. George was editor of *The Wilson Bulletin* and it was to him that I submitted my first manuscript—one that I would judge today to be of little significance, perhaps worthy of a note in a state journal. But reviewers were kind and I learned later that George was always one to encourage students. This was a philosophy that I benefited from and later adopted during my own tenure as editor. Aside from my elation over George’s judgement that my manuscript should be published (pending heavy revision and shortening!), what I remember most—and what anyone who knew George Hall as editor of *The Wilson Bulletin* fondly remembers—is the appearance of George’s typed correspondence. George is by profession a chemistry professor, not an ornithologist. His editorial work was done in his “spare” time. His letters were obviously done on an old manual typewriter that was in need of some adjustment—the individual letters seemed to be trying to escape the page, not two resting on the same plane!

In 1972, Treasurer Bill Klamm also stepped down and the Council was in urgent need of a new Treasurer—a time-consuming job and a difficult position to fill. With no candidates in mind, the Council’s questionnaires were pulled into play—and there I was. Naively I accepted the position. At that time, the Treasurer got Allen Press to mail out dues notices, then carefully logged the dues in, kept checking and savings accounts, mailed reminder notices, managed membership and subscription lists, paid the Society’s bills, and assisted with management of the Society’s investments. Quite honestly, I was out of my element! I persevered for a year, with luck, careful guidance from Bill Klamm, and a great deal of assistance from my businessman father-in-law.

The next year the Council had the difficult task of finding a new editor, when John Hubbard retired after only one year. Once again my name came up as a volunteer! The editor’s job was a position that I really wanted and one for which I had experience as an editorial assistant for *The Auk* under Robert Mengel, and as Assistant Editor for the *Kansas Ornithological Society Bulletin* under Richard Johnston. The position could be mine, but only if we could find a new Treasurer. I had the perfect answer. Ernest E. Hoover, an amateur from Grand Rapids, Michigan,
was also employed at a bank. Ernie and I had corresponded over the years because of a mutual interest in woodpeckers and had even published a note together. What more likely candidate for Treasurer than a banker! Ernie accepted the nomination and we were both elected to our respective posts. I don't know whether I was more delighted to be ex-Treasurer or new Editor!

When George Hall was elected President in 1979, the biggest problem he faced was a financial crisis. The Society's assets had dwindled and costs of publication were skyrocketing. Treasurer Ernie Hoover resigned and Bob Burns was elected to pick up the pieces. What Bob and the Council discovered helped explain the financial crisis. While the annual check of Ernie's books by the Auditing Committee always revealed the books to balance, the check did not reveal that Ernie had in later years been paying himself a substantial monthly salary! Over a few years the amount had added up to several thousand dollars. Having been Ernie's predecessor as Treasurer, I knew the work could consume as much time as a full-time job. To Ernie it had become a thankless task. While the editor received an honorarium for his services, the treasurer received naught for his equally time-consuming efforts. When confronted with the possibility of legal action by the Society, Ernie repaid the money.

Under Bob Burns' prudent management of incoming funds and expenditures, with exceptional management of invested funds by the investment committee headed by Phil Street, and with a dues increase, the Society regained a sound financial status. When Bob became Treasurer, the Council had been discussing the possibility of joining with the American Ornithologists' Union and the Cooper Ornithological Society in a business arrangement that would facilitate receipt of dues and management of membership lists and subscriptions. Such a venture finally came about in 1979 with the incorporation of "OSNA"—the Ornithological Societies of North America—under the direction of Sandra L. Gaunt. One result of the effort has been publication of joint membership lists called "The Flock" in 1979, 1985, and 1988.

Management of OSNA was transferred to the Cornell Laboratory of Ornithology in mid-1982, but was returned to Sandra Gaunt at The Ohio State University in early 1984, where it has remained to the present. In 1988 the Association of Field Ornithologists (formerly the Northeastern Bird Banding Association) also became affiliated with OSNA.

In conjunction with the consolidation of membership lists, the OSNA member societies began publishing the quarterly *Ornithological Newsletter* in 1980 under the editorship of Richard Banks. A newsletter had been published by the AOU in 1976 and was inspiration for the development of joint membership lists, dues notices, and OSNA. Publication of the
The Wilson Bulletin newsletter greatly reduced the need for using the more expensive journal space for news items and has also stimulated a greater exchange of news, notices of grants and positions available, and other announcements.

The fourth joint Wilson/Cooper meeting was held at the University of Colorado, Boulder, in 1985. It was well-attended and included outstanding programs and field trips. But, the meeting may be remembered for an unusual streak of bad luck. An unprecedented heat wave plagued attendees; Wilson 2nd Vice-President Mary Clench fell and broke her arm; a bus enroute to the banquet had two flat tires; and the caterer came up short on food for the banquet!

The Wilson Bulletin continued to grow in size and stature during the past few decades, culminating in 1987 in the largest volume ever published: Volume 99 was completed with 783 pages! Certainly our Founders could not have imagined that their journal, which in 1896 cost only $77 to publish, could evolve into the major international journal that it is today—or that inflation could result in publication costs in excess of $62,000 per volume!

Two of the most cited papers published in The Wilson Bulletin in this period are an article by Harold Mayfield (1961) on calculating nesting success in birds, and Frances James’ paper on habitat ordination (James 1971). This was apparently the first ornithological paper to apply these now standard statistical techniques to bird ecology.

The 1968 volume of The Wilson Bulletin was dedicated to George M. Sutton in honor of his seventieth birthday and for his devotion to the WOS. The volume included many papers on Arctic ornithology by his colleagues and students and a biographical tribute by Andrew J. Berger (1968) which summarizes many of Doc’s contributions to the Wilson Society.

Bird art has always been of interest to ornithologists, and the role of bird art in the affairs of the WOS has always been prominent. Undoubtedly such prominence has been in part due to the Wilson Society leadership roles of ornithologist-artists such as George Sutton and Walter Breckenridge (President 1952–1954). Art shows featuring the work of regional artists have become an expected—and much enjoyed—feature at annual meetings. Artwork has also been a prominent feature in The Wilson Bulletin. Publication of color plates was at first only occasional and funded by contributions from individuals or groups such as the Oklahoma Ornithological Society or Nebraska Ornithologists’ Union, but in 1973 George Sutton generously established a Color Plate Fund endowment to ensure that a color plate could be published in each issue of the journal.
At the Wilson meeting in Omaha and then later in *The Wilson Bulletin*, President Douglas James (1978) proposed changing the name of *The Wilson Bulletin* to one that would more readily identify the journal's contents to non-ornithologists. However the proposal was not met with much enthusiasm.

**GRANTS AND PRIZES**

By 1972 the WOS had the full complement of awards that it now gives: The Louis Agassiz Fuertes Award, Margaret Morse Nice Award, Ernest P. Edwards Prize, Alexander Wilson Prize, Paul A. Stewart Awards, George M. Sutton Prize for Ornithological Art, and Student Membership Awards. These awards are largely a product of this last third century of the Society's history. Another award, the S. Morris Pell Award, was established with a contribution of $75 made during the late 1940s to provide grants to young bird artists. The $75 first shows in the Treasurer's report for 1949, although little mention was subsequently made of the fund. At the 1956 annual meeting, a Pell award of $25 was given to Donald R. Altemus; at the 1957 meeting, awards of $25 each were given to Colleen Nelson and Albert Earl Gilbert, "thus exhausting the S. Morris Pell Fund."

A brief history of existing awards and prizes follows:

*Louis Agassiz Fuertes Award.*—The Louis Agassiz Fuertes Award was established in 1947 to honor the memory of the eminent bird artist. The
force behind establishment of the award was undoubtedly Fuertes' student, and then President of the Wilson Ornithological Club, George Miksch Sutton. The intent of the award has always been to encourage ornithological research, and the Society has always held this award as the most prestigious of those given. Efforts have often been made to assure that it is also the most monetarily rewarding, with the value of the award ranging to $400 in recent years. Although there are no restrictions as to eligibility for the Fuertes Award, applications from non-professionals and students have been preferred.

Contributions to the Fuertes Research Fund were exhausted in 1957, and Council agreed that in the future funds should be made available from the general fund of the Society to assure continuation of the Fuertes Grants. Nevertheless, as a result of misunderstanding and the belief that no funds were available, no Fuertes grant was made in 1958. Contributions have frequently been solicited for the fund—and received. But the “giving” urge of the grants committee, officers, and Council has always been high and general operating funds have often been used to support student research grants.

In 1982 a fund-raising effort carried out under the direction of C. John Ralph netted more than $7000 for the Fuertes and Nice award funds. Many past winners of the awards assisted with the effort, and several commented that what really counted was not the prize money, but the recognition by peers that their efforts were worthwhile.

Margaret Morse Nice Award.—This award, established by an anonymous contribution of $500 in 1970, is restricted to applicants not associated with a college or university. The award is intended to encourage the independent researcher without access to funds and facilities usually available at academic institutions. High school students are eligible. In recent years these awards have ranged to $200.

Ernest P. Edwards Prizes.—These awards, in amounts up to $350, have been funded each year since 1971 by Ernest P. Edwards and are given for the best and, at times, also the second best papers published in the previous year’s volume of The Wilson Bulletin. The judging for these awards is done by a committee appointed by the President. The committee always includes the Editor as one member.

Alexander Wilson Prize.—At the 1968 meeting, the Council approved an award of $100 for the best paper presented by a student or non-professional at each annual meeting. Papers by invited participants in symposia, and papers coauthored by a holder of a doctorate are ineligible. The amount of this award has ranged up to $200 in recent years.

Paul A. Stewart Awards.—Paul A. Stewart initiated these awards with
a generous endowment to the Wilson Society in 1978. The awards are intended to support research in ornithology, especially studies of bird movements based on banding and analysis of recoveries and returns, and investigations pertaining to economic ornithology. Several Stewart Awards in the amount of $200 each are available each year. In recent years the awards have ranged up to $275.

**George M. Sutton Prize for Ornithological Art.**—At the 1983 annual meeting, the Council voted to establish an annual competition in ornithological art in memory of George M. Sutton. The competition was to consist of paintings and drawings to be shown at the Society's annual meetings. The winner of the competition was to receive a cash prize of $500. One feature of the fourth joint meeting of the Wilson and Cooper societies was the first Sutton Art Show, which was won by Karen Allaben-Confer.

Later it became obvious that a Sutton Art Show would not be possible each year because of the specific facility requirements for safe-guarding and displaying art work, and the annual nature of the competition was modified to “occasional.” The second George M. Sutton Prize competition was scheduled for our Centennial meeting in Philadelphia.

**Student Membership Awards.**—At the 1966 annual meeting, Council empowered a committee, to be appointed by the President, to establish 25 complimentary, one-year Wilson Ornithological Society memberships for undergraduate students showing an interest and promise in ornithology. In 1973, Mrs. Aaron M. Bagg, wife of the late President (1966-68), provided a generous gift, funding the student membership awards for several years. During this interval they were known as the Aaron M. Bagg Student Membership Awards. In practice, awards were given to both undergraduate and graduate students and the number of awards varied from year to year depending on the number and quality of applicants.

**THE JOSSELYN VAN TYNE MEMORIAL LIBRARY**

The Wilson Club Research Library that was established at the University of Michigan in 1930 grew slowly, but served members well. Ground rules laid down at its initiation, and in effect today, provide for members to borrow publications with their only expense being the postage to return them. The library has certainly also been a special asset to the students and professionals at the University of Michigan Museum of Zoology, and no doubt greatly facilitated Josselyn Van Tyne's efforts as Editor of *The Wilson Bulletin*.

Following his death in 1957, Josselyn Van Tyne's personal library was donated to the Wilson Society by his widow, Helen Bates Van Tyne. At
the 1957 annual meeting, Council voted to name the Society library “The Josselyn Van Tyne Memorial Library,” as a tribute to the past-President and long-time Editor of The Wilson Bulletin.

Our library has continued to prosper, thanks to the efforts of members such as past-President Andrew J. Berger, who have made substantial contributions to library holdings, and to the Society librarians such as current librarian Janet Hinshaw. Janet quickly responds to all loan requests and also actively seeks contributions of materials for the library. In this day and age when interlibrary loan requests can take weeks to process and can be very expensive, access to the Josselyn Van Tyne Memorial Library is a privilege well worth membership in the Wilson Ornithological Society.

THE WILSON ORNITHOLOGICAL SOCIETY—WHERE WE ARE

The past few decades have brought many changes to the Wilson Ornithological Society—most reflected in changes in The Wilson Bulletin. Compilation of data on membership and publication of The Wilson Bul-
letin reveal a continuous healthy growth (Figs. 1 and 2). Data on dues and costs of publication unfortunately also demonstrate continuous—and nearly exponential—growth (Fig. 3!)

We take great pride in our professional/amateur mix of membership—which runs the gamut from backyard birder to museum systematist and from high school student to college professor. Our journal has always been a common ground, but perhaps the biggest challenge for the future is to maintain a journal that is readable and informative to such a diverse membership. The range of subject matter in The Wilson Bulletin still focuses on field ornithology, and wild birds pique curiosity and stir excitement no matter how sophisticated our approach to studying them. Two threads unite our diverse membership: the thread of uncertainty at how wild birds will respond to their environment, and the marvel at the mechanisms by which they do so.

Thomas L. Hankinson (1922), in his President’s address delivered at the joint WOC/AOU meeting in Chicago in 1922, noted the special role of the Wilson Club relative to other organizations: “The Wilson Club has especially encouraged outdoor ornithology.” He also noted the role of field ornithology in documenting the influences of habitat destruction on bird populations. Significantly he pointed out that: “It is outdoor orni-
thology that attracts the amateur; and professionals come from amateurs. It is important, then, to aid the amateur, and this has been a function of the Wilson Ornithological Club.” Such sentiments have been echoed by Wilson officers to the present, but in recent years we have also recognized how terribly important—how professional—the contributions of amateurs have been to our science. The only distinction that truly separates amateur and professional ornithologists is the source of their paychecks.

LITERATURE CITED


### Appendix A

**Presidents of The Wilson Ornithological Society**

<table>
<thead>
<tr>
<th>President</th>
<th>Years</th>
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<tbody>
<tr>
<td>J. B. Richards</td>
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<td>Clait E. Braun</td>
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<td>Mary H. Clench</td>
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APPENDIX B

VICE-PRESIDENTS OF THE WILSON ORNITHOLOGICAL SOCIETY

C. C. Maxfield, 1893
R. M. Strong, 1894
Ned Hollister, 1895–1903
W. L. Dawson, 1904–1905
R. L. Baird, 1906–1908
W. E. Saunders, 1909–1911
Bradshaw H. Swales, 1912–1913
George L. Fordyce, 1914–1919
H. C. Oberholser, 1920–1921
Dayton Stoner, 1922–1923
William I. Lyon, 1924
Thomas H. Whitney, 1925–1928
George Miksch Sutton, 1929–1931
Edwin L. Mosely, 1932–1933
Josselyn Van Tyne, 1933–1934
Alfred M. Bailey, 1935–1936
Margaret Morse Nice, 1937
Lawrence E. Hicks, 1938–1939
George Miksch Sutton, 1940–1941
S. Charles Kendeigh, 1942–1943
Olin S. Pettingill, Jr., 1944–1947
Maurice Brooks, 1948–1949

Walter J. Breckenridge, 1950–1951
Burt L. Monroe, 1952–1954
Harold F. Mayfield, 1954–1955
John T. Emlen, Jr., 1955–1956
Lawrence H. Walkinshaw, 1956–1958
Harold F. Mayfield, 1958–1960
Phillips B. Street, 1961–1962
Roger Tory Peterson, 1962–1964
Aaron M. Bagg, 1964–1966
H. Lewis Batts, Jr., 1966–1968
Pershing B. Hofslund, 1969–1971
Andrew J. Berger, 1973–1975
Douglas A. James, 1975–1977
George A. Hall, 1977–1979
Clait E. Braun, 1983–1985
Mary H. Clench, 1985–1987
Jon C. Barlow, 1987–

SECOND VICE-PRESIDENTS OF THE WILSON ORNITHOLOGICAL SOCIETY

Josselyn Van Tyne, 1932–1933
Alfred M. Bailey, 1933–1934
Margaret Morse Nice, 1935–1936
Lawrence E. Hicks, 1937
George Miksch Sutton, 1938–1939
S. Charles Kendeigh, 1940–1941
Olin S. Pettingill, Jr., 1942–1943
Harrison F. Lewis, 1944–1946
Maurice Brooks, 1947
Walter J. Breckenridge, 1948–1949
Burt L. Monroe, 1950–1951
Harold F. Mayfield, 1952–1954
Lawrence H. Walkinshaw, 1954–1956
Phillips B. Street, 1956–1960
Roger Tory Peterson, 1961–1962

Aaron M. Bagg, 1962–1964
H. Lewis Batts, Jr., 1964–1966
Pershing B. Hofslund, 1968–1969
Kenneth C. Parkes, 1969–1971
Andrew J. Berger, 1971–1973
Douglas A. James, 1973–1975
George A. Hall, 1975–1977
Abbot S. Gaunt, 1977–1979
Clait E. Braun, 1983–1985
Mary H. Clench, 1985–1987
Jon C. Barlow, 1987–
## APPENDIX C

### Secretaries of The Wilson Ornithological Society

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<td>J. E. Dickinson</td>
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<td>W. L. Dawson</td>
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<td>John W. Daniel, Jr.</td>
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<td>C. W. G. Eifrig</td>
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<td>Orpheus M. Schantz</td>
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<td>G. A. Abbott</td>
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<td>Albert F. Gavier</td>
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<td>Howard K. Gloyd</td>
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<td>Jesse M. Shaver</td>
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<td>James Tate, Jr.</td>
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## APPENDIX D

### Treasurers of The Wilson Ornithological Society

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<td>Reuben M. Strong</td>
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<td>S. E. Perkins III</td>
<td>1936-1938</td>
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<td>Gustav Swanson</td>
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APPENDIX E
EDITORS OF The Wilson Bulletin

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<td>Charles R. Blem</td>
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### Appendix F
**Annual Meetings of The Wilson Ornithological Society**

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For the 75th anniversary volume of *The Wilson Bulletin*, I compiled (Parkes 1963) a brief history of the illustrations that have appeared in the journal since the first in Volume 7, no. 2 (1900) and the first colored plate, in Volume 38, no. 2 (1926). This was followed by an annotated list of the 41 colored plates that had appeared through 1962, together with a list of the artists or photographers whose work had been reproduced.

For this, the Centennial Volume of *The Wilson Bulletin*, it is appropriate to continue this project by listing the colored plates that have appeared in the subsequent quarter century, a period during which the readers of the journal have been treated to an exceptionally fine cross-section of modern ornithological illustration. The *Bulletin*'s fourth quarter century began auspiciously with a newly designed Wilson's Warbler cover by Dr. George Miksch Sutton, essentially the same cover design that is still being used.

As is known to all scientific societies that publish journals, high quality color printing is very expensive. In the March 1967 issue of *The Wilson Bulletin* (Vol. 79:122), a note in the "Ornithological News" page solicited contributions to a Color Plate Fund, stating that "the cost of the color work precludes having more than one [plate] a year." One response to this request came quickly. Editor George Hall announced that Volume 80 (1968:111) would be dedicated to George Miksch Sutton on the occasion of his 70th birthday, and would be in part a symposium on Arctic ornithology, this being a favorite topic of Dr. Sutton. Two issues later, the color frontispiece that reproduced a Sutton painting of Hudsonian Godwit (*Limosa haemastica*) heads was "subsidized by the Oklahoma members of the Wilson Society and many other friends and former students of Dr. George M. Sutton in Oklahoma and nearby states [p. 344]."

In 1973 Dr. Sutton created a generous endowment fund for the sole purpose of ensuring the publication of a color plate in every issue of the *Bulletin*. The George Miksch Sutton Colorplate [Dr. Sutton's preferred spelling] Fund was announced by the Council of the Wilson Ornithological Society on p. 486 of Volume 85 (1973). In my "President's Page" in the March 1974 issue (Vol. 86:87), I commented on Dr. Sutton's gift, and pointed out the opportunity it afforded to authors of *Wilson Bulletin* articles to submit manuscripts that could appropriately be illustrated in color, even "commissioning colored plates to accompany articles that virtually cry out for such illustration," a practice that was to be followed on numerous occasions in subsequent years.

In its original announcement, the Council solicited contributions to the fund to supplement Dr. Sutton's gift. In a later note (Vol. 86, 1974:182), the Council explained that there had been a misunderstanding, in that Dr. Sutton wished that additions to the fund bearing his name be obtained only through his own efforts. Gifts to the Wilson Society by former students and other friends of Dr. Sutton, the Council stated, could appropriately be made to the Louis Agassiz Fuertes Research Grant Fund, which he had also founded. With Dr. Sutton's passing in 1982, the restriction on gifts to the Colorplate Fund was lifted, and additions to this fund, ensuring continued publication of color reproduction in the face of inflationary rises in costs, will be welcomed by the Treasurer.

In 1985 the first George Miksch Sutton Award for ornithological art, intended to encourage...
relatively new, non-professional (at the time of entry) bird artists, was presented to Karen Allaben-Confer. Her winning painting, of Razorbills \((Alca torda)\), was reproduced as the frontispiece of the March 1986 issue of *The Wilson Bulletin*. The competition was held again in 1988, and it is expected that the winning painting, of a Zigzag Heron \((Zebrilus undulatus)\) by Tracy Pedersen, will be reproduced in an early issue in 1989.

One of the outstanding features of the ornithology of the past quarter-century has been the discovery of striking new taxa of birds in South America, most notably in Peru, by workers from Louisiana State University, the Field Museum of Natural History, and other institutions. Several of the papers describing these species and subspecies were submitted to *The Wilson Bulletin* in the knowledge that they could be accompanied by a colored plate of the new form (and sometimes of its relatives as well). In the checklist of figured species beyond, an asterisk (*) indicates that the plate accompanied the original description of the form listed.

In all, 76 colored plates appeared in *The Wilson Bulletin* in the years 1963–1987 (vols. 75–99). Of these, 23 were reproductions of photographs, the rest of paintings. A total of 104 avian species has been figured, in addition to 4 plates of hybrids. The artists represented, in alphabetical order, are as follows (with number of plates published):

<table>
<thead>
<tr>
<th>Artist</th>
<th>Plates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allaben-Confer, Karen</td>
<td>1</td>
</tr>
<tr>
<td>Bennett, F. P., Jr.</td>
<td>1</td>
</tr>
<tr>
<td>Breckenridge, Walter J.</td>
<td>1</td>
</tr>
<tr>
<td>Butler, Murrell</td>
<td>1</td>
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<tr>
<td>Coe, James</td>
<td>1</td>
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<tr>
<td>Dilger, William C.</td>
<td>1</td>
</tr>
<tr>
<td>Donahue, Paul K.</td>
<td>1</td>
</tr>
<tr>
<td>Duffin, Kathleen</td>
<td>2</td>
</tr>
<tr>
<td>Eckelberry, Don R.</td>
<td>4</td>
</tr>
<tr>
<td>Fitzpatrick, John W.</td>
<td>1</td>
</tr>
<tr>
<td>Gautheaux, Sidney A., Jr.</td>
<td>1</td>
</tr>
<tr>
<td>Gilbert, Albert E.</td>
<td>1</td>
</tr>
<tr>
<td>Halliday, Nancy</td>
<td>1</td>
</tr>
<tr>
<td>Isler, Morton L.</td>
<td>1</td>
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<tr>
<td>Jaques, Francis Lee</td>
<td>1</td>
</tr>
<tr>
<td>Lekagul, Boonsong.</td>
<td>1</td>
</tr>
<tr>
<td>Lunk, William A.</td>
<td>1</td>
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<tr>
<td>McQueen, Larry B.</td>
<td>2</td>
</tr>
<tr>
<td>Miley, Theodore R.</td>
<td>1</td>
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<tr>
<td>Nelson, Colleen H.</td>
<td>1</td>
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<tr>
<td>O’Neill, John P.</td>
<td>13</td>
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<tr>
<td>Peterson, Roger T.</td>
<td>1</td>
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<tr>
<td>Pineo, Christopher</td>
<td>1</td>
</tr>
<tr>
<td>Pratt, H. Douglas</td>
<td>1</td>
</tr>
<tr>
<td>Sandström, George</td>
<td>2</td>
</tr>
<tr>
<td>Sutton, George M.</td>
<td>7</td>
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<tr>
<td>Tudor, Guy A.</td>
<td>1</td>
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<tr>
<td>Zimmerman, William</td>
<td>1</td>
</tr>
</tbody>
</table>

It is of interest to note that only 5 artists (Breckenridge, Dilger, Eckelberry, Peterson, and Sutton) appear on both the 1926–1962 and 1963–1987 lists. One artist, Francis Lee Jacques, was represented posthumously in 1975.

Bird photography has advanced considerably during the past quarter-century, and this is reflected by the 23 colored plates based on photographs, as contrasted with a mere 2 prior to 1963. Photographers were represented by only a single colored plate each in 1963–1987, with the exception of Joseph R. Jehl, Jr., who contributed 4. In the following list, [brackets] indicate that photographs were not specifically credited, and are here assigned to the author(s) of the accompanying paper.

<table>
<thead>
<tr>
<th>Photographer</th>
<th>Plates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bierregaard, Richard O., Jr. [Binford, Laurence C., Bruce G. Elliott, &amp; Steven W. Singer]</td>
<td>1</td>
</tr>
<tr>
<td>Cottrille, Betty D.</td>
<td>1</td>
</tr>
<tr>
<td>Giezentanner, Keith</td>
<td>1</td>
</tr>
<tr>
<td>Gill, Frank B.</td>
<td>1</td>
</tr>
<tr>
<td>Haney, J. Christopher</td>
<td>1</td>
</tr>
<tr>
<td>Kuhnigk, Albert [Labisky, Ronald F., &amp; Gary L. Jackson]</td>
<td>1</td>
</tr>
<tr>
<td>[Mock, Douglas W.]</td>
<td>1</td>
</tr>
<tr>
<td>Peckover, William S. [Raitt, Ralph J., &amp; John William Hardy]</td>
<td>1</td>
</tr>
<tr>
<td>Ryder, John P.</td>
<td>1</td>
</tr>
</tbody>
</table>
The following checklist of species figured in color in *The Wilson Bulletin* 1963–1987 is arranged taxonomically rather than chronologically. The sequence and nomenclature are those of the A.O.U. Check-list (A.O.U. 1983), with a few extralimital families interpolated. English names are those used on the plate; if different from the A.O.U. name, the latter is given in brackets. For South American birds, the name used by Meyer de Schauensee (1966) is given, credited to “M. de S.,” if different from the caption name. Subspecific names are used only if these are indicated in the caption of the plate. Page references are given only for the one instance in which the plate was not a frontispiece. The stated month of issue has been constant: March (No. 1), June (No. 2), September (No. 3), and December (No. 4). Unless the word “photo” appears, the plate was reproduced from a painting.

**FAMILY PROCELLARIIDAE**

Antarctic Petrel (*Thalassoica antarctica*): adult.  
Vol. 93, No. 1, 1981  
Photo, Jehl

Black-capped Petrel (*Pterodroma hasitata*): adult.  
Photo, Haney

**FAMILY ARDEIDAE**

Great Blue Heron (*Ardea herodias*): adult male in stretch display.  
Vol. 88, No. 2, 1976  
Photo, Mock

**FAMILY THRESKIORNITHIDAE**

Madagascar Crested Ibis (*Lophotibis cristata*): adult.  
Vol. 86, No. 3, 1974  
Photos, Gill

**FAMILY ANATIDAE**

Mute Swan (*Cygnus olor*): 2 color phases of downy young.  
Vol. 88, No. 1, 1976  
Nelson

Lesser Snow Goose (*Chen hyperborea hyperborea*): adult males and females at nests.  
Vol. 82, No. 1, 1970  
Photo [Ryder]

Ross’s Goose (*Chen rossii*): adult males and females at nests.  
Vol. 82, No. 1, 1970  
Photo [Ryder]

Blue-winged Teal (*Anas discors*) × Cinnamon Teal (*A. cyanoptera*) hybrids: heads of 5 males.  
Vol. 91, No. 3, 1979  
Sutton

Canvasback (*Aythya valisineria*): adult male (head and breast).  
Vol 75, No. 1, 1963  
Sutton

**FAMILY ACCIPITRIDAE**

Vol. 91, No. 4, 1979  
Photo [Sykes]

Guiana Crested Eagle [=Crested Eagle of M. de S.] (*Morphnus guianensis*): adult male and female at nest.  
Vol. 96, No. 1, 1984  
Photo, Bierregaard
Vol. 89, No. 1, 1977
O’Neill

Ornate Hawk-Eagle (*Spizaetus ornatus*): adult male at nest.
Vol. 97, No. 2, 1985
Photo, Kuhnigk

**FAMILY CRACIDAE**

Crested Guan (*Penelope purpurascens*): adult head.
Vol. 94, No. 3, 1982
O’Neill

Spix’s Guan (*P. jacuacu*): adult head.
Vol. 94, No. 3, 1982
O’Neill

White-winged Guan (*P. albipennis*): adult head.
Vol. 94, No. 3, 1982
O’Neill

**FAMILY PHASIANIDAE**

Ring-necked Pheasant (*Phasianus colchicus*): 98 eggs laid by 1 female.
Vol. 78, No. 4, 1966
Photo [Labisky and Jackson]

Lesser Prairie Chicken (*Tympanuchus pallidicinctus*): adult male booming.
Vol. 89, No. 4, 1977
Photo, Giezentanner

**FAMILY RALLIDAE**

Nkulengu Rail (*Himantornis haematopus*): downy young.
Vol. 85, No. 4, 1973
Zimmerman

Madagascar Gray-throated Rail (*Canirallus kioioides*): downy young.
Vol. 85, No. 4, 1973
Zimmerman

Forbes’s Forest-Rail (*Canirallus forbesi*): downy young.
Vol. 85, No. 4, 1973
Zimmerman

Gray-breasted Crake (*Laterallus exilis*): adult.
Vol. 93, No. 2, 1981
Lunk

Rufous-faced Crake (*L. xenopterus*): adult.
Vol. 93, No. 2, 1981
Lunk

Rufous-sided Crake (*L. melanophaius*): adult.
Vol. 93, No. 2, 1981
Lunk

Red-and-white Crake (*L. leucopyrrhus*): adult.
Vol. 93, No. 2, 1981
Lunk

San Cristobal Gallinule (*Pareudiastes silvestris*): adult (unique holotype).
Vol. 87, No. 1, 1975
Jaques

**FAMILY HAEMATOPODIDAE**

Magellanic Oystercatcher (*Haematopus leucopodus*): adult.
Vol. 92, No. 2, 1980
Photo, Jehl

**FAMILY SCOLOPACIDAE**

Solitary Sandpiper (*Tringa solitaria*): 1-day old chick.
Vol. 80, No. 4, 1968
Breckenridge

Hudsonian Godwit (*Limosa haemastica*): adult male and female, heads.
Vol. 80, No. 3, 1968
Sutton

White-rumped Sandpiper (*Calidris fuscicollis*): newly hatched chick.
Vol. 80, No. 1, 1968
Sutton

Stilt Sandpiper (*Calidris himantopus*), adult male and chick.
Vol. 85, No. 2, 1973
Photo, Kuhnen
Vol. 93, No. 4, 1981
Photo, Cottrille

FAMILY LARIDAE

Thayer’s Gull (Larus thayeri); 3½ yr old (head).
Vol. 90, No. 4, 1978
Sutton
Sabine’s Gull (Xema sabini): adult.
Vol. 96, No. 2, 1984
Photo, Kehoe
Roseate Tern (Sterna dougallii): 10 heads illustrating bill color change 8 June-14 August.
Vol. 88, No. 3, 1976: 2 plates, between pp. 380 and 381
Duffin

FAMILY ALCIDAE

Razorbill (Alca torda): adults (winner 1985 Sutton Award).
Vol. 98, No. 2, 1986
Allaben-Confer
Marbled Murrelet (Brachyramphus m. marmorata): chick and nest.
Vol. 87, No. 3, 1975
Photo [Binford, Elliott, and Singer]
—: adult at nest cavity.
Vol. 97, No. 1, 1985
Photo, Johnston

FAMILY PSITTACIDAE

Red-bellied Parrot (Pyrrhura frontalis): adult.
Vol. 77, No. 2, 1965
Eckelberry
Monk Parakeet (Myiopsitta monachus): adult.
Vol. 85, No. 3, 1973
Butler

FAMILY STRIGIDAE

Cinnamon Screech-Owl (Otus *petersoni): adult.
Vol. 98, No. 1, 1985
Peterson
Vol. 78, No. 1, 1966
Eckelberry

FAMILY TROCHILIDAE

Royal Sunangel (Heliangelus *regalis): adult male & female.
Vol. 92, No. 2, 1979
Fitzpatrick
Viridian Metaltail (Metallura williami atrigularis): adult male.
Vol. 92, No. 1, 1980
O’Neill
Violet-throated Metaltail (M. baroni): adult male & female.
Vol. 92, No. 1, 1980
O’Neill
Neblinka Metaltail (M. *odomae): adult male & female.
Vol. 92, No. 1, 1980
O’Neill
Coppery Metaltail (M. theresiæ): adult male & female.
Vol. 92, No. 1, 1980
O’Neill
Fire-throated Metaltail (M. eupogon): adult male & female.
Vol. 92, No. 1, 1980
O’Neill
Scaled Metaltail (M. a. aeneocauda): adult male.
Vol. 92, No. 1, 1980
O’Neill
FAMILY RAMPHASTIDAE

Saffron Toucanet (Baillonius bailloni): adult. Vol. 76, No. 1, 1964

Eckelberry

FAMILY PICIDAE


Golden-olive Woodpecker (Piculus rubiginosus): adult male head, either P. r. yucatanensis or maximus; adult male heads P. r. aeruginosus, 2 variants. Vol. 90, No. 2, 1978

Guayaquil Woodpecker (Campephilus gayaquilensis): adult female at nest. Vol. 92, No. 4, 1980

Gilbert

FAMILY FURNARIIDAE

Marcapata Spinetail (Cranioleuca m. marcapatae & C. m. weskei): adults. Vol. 96, No. 4, 1984


Bennett

FAMILY FORMICARIIDAE (Including “Conopophagidae”)

Bluish-slate Antshrike (Thamnomanes schistogynus): adult female. Vol. 95, No. 4, 1983


[N.B.: the 3 species above are considered races of H. pileatus, Black-capped Antwren, by M. de S.]

Bare-eyed [=Sooty of M. de S.] Antbird (Rhegmatorhina gymnops): adult male and female. Vol. 81, No. 4, 1969


White-breasted Antbird (Rhegmatorhina hoffmansi): adult male and female. Vol. 81, No. 4, 1969


Bennett

O’Neill
Rufous Antpitta (*Grallaria rufula*): adult.
Vol. 99, No. 3, 1987

O’Neill

Chestnut Antpitta (*G. *blakei*): adult.
Vol. 99, No. 3, 1987

O’Neill

Ochre-fronted Antpitta (*Grallaricula *ochraceifrons*): adult male and female.
Vol. 95, No. 1, 1983

O’Neill

Chestnut-belted Gnateater (*Conopophaga aurita*): adult male & female.
Vol. 96, No. 3, 1984

FAMILY TYRANNIDAE

Rufous Flycatcher (*Myiarchus semirufus*): adult at nest.
Vol. 87, No. 4, 1975

Pineo

FAMILY PIPRIDAE

Band-tailed Manakin (*Pipra fasciicauda*): adult male.
Vol. 95, No. 3, 1983

Bennett

Golden-winged Manakin (*Masius chrysopterus*): adult male & female.
Vol. 99, No. 4, 1987

Donahue

FAMILY CORVIDAE

Blue Jay (*Cyanocitta cristata*) × Steller’s Jay (*C. stelleri*) hybrid: adult.
Vol. 83, No. 4, 1971

Photo, Wheat

Vol. 75, No. 4, 1963

Eckelberry

Yucatan Jay (*Cyanocorax yucatanica [=yucatanicus of A.O.U.]): adult (4+ yr), juv.
2-yr old, 1-yr old.
Vol. 88, No. 4, 1976

Halliday

Vol. 91, No. 1, 1979

Photo [Raitt & Hardy]

Vol. 83, No. 1, 1971

Sutton

Florida Scrub Jay (*Aphelocoma c. coerulescens*): pipped egg, young of 0, 5, 11 & 18 days.
Vol. 90, No. 1, 1978

Photo [Woolfenden]

FAMILY PARADISAEIDAE

Pale-billed Sicklebill (*Epimachus bruijni*): male in display.
Vol. 98, No. 4, 1986

Coe

Goldie’s Bird-of-Paradise (*Paradisaea decora*): adult male.
Vol. 92, No. 3, 1980

Photo, Peckover

FAMILY CAMPEPHAGIDAE

Scarlet Minivet (*Pericrocotus flammeus*): adult male and female.
Vol. 79, No. 2, 1967

Lekagul

FAMILY AEGITHINIDAE

Green Iora (*Aegithina viridissima*): [adult female].
Vol. 79, No. 2, 1967

Lekagul

Greater Green Leafbird (*Chloropsis sonnerati*): adult male.
Vol. 79, No. 2, 1967

Lekagul
FAMILY TROGLODYTIDAE

Nightingale Wren (*Microcerculus philomela*): adult & juvenile.  
Vol. 95, No. 2, 1983  
McQueen

Whistling Wren (*M. luscinia*): adult & juvenile.  
Vol. 95, No. 2, 1983  
McQueen

FAMILY MUSCICAPIDAE (*Muscicapa thalassina*)

Verditer Flycatcher (*Muscicapa thalassina*): adult male.  
Vol. 79, No. 2, 1967  
Lekagul

Verditer Flycatcher (*Muscicapa thalassina*): adult & juvenile.  
Vol. 95, No. 2, 1983  
McQueen

FAMILY MUSCICAPIDAE (*Chasiempis sandwichensis gayi*)

Oahu 'Elepaio (*Chasiempis sandwichensis gayi*): adult & immature.  
Vol. 89, No. 2, 1977  
Pratt

FAMILY MUSCICAPIDAE (*Turdus graysoni*)

Grayson's Robin (*Turdus graysoni*): adult.  
Vol. 93, No. 3, 1981  
Pulich

Grayson's Robin (*Turdus graysoni*): adult male.  
Vol. 93, No. 3, 1981  
Pulich

FAMILY MIMIDAE

Socorro Mockingbird (*Mimodes graysoni*): adult.  
Vol. 94, No. 1, 1982  
Photo, Jehl

FAMILY VIREONIDAE

St. Andrew Vireo (*Vireo caribaeus*): adult at nest.  
Vol. 97, No. 3, 1985  
O'Neill

Bachman's Warbler (*Vermivora bachmanii*) adult male & female.  
Vol. 89, No. 3, 1977  
Gauthreaux

Yellow-rumped Warbler (*Dendroica coronata*): adult males in definitive alternate plumage of *D. c. coronata*, *auduboni*, *nigrifrons*, and *goldmani*.  
Vol. 82, No. 4, 1970  
Miley

Bachman's Warbler (*Vermivora bachmanii*): adult male & female.  
Vol. 89, No. 3, 1977  
Gauthreaux

Yellow-rumped Warbler (*Dendroica coronata*): adult males in definitive alternate plumage of *D. c. coronata*, *auduboni*, *nigrifrons*, and *goldmani*.  
Vol. 82, No. 4, 1970  
Miley

FAMILY EMBERIZIDAE (Parulinae)

Scrub Tanager (*Tangara vitriolina*): adult male & female.  
Vol. 97, No. 4, 1985  
O'Neill

Vol. 97, No. 4, 1985  
O'Neill

Green-capped Tanager (*T. *meyerdeschauenseei*): adult male and female.  
Vol. 97, No. 4, 1985  
O'Neill

Green-capped Tanager (*T. *meyerdeschauenseei*): adult male and female.  
Vol. 97, No. 4, 1985  
O'Neill

Black-capped Tanager (*Tangara heinei*): adult male and female.  
Vol. 99, No. 1, 1987  
Isler

Sira Tanager (*T. *phillipsi*): adult male and female.  
Vol. 99, No. 1, 1987  
Isler

Silvery Tanager (*T. v. viridicollis*): adult male and female; (*T. v. fulvigula*): adult male.  
Vol. 99, No. 1, 1987  
Isler

Green-throated Tanager (*T. argyrofenges caeruleigularis*): adult male and female.  
Vol. 99, No. 1, 1987  
Isler
Parodi's Tanager [=Parodi's Hemispingus of Isler and Isler 1987] (*Hemispingus* *parodi*): adults, 2 plumage variants.
Vol. 86, No. 2, 1974

Rufous-browed Hemispingus (*Hemispingus* *rufosuperciliaris*): adult.
Vol. 86, No. 4, 1974

Golden-back Mountain-Tanager (*Buthraupis aureodorsalis*): adult.
Vol. 86, No. 4, 1974

**FAMILY EMBERIZIDAE** (Cardinalinae)

Rose-breasted Grosbeak (*Pheucticus ludovicianus*) × Black-headed Grosbeak (*P. melanocephalus*) hybrids: 4 adult male variants and one 2nd year male.
Vol. 86, No. 1, 1974

Indigo Bunting (*Passerina cyanea*) × Lazuli Bunting (*P. amoena*) hybrids: 2 adult male variants.
Vol. 87, No. 2, 1975

**FAMILY EMBERIZIDAE** (Emberizinae)

Zapata Sparrow (*Torreornis inexpectata*): adult.
Vol. 94, No. 4, 1982

Smith’s Longspur (*Calcarius pictus*): female at nest.
Vol. 80, No. 2, 1968

**FAMILY ESTRILDIDAE**

Red-headed Parrotfinch (*Erythrura cyaneovirens*): adult males of *E. c. cyaneovirens, * *gaughrani, pealii, regia, serena.*
Vol. 84, No. 4, 1972

**LITERATURE CITED**


SHORT COMMUNICATIONS

Where were Kirtland’s Warblers during the last ice age?—The nesting requirements of the Kirtland’s Warbler (Dendroica kirtlandii) are highly specialized. It nests only on level or gently rolling sandy soil among young jack pines (Pinus banksiana) when they are about 2-4 m tall (8-20 years old) in nearly homogeneous stands. The nest is embedded in the ground and concealed under low vegetation. These conditions occur naturally only after extensive fires in jack pine woodlands. Very large tracts of potential habitat are necessary to provide a sufficient amount of forest in exactly the right stage at all times to sustain the nesting population. Although the range of the jack pine almost spans the continent, the bird nests in only one portion of northern Lower Michigan (Mayfield 1960:9-12). Here at any one time it has utilized only about 4,000 ha within the 100,000 ha of predominantly jack pine forest of the historical nesting range (Zimmerman 1956:31).

In the heart of its range the warbler has nested occasionally in suitable tracts as small as 30 ha, but this detail may be misleading because there have always been larger occupied tracts in the vicinity. The bird seems to be attracted only by extensive areas of the right kind. Even nonbreeding strays in nesting season (males seen in Wisconsin, Upper Peninsula of Michigan, Ontario, and Quebec) have been found in very large tracts somewhat similar in appearance to the nesting ground.

Until recently we supposed that suitable nesting conditions were widespread across the Midwest on the sandy outwash plains at the foot of the Wisconsin Glacier (Mayfield 1960: 24, 31). Now, however, we need to review that opinion. Pollen analyses have shown that jack pines were almost nonexistent in the Midwest 18,000 years ago at the height of the last glacial advance. The tree probably survived in that enormous region only in small isolated refugia, while at the same time jack pine covered most of the Appalachian highlands and the Atlantic Coastal Plain. It re-entered the Midwest about 10,000 years ago, replacing spruce because of its greater tolerance of repeated fires (Wright 1981, Critchfield 1985).

It is unlikely that the warbler was a significantly different creature in the late Pleistocene. It is a well-marked species, and Charles G. Sibley (pers. comm.) has expressed the opinion from DNA-based analysis that it probably separated from closely related Dendroica more than 100,000 years ago. We cannot be sure it has not changed its nesting behavior and habitat during the last 10,000 years, but its present rarity argues against its adaptability.

I suggest, therefore, that for a time near the end of the Pleistocene the bird’s nesting range may have been restricted to the sandy coastal plain of the South Atlantic States. Similarly, other birds now breeding in the northern-coniferous forest zone, may have been limited to the southeastern corner of the United States by the concentration of pinelands there. This circumstance, along with the possible origin of these species in the West Indies or beyond, may help explain why their fall migration route carries them southeast toward the sea instead of south across the midcontinent toward Mexico and Central America.

Acknowledgment.—I thank E. Tramer for comments on a draft of this paper.

LITERATURE CITED


Natal philopatry, site tenacity, and age of first breeding of the Semipalmated Sandpiper.—

Adults of many species of birds usually return to breed in areas where they have bred previously (Greenwood 1982). Therefore, in these species one would expect more obvious sexual biases in natal, compared to adult, dispersal, if sex-biased dispersal functions in inbreeding avoidance (Greenwood 1982), or to minimize intraspecific competition. It should, then, be most useful to examine sex biases in natal, rather than adult, dispersal. However, relatively few studies have examined sex biases in natal philopatry of birds (e.g., Greenwood 1980, Oring and Lank 1984).

The present note examines the effect of sex on natal philopatry, site tenacity, and age of first breeding from an eight-year study of a breeding population of Semipalmated Sandpipers (Calidris pusilla). The Semipalmated Sandpiper is a small, migratory shorebird with a monogamous, male-territorial mating system. I studied sandpipers at La Pérouse Bay, 40 km east of Churchill, Manitoba, in the summers of 1980 through 1987. During this period, I gradually increased the study area from 2 to 3 km². Approximately 40 to 130 pairs nested in the study area each year. Nests were mapped on 10 × enlargements of aerial photographs (scale 1:2500, allowing accuracy to at least 3 m; Abraham 1980). Adult birds were given individual color-band combinations, while young nestlings were banded with one stainless steel band, and often a single color band. Adults were sexed by bill length and behavior (see Gratto and Cooke 1987). For a more complete description of the study site and methods see Gratto et al. (1985).

I defined natal philopatry as the return of birds banded as nestlings to breed in the study area. Natal site tenacity was defined as the distance from a bird’s natal nest to the nest where it was first found breeding. Age of first breeding refers to the age a bird was first found with a nest. I might have missed the first breeding of a few individuals if their nests had been depredated very early, or if they had nested at the extreme edge of the study area (as did one female first found breeding at age 6). This should not have affected differences between sexes.

Because some individuals were first found breeding at age 4, returns of nestlings banded from 1980 to 1983 should be most complete (Table 1). Average return from these four years was 7 percent. Over all years, almost 90% of all young hatched in the study area were banded as nestlings. However, only 33.3% (8/24) of all yearling breeders from 1981 to 1987 (identified by the presence of partial postjuvenal wing molt, Gratto et al. 1983), were banded in
Table 1

Return Rates of Semipalmated Sandpiper Nestlings Banded at La Pérouse Bay from 1980 to 1986 and Later Found Breeding There, 1981 to 1987

<table>
<thead>
<tr>
<th>Year</th>
<th>Nestlings banded</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
<th>Percent return</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>60</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>6.7</td>
</tr>
<tr>
<td>1981</td>
<td>36</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>7.1</td>
</tr>
<tr>
<td>1982</td>
<td>142</td>
<td>4</td>
<td>2</td>
<td>6</td>
<td>4.2</td>
</tr>
<tr>
<td>1983</td>
<td>117</td>
<td>8</td>
<td>6</td>
<td>14</td>
<td>12.0</td>
</tr>
<tr>
<td>1984</td>
<td>198</td>
<td>1</td>
<td>5</td>
<td>6</td>
<td>3.0</td>
</tr>
<tr>
<td>1985</td>
<td>166</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0.7</td>
</tr>
<tr>
<td>1986</td>
<td>31</td>
<td>0</td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>Total</td>
<td>770</td>
<td>18</td>
<td>17</td>
<td>35</td>
<td>4.5</td>
</tr>
</tbody>
</table>

the study area as nestlings, suggesting that more than half of all new breeders must emigrate into the study area from elsewhere.

Assuming a 1:1 sex ratio at hatch, there was no sex bias in the return of nestlings breeding in the study area (G-test, $P > 0.05$, see Table 1). Similarly, there was no significant sex difference in natal site tenacity (males: $N = 15$, median = 603 m, range 128–1425 m; females: $N = 14$, median = 742 m, range 145–1492 m; Mann-Whitney $U$-Test, $P > 0.05$).

There may be a tendency for females to begin breeding at an earlier age than males, although the difference was not significant (Table 2). Most females bred first at age 2, while equal proportions of males first bred at ages 1 to 4. There are indications that adult females may have slightly higher mortality rates than males, with an easier entrance into the breeding population (C. L. Gratto, unpubl. data). In fact, 69.7% (23/33) of all yearling breeders from 1980 to 1987 (identified by the presence of partial postjuvenal wing molt) were females, and only 30.3% (10/33) males.

Table 2

Age at which Semipalmated Sandpipers Banded as Nestlings Were First Found Breeding at La Pérouse Bay, 1980 to 1987

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>Females (N)</th>
<th>Males (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>4</td>
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<td>4</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>1*</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>17</td>
<td>18</td>
</tr>
</tbody>
</table>

* Found at extreme edge of study area, and not included in statistics.
Yearlings bred closer to their natal nest than did those first breeding at age 2, or older (Table 3). It is not known why this should occur, unless birds first breeding as two year olds or older, many of which apparently do not migrate north as yearlings (Gratto and Morrison 1981, Spaans 1984), are less able to obtain territories near their natal site.

In conclusion, the results of this study indicate no sex bias in natal philopatry. This finding disagrees with the ideas of Greenwood (1980), and Liberg and von Schantz (1985), who predicted male-biased natal philopatry in monogamous birds due to greater advantages of site familiarity for males, in territory acquisition. However, since Semipalmated Sandpipers show near-equal parental investment (both parents incubate and young are precocial), and sexes are monomorphic and of near-equal size (Prater et al. 1977), neither dominance (Gauthreaux 1978) nor sexual selection (Oring and Lank 1982) are likely to be a cause of sex-biased dispersal. Additionally, in such short-lived, nonsedentary birds, the potential for close inbreeding is reduced (Redmond and Jenni 1982). Therefore, neither of the suggested ultimate causes of sex-biased dispersal are likely to be important in this species, so it is perhaps not surprising to find a lack of sex bias in natal philopatry. Results from other small calidridine sandpipers with equal parental investment are similar (Dunlin [C. alpina] Soikkeli 1970; Temminck’s Stint [C. temminckii] Hildén 1979; and Western Sandpiper [C. mauri] R. T. Holmes in Oring and Lank 1982).

Acknowledgments.—I particularly appreciate the support of F. Cooke, L. Oring, and A. Fivizzani during this project. I thank everyone at the La Périouse Bay Tundra Biology Station for their help, especially J. Hamann, E. Mallory, J. Reynolds, E. Smith, M. Stalker, and L. Stephenson. Comments of J. Carroll, M. Colwell, C. Hass, W. Jenson, and P. Pickett were appreciated. I thank the Churchill Northern Studies Centre for logistic support. This research was supported financially by the Natural Sciences and Engineering Research Council of Canada, the Northern Training Grants Program of the Canadian Department of Indian and Northern Affairs, United States National Science Foundation Grants PCM 8315758 and DCB 8608162 to L. Oring and A. Fivizzani, the Arctic Institute of North America, an AOU Carnes Award, a Chapman Research Award, a Sigma Xi Grant-in-aid of Research, the E. A. Bergstrom Memorial Research Fund, and the Eastern Bird Banding Association Research Fund.

LITERATURE CITED


Interspecific egg pecking by the Black-capped Chickadee. — Few passerines are known to destroy eggs of other birds, and documentation is restricted mainly to members of the Troglodytidae and Mimidae (e.g., Orians and Wilson 1964; Verner 1975; Picman 1977; Belles-Isles and Picman 1986a, b). The relative rarity of egg-pecking behavior among passerines could be explained by costs associated with the destruction of eggs of other birds, such as aggression by nest owners toward the aggressor. Alternatively, it is possible that this phenomenon is more common and that its apparent “rarity” is the result of difficulties in obtaining evidence for it. In 1984–1986, while studying House Wrens (Troglodytes aedon) at Presqu’ile Provincial Park, Ontario, and in the Mer Bleue Bog near Ottawa, Ontario (description of these study areas given in Belles-Isles and Picman 1986a, b), we obtained evidence of seven cases of egg pecking by Black-capped Chickadees (Parus atricapillus). Because we could find no previous reports on egg-destroying behavior by this species, we describe these cases below.

Case 1: We used a trap for House Wrens that exploits their egg-pecking tendency (e.g., Belles-Isles and Picman 1986b). The trap consists of a 28 × 22 × 8 cm cage containing a Red-winged Blackbird (Agelaius phoeniceus) nest and egg. The egg is glued to a trigger which sets off a hoop-netting trap when a bird pecks the egg (Picman 1980). In one of these traps on May 26, 1984, in Presqu’ile Provincial Park, we accidentally captured a female chickadee with a well developed brood patch. However, we did not observe the bird pecking the Red-winged Blackbird egg. No chickadee nest was found within a 20-m radius.

Case 2: On May 14, 1985, in Presqu’ile Provincial Park, we found a chickadee nest in the laying stage. We placed a ‘blackbird nest trap 3 m from the nest while chickadees were away. Two chickadees approached the trap approximately 60 min later. One of them flew directly into it, perched on the nest edge, and pecked the Red-winged Blackbird egg. The captured bird was again a female with a fully developed brood patch.

Cases 3–7: In the spring and summer of 1985 and 1986, one of us (JP) investigated predation of passerine nests. Predators were photographed using camera setups that took pictures when eggs were disturbed in an experimental nest (see Picman 1987). During this study, artificial nests with one or two Japanese Quail (Coturnix coturnix) eggs were offered to predators in different habitats (marsh, meadow, scrubland, forest). This produced approximately 700 pictures of predation events in habitats suitable for chickadees (scrubland, forest). Of these, five were of Black-capped Chickadees (2 in 1985 and 3 in 1986). Chickadees in these pictures were in an egg-pecking position (i.e., the birds perched on the nest edge had their bills touching the egg, or their raised head was pointing toward the egg). Four of these events occurred in scrubland and one in a coniferous forest. All five chickadee pictures were obtained during the breeding season in June or July. Unfortunately, the pictures of these events did not allow us to determine the sex and the breeding stage of the individuals involved. The rate of egg attacks by Black-capped Chickadees was generally low, suggesting that this species is a relatively unimportant egg predator. This low frequency of egg attacks could be the result of: (1) the behavior being limited to a few individuals within a population, (2) the relative rarity of this species in our study areas, and/or (3) the lack of appropriate stimuli eliciting the egg-pecking behavior in this species. We do not have data to discriminate among these alternatives. Therefore, more research is needed to establish the frequency of occurrence of egg-pecking behavior in the Black-capped Chickadee, the stimuli that elicit this behavior, and the ecological significance of this behavior.

Acknowledgments.—We thank C. Blem, W. Elden, M. Ficken, M. McLaren, M. Milks, J. Verner, and an anonymous referee for constructive comments on the manuscript. The Ontario Ministry of Natural Resources and the National Capital Commission kindly allowed
A possible case of intraspecific killing in the Lesser Snow Goose.—Most species of birds aggressively defend their territories, nests or mates against intraspecific intruders, but it is rare for either the resident or the intruder to be injured seriously or killed during such confrontations (Maynard Smith and Price 1973). There is evidence, direct and circumstantial, indicating that intraspecific killing, associated with defense of territory, nest or mate, or with forced copulation attempts, occurs (Cottrille 1950, Grubbs 1977, Loflin 1982, McKinney et al. 1983, Lombardo 1986, Belles-Isles and Picman 1987). Relatively little is known of the frequency of these events. The Lesser Snow Goose (Chen caerulescens caerulescens) is a monogamous, colonial, Arctic nesting bird with vigorous mate defense. Interactions are particularly aggressive during the incubation period, and are associated with a high frequency of extra-pair bond copulation attempts (Mineau and Cooke 1979). It is estimated that 2.4% of all goslings are fathered by extra-pair fertilization (Lank et al. 1988). In June 1985 at La Pérouse Bay, Manitoba, Canada (58°24'N, 94°24'W), we encountered an unusual situation in which a Lesser Snow Goose was apparently killed by a pair of Lesser Snow Geese, while intruding on a nesting territory.

On 27 May 1985 an incubated nest (P108) of a pair of blue phase Lesser Snow Geese was found. This nest was one of approximately 3100 nests found in 1985 as part of a long term study at La Pérouse Bay (see Cooke 1987). The nest was located on the periphery of the main nesting colony and was at least 100 m from another nest. When the nest was revisited on 17 June, a white phase goose which had recently died was found beside the nest cup. Its foot was wedged firmly between two branches of a small willow bush (Salix brachycarpa), and the feathers on the head and back of its neck were missing. On dissection
the bird proved to be a male with fully developed testes and average reserves of subcutaneous fat. Plumage characteristics indicated the bird was at least two years old. The nest had not been disturbed and all four eggs subsequently hatched successfully.

We believe that this bird entered the nest territory of the resident pair, and then, unable to escape, was subsequently killed. To our knowledge, this is the first case in which an adult Snow Goose has successfully killed another during the 19 years of our studies at La Pérouse Bay. We can only speculate as to why the goose which died visited the nest of the blue pair, but extra-pair bond copulation (EPC) seems to be the most likely explanation. This behavior is common in colonial birds (Gladstone 1979) and waterfowl (McKinney et al. 1983), and has been observed frequently during the incubation period in Snow Geese (Mineau and Cooke 1979), with males visiting and copulating with females on the nest. When an EPC is detected by the mate of an incubating female, the intruding male is attacked vigorously and chased off. A typical defense involves pecking and tugging at the head, neck and shoulder regions of the intruder (Mineau and Cooke 1979), resulting in wounds similar to those of the dead male we found. It appears that in this case the intruding male was unable to escape, and subsequently beaten to death by the defending male. Although the demise of this particular goose was probably the result of a rare accident, it demonstrates the potential for intraspecific killing associated with EPC’s and mate or territory defense.

Acknowledgments.—Research of the breeding biology of the Lesser Snow Goose is supported in part by the Natural Sciences and Engineering Research Council of Canada, the Canadian Wildlife Service, and the Mississippi and Central Flyway Councils. We thank S. Jackson, F. McKinney, J. Reynolds, R. Rockwell, and three reviewers for comments on the manuscript.

LITERATURE CITED


Interspecific learning and cultural transmission of song in House Finches. — House Finches (Carpodacus mexicanus) recently have extended their range in eastern North America and changed their songs by a process of cultural evolution, with song neighborhoods developing along the east coast apparently from a single ancestral population between 1939 and the late 1960's (Mundinger 1975, 1980). Here we report a rapid cultural change in songs of wild House Finches and an instance of reciprocal learning of song elements between species, the House Finch and the Common Canary (Serinus canaria).

On 21 and 24 May 1987, an unbanded House Finch was observed for 1 h in a residential area of Ann Arbor, Washtenaw County, Michigan (42°18'N, 83°43'W) and its songs were recorded on a Sony TCM-5000 cassette tape recorder with a Sennheiser ME-40 microphone in a 330-mm parabolic reflector. It was brightly colored with red underparts; the flanks were streaked but not the breast or most of the belly. The male repeatedly sang while perched and during slow flight displays away from his mate, which remained on a nest high in a spruce. This flight display is typically seen during courtship (Thompson 1960). The male fed the female near the nest. The same male apparently had nested earlier; he fed two grown fledglings perched 10–20 m from the nest, and the female joined them from the nest.

Songs were audiospectrographed at 300-Hz band on a Kay Elemetrics Co. Vibralyzer. The male had two recognizable song types or themes, and both were "mixed" with elements of two species, phrases ("tours") of canaries in the middle of the song and phrases typical of local House Finches at the beginning and ending of the songs (Fig. 1). The two song themes were given in irregular alternation and in approximately equal numbers. The canary tours were recognizable by rapid trilling of simple notes, in contrast to usual House Finch songs which do not repeat notes in series and which have longer, more complex notes (Mundinger 1975, Bitterbaum and Baptista 1979).

On 31 May 1987, RBP found more House Finches with canary tours, two neighboring males on the campus of the University of Michigan, 2.9 km from the area where the first male sang. Each had two similar recorded song themes; one theme had a canary tour introduction and the other had a tour in the middle. One theme is illustrated in Fig. 1; the other ("d") also was shared by the two House Finches, indicating a matching of song repertoires. One male was brightly plumaged, reddish, with heavy streaking below and had a metal band on one leg; the other was dull with a patch of pink on one side of the breast and was unbanded. Each male repeatedly accompanied its nest-building female to her nest. Other finches on campus had normal House Finch songs (theme "a" and other themes).

House Finches were first seen in Ann Arbor in 1981 and nested in 1982 (Payne 1983). In 1987, they were the most numerous songbird on campus and at least 200 pairs lived in Ann Arbor. Songs of six males were recorded in early spring during 1985, and 12 others were recorded in February and March 1987; none had canary elements.

Both the campus and residential House Finches may owe their canary tours to the same canary. In 1983, SW observed a banded canary feeding with several House Finches at an outdoor feeder on campus from late April through the summer. During summer, she captured it and released it on campus; she recaptured it again in early October. She moved it from the campus into a home, where it lived next to a window where wild House Finches visited a window feeder. The finches and canary often sang back and forth. The canary site is only 150 m from the nest of the residential canary-tour House Finch and 100 m from one of the finch's singing perches. The canary several times was seen flying toward the canary site from this perch. The tours in the mixed songs of House Finches on campus and in the residential area had notes like the suspect song-model canary, perhaps significant because canaries have many kinds of notes in their songs (Güttinger 1985). The canary's songs were recorded later.
House Finch

Canary

kHz

f1

mc3

mc1

mc4

mc2

mc4

c2

mf1

c1

f1

1.0 s

0
in 1987; it is uncertain whether its repertoire was completely sampled. Not only did the wild House Finches learn song elements from the canary, but the canary sang parts of the song of the House Finches as well as characteristic canary songs and had apparently learned these themes from the House Finches (Fig. 1; compare audiospectrograms of normal canary song in Güttinger 1985). The canary had the House Finch themes in its repertoire for at least a year.

The canary tours were apparently transmitted from one House Finch to another as well as between canary and House Finch, because the neighboring birds on campus had nearly identical mixed song themes. House Finches have occasionally learned the songs of other species in the field (Baptista 1972), and canaries and other cardueline finches sometimes imitate the notes and song organization of other species (Güttinger 1974, Remsen et al. 1982). The more brightly colored, banded House Finch on campus had some longer canary tours than any heard from the duller male. The plumage difference suggests that the younger copied the themes of the older; male House Finches in their first year tend to be less reddish than older males, though plumage colors of the age classes may overlap (Michener and Michener 1931).

Mundinger (1975, 1980) interpreted the microgeographic variation in song among House Finches on the east coast as a result of errors or “cultural mutations” in learning the songs of older individuals and with their subsequent dispersal and being copied themselves when they are the only song models in the neighborhood for younger finches. By this reasoning, we predict that the mixed-species song themes of the House Finches in Ann Arbor will degrade rapidly, because most neighboring finches have more species-typical songs. On the other hand, if House Finches learn from single song tutors, we predict a persistence of the mixed song themes in Ann Arbor.

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LITERATURE CITED


Fig. 1. Songs of House Finches and canaries in Ann Arbor, Michigan. a–f, House Finch; a, campus, 14 April 1985; b, c, two song themes of residential House Finch on 21 May 1987, with three canary tours; d, e, two song themes of a banded House Finch on 31 May 1987; f, one song type of an unbanded House Finch on 31 May 1987 (note resemblance of song themes e and f and perhaps also c, indicating song transmission between House Finches); g, song of a captive canary that had lived with wild House Finches; h, i, normal tours of the same canary, edited from longer themes. For evidence that House Finches copy canary song elements, compare m1 and c1 (b and i), m2 and c2 (d and g), and m1 and m4 with canary tours in Fig. 1 of Güttinger (1985); m3 is tentatively identified as a canary note because it is given in a tour like the other canary notes. For the canary copying House Finch song, compare the nonrepeated elements of g with song of a normal House Finch (a) and with Thompson (1960), Mundinger (1975), and Bitterbaum and Baptista (1979); and the terminal song element m1 (g) with f1 (a, d, and f) and with syllable 94 in Bitterbaum and Baptista (1979).
Sequential polyandry by a female Killdeer.—The Killdeer (Charadrius vociferus) is considered to be monogamous (Bunni 1959, Lenington 1980), with males taking a greater role in parental care than females (Mundahl 1982; Brunton 1987, 1988a, b). Female desertion of mate and nesting attempt has been observed in some populations, especially late in the breeding season or after a second clutch (Bunni 1959, Lenington 1980), but apparently is rare or absent in others (Brunton 1987). Reproductive success of deserted males generally is lower than that of pairs, but few data exist for comparisons (Lenington 1980, Brunton 1988a). Also, the subsequent behavior of deserting females rarely has been observed because of the difficulties of following these birds over a large area. Here I report the first documented case of a sequentially polyandrous female Killdeer.

I studied Killdeer in the Houghton Lake region of Michigan from April through August 1984 and 1985. Nesting attempts of 41 pairs of Killdeer were monitored, and 37 males and 27 females were captured and color banded. During the study, 66% (27/41) of all nesting pairs remained monogamous and stayed on the same territory throughout the breeding season. Pairs that failed in consecutive nesting attempts in a single year were more likely to change territories than those having a successful nesting ($x^2 = 16.2, P < 0.001$). During 1985, a pair color banded in 1984 was first observed on their territory on 11 April and their nest containing two eggs was discovered on 21 April. Incubation began on 25 April, and chicks hatched on 17 May. The female was last observed foraging in the territory on 20 May. The male (M1) continued to care for the chicks and successfully raised one chick to fledging. M1 remained on the territory but did not remate in 1985. On 18 May 1985, the female was observed copulating with an unmated male (M2) on a territory approximately 0.5 km away from where M1 was still caring for their offspring. M2 was banded during 1984 on the same territory. He returned alone and remained unpaired during 1985 up until the appearance of the female. On 22 May a nest containing three eggs was discovered. Both
members of this new pair incubated. The clutch, however, was depredated after ten days. The pair remained in the area performing nest building and territory defense until early August. It is possible that two other females also were polyandrous; they disappeared during brooding late in the breeding season, and their mates attempted to raise the offspring alone.

In sequential polyandry, the female forms a monogamous pair bond with a male, abandons him and their offspring, and then nests with a new male within one breeding season. The system is similar to sequential monogamy, except that female variance in reproductive success probably is larger than male variance (Daly and Wilson 1978). This is because males do not remate immediately but provide extensive parental care. Mating systems with greater female than male variance in reproductive success are rare (Emlen and Oring 1977, Lenington 1980), and, among higher vertebrates, occur only among birds (Jenni 1974) and humans (Daly and Wilson 1978). Sequential polyandry has been reported or suspected to occur in a number of shorebird species, including Spotted Sandpipers (Actitis macularia, Oring and Knudson 1972), Black-bellied Plovers (Pluvialis squatarola, Hustel and Page 1976), Wilson's Phalaropes (Phalaropes tricolor, Hohn 1967), and Willets (Catoptrophorus semipalmatus, Howe 1982). Theories explaining the evolution of sequential polyandry include factors such as predation rates (Graul et al. 1977), energetic costs of egg production and food availability (Oring and Knudson 1972, Faaborg and Patterson 1981), and biased sex ratio (Erckmann 1983). As with other forms of polyandry, sequential polyandry is suggested to have evolved from monogamy, through increasing male parental care and female desertion (Erckmann 1983, Oring 1985). The advantages of switching mates needs to be considered when explaining the evolution of sequential polyandry. Females may benefit from energy and time savings and be able to raise more offspring in a given period of time. They may also be in better condition for migration at the end of the breeding season (Oring and Knudson 1972; Maxson and Oring 1980; Brunton 1988a, b). The major disadvantage of abandoning a nest and mate is potentially lower offspring survival. This cost can be minimized by abandoning when offspring are more independent and less vulnerable (Brunton 1987). Female Killdeer have been observed to desert their mates and chicks (Bunni 1959, Lenington 1980). Male Killdeer perform a greater proportion of the parental activities than females, and this disparity between the sexes increases as the nesting cycle progresses (Brunton 1987, 1988a, b). Although only a single observation, the circumstances of the present case are consistent with the hypothesis that extensive male parental care and female desertion may be important factors in the evolution of polyandry.

Acknowledgments. — Financial support for this study was provided by the University of Michigan and Sigma Xi Grants-in-aid of Research. The Houghton Lake Waste-Water Treatment Authority, Roscommon County, gave permission to work on their land. The Department of Natural Resources of the State of Michigan provided lodging. For reviews of various drafts of this manuscript I thank S. Beissinger, C. Blem, J. Farley, B. Low, and an anonymous reviewer.

LITERATURE CITED


A hunting technique of the Black-and-white Hawk-Eagle (*Spizastur melanoleucus*).—The Black-and-white Hawk-Eagle ranges from Mexico to Argentina (Brown and Amadon 1968), but its hunting techniques have not been recorded. Wetmore (1965:265) noted that one collected at Chepo, Panama, “came with considerable force through high forest to strike at Araçari toucans that chattered and dashed about in the branches, much excited.” The Brazilian name, “gavião-pato” or “duck hawk,” suggests that it captures ducks. W. H. Partridge (fide Brown and Amadon 1968) reported it hunting Brazilian Mergansers (*Mergus octosetaceus*) and Olivaceous Cormorants (*Phalacrocorax olivaceus*) near Iguazu Falls, Argentina. Russell (1964) reported a collared Araçari (*Pteroglossus torquatus*) and a Scaled Pigeon (*Columba speciosa*) as prey for individuals collected in Belize. Alvarez del Toro (1980:43) added tinamous, chachalacas, guans and other large and wary animals. Sick (1985:213) listed toads and oropendolas. How the species catches large and fast-moving prey seems to be unknown.
On 29 July 1987, near the headquarters of the Ecological station of Serra das Araras (Macaw Mountains) in southwestern Mato Grosso, Brazil, I observed an individual hunting with a technique that could explain the above observations. The Serra das Araras are parallel mountain ridges, reaching 800-m elevation, and the station headquarters is at a T-fork of the Salobra River, on a long but narrow intermontane plain at 200-m elevation (15°38'S, 57°12'W). Dry riverine woodlands, open campos, and semi-open savannas (cerrado) give way to dry woodlands on the steep slopes of ridges on either side. The top of the ridge to the southeast is in cerrado or dry woodlands, and is a flat-topped narrow remnant of the “chapadas” or mesas of the Brazilian Shield. July is dry, and many trees are leafless. At 06:55 the screeches of a band of small Red-shouldered Macaws (Ara nobilis) called my attention to a plummeting closed-winged hawk-eagle, which looked small as a tityra until it alighted near the tight group of fleeing macaws. By circling, I could see the hawk-eagle well, atop a leafless snag of a tree near the clearing. It soon flew 200 m to the top of a tree near the fork of the river, still in plain sight. For over two hours it waited in upright posture, preening the upper back or base of the fairly long tail or upper breast at intervals or turning and looking about and below. At times it stood high and horizontal on long white-feathered legs, especially when it turned 180°. A pair of Purplish Jays (Cyanocorax cyanomelas) yelled at it from a distance the first ten or fifteen minutes, but gave up and moved to the clearing. Amadon and Eckelberry (1955) reported similar scolding by Brown Jays (Psilorhinus morio) in Mexico. At 09:07 the hawk-eagle flew off upriver (south) some 500 m, gaining a little elevation, and then turned and glided northwest downriver to a perch out of sight. At 09:23 it took wing again, flapping and soaring to the notch where the Salobra breaks through the ridge to the northwest. It then began to circle and soar on the northwest wind that had just started blowing up the south side of the notch. It quickly soared up past two King Vultures (Sarcoramphus papa) already using the updraft, high over the notch. On wide and long wings, it is better adapted to soaring than are Spizaetus species, which have broad but shorter wings.

The soaring bird drifted downwind over the plain to at least 400 or 500 m above the ground, as high as the ridge to the east, and 200 m over the ridge to the northwest. It then slightly folded its wings and began a slow drift northwest into the wind, losing little if any altitude, a speck in the sky moving gradually toward the forested ridge to the north of the notch. Once it nearly closed its wings and started to drop, but recovered and resumed the wide “M” folding of the wings and the slow drift upwind. Two minutes later, it folded the wings and plummeted out of the sky, passing the wooded face of the serra at great speed and disappearing through the bare treetops, undoubtedly a stoop after prey. J. M. Thiollay (in litt.) saw two unsuccessful dives through the canopy at cotingas, Ramphastos spp. and other birds at a fruiting tree in French Guiana, although he did not see the start of the dives. At 16:00 on 10 January 1988, along the tops of the cliffs just west of the tourist site at the geographical center of the continent (15°30'S, 55°30'W) near Chapada dos Guimarães, two hunting hawk-eagles were using updrafts to soar high over the forest. One hawk-eagle dove suddenly past the face of the mesa, soared upward and dove again to a tree over the abyss. It ran up a limb and looked down for 15 minutes, flew to the center of another overhanging tree, ran out on a limb to an exposed site for five minutes, and finally soared out of sight along the cliff. Active foraging from great heights resembles hunting in the Old World genus Hieraaetus, which Amadon (1982) considered morphologically similar to Spizaetus and possibly congenic. However, convergence is possible.

Foraging by stooping from great heights probably explains how this hawk-eagle can capture large and alert prey in the treetops or edges of forests. Its wings are too long to fly after prey through the forest in the manner of Accipiter spp. or Spizaetus spp. Its tail is long enough...
to be angled for last-second changes in direction after prey fleeing through the branches, but is too long for a bird that hunts by waiting for prey in the manner of many *Buteo* spp. or *Leucopternis* spp. I should note, however, that the Short-tailed Hawk (*Buteo brachyurus*) is also a soar-stoop hawk, soaring 100–200 m up and stooping abruptly past tree crowns at forest edges for small birds; probably it does not need a long tail to change course within the treetops.

This type of foraging also could explain why *S. melanoleucus* often occurs at forest edges. It would have less success detecting and chasing prey in dense, continuous foliage of unbroken forests. Cade (in McFarland et al. 1985:433) indicates that soar-stooping is used mainly by open-country raptors, so that use even at forest edges may be somewhat unusual. It may also be that updrafts at forest edges or along ridges could help *S. melanoleucus* soar upward. The Serra das Araras bird could have roosted atop the serra to make its first stoop of the morning, at an hour when winds were too weak to have carried it upward. It then had to wait almost three hours for its next attempt. Since semi-open habitats are usually settled and cleared very rapidly in the tropics, human interference may be a problem for this species.

The spectacular color pattern of this hawk-eagle perhaps would not alert the prey in time, or could even confuse it in the last-minute chase. I was struck that, when soaring, the hawk-eagle resembled a King Vulture. That species soars high also (Houston 1984), and occurs throughout the range of *S. melanoleucus* in the same habitats. *S. melanoleucus* has an unusual white forward margin atop the wings, well illustrated in a picture by Tony Luscombe (Clinton-Eittierie 1987) and very noticeable in the individuals I have seen. This margin suggests the white upper wing coverts of the King Vulture. Underneath, the two species are white except for relatively dark primaries and rectrices. Being smaller than the King Vulture, it would seem higher and more distant than it really is to an animal that mistakes it for one. Some other accipitrids are white below, however, including young *Hieraaetus* (Amadon 1982).

The young Cayenne Kite (*Leptodon cayanensis*) is colored surprisingly like *S. melanoleucus*, but lacks the white anterior wing margin and has barred black-and-white remiges. If it is a mimic, it perhaps resembles the larger and more dangerous species to avoid close mobbing by small birds or attacks by larger species that take it for a *S. melanoleucus*. I have not seen it soar-stooping, and indeed its prey are mostly small and not very wary species.

**Acknowledgments.**—I appreciate research support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) of Brazil, collaboration of Yoshiko Oniki of the Programa Polonoroeste (Universidade Federal de Mato Grosso), help from the Secretaria Especial do Meio Ambiente (SEMA, Brasilia) and from workers at the Estação Ecológica da Serra das Araras, and information from D. Amadon and J. M. Thiollay.

**LITERATURE CITED**


Post-breeding migration of Oilbirds. —There are few indications in the literature suggesting that Oilbirds (*Steatornis caripensis*) perform a post-reproductive migration, leaving their breeding caves at the end of the breeding season. Indirect evidence comes from the observations of Tannenbaum and Wrege (1978) and Snow (1979). The former two authors visited Cueva de Coy-Coy in western Venezuela in January 1977 and found only two birds from a colony that previously had a breeding population of several hundred birds. During a second visit in March 1977, they found at least 50 birds in the same cave. Tannenbaum and Wrege suspected that birds were beginning to return to the cave in March for their annual breeding. In the Los Tayos Cave in Ecuador, Snow (1979) estimated a population of 170 Oilbirds in July 1976, which declined by August to approximately 13 birds. Snow visited the cave near the end of the breeding season and estimated from the number of chicks harvested by the local Indians, in April of the same year, that the Los Tayos population could have been at least 1500 birds.

The postbreeding exodus from Los Tayos, and possibly Coy-Coy, was in sharp contrast to the behavior of these birds in Trinidad where Snow (1961, 1962) carried out a long-term study of a small colony. There, Oilbirds occupied their nesting ledges throughout the year. Snow (1979) indicated that many birds also are always present at the Caripe Cave in eastern Venezuela. The purpose of the present note is to document a massive postbreeding migration of Oilbirds from their breeding site at the Caripe Cave.

The Caripe Cave or Cueva del Guacharo, the site of Humboldt’s (1833) description of the species, hosts one of the largest known Oilbird populations. Although there are no reliable censuses of this colony, estimates of its numbers have been as high as 20,000 birds (De Bellard Pietri 1979). Since May 1985, we have visited the cave at monthly or bimonthly intervals. During the last three breeding seasons, the bulk of egg laying occurred in late April and May, but eggs occasionally were laid as early as mid-March and as late as mid-July. Most nests had nestlings by July and August and fledging occurs from mid-August through early September. Few birds fledged as late as the end of September. This breeding schedule is roughly similar to that observed by Tannenbaum and Wrege (1978) during 1976 in the same cave.

Population density at the Caripe Cave is highest during the breeding period, probably reaching 10,000 birds or more, but we have not found a reliable way to count them at these times. However, we counted the birds at times when their numbers were lower, and observed dramatic declines in density during the nonbreeding season. Birds start leaving the cave at sunset for their nightly foraging and return to it before sunrise. Our population estimates, using hand counters, have been made by counting the birds that leave the cave during the first hour of their departure. Since not all birds left the cave, a walk through the initial 700-m
chamber, where birds are, was made at the end of the counting period, when possible, and the number of birds remaining was estimated.

By November 1985, a dramatic decline in birds was evident, and we estimated a population of 200 birds on 12 November. Birds were counted on the nights of 15, 18, and 20 December when 80, 192, and 150 birds, respectively, departed from the cave during the first hour. Population size remained low during early 1986 as evidenced by a count made on the night of 4 January. Two observers counted 94 and 96 birds each during the first hour of departure and estimated that 25 and 30 birds remained inside the cave, indicating a total population of around 125 birds. By February, large numbers of birds had returned to the cave. On the night of 17 February, two observers counted 3198 and 2902 individuals during the first hour of the birds' departure. A walk through the main chamber indicated that at least several hundred birds remained inside. By March the number of birds in the cave was again so high that it was not possible to count them.

During 1986, the postbreeding exodus occurred later than in the previous year. On the night of 16 November we counted 976 individuals during the first 7 min of the birds' departure. We then stopped because we were unable to count the large number of birds coming out of the cave. Several thousand birds remained inside. A large population decline was evident on the night of 21 December when we counted 279 birds during the first half hour of the departure, before it became too dark and misty for seeing the birds. At that time the echolocation clicking of a few departing birds could still be heard. Probably another 200 or 300 birds remained in the cave. We were not able to count the birds in January or February 1987, but their numbers were high again in March, prior to their annual breeding.

Those observations indicate that a large post-breeding exodus occurs from the Caripé Cave similar to that suspected to occur at Cueva Coy-Coy, Los Tayos, and possibly Cueva de los Güácharos in Colombia's Cordillera Oriental (Kyshakevych 1983). We have not been able to assess if this migration is an occasional phenomenon or if it is a recurrent event in the birds' life. Questioning of the cave guides that have worked there for decades has provided contradictory information. Tannenbaum and Wrege (1978) did a detailed study of Oilbirds from early May through November 1976, with a second study period in January 1977, in the Caripé Cave and made no reference to a large exodus from the cave. It is possible, then, that postbreeding migration is a more recent event, or that it does not occur every year.

Where Oilbirds migrate, or the causes of their movement are not precisely known. The Caripé Cave is located within an extensive karst area that extends for tens of kilometers along northern Monagas State, where 20 other caves with Oilbirds have been explored so far (Bosque 1978, 1986). Some of those caves also contain colonies of several thousand birds. Thus, it is likely that extensive migrations occur between caves in that region. Lack of adequate food supply has been suspected to be an important factor in determining the birds' movement. Tannenbaum and Wrege (1978) speculated that food supply was insufficient to support the Coy-Coy colony throughout the year and Snow (1979) considered that changes in the birds' diet at Los Tayos suggested a food shortage within an energetically economic foraging distance from the cave.

In the Caripé Cave, the fruits of Lauraceae, Burseraceae and Palmae are the main food supply during the breeding season, but during the nonbreeding season birds rely mostly on palms (Tannenbaum and Wrege 1978, unpubl. data). Tannenbaum and Wrege concluded that the enormous Güacharo colony could coexist with agricultural activities in the surroundings. In the Caripé area, agriculturists selectively spared certain lauraceous trees to shade their coffee plants, and those trees support the birds during the breeding season. In contrast, palms have been cleared from the area; the number of palms remaining near the cave at the time of Tannenbaum and Wrege's (1978) study was very low. Agricultural activities have been intensified since then. If postbreeding migration is a recent event, it
suggests rapidly deteriorating foraging conditions that could eventually threaten the Caripe colony. The existence of local movements of Oilbirds has important consequences on the design of conservation strategies for this species as refuge areas created around caves might prove to be insufficient for its proper conservation.

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LITERATURE CITED


The shoulder spot in Gray Partridge.—The shoulder-spot display has been described in all grouse species (Tetraoninae), except several species of ptarmigan (Lagopus spp.) and the Hazelhen (Tetrastes bonasia) (Hjorth 1970, Lumsden 1970, Garbutt 1981, Jamieson 1983). However, the shoulder-spot display has not been described for other species within the family Phasianidae.

In grouse, the shoulder spot consists of a small light-colored patch of feathers on the
Lig. 1. Gray Partridge displaying shoulder spot during handling.

shoulder area of the bird that may be exposed by shifting the position of underwing coverts on the patagium to an exposed position on the upper surface of the wing (Lumsden 1970, Garbutt 1981). These feathers usually are white or gray in color and contrast with the darker color of the bird's contour feathers (Fig. 1). The shoulder spot occurs in both sexes of many species and is variable in size among species (Lumsden 1970). In grouse, the shoulder-spot display is thought to have evolved from flight intention movements as a signal of fear. In some species the display is also associated with intraspecific aggression and courtship (Lumsden 1970).

The Gray Partridge (Perdix perdix), introduced to the northern plains of North America during the early 1900s, is now distributed widely across the northern prairie region (Potts 1986). While trapping Gray Partridges in North Dakota during the winters of 1985-1987, I observed many trapped partridges displaying shoulder spots. Observations were made while the birds were in baited walk-in funnel traps similar to those described by Gaither (1969). Partridges were generally not alarmed while in the trap, and I observed many birds feeding and roosting. When I approached the traps, birds on the outside would quickly flush while those inside attempted to escape by flying, then running, along the trap margin. It was during this time that some birds displayed a shoulder spot. Several individuals also displayed while being handled. During 1986, a sample of 9 of 10 partridges captured from four coys displayed a shoulder spot while in the trap or during handling. Both sexes and both adults and subadults were observed to display. Four partridges raised in captivity revealed shoulder spots when disturbed by human presence in the pen area. However, not all birds in a pen displayed simultaneously, and use of display or size of the spot was not related to level of disturbance. The display was not observed during aggressive interactions between captive males. Jenkins (1961) and Beani and Dessi-Fulgheri (1984, 1986) did not report seeing a
shoulder-spot display during their observations of behavior in partridges. In all cases that I observed, the shoulder spot appeared to be a fear or flight intention display as described by Lumsden (1970). However, the display seemed secondary in importance compared to vocalizations and "tail flicking" during periods of extreme alarm. Examination of the shoulder spot of a partridge confirmed the realignment of white underwing coverts to the top of the wing in the patagial region. The manipulation by the bird of underwing feathers appeared to be identical to that of Ruffed Grouse (Bonasa umbellus) (Garbutt 1981). Since "display" implies actual communication between individuals further investigation is needed to determine if, in fact, the shoulder spot actually is serving a communication function in Gray Partridge.

The shoulder spot in Gray Partridges and the display seen in grouse are morphologically similar. Lumsden (1970) concluded that the widespread occurrence of this display among grouse indicated it appeared relatively early in evolution. The morphological and behavioral similarities between the display in grouse and partridges suggest that the shoulder spot may have evolved even earlier. Since this is an escape behavior, and since many species of partridges and pheasants are difficult to observe in the wild, it may have been overlooked.

Acknowledgments.—These observations were made while the author was supported by funds from the North Dakota Game and Fish Department through Pittman-Robertson Project W-67-R. Additional support was provided by the Biology Department and Institute for Ecological Studies at the University of North Dakota. Helpful editorial comments were provided by R. Crawford, S. Haig, C. Gratto, and F. Zwickel.

LITERATURE CITED


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Head-scratching method in swallows depends on behavioral context.—Birds scratch the head by raising the foot dorsal to the lowered wing (overwing or indirect method) or by passing the foot ventral to the folded wing (underwing or direct method). The adaptive significance of the two methods has puzzled ornithologists since Heinroth (1917) first de-
scribed the behavior. Intraspecific variation appears rare (Simmons 1961, Burtt 1983) and confined to ontogenetic changes from underwing to overwing head-scratching, to captive or injured birds that revert from overwing to underwing head-scratching, and to rare, isolated underwing head-scratching in species that normally head-scratch over the wing (Burtt and Hailman 1978). Only the Black-and-white Warbler (Mniotilta varia, Burtt 1980) and Hairy Woodpecker (Picoides villosus, Dunham 1963) have been seen using both head-scratching methods interchangeably. Individuals of both species were preening when observed, but preening is the behavioral context most often associated with head-scratching (Burtt and Hailman 1978). Observations of swallows suggest that, in flight, underwing head-scratching is used by healthy, adult birds that head-scratch over the wing in other behavioral contexts.

Our data are based on field observations by Burtt in Delaware County, Ohio from 1978 to 1987; by Bitterbaum in Florida, Trinidad, Tobago, and Mexico from 1977 to 1980; and by Hailman throughout North America and the West Indies from 1960 to 1987. The data are presented taxonomically according to the A.O.U. Check-list (1983), supplemented by Meyer de Schauensee (1970).

When perched or standing on the ground, all species of swallows listed in Table 1 head-scratched over the wing. Head-scratching was relatively rare, but occurred most often during maintenance behavior and less often during resting, vocal, or locomotory behavior. In Delaware County, head-scratching was most frequent from mid-July through August and may be associated with molt of the head feathers as observed in Kirtland’s Warbler (Dendroica kirtlandii, Mayfield 1960). Alternatively, swallows congregate in mixed-species, premigratory flocks from mid-July through August when head-scratching may be more easily observed than at other times of the year.

On eleven occasions flying swallows were observed scratching their heads (Table 1). While head-scratching, swallows glided with the wings stretched horizontally or down to 10° below the horizontal. The tail was depressed 30-40° below the horizontal, the head was lowered and turned so that the side to be scratched was toward the extended foot. The foot was extended forward ventral to the wing and the shoulder in a position analogous to that of underwing head-scratching in perched birds. The foot not scratching remained tucked into the ventral plumage. Head-scratching in flight followed in-flight bathing on 5 of 6 occasions observed by Burtt, but was not limited to such occurrences as illustrated by one Tree Swallow (Tachycineta bicolor) observed head-scratching while gliding over a field.

Head-scratching with the wings extended may not be analogous to head-scratching when perched with the wings folded. Nonetheless, swallows extend the leg ventral to the shoulder during in-flight head-scratching, whereas perched swallows extend the leg dorsal to the shoulder during overwing head-scratching. Furthermore, swallows can glide with the wings depressed 30° below the horizontal, a negative dyhedral that would seem to allow overwing head-scratching in flight. Thus, head-scratching in flight resembles underwing head-scratching, and swallows appear capable of reaching over a depressed wing while gliding.

Swallows commonly drink and bathe on the wing, dipping into the water from an extended glide then rising into the air on rapidly flapping wings and shaking the entire body (Slessers 1970, Wolinski 1985, Burtt pers. obs.). Parents also feed fledged young while in flight. Parent and young approach, hover, and exchange food (Burtt 1977, Hailman pers. obs.). Such complex aerial behavior suggests that the method of aerial head-scratching is not restricted by behavioral limitations of flight.

Without exception, all observations of perched or standing swallows are of overwing head-scratching (Table 1). Thus overwing head-scratching appears to be the usual method among perched swallows. Six of 12 species have been observed head-scratching in flight and all six species used the underwing method (Table 1). Two species have been seen head-scratching in flight more than once (Table 1) and all observations were of underwing head-scratching.
### Table 1
**Comparison of Head-scratching Method in Perched and Flying Swallows**

<table>
<thead>
<tr>
<th>Species</th>
<th>Perched</th>
<th></th>
<th>In flight</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Underwing</td>
<td>Overwing</td>
<td>Underwing</td>
<td>Overwing</td>
</tr>
<tr>
<td>Purple Martin <em>(Progne subis)</em></td>
<td>0</td>
<td>29</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Caribbean Martin <em>(P. dominicensis)</em></td>
<td>0</td>
<td>0</td>
<td>X*</td>
<td>0</td>
</tr>
<tr>
<td>Gray-breasted Martin <em>(P. chalybea)</em></td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tree Swallow <em>(Tachycineta bicolor)</em></td>
<td>0</td>
<td>17</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>White-winged Swallow <em>(T. albiventer)</em></td>
<td>0</td>
<td>52</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Violet-green Swallow <em>(T. thalassina)</em></td>
<td>0</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Blue and White Swallow <em>(Pygochelidon cyanoleuca)</em></td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Northern Rough-winged Swallow <em>(Stelgidopteryx serripennis)</em></td>
<td>0</td>
<td>13</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Southern Rough-winged Swallow <em>(S. ruficollis)</em></td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cliff Swallow <em>(Hirundo pyrrhonota)</em></td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cave Swallow <em>(H. fulva)</em></td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Barn Swallow <em>(H. rustica)</em></td>
<td>0</td>
<td>23*</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>0</td>
<td>163</td>
<td>11*</td>
<td>0</td>
</tr>
</tbody>
</table>

* Observed, but number unknown; C. R. Brown pers. comm.
* Wolinski 1985
* One observation was of a Barn Swallow standing on a road sunbathing when it head-scratched over the wing.

Thus underwing head-scratching appears to be the usual method among flying swallows. These data indicate that head-scratching method in swallows is context-dependent.

Earlier studies (Heinroth 1917, 1930; Lorenz 1950; Burtt and Hailman 1978) showed that all variation in head-scratching method was among species that normally head-scratch over the wing, but as nestlings, when captive or injured, or on rare occasions, head-scratched under the wing. Such consistency in the pattern of variation suggests that underwing head-scratching is primitive and overwing head-scratching derived. But what is the adaptive significance of the alternative head-scratching patterns? Swallows head-scratch over the wing while perched and under the wing while flying. The center of gravity is above and between the feet while perched, below and slightly behind the wings while flying. The swallow's shift in head-scratching method associated with its shift in center of gravity relative to its loco-
motory systems suggests that subtle differences among species' center of gravity may explain
the adaptive significance of interspecific differences in head-scratching method.

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The usefulness of taped Spotless Crake calls as a census technique.— Playing taped calls
of Spotless Crakes (Porzana tabuensis) has been used successfully to determine the presence
of crakes and to identify the habitat they use in New Zealand (Ogle and Cheyne 1981). In
this study, calls of Spotless Crakes were broadcast throughout the breeding season at given
locations to evaluate the crake's consistency of reaction to taped calls. This study was
conducted at Pupekuke Lagoon, an 86-ha management reserve of the New Zealand Wildlife
Service in the Manawatu district of the North Island, New Zealand, latitude 40°20'S, lon-
Table 1

<table>
<thead>
<tr>
<th>Time (min)</th>
<th>0-1</th>
<th>1-2</th>
<th>2-3</th>
<th>3-4</th>
<th>4-5</th>
<th>5-6</th>
<th>6-7</th>
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</thead>
<tbody>
<tr>
<td>No. responses</td>
<td>42</td>
<td>31</td>
<td>26</td>
<td>23</td>
<td>22</td>
<td>11</td>
<td>38</td>
</tr>
<tr>
<td>% of total</td>
<td>22%</td>
<td>16%</td>
<td>13%</td>
<td>12%</td>
<td>11%</td>
<td>6%</td>
<td>20%</td>
</tr>
</tbody>
</table>

Table 2

<table>
<thead>
<tr>
<th>Type of call</th>
<th>No. responses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soft calls (&quot;bubblings&quot; and &quot;murmurings&quot;)</td>
<td>65</td>
</tr>
<tr>
<td>Intermediate (&quot;pit-pits&quot; and whistles)</td>
<td>40</td>
</tr>
<tr>
<td>Intermediate and soft</td>
<td>32</td>
</tr>
<tr>
<td>Loud (&quot;purrs&quot;)</td>
<td>15</td>
</tr>
<tr>
<td>Loud and soft</td>
<td>22</td>
</tr>
<tr>
<td>Loud and intermediate</td>
<td>7</td>
</tr>
<tr>
<td>Loud, soft, and intermediate</td>
<td>13</td>
</tr>
</tbody>
</table>

Latitude 175°16'E. Dominant emergent plants within this marshland are raupo (Typha orientalis), flax (Phormium tenax), tussock sedge (Carex secta), and cabbage tree (Cordyline australis). The vegetation, climate, and history of the lagoon have been described by Ogden and Caithness (1982). Taped calls of Spotless Crakes were played for 6.5 min at slightly greater than normal amplitude at 45 stations from 14 September to 14 December 1982 for a total of 13 times. Maximum amplitude one m from the source was 90 db. The stations were approached carefully by walking on pathways or boardwalks about the swamp, and by rowing along the swamp edge of the lagoon. Tapes were played consecutively from stations 1 through 31 in the morning and usually in the evening (occasionally mornings) at stations 32 through 45. On land, I walked 5-7 m away from the tape recorder to listen; in the boat I turned down the amplitude of the tape recorder at frequent intervals to listen. This tape is listed in the N.Z. Wildlife Service sound library catalogue as checklist No. 136, reel No. 71, Spotless Crakes—Whangarei. The tape segment used consisted of five loud "purrs" in the first min, 35 soft "pips" the next 25 sec, followed by 279 moderately loud calls, mostly "pit-pits," during the following 5 min, and ended with a second series of loud "purrs." These descriptive terms of Spotless Crake vocalizations are from Hadden (1970) and Kaufmann and Lavers (1987). Tapes were played at the stations on the least windy day of each 7-10 day period.

The adjoining areas of marsh, especially raupo and tussock sedge, were searched for nests with the help of A. Grant, several members of the Faunal Survey crew, and my son Matthew. Active nests were checked regularly, and several were observed from a blind. In this way the extent of crake response could be correlated with the stage of their breeding cycle.
Spotless Crakes varied in time to respond to taped calls, the kinds of calls given, their intensity, and their frequency. The initial response of the crakes was most frequently given during the first minute of tape playing (Table 1). Fewer responses were given as tape playing progressed, until the end, when nearly as many birds responded as during the first minute.

In one instance the tapes were played continuously for 21 min before a response was given. At times, the tape did not elicit a response but appeared to make the crakes more sensitive to disturbance. For example, walking from station 15 to 16 required passing stations 12 and 13. Several times crakes called as I walked by these stations even though they had remained silent during the playing of tapes there.

The Spotless Crakes usually responded with calls of low amplitude; "bubblings" and "murmurings" were soft and low, "pit-pits" and short whistles were intermediate, and "purrs" were loud. The main exception were the "purrs," which became more variable in form and amplitude toward the end of the study. Less than one-third of the responses contained loud calls (Table 2). For this reason, the broadcasting of calls was restricted to calm days.

While some birds called as they were approaching the recorder, others did not respond until after they had approached the edge of the swamp vegetation. Some birds, which were responding close to the recorder, appeared to return to the center of their territory before giving loud "purrs." Some of the birds which interacted with the tapes during the "pit-pits" appeared intimidated by the second series of loud "purrs" and ceased calling. However, the
large number of responses during the first minute and after the last minute of taped calls coincided with the “purrs” on the tape recording.

Stage of breeding cycle was the most significant cause of variation in responding to tapes. Nesting pairs responded quickly, vigorously, and continuously to calls broadcast during the two weeks prior to egg laying. Once incubation began they did not call, although several times splashings were heard. After their eggs hatched, they answered the calls sporadically, with soft or intermediate calls of short duration. One pair of crakes never responded to tapes. The behavior of this pair suggests crakes may not respond during renesting, since two months prior to finding their active nest, I located two empty nests nearby. The large number of responses obtained from the 22 September to 27 October indicate this is the major pre-incubation period at Pukepuke Lagoon (Fig. 1). In contrast, the response rate of Soras (P. carolina) to recordings played weekly peaked at the beginning of egg laying and steadily diminished thereafter (Johnson and Dinsmore 1986).

Water levels may influence the concentration of crakes and thereby affect their response to tape recordings. A large number of Spotless Crakes responded to taped calls 21 October when the water level in the lagoon was at its lowest. Multiple responses, often resulting in interactions between birds, were most frequent that day, and the largest number of birds appeared at the edge along the lagoon.

The full roles of the sexes in calling has yet to be determined. I assumed that soft calls, such as “bubblings,” “murmurings” and whistles performed by two birds close together, often in a duet, were made by members of a pair. I assumed that loud calls, such as “cracks” and “purrrings,” were performed by males, as these were followed by chasing and fighting when two birds were close together.

One or two Marsh Crakes (P. pusilla) responded to tapes of Spotless Crakes at two stations on four occasions. Marsh Crake calls were broadcast on the dark, calm evenings of 22 September and 26 October and the morning of 25 October. No Marsh Crakes responded and only two (possibly five?) Spotless Crakes responded weakly at the cessation of the Marsh Crake tape broadcast. The Spotless Crakes appeared unstimulated, if not intimidated, by the Marsh Crake calls. In contrast, Glahn (1974) found that Virginia Rails (Rallus limicola) and Soras responded equally well to conspecific and interspecific calls during the breeding season in the western U.S. However, Johnson and Dinsmore (1986) found that the Sora’s call could be used to count both species during the prelaying season in central U.S., but during the postlaying season best results were achieved by alternating broadcast calls of the two species. Virginia Rails respond as readily to broadcast calls of the other species as well as their own (Glahn 1974). Greise et al. (1980) used a sequence of alternating calls of both species, incorporating 1 min listening periods between calls, to census rails in Colorado. The difference in responses to taped calls between Spotless and Marsh crakes may have been caused by the low population density of Marsh Crakes at Pukepuke Lagoon.

To standardize census methods I suggest: (1) the use of the same recording having a variety of calls including several bursts of purrs; (2) playing recording for 5 min; (3) using a slightly above-normal amplitude; (4) using 1 min breaks during the recording as silent listening periods; (5) playing recordings on calm mornings; (6) playing during the peak of the breeding season, mid-September to mid-October; and (7) only one person should make each census to avoid frightening crakes.

Acknowledgments.—I am indebted to many people of the N.Z. Wildlife Service for support, encouragement, and ideas, particularly Adams and Crawley for logistic support and use of Pupeke facilities; Williams for making the arrangements and reviewing this manuscript, and Grant for helping with field work; and all those who made us welcome during our stay. P. Barber allowed free access through his property. The Loras College Environmental Research Center provided funds for films and use of some field equipment.
LITERATURE CITED


Notes on Hooded Merganser nests in the coastal plain of South Carolina.—Densities of breeding Hooded Mergansers (Lophodytes cucullatus) in the southeastern United States are low (Bellrose 1980), and information on their breeding biology is limited. We document the frequency of nesting at a site located in the Coastal Plain of South Carolina, examine the relationship between fresh egg mass and duckling mass, and report sex ratios of hatching broods. We also report changes in body mass of two female Hooded Mergansers during incubation.

Study area and methods.—Nest boxes were erected for Wood Ducks (Aix sponsa) in the mid-1970s on the Department of Energy's Savannah River Plant (SRP) in western South Carolina. Twenty-six nest boxes were placed along a 2.5-km portion of Upper Three Runs Creek, a mixed-hardwood swamp forest typical of the southeastern coastal plain (Sharitz et al. 1974). Nest boxes (N = 41–47) also were available in Steel Creek, a section of the Savannah River swamp recovering after the termination of thermal stress from nuclear reactor effluent (McCort 1987). Additional nest boxes (N = 30–59) were located in Carolina bays (see Richardson et al. 1981). Variation in the number of available boxes was due to additions and removals. From 1982–1988, all nest boxes were checked weekly from late January to early July. Length (mm) and breadth (mm) of Hooded Merganser eggs were noted. Fresh egg mass (nearest 0.1 g) of unincubated eggs was recorded with a digital balance. Nesting females were captured, banded, and body mass was recorded during early incubation. Eggs were candled to determine incubation stage and nest initiation date. Females were recaptured when eggs were pipping to measure body mass. Ducklings were web-tagged in pipping eggs (Alliston 1975) to examine the relationship between egg mass and duckling mass. Duckling mass was recorded before the protective keratin sheath on most feather tracts had been preened off. Ducklings were sexed by cloacal examination.

Linear regression of egg dimensions on fresh egg mass was performed with the Statistical
Table 1

CHARACTERISTICS OF HOODED MERGANSER NESTS IN SOUTH CAROLINA

<table>
<thead>
<tr>
<th>Initiation date</th>
<th>Mean egg mass (g)</th>
<th>Clutch size</th>
<th>Clutch mass (g)</th>
<th>Duckling mass (g)</th>
<th>Female mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 Mar 85</td>
<td>60.6 ± 1.1</td>
<td>8</td>
<td>484.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24 Feb 87</td>
<td>59.3 ± 0.9</td>
<td>10</td>
<td>593.1</td>
<td>35.7 ± 0.6</td>
<td>565</td>
</tr>
<tr>
<td>28 Feb 87</td>
<td>58.6 ± 0.7</td>
<td>11</td>
<td>645.1</td>
<td>35.9 ± 0.5</td>
<td>515</td>
</tr>
<tr>
<td>10 Mar 88</td>
<td>59.6 ± 1.1</td>
<td>11</td>
<td>655.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Values are means ± 1 SE.

**Mass recorded <12 hours from hatching.

***Body mass from early incubation (< day 9).

Analysis System's general linear models procedure (SAS 1985). Spearman's correlation coefficient was used to describe the relationship of duckling mass and egg mass, and a Wilcoxon Two-sample Test was used to test for differences between sexes in duckling body mass at hatching. Values presented are means ± 1 SE and statistical tests were considered significant at the 0.05 probability level (P < 0.05).

Results and discussion. —Hooded Merganser nests were found in 1983 (1), 1985 (1), 1987 (2), and 1988 (1). Nest-box use by Hooded Mergansers averaged 0.6 ± 0.2% of available boxes. Similar results were reported in central Georgia (Odom 1970), where only one successful Hooded Merganser nest was found among 194 available nest boxes.

On the SRP, one female Hooded Merganser produced clutches in 1985 and 1987 along Upper Three Runs Creek. Three females nested in Steel Creek boxes, and three nests incubated by Wood Ducks contained Hooded Merganser eggs. No Hooded Merganser nests were found in Carolina bays, although these areas were used extensively by nesting Wood Ducks. Hooded Mergansers prefer nesting adjacent to water (Morse et al. 1969). Many Carolina bays dry by mid-to-late summer, and therefore, may not provide suitable habitat near the nest boxes. Clutch size of Hooded Mergansers nesting on the SRP averaged 10.0 for four nests (Table 1). In Maryland, clutch size of four successful nests averaged 10.0 (McGilvrey 1966). Morse et al. (1969) reported clutch size of adults (10.8) and first-year breeders (9.4) in Oregon. Length (L), breadth (B), and fresh mass (M) averaged 53.6 ± 0.3, 43.7 ± 0.1, and 59.0 ± 0.6, respectively, for 26 eggs. The equation: M = -0.389 + 0.00058(LB^2), R^2 = 0.91, P < 0.0001, was used to estimate mass of eggs that were incubated (N = 16), and actual fresh mass was unavailable. Clutch mass of four completed clutches averaged 594.7 g (Table 1). The eggs of Wood Ducks are considerably smaller (43.9 g), but because of larger average clutch size in Wood Ducks (Bellrose 1980), clutch masses do not differ greatly (Wood Duck: 610.5 g) (Kennamer and Hepp 1987).

Two of the five nests were successful in producing ducklings, and 95% of the eggs in successful nests hatched. The eggs of one unsuccessful nest were punctured, probably by a Red-headed Woodpecker (Melanerpes erythrocephalus) observed leaving the nest box. Eggs of another nest were consumed by a black rat snake (Elaphe obsoleta). A third nest was predated by a raccoon (Procyon lotor). In two successful nests, 60% of the ducklings were males. Body mass of males (N = 11) and females (N = 7) did not differ (P > 0.58) at hatching. Duckling mass prior to leaving the nest averaged 35.8 g and was correlated positively with egg mass (r = 0.88, P < 0.0005).

One nesting female had a body mass of 565 g when captured on day 9 of incubation. This female incubated for 34 days and by hatching had lost 13.3% of the first recorded mass.
Another female was captured on day 4 of incubation and had a body mass of 515 g. This female lost 8.7% of her initial body mass during a 33-day incubation period. Our data, though limited, indicate that female Hooded Mergansers lose relatively little body mass during incubation compared to other North American anatids (see review, Gatti 1983).

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LITERATURE CITED


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Nonfish prey of wintering Bald Eagles in Illinois.—Many Bald Eagles (Haliaeetus leucocephalus) winter in Illinois (Fawks 1979), where they feed primarily on fish (e.g., Southern 1966, Fischer 1982, Harper 1983). However, few reports have been published documenting their use of mammalian and avian prey in the midwestern United States (Lingle and Krapu 1986, Stalmaster 1987). This paper describes the almost exclusive use of nonfish prey in an upland population of Bald Eagles, and discusses related management implications.
Table 1

| Prey Items Determined from 489 Bald Eagle Pellets Collected in 1981-1985 from Two Upland Night Roosts in Illinois |
|--------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------|
| **Number of pellets containing prey** | **Percent of pellets containing prey** |
| Birds | | |
| Unidentified Passeriformes | 17 | 3.5 |
| Eastern Meadowlark (*Sturnella magna*) | 4 | 0.8 |
| Ring-necked Pheasant (*Phasianus colchicus*) | 2 | 0.4 |
| Mammals | | |
| Domestic Pig (*Sus scrofa*) | 362 | 74.0 |
| Eastern Cottontail (*Sylvilagus floridanus*) | 196 | 40.1 |
| Eastern Fox Squirrel (*Sciurus niger*) | 13 | 2.7 |
| Opossum (*Didelphis marsupialis*) | 7 | 1.4 |
| Eastern Grey Squirrel (*Sciurus carolinensis*) | 3 | 0.6 |
| Domestic Cow (*Bos taurus*) | 3 | 0.6 |
| Raccoon (*Procyon lotor*) | 2 | 0.4 |
| Prairie Vole (*Microtus ochragaster*) | 2 | 0.4 |

* Some pellets contained more than one prey item.

During the winters of 1981–1985, regurgitated pellets were collected from two Bald Eagle night roosts. The roosts were located in Pike County, Illinois, 13 and 20 km from the Mississippi River in upland forests dominated primarily by oaks (*Quercus* spp.) and maples (*Acer* spp.). Both roosts combined were used by as many as 90 eagles in one evening. The remains of eight species of mammals and five species of birds were identified in 489 pellets; 99.2% (485/489) of the pellets contained mammals, and 5.3% (26/489) contained birds (Table 1). We never saw eagles attempting to capture live prey, but we often observed them scavenging carrion. As many as 30 eagles were seen feeding on domestic pig (*Sus scrofa*) carcasses at one time in the vicinity of both roosts, which were located in close proximity to livestock operations. All prey except pigs, domestic cows (*Bos taurus*), and voles (*Microtus* spp.) were observed as road kills in areas frequented by eagles. Although no remains were found in pellets, we also saw eagles feeding on skinned carcasses of Coyotes (*Canis latrans*) discarded by trappers. A bias toward nonfish prey species may exist in our pellet analysis as fish skeletons are more completely digested than those of other vertebrates (Todd et al. 1982). However, in approximately 1000 h of observations on foraging eagles, none was seen to feed on fish. In addition, fish were unavailable to the eagles because streams in the immediate area were completely frozen during the winters. This corroborates our data from pellet analyses that mammalian species were the primary prey rather than fish.

There are two implications related to these findings. First, eagles may die from secondary poisoning if livestock have been treated with pesticides. Farmers often use organophosphate insecticides in autumn for control of warbles in livestock (Henny et al. 1985). DeVries (pers. comm.) stated that in 1984 five Bald Eagles died in Iowa after scavenging domestic pigs treated with the pesticide fenthion. Second, upland areas should not be excluded when censusing wintering Bald Eagles (also see Russell 1968). In 1984 we saw 100 eagles in one
upland area of Illinois shortly after the midwinter Bald Eagle census conducted by the National Wildlife Federation. Since this census covered areas primarily along the Mississippi and Illinois rivers, eagles in upland habitat may not have been counted, resulting in an inaccurate estimate of eagles wintering in Illinois.

Acknowledgments.—We thank C. Thompson, N. Drilling, D. James, G. Krapu, and J. Harper for making comments on this manuscript.

LITERATURE CITED


Breeding-season diet of Northern Saw-whet Owls in southwestern Idaho.—The Northern Saw-whet Owl (Aegolius acadicus) is a common inhabitant of forested lands from central Canada south to the central United States (Godfrey 1986). Despite its wide range, very little is known of its breeding biology (Cannings 1987). Catling (1972) noted that food habits data from the breeding season are "very meagre." Indeed, we know of only one large sample of Northern Saw-whet Owl food habits from the breeding season (Cannings 1987).

Eight Northern Saw-whet Owl nests (1 in 1986 and 7 in 1987) were found in the Snake River Birds of Prey Area (BOPA) in southwestern Idaho. Unlike typical Northern Saw-whet Owl nesting habitat, the vegetation of the BOPA is shrub-steppe desert dominated by big sagebrush (Artemisia tridentata). Trees are scarce and are confined to watercourses and farm settlements. All Northern Saw-whet Owl nests were in nest boxes, either in native riparian willows (Salix sp.) or in groves of exotic Russian olives (Elaeagnus angustifolia) and black locusts (Robinia pseudoacacia). Three of the nesting females in 1987 mated with the same male (Marks et al., unpubl. data).

We present data on diet composition and prey size of these owls during the breeding
Table 1

<table>
<thead>
<tr>
<th>Prey</th>
<th>Weight (g)</th>
<th>No. of prey</th>
<th>Percent of total</th>
<th>Total prey biomass (g)</th>
<th>Percent of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sorex sp. (shrew)</td>
<td>6</td>
<td>2</td>
<td>0.3</td>
<td>12</td>
<td>0.1</td>
</tr>
<tr>
<td>Mus musculus (house mouse)</td>
<td>17</td>
<td>219</td>
<td>30.7</td>
<td>3723</td>
<td>26.2</td>
</tr>
<tr>
<td>Reithrodontomys megalotis (harvest mouse)</td>
<td>11</td>
<td>214</td>
<td>30.0</td>
<td>2354</td>
<td>16.6</td>
</tr>
<tr>
<td>Peromyscus maniculatus (deer mouse)</td>
<td>19</td>
<td>104</td>
<td>14.6</td>
<td>1976</td>
<td>13.9</td>
</tr>
<tr>
<td>Microtus montanus (montane vole)</td>
<td>35</td>
<td>175</td>
<td>24.5</td>
<td>6125</td>
<td>43.2</td>
</tr>
<tr>
<td>Total</td>
<td>714</td>
<td>100.1</td>
<td>14,190</td>
<td>100.0</td>
<td></td>
</tr>
</tbody>
</table>

season. We also compare our data with those from the recent studies of Boula (1982), Grove (1985), and Cannings (1987) to characterize the trophic niche of Northern Saw-whet Owls, based on data available from the Pacific Northwest.

After the young left the nest, we collected the mass of broken pellets that had accumulated in the bottom of each nest box (no pellets were recovered from two nests that failed before the eggs hatched). Because male Northern Saw-whet Owls do almost all of the nest provisioning (pers. obs.; R. Cannings, pers. comm.), and because female Aegolius owls keep the nest very clean during incubation and early brood-rearing (Korpimäki 1981, Cannings 1987), these prey remains probably represented food brought to the nest by the male during the last half of the nestling period. After searching for feathers, we soaked the pellet material in a weak solution of NaOH to separate bones from the rest of the material. Prey were identified by standard methods (Marti 1987). In most cases, dentaries were the most useful bones for identification of prey species.

Table 2

<table>
<thead>
<tr>
<th>Prey</th>
<th>Strike Camp</th>
<th>Treeline 2</th>
<th>Harris</th>
<th>Bruneau Marsh</th>
<th>Bruneau Marsh S</th>
<th>Boat launch*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sorex sp.</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>0.6</td>
<td>0.9</td>
<td>--</td>
</tr>
<tr>
<td>Mus musculus</td>
<td>56.1</td>
<td>23.5</td>
<td>33.8</td>
<td>3.7</td>
<td>11.6</td>
<td>62.9</td>
</tr>
<tr>
<td>Reithrodontomys megalotis</td>
<td>15.1</td>
<td>21.6</td>
<td>15.0</td>
<td>53.4</td>
<td>58.9</td>
<td>5.6</td>
</tr>
<tr>
<td>Peromyscus maniculatus</td>
<td>18.0</td>
<td>7.8</td>
<td>14.4</td>
<td>15.3</td>
<td>16.1</td>
<td>10.1</td>
</tr>
<tr>
<td>Microtus montanus</td>
<td>10.8</td>
<td>47.1</td>
<td>36.9</td>
<td>27.0</td>
<td>12.5</td>
<td>21.4</td>
</tr>
<tr>
<td>Total prey items</td>
<td>139</td>
<td>51</td>
<td>160</td>
<td>163</td>
<td>112</td>
<td>89</td>
</tr>
<tr>
<td>MMMP (g)</td>
<td>18.4</td>
<td>24.3</td>
<td>23.0</td>
<td>18.9</td>
<td>15.9</td>
<td>20.7</td>
</tr>
<tr>
<td>(SE)</td>
<td>(0.5)</td>
<td>(1.5)</td>
<td>(0.8)</td>
<td>(0.8)</td>
<td>(0.8)</td>
<td>(0.8)</td>
</tr>
</tbody>
</table>

* 1986 nest; all other nests from 1987.
Table 3

Food-niche Overlaps among Six Northern Saw-whet Owl Nests in Southwestern Idaho. Overlap Values May Range from 0 (No Dietary Overlap) to 1 (Complete Dietary Overlap)

<table>
<thead>
<tr>
<th>Nests</th>
<th>Treeline 2</th>
<th>Harris</th>
<th>Bruneau Marsh</th>
<th>Bruneau Marsh S</th>
<th>Boat launch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strike Camp</td>
<td>0.572</td>
<td>0.740</td>
<td>0.449</td>
<td>0.536</td>
<td>0.826</td>
</tr>
<tr>
<td>Treeline 2</td>
<td>-</td>
<td>0.831</td>
<td>0.601</td>
<td>0.535</td>
<td>0.583</td>
</tr>
<tr>
<td>Harris</td>
<td>-</td>
<td>-</td>
<td>0.600</td>
<td>0.534</td>
<td>0.708</td>
</tr>
<tr>
<td>Bruneau Marsh</td>
<td>-</td>
<td>-</td>
<td>0.855</td>
<td>0.408</td>
<td></td>
</tr>
<tr>
<td>Bruneau Marsh S</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.398</td>
</tr>
</tbody>
</table>

We calculated the following niche metrics: (1) mean body mass of mammalian prey (MMMP, Marks and Marti 1984), (2) food-niche breadth (Levins 1968), (3) dietary evenness (a modification of Hill's [1973] ratio proposed by Alatalo [1981]), and (4) food-niche overlap (Schoener 1968). Estimated mean weights of prey species were obtained from Marti (1976), Steenhof (1983), and Cannings (1987). Food-niche breadth and dietary evenness were calculated using mammalian prey at the generic level of resolution (see Marks 1984).

Breeding Northern Saw-whet Owls in our study area fed exclusively on five species of small mammals, but did not seem to specialize on any one prey species. House mice (Mus musculus) and harvest mice (Reithrodontomys megalotis) were the most numerous prey by number, whereas montane voles (Microtus montanus) contributed the greatest amount of prey biomass (Table 1). Overall, these three species constituted 85.2% of the diet by number and 86.0% by biomass (Table 1). The relative frequencies of prey species in the diets differed significantly among nests ($G = 275.9$, df = 15, $P < 0.0001$). Mus, Reithrodontomys, and Microtus each were the most common prey at two nests (Table 2). MMMP ($\pm$SE) ranged from 15.9 $\pm$ 0.8 g to 24.3 $\pm$ 1.5 g (Table 2) and differed significantly among nests (one-way Kruskal-Wallis test, $H = 65.8$, df = 5, $P < 0.0001$).

Dietary overlap among nests ranged from 0.398 to 0.855 (Table 3). Nearest-neighbor distances between nests for which we had food habits data ranged from 130 to 400 m. In most cases, the closest nests had the most similar diets. Dietary overlap was significantly negatively correlated with distance between nests ($r_s = -0.78, N = 15, P = 0.0005$), suggesting that the owl diets were related to the habitat features (and resultant make-up of the small mammal faunas) in the vicinity of nest sites. Interestingly, prey species composition was significantly different ($G = 31.2$, df = 3, $P < 0.001$) at the two nests of the polygynous male for which we had food data (Strike Camp and Harris). The diets at these nests were more similar to those at other close nests than they were to each other (Table 3). This suggests that either: (1) the male was provisioning the two nests from different areas in his territory, or (2) prey species availability varied temporally. Although these nests were only 130 m apart, their hatching dates differed by 15 days.

Eleven genera of small mammals have been recorded in Northern Saw-whet Owl diets in the Pacific Northwest (Forsman and Maser 1970, Boula 1982, Grove 1985, Cannings 1987, this study). Small mammals constituted 95-100% of the diets in these studies. Individuals wintering in shrub-steppe in north-central Washington fed primarily on Microtus (Grove 1985), whereas those breeding in coniferous and deciduous forests in south-central British Columbia (Cannings 1987) and in coniferous forests in northeastern Oregon (Boula 1982).
Table 4

Trophic Parameters of Northern Saw-whet Owls in the Pacific Northwest. S is the Number of Small Mammal Genera in the Diet at Each Locality

<table>
<thead>
<tr>
<th>Location</th>
<th>N</th>
<th>MMMP (SE) g</th>
<th>Food-niche breadth</th>
<th>Dietary evenness</th>
<th>Major prey (percent of prey items)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Washington</td>
<td>770</td>
<td>26.7 (0.4)</td>
<td>6</td>
<td>2.69</td>
<td>0.703 Microtus (54)</td>
<td>Grove (1985)</td>
</tr>
<tr>
<td>British Columbia</td>
<td>584</td>
<td>21.4 (0.3)</td>
<td>6</td>
<td>2.54</td>
<td>0.636 Peromyscus (58)</td>
<td>Cannings (1987)</td>
</tr>
<tr>
<td>Oregon</td>
<td>77</td>
<td>20.8 (0.8)</td>
<td>7</td>
<td>1.68</td>
<td>0.402 Peromyscus (77)</td>
<td>Boula (1982)</td>
</tr>
<tr>
<td>Idaho</td>
<td>714</td>
<td>19.9 (0.3)</td>
<td>5</td>
<td>3.77</td>
<td>0.950 Mus (31) Reithrodontomys (30)</td>
<td>This study</td>
</tr>
</tbody>
</table>

* Winter diet; all other studies are breeding diet.

b Peromyscus made up 84% of the diet in coniferous forest and 36% in deciduous forest.

fed mostly on Peromyscus (Table 4). In Idaho, they ate similar proportions of Mus, Reithrodontomys, and Microtus during the breeding season (Table 1). Dietary differences were also reflected in food-niche breadth and evenness measures. Although the number of prey genera in Northern Saw-whet Owl diets was similar across Pacific Northwest localities, food-niche breadth was 1.5–2 times greater in Idaho than in the other areas (Table 4). Dietary evenness was also much greater in Idaho than in the other areas (Table 4). MMMP ranged from 20 to 27 g (Table 4), and 99% of the mammalian prey items (N = 2092) weighed between 10 and 35 g.

The variation in food habits among nests in southwestern Idaho and among localities in the Pacific Northwest suggests that Northern Saw-whet Owls are opportunistic predators that feed on a wide variety of small mammal species, most of which weigh less than 40 g. Nonmammalian prey apparently are seldom taken by Northern Saw-whet Owls in this region. Geographic differences in the diets of Northern Saw-whet Owls probably reflect differences in the local availability of prey species (see Jaksic 1983, Marks 1984). There is an obvious need for data from additional localities within the Pacific Northwest coupled with measurements of the relative availability of prey species.

Acknowledgments.—We thank D. Orcutt, Idaho Department of Fish and Game, for allowing us to study owls on the C. J. Strike Wildlife Management Area. The manuscript was improved by the comments of R. Cannings, C. Marti, V. Marks, and J. Vemer. Logistical support was provided by the Bureau of Land Management’s Snake River Birds of Prey Research Project.

LITERATURE CITED


Identification Guide to North American Passerines. By Peter Pyle, Steve N. G. Howell, Robert P. Yunick, and David F. DeSante. Slate Creek Press, Bolinas, California, 1987:278 pp., 219 numbered text figures, 7 tables. $19.50.—With the exception of a few comparatively minor detractions, this book represents a superb effort on the parts of its authors. It contains an impressive amount of information which, we think wisely, was not crammed into the small pocket book format of its European counterpart. At about 9 × 6 inches, or somewhat larger than most field guides, it still manages to condense information that most bird handlers typically have scattered through several three-ring binders, reprint files and reference books. Also, by choosing a larger format, the authors have been able to avoid the telegraphic style and many of the abbreviations that make “Identification Guide to European Passerines” (Svensson 1970, 1975, 1984) less readable. Armed with this new reference, many bird handlers, and particularly those less experienced, can breathe a collective sigh of relief—the best and most current identification, ageing and sexing methods are at their fingertips.

The book begins with a very well written introduction that includes sections on Bird Topography, Measurements, Wing Formula, Skulling, Molt, Plumage, Juveniles and Soft Parts, Feather Shape and Wear, Growth Bars, Breeding Characteristics, and Directions for Use (of the guide). The introduction is followed by accounts that treat 276 species, plus 20 additional subspecies or hybrids. The book was apparently in press prior to publication of the 36th supplement to the A.O.U. check-list of North American birds (Auk 104:591-595), since it assigns subspecies, rather than species status to the Yellow-green Vireo (Vireo flavoviridis).

Brief but useful summaries of familial or subfamilial characteristics (e.g., general wing morphology, patterns of molt, generalized ageing and sexing criteria) are provided in the appropriate places throughout the guide. Also interspersed among the accounts are seven tables which provide summaries of measurements and/or key characteristics for distinguishing among four eastern and four western Empidonax species; between Alder (E. alnorum) and Willow flycatchers (E. traillii), Tropical (Tyrannus melancholicus) and Couch’s kingbirds (T. couchii), Red-winged (Agelaius phoeniceus) and Tri-colored blackbirds (A. tricolor), and among the juveniles of six species of Ammodramus sparrows; also information on the waxy appendages and/or tail band width of Bohemian (Bombycilla garrulus) and Cedar waxwings (B. cedrorum). Short sections of text are provided on Identifying Empidonax Flycatchers and Ageing and Sexing Dendroica Warblers.

Each account gives the English and scientific name, a four-letter code derived from the former, the A.O.U. number and recommended band size for each species and subspecies. Bird-banders should note that the four-letter alpha codes in this book are not necessarily those accepted by the Bird Banding Laboratory. The body of each account does not take the form of a dichotomous key (unlike most previously published ageing and sexing information about North American species), but rather provides sufficient information on the timing and extent of molt and skull pneumatization, and on age- and sex-related plumage and morphometric criteria, so that users can deduce the correct assignment of an individual bird to species (when there are potentially confusing look-alike species) and to age and sex class (when such distinctions can be made reliably). Finally, the reader is given a list of references which either were the sources of, or which provide further details about the identification criteria outlined in each account. It will be clear, however, to anyone familiar with the literature, that the experience and expertise of the authors have given rise to much new information.
Careful use of this guide (i.e., heeding the numerous wise cautions and good advice given by the authors in the introduction and throughout the text) will no doubt increase the frequency and accuracy of bird handlers' attempts to identify, age, and sex passerines, including both live birds in-hand and study skins in museum collection. Anyone who is used to the dichotomous key format will have to adjust to making decisions based on a combination of perhaps several variable criteria, but the authors have made every effort to provide all the information necessary to ease this transition. In particular, we recommend that the introduction to this book be read thoroughly; in fact, we consider this to be essential for the accurate application of the specific information provided elsewhere in the guide.

Among the few detractions that we noted are several that could have been avoided with a more careful proofreading of the manuscript. There are, for instance, a surprising number of outright spelling errors, in addition to numerous typos. On p. 25, the authors write, "Some individuals disburse [italics ours] from their breeding grounds . . . ," instead of disperse. Calendar is misspelled "calender" seven times on pp. 26-27. At least one text reference, Willoughby (1986), could not be found in the "Literature Cited" section, and not all figures are correctly cited in the text.

From a content standpoint we have a few misgivings, but none seriously detracts from our overall opinion that this book is a laudable work. Figure 1, referred to in the section on Bird Topography, illustrates but does not identify the carpal covert (the short covert located adjacent and distal to the outermost greater secondary covert), and the alula covert (the short, proximal feather of the three-feathered passerine alula) is neither illustrated nor discussed anywhere in this work. We have found that these two feathers can be very useful (with practice) for ageing birds of many species that have a partial prebasic molt, since they are frequently the last feathers of the upper alar tract to be replaced at this molt. The contrast between a molted carpal covert and an adjacent, unmolted alula is often at least as distinctive as the contrast between molted greater secondary coverts and unmolted greater primary coverts (only the latter are described in this guide). When the alula covert is molted (e.g., in many Parulinae and Emberizinae), contrast can be seen between it and the unmolted alular feathers, even when the difference between molted greater secondary coverts and retained greater primary coverts is not so clear (e.g., in many brownish or greenish birds).

Also, examination of the alula covert is particularly useful for species in which both the first-year and older birds undergo a partial prealternate molt involving some or all of the greater secondary coverts. As the authors point out on p. 19, both age groups in these species will show contrasts between coverts in the spring. Contrast between the alula covert and the other alular feathers, however, will still be characteristic only of first-year birds (= second-year, following the prealternate molt). In these birds three feather generations can sometimes be distinguished, when only two will be present in birds having undergone a definitive prealternate molt (i.e., after second-year birds).

Another feather group not identified in this work, but nonetheless of some use in ageing birds, is the upper middle primary coverts. We have found that these small feathers, seen by pushing the alular feathers aside, are not included in the first prebasic molt of some passerines, notably the Catharus thrushes. In about 20% of the Swainson's Thrushes (C. ustulatus) that we handled at our banding station (Powderrill Nature Reserve) in southwestern Pennsylvania last fall, the only retained juvenile coverts (i.e., those with the characteristic terminal spots) were upper middle primary coverts. While all thrushes can be aged by degree of skull pneumatization through the fall migration period, and while we endorse skulling as the single most reliable ageing criterion for most passerines in the fall, the presence of retained feathers in this group should increase the number of second-year birds that can be distinguished in the spring. We should point out, as the authors are careful to do, that
the distinctions between molted and unmolted feathers are rarely easy to make; they require, among other things, very well-lighted surroundings, careful scrutiny, and practice.

We have some concerns about a few of the identification criteria presented in this guide. We think that differences in rectrix shape and the color patterns of individual feathers between young and adult age classes are probably overemphasized, and the former, in particular, is overillustrated. We suspect that despite the authors' cautions, some readers may latch onto these characteristics (precisely because they are so prominently featured), without appreciating that they are among the more variable and less reliable criteria presented in the book.

Although the abundance of illustrations certainly contributes to the very attractive layout of this guide, we are not convinced that so many wing formula drawings were warranted. Most simply show that one primary is longer or shorter than another (information that is well enough conveyed in equation form in the Species subsection of each account), and they may give the incorrect impression to anyone who fails to read the authors' introductory instructions, that this measurement is taken on a partially opened wing. In fact, we have real misgivings about the inclusion in any form of so much wing formula information, given that pertinent data for North American passerines are scarce. If the authors acquired these data themselves, they make no mention of the sample sizes involved, nor of the full extent of intraspecific variation. Mulvihill and C. Ray Chandler (MS in prep.) have documented a significant amount of wing formula variation both between and within the age/sex classes of the Dark-eyed Junco (*Junco hyemalis*), including differences in the relative positions of certain primaries. As a means for distinguishing among look-alike species, wing formulae of North American passerines should probably only be applied to those few species for which adequate studies have been completed (e.g., Phillips et al. 1966. Bird-Banding 37: 153-171; Phillips and Lanyon 1970. Bird-Banding 41:190-197).

In as much as it facilitates the ageing and sexing of many North American passerines for which the criteria enabling such determinations were poorly known, this book should have a substantial impact on many bird studies, particularly on those studies of behavioral ecology heretofore unable to account for the influence of these important variables. While a few of the specific ageing and sexing methods outlined in this guide are open to question, and while the authors have not presented all known criteria, this is an excellent first edition. Any subsequent editions will no doubt benefit if readers follow the senior author's suggestion "... to publish contradicting, additional, or supporting information... so that it may be incorporated into future editions."

We recommend this book highly to bird banders and to field and museum ornithologists, alike.—Robert S. Mulvihill and Robert C. Leberman.
A majority of the 60 papers presented deal with birds. Although many chapters require a strong quantitative background, especially in multivariate statistics, many others do not. When one compares this publication with previous habitat-modeling symposia proceedings, one realizes what a superior contribution “Wildlife 2000” is, and how incredibly far wildlife-habitat modelers have come in a short time. There are very few redundant papers or “nonpapers” in this volume. The wide array of modeling procedures, statistical methods, and computer software developed and used by the authors is impressive; we have indeed learned how to build models. Whether or not we have learned how to build good models is another question.

Sections I and II encompass a variety of modeling concepts, techniques and applications, tests of model assumptions, and modeling pitfalls. Many of the chapters in Section I deal with descriptive models developed from literature search and expert opinion, such as the U.S. Fish and Wildlife Service’s Habitat Evaluation Procedures (HEP) and the U.S. Forest Service’s Wildlife Habitat Relationships (WHR) models. Descriptive models are usually not field validated and have been criticized because of their poor predictive ability, yet widely accepted alternatives have not been developed. A variety of other approaches, mostly multivariate, are covered in the bulk of the rest of these sections. Capen et al. (Chapter 26) present an excellent description of study design and use of discriminant analysis and more robust logistic regression models to classify used and unused sites for four songbird species. They observed good results when jackknife and cross-validation procedures were used within the same data set. However, an independent data set showed poor classification when applied to the derived models. These results point out an important problem with developing wildlife-habitat models from data at a single site, namely, that a model developed in one area will reflect the peculiarities of those data, be they real or statistical outliers (i.e., the model is overfitted). The development of models that are applicable over a wide geographic range is considerably more difficult.

Section III, “When Habitats Fail as Predictors,” provides ample evidence that there are many situations where habitat alone is simply not enough to predict the presence or abundance of a species. Long-term studies by Rotenberry (Chapter 31), Gaud et al. (Chapter 32), Diehl (Chapter 33), and O’Connor (Chapter 34) all report extreme yearly fluctuations in bird numbers apparently unrelated to habitat change. Most researchers, however, probably recognized the importance of long-term studies to examine wildlife-habitat or any other ecological relationship, and would place little faith in a habitat model developed from one season in the field.

Section IV, “Predicting Effects of Habitat Patchiness and Fragmentation,” is a natural successor from the previous sections; many similar types of models are developed except that explanatory variables include such names as island area, insularity (Rosenberg and Raphael, Chapter 38), and core area (Temple, Chapter 43). Other papers in this section (Seagle, Chapter 40; Urban and Shugart, Chapter 39) discuss the relatively new area of “landscape ecology” that involves the study of habitat mosaics. I suspect that wildlife/habitat relationships will be examined on this scale with greater frequency in the future.

Section V, “Linking Wildlife Models with Models of Vegetation Succession,” involves using dynamic computer simulation models to depict forest successional change, then linking wildlife-habitat models to the characteristics of the predicted ecosystem changes, primarily in light of various timber production and harvesting scenarios. This final section of research papers leaves one feeling optimistic about the potential of habitat modeling. However, forest succession models for wildlife planning are only as good as the wildlife-habitat models that are used to link with them. Most of the chapters in this section use planning models like HEP or WHR models to link with successional models. Yet if one does not place much faith in these descriptive models, then how much faith can one have in more sophisticated
models that incorporate them? Or, it may be that descriptive models can be valuable in planning scenarios that do not require the high confidence levels, precision, and certainty of models used in scientific research.

This dichotomy is reflected in the sectional summaries written from the manager's and researcher's viewpoints. Several managers express the valid point that models that are not as accurate as we would like are still practical to use and therefore of value. Others express the concern that more sophisticated modeling methods are outdistancing the ability of managers to use them. It may well be that managers will continue to use descriptive models, enhanced in utility by such features as expert systems (Marcot, Chapter 23) and successional simulation models. Researchers are likely to continue to use more sophisticated models that are more appropriate for their needs on individual study areas. This dichotomy is not necessarily a bad thing, especially if descriptive planning models can be improved through use of scientific models by testing hypotheses, assumptions, and components of the former.

In summary, then, "Wildlife 2000" is a timely, attractive, well-edited and well-produced publication that is of value to researchers and managers alike. My only criticism is that, while an impressive array of techniques and software is presented, I wonder how good many of these models are. Model building is an iterative process in that, after specifying and fitting the model, diagnosis and validation serve to respecify and improve the model, and in testing the new model the procedure is started anew. Of the numerous models introduced in the first two sections, very few are validated using independent data from another area, if at all. Also, several models are developed using only 1–2 years of data. It is apparent that not many of the models presented in these sections have progressed very far in the overall modeling process. In fairness, though, the objective of at least some of these studies when they were initiated years ago was not to build wildlife-habitat models. Rather, in the course of their work researchers developed some interesting modeling ideas that they wished to impart to their colleagues. Others undoubtedly collected data specifically for a topic they wished to present at this symposium and did not have time to collect more data. Modeling is still a new area in wildlife ecology. When the next symposium on habitat modeling appears several years from now, I have no doubt that huge advances will be made over these and other problems.

Just one final word on value; the quality of the content of "Wildlife 2000" is obvious. In addition, the publication is presented in an attractive style, hardbound, for an extremely reasonable price. How did the editors do it? Or, more to the point, why haven't other symposium editors been able to do it? You know what I am referring to; these publications often have photocopied text, frequently with different type in different papers, and are loaded with typographic errors. But add a hard cover, and the publishing company asks a price several times more than this volume. Both the editors of this volume and Wisconsin Press should be congratulated, if for no other reason than giving impoverished biologists a break. —Robert J. Cooper.

An Introduction to Behavioural Ecology. By J. R. Krebs and N. B. Davies. 2nd Edn. Sinauer Associates Inc., Sunderland, Massachusetts, 1987:389 + ix pp., 118 figures, 33 tables. $19.95.—In 1981, John Krebs and Nick Davies published the first edition of a textbook based on their lectures in behavioral ecology at Oxford and Cambridge. That first edition filled an important niche, because it was written for students who were already familiar with the basic concepts of ethology and ecology, but were focusing squarely on questions about the function and evolution of behavior. The original text found an approving audience, as evidenced by its four printings. In 1987, the second edition became available
on the North American market, and this thoroughly revised version should be as well received as their first effort.

In revising the text, Krebs and Davies have retained the 13 chapters of the first edition and have added two new ones that are detailed discussions of competition for resources, and altruism. After first describing the aims and methods of studying the survival value of behavior, the authors discuss, in separate chapters, the theoretical ideas and empirical results of studies dealing with how “well-adapted” animals make decisions, how fighting strategies and territoriality result from competition, the causes and consequences of group living, mating decisions, parental care, alternative reproductive strategies, cooperative breeding, and the ecology of signaling behavior. The concluding chapter re-evaluates the plausibility of some of the authors’ main premises (e.g., the evolution of selfish genes as opposed to groups) and the value of optimality models in understanding the evolution of behavior.

Each chapter in the current edition has been carefully revised. For example, where researchers have continued a particular study, the authors have thoroughly reworked the text to include their most recent findings (e.g., Woolfenden and Fitzpatrick’s study of Florida Scrub Jays, *Aphelocoma coerulescens*). In addition, there are many examples of new studies that have been incorporated into the text (e.g., Alatalo and associates’ studies of polygyny in Pied Flycatchers, *Ficedula hypoleuca*). With over 500 references, half of them different from the first edition’s, the bibliography is about one-third larger than the earlier one. Given the rate at which information is accumulating in this young field, the value of this text as a timely synthesis cannot be overstated.

From a technical viewpoint, the second edition has been improved in several ways: the size of the print is larger, typographical errors have been largely eliminated, several new photographs have been added, and the quality of those reproduced from the first edition has been improved. Where appropriate, the authors have introduced new figures and tables to complement the revised text, and several expanded discussions of difficult concepts have been added. Finally, color has been used to highlight titles and graphs in the current edition, making it quite a handsome text.

The most appropriate audience for the text will remain an upper-year undergraduate class. The inclusion of “topics for discussion” at the end of each chapter can be used to stimulate class debates, and the division of the book into 15 chapters makes it convenient for use in a one-semester course. The text could equally well serve as a “handbook” of terms and basic ideas for a graduate level course in behavioral ecology. Students at either level will find the relaxed, conversational, writing style enjoyable, and the authors’ discussions of even rather difficult concepts clear.

In summary, the second edition of Krebs’ and Davies’ text is a fresh and timely synthesis of the literature in a rapidly changing field, presented in an attractive and enjoyable format. The text is a valuable aid for teaching an undergraduate class, and it can be recommended without hesitation.—T. E. DICKINSON and N. J. FLOOD.
He reviews the King-Clapper complex and concludes that although he believes that one "polytypic biological species" is involved, to facilitate comparisons, he treats King and Clapper rails as distinct species! The wise reversion to using established common names for subspecies both makes such comparisons lucid and permits being consistent. Tables of measurements—including weights—are presented for series of rails from the Colorado River valley and from adjacent populations of the coast of Mexico with the hour and minute when the bird was collected, but without identifying the museum where they were deposited or giving specimen numbers!

Chapters two to five form the bulk of the report. They deal with ecology, special investigations (population sizes), and historical trends of the Yuma Clapper Rail. Defining the relative importance of the various habitats used by the rails (vegetation components are described in detail), and documenting the often contradicting "conservation" forces affecting those habitats, usually destructively, is the most important contribution of the report. The author rather well demonstrates that the Yuma Clapper Rail was simply overlooked by earlier collectors—including Grinnell—who concentrated on the larger lakes and marshes of the Colorado River valley. The population has not witnessed a recent expansion into man-made habitats, but probably was always there, and indeed is now living in largely imperiled habitats.

Little new life history work has been done on the subspecies, and there are a lot of references to other populations of Clapper Rails to fill in lacunae.

Chapter six is on research and management recommendations. Interesting is the simple suggestion that the wintering range of the subspecies, and the taxonomic relationship of *yumanensis* to *rhizophorae* and *nayaritensis* of the contiguous coast of Mexico be determined! Would this journal publish such a taxonomic manuscript? The author also suggests that radio telemetry be used to study life history and movements of this secretive bird. One heartily concurs with the author who concludes with his hope that this report will help in efforts to manage and to increase protection of this restricted subspecies.

The report is illustrated extensively. I'm sure the original photographs were excellent but the reproduction by photo-offset is poor and the illustrations are all middle gray. The author must be disappointed. There are 33 pages of references cited. It is a useful compendium of Clapper Rail literature and a vital report for all involved in the management of wetlands.

Robert W. Dickerman.

**Bruno Liljefors The Peerless Eye.** By Martha Hill, Doubleday and Company, Garden City, New York, 1987:174 pp., quarto (27 × 29 cm.), 58 black-and-white illustrations, 112 in color. $60.—The spirit of Bruno Liljefors, and that of author Martha Hill as well, is well expressed in her account of seeing, for the first time, one of Liljefors's originals:

Upon opening the heavy main door (of the Thiel Gallery), the visitor ascends a broad, dark wood staircase leading to the sky-lighted main galleries. Halfway up, he is distracted by a flash of white from the side. Turning to confront a sixteen-foot-long canvas on the opposite wall, he sees forty eiders, life size, whirring across the wintry sea, their blurred wings ruffling the trough of a wave. The black-green sea is chilling, and so is the sensation of wind. The impact of this monumental vision leaves the onlooker breathless as he surveys the phalanx of birds flying past, finally noticing the few brown females which at first were eclipsed by the dazzling nuptial plumage of the drakes. This feeling of sudden encounter, of witnessing an event in nature without intruding—this is the incomparable art of Bruno Liljefors.

Martha Hill, who has long served as picture editor of Audubon magazine, has done a masterly job in bringing to the English-speaking audience the art of this Swedish painter of
birds and mammals. Widely considered the finest of all wildlife artists, he is little known in the United States. By using Liljefors's letters, journals, and publications as well as the several books about him by art critics, she has succeeded in following his development as an artist very well. I am impressed with her diligence and dedication, because virtually all of the source material was in Swedish, which she had translated. She made several trips to Sweden to confer with museum curators and private owners of Liljefors paintings. The product is both informative and readable. It is in the form of what I would call essays, rather than chapters, each one enjoyable by itself.

Hill traces the life of the artist from his birth in 1860 to his death in 1939 and the resurgence of public acclaim in 1960. His popularity is still rising, so much so that in recent years individual paintings have sold in Sweden for more than a hundred thousand kronor. Of the many interesting tidbits which make the book so interesting, I select just a few as illustrations. Though Liljefors began his art work and training as a child it was not until he was 47 years old that he became a smashing success financially, when a one-man show sold for enough so that he could purchase the archipelago Bullerö, with its 365 rocky islets, rich with sea life. He made it his private wildlife sanctuary, employing a caretaker to patrol and prevent the shooting of wildlife, including his favorite sea eagles, on which a bounty was paid at that time. The area is a nature reserve today.

He was represented in the Swedish exhibits at two major world fairs, the Field-Columbian Exposition at Chicago in 1893, with 17 paintings, and the Louisiana Purchase Exposition at St. Louis in 1904, where his 19 paintings won several gold medals. This type of acclaim, however, did not translate into enough money for a comfortable living for his large family (eleven children), and his wife was quoted as scorning gold medals and wishing for cash. However, he did have several good friends who were helpful in arranging sales of his paintings, and who bought many themselves. Among them were banker Ernest Thiel, the king's son, Prince Carl Eugene, and artist Anders Zorn.

Hill discusses the fact that most curators of fine art refuse to recognize animal paintings as worthy of their attention, and relates her experience in trying to persuade the Metropolitan Museum in New York City to put on a Liljefors exhibit, but brings out that in Sweden several art museums bought his paintings, and the National Museum of Art in Stockholm has 552 Liljeforses in their archives. They represent all of his favorite subjects, foxes, hares, black grouse, ducks and geese, and both golden and sea eagles.

Anyone interested in bird art will find this fine book rewarding, both for its information and for the beautiful reproductions of so many Liljefors paintings.—Gustav A. Swanson.


Fifty years ago, the Congress passed what is considered by many the most important of all conservation laws, the Federal Aid in Wildlife Restoration (Pittman-Robertson) Act. This book reviews its programs as seen by 35 authors. Usually considered primarily a funding provision, the P-R Act has conferred far broader benefits, upgrading the effectiveness and professionalism of the state wildlife agencies as nothing else had ever done.

The provisions of the P-R Act are fairly simple: an 11% excise tax on sporting arms and
ammunition is collected by the federal government and distributed to the states for wildlife restoration work. Each project is conducted by the state, which is reimbursed for ¾ of its cost by the fund. The U.S. Fish and Wildlife Service has exercised central supervision so successfully that the Act has been amended to add other sources of income, from excise taxes on handguns and on archery equipment used for hunting, and to inspire a parallel Act in 1950, the Dingell-Johnson Act for Federal Aid in Sport Fisheries Restoration. These two important measures are shining examples of good and effective federal intervention.

Why has the P-R Act been so important? First, of course, is the money it has distributed to the states: in 1986 alone over $100 million. During the first fifty years the states received more than $1.5 billion. To use my home state as an illustration, Minnesota's 997 Wildlife Management Areas, totalling more than 500,000 acres, were purchased in large part with P-R funds participating. Minnesota has generally spent almost all of its P-R funds on land acquisition and development, with hunter education about 4% and research only about 1.3%.

The benefits other than funding were equally important. When the P-R Act was passed in 1937 the typical state wildlife agency was strongly political, with staff appointments reflecting largely politics rather than professional training or competence. Major activities were law enforcement, game farming, and predator control. The P-R Act made drastic improvements. Important requirements were that eligible projects be "substantial in character and design" and that staff employed must be the best qualified that were available. The quality of state wildlife programs and personnel were quickly improved nationwide.

Individual chapters deal with more than a dozen species of wildlife which have increased remarkably with improved management resulting in part from the P-R programs. One deals with the Giant Canada Goose (Branta canadensis maxima), thought to be extinct by DeLacour when he described it in 1951. Then 25 years ago a small nonmigrating population was discovered on Silver Lake in Rochester, Minnesota, where it had been fed and protected by Dr. Charles Mayo and others. Since then an active restoration program has succeeded far beyond expectations, and the Giant Canada is again a nesting species by the thousands in the Great Plains states and elsewhere.

Other wildlife successes under the Federal Aid programs include the Wild Turkey (Meleagris gallopavo), the white-tailed and mule deer (Odocoileus virginianus and O. hemionus), Wood Duck (Aix sponsa), black bear (Ursus americanus), pronghorn (Antilocapra americana), elk (Cervus canadensis), mountain lion (Felis concolor), beaver (Castor canadensis), bobcat (Lynx rufus) and sea otter (Enhydra lutris). All of these species are now more numerous and many of them have been restored to areas from which they had been exterminated, and P-R projects have usually been a key to the success. Some states have conducted much of their non-game wildlife work under the P-R Act.

The account of the initiation of the Act includes some fascinating and little known details. Congressman Willis Robertson agreed to sponsor the bill only if 29 words which he pencilled into the draft were added: "... and which shall include a prohibition against the diversion of license fees paid by hunters for any other purpose than the administration of said State fish and game department..." This provision alone has saved for the state wildlife agencies many millions of dollars, because it was a common practice for state legislatures to use hunters' license fees for other purposes.

The book can be recommended enthusiastically to anyone interested in wildlife conservation, and it is suitable for display on your library table, it is such an attractive production, lavishly illustrated with more than 200 photos and maps, most of them in color. It is amusing that President Reagan and Interior Department Secretary Hodel, who had nothing to do with the Act, are honored with full-page color photos and prefatory remarks.—GUSTAV A. SWANSON.
SONGBIRDS IN YOUR GARDEN; HOW TO ATTRACT, FEED, AND ENJOY BIRDS IN YOUR GARDEN OR BACKYARD. BY JOHN K. TERRES, ILLUS. BY MATTHEW KALMENOFF. HARPER AND ROW PUBLISHERS, INC., NEW YORK, NEW YORK, 1987: XIV + 306 PP. $9.95.—TO REVIEW THIS REPRINT OF TERRES’ CLASSIC WORK, WHICH WENT THROUGH THREE EDITIONS BETWEEN 1953 AND 1977, I COMPARED THIS INEXPENSIVE, SEMI-HARD-COVER PERENNIAL LIBRARY EDITION WITH MY COPY OF THE ORIGINAL TO SEE WHAT CHANGES HAVE BEEN MADE OVER THE YEARS. THE NEW EDITION IS ABOUT ½ LARGER IN PAGE SIZE AND IS 32 PAGES LONGER, BUT MOST OF THE INCREASE IS IN WIDER MARGINS (THE TYPE BED IS IDENTICAL IN PAGE WIDTH, BUT IT IS 4 LINES LONGER) WITH MANY MORE, OFTEN DELIGHTFUL, MARGINAL ILLUSTRATIONS, AND AMPLIFIED APPENDICES. BUT IS THIS EDITION WORTH BUYING TODAY? AT ITS PRICE, I THINK SO.

fter the obligate Foreword by Roger Tory Peterson, a Preface by Terres, and an Introduction by Edwin Way Teale, the book begins with a “new” (not in the first edition) chapter on the history of bird feeding, augmented by the author’s own stories about feeding. It then continues, almost unchanged, through chapters on how to feed, make birdhouses, help birds at nesting time, provide water, care for young birds, attract hummingbirds, plant garden ornamentals that are used by birds, make sounds to attract birds, build a bluebird trail (a new chapter), and a list of problems and how to solve them. The book ends with almost 100 pages of appendices, an updated list of references, and a good index.

This has always been a very personal book, filled with Terres’ stories about his experiences with birds. Therein lies its charm. To some extent, however, a 1980s reader may also find it quaint, filled with anthropomorphisms and “cute” tales, a friendly and useful book, possibly entertaining, possibly over the hill. In spite of Terres’ cosmetic updating, the book’s basic age shows and thereby lessens its utility. For instance, feed prices have been updated to 1986, and honey water is no longer a recommended feeder food for hummingbirds, but many items such as range changes (e.g., by Carolina Wrens [Thryothorus ludovicianus] and Bewick’s Wrens [Thryomanes bewickii, pp. 58–59] have not been modernized, only a few of the birds’ names have been brought into conformity with the 1983 A.O.U. Check-list, and I doubt if submersion heaters for heating birdbaths in winter are still available for $2.00, even if it’s wise to use them. Most of the datedness of the book, however, is apparent in what was omitted: I cannot imagine discussing bird feeding today without mention of that finch “magnet,” thistle (niger) seed. Nor are some of the other seeds now generally available (e.g., safflower and the different types of sunflower seeds) even mentioned. There is much about “squeaking” and imitating birds’ calls to attract them but nothing on tape-recorder playback. The section on feeding orphaned young birds is still poor, as is the discussion of preventing window kills and birds fighting their reflections in windows—subjects that come up constantly in questions from the general public. The book’s organization also would have been improved if the problems noted in the last chapter and those in the Hints and Suggestions appendix had instead been inserted in the appropriate places in the main text, such as placing squirrel-proofing in the chapter on feeders, and cleaning in the birdhouse chapter. I suspect that a publisher was unwilling to pay for a thoroughly revised edition, resulting in new material being relegated to add-on appendices. They are, however, indexed adequately. The book also has a strong Northeastern bias, understandable in view of Terres’ own experiences and the personal nature of this book, but that is largely counteracted by the detailed, coast-to-coast listings of suggested plantings and food and nest-site preferences in the appendices.

On the positive side, the book retains its basic worth—clear instructions for feeding and attracting birds and for making birdhouses (even I, certainly no carpenter, have successfully built a few from Terres’ plans), interspersed with delightful tales of his years of experience in caring for the needs of wild birds, and a nice collection of new line drawings that greatly add to the appeal of the book. At $9.95, it is a bargain reference source as well as enjoyable reading for almost anyone.—MARY H. CLENCH.
STATUS AND DISTRIBUTION OF THE FLORIDA SCRUB JAY. By Jeffrey A. Cox. Florida Ornithological Society, Special Publication No. 3, 1987:109 pp., 36 figs., 7 tables. $8.00 from FOS, 1701 N.W. 24th St., Gainesville, Florida 32605.—In Florida, Scrub Jays ( Aphelocoma caerulea sens) form a disjunct eastern population that is restricted to habitats on soils of white, well-drained sands. As much of this land has been cleared for citrus and housing developments, Scrub Jays are listed as a threatened species in the state. The author did a comprehensive, state-wide survey by thoroughly searching for Scrub Jay records in the literature, in egg and skin collections, in the Bureau of the Biological Survey files, in the Breeding Bird Survey files of U.S. Fish and Wildlife Service, and through correspondence with people working in Florida. In addition, in 1981 he conducted extensive field surveys of all known or suspected locations for Scrub Jays.

The monograph is organized alphabetically by Florida counties. For each county Cox discusses the historical distribution and the current distribution of jays. Each county has a map with numbered locations for each former and current population. At the end of each county summary, a listing by each numbered locality is given which includes details of the exact site, its habitat, and number of jays seen. A separate section is provided for Ocala National Forest, which spans parts of three counties, and is given special attention because of its importance as jay habitat. A follow-up survey could be done from the information provided in these summaries.

Cox estimates the total population of Scrub Jays in Florida at 15,600 to 22,800 birds, an estimated decrease of 50% from late 1800s levels. More than 80% of these birds are on Merritt Island/Cape Canaveral and Ocala National Forest lands. Clearly the preservation of the species is dependent on correct management of these areas by the appropriate federal agency. Scrub Jays have been extirpated from five counties and show substantial decreases in most others. He recommends the purchase of several pieces of private property that would add important populations into protected ownership.

The book is well organized but rather dry reading. Lacking from the book and important for the conservation of Scrub Jays is a thorough discussion of the size of prime Scrub Jay habitat required to preserve a population. He appears overly optimistic that some small populations will survive. For those interested in Florida Scrub Jays or conservation of important scrub habitats it will be an important reference.—G. Thomas Bancroft.

HINDLIMB MYOLOGY AND EVOLUTION OF THE OLD WORLD SUBOSCINE PASSERINE BIRDS (ACANTHISISITIDAE, PITIDAE, PHLEPETIDAE, EURYAIMIDAE). By Robert J. Raikow, Ornithological Monographs, No. 41, published by the American Ornithologists Union, Washington, D.C., 1987:viii + 81 pp., 37 numbered text figures, 3 tables. $12.50 ($9.50 to AOU members).—This is the latest in a long series of myological descriptions of higher landbirds by Robert Raikow, one of the most prolific recent authors of avian comparative anatomy. It is an important piece of work because it is the first detailed description for the hindlimb musculature of the Old World suboscine families. The emphasis is equally distributed between pure description and phylogenetic analysis. It is typical of Raikow's work.

Raikow's description and analysis are clearly defined and logical. The work is not presumptuous. Raikow provides a very level-headed discussion of his methodologies and their limitations. Anyone who questions Raikow's conclusions has all the material available to him in this monograph to follow step by step, from the collection of data on through the analysis. His statistical methods are robust and widely available. He discusses alternative and consensus trees. His phylogenetic conclusions gain credibility by their general congruence with those of Sibley and Ahlquist's DNA solution hybridization studies, as Raikow notes.
himself, together with the biogeographical plausibility of his conclusions, which he did not discuss. Ironically, Raikow relies on the corroboration of genetic distance data for support of his conclusions, at the same time downplaying its significance as a competing alternative to morphological studies.

Virtually any phylogenetic analysis is guaranteed to elicit some opposition, and the present study is no exception. Raikow's treatment of the suboscines most clearly differs from the classifications of other ornithologists in his treatment of the broadbills (Eurylaimidae). Most early authors treated broadbills as a major subdivision of all of the passerines or of the suboscines. Olson (Ibis 113:507–516, 1971) believed that eurylaims are closely related to the cotingas (Cotingidae) of the New World. Raikow found little to unite the Eurylaimidae as a family. He disagrees with Sibley, Williams, and Ahlquist (Notornis 29:113–130, 1982) that the New Zealand Wrens (Acanthisittidae) are suboscines, but he agrees with Sibley and Ahlquist (Ornithol. Monogr. 36:396–428, 1985) that the remaining Old World suboscines comprise a monophyletic group. This latter opinion certainly makes the greatest amount of sense from a biogeographic point of view. In such a scenario, similar environmental and behavioral selective factors resulted in parallel evolution between the Old World suboscines and the New World suboscines, for example between the antpittas (Formicariidae) and the pittas (Pittidae), and the cotingas and the broadbills. Unlike Sibley and Ahlquist (1985), Raikow does not resolve the branching order of the New World suboscines. His phylogenetic reconstruction is potentially consistent with the controversial hypothesis that tapaculos (Rhinocryptidae) and the Australian Menuridae are similar because of retained primitive characters (Feduccia and Olson, Smithsonian Contrib. Zool. 366:1–22, 1982; see also Bock and Clench, Records Australian Mus. 37:243–254, 1985). Raikow makes no mention of this.

The only serious deficiency in this paper, as in all of Raikow's descriptions, is his neglect of osteology. There are no figures of the bones showing muscular origins and insertions. When bones are included in illustrations of dissections of muscles, they are practically amorphous. This is particularly unfortunate because the people most likely to use this paper as a reference on a continuing basis are paleontologists. In contrast, few other systematists are likely to read carefully the descriptive parts of this monograph more than once, if even that.

Raikow discusses a few nonpelvic, nonmyological characters in a very cursory fashion. He did not address several of the diverse characters cited by Olson (1972) in support of a relationship between the broadbills and cotingas. Nonetheless, Raikow cannot be faulted for omitting such data from his analysis, which is expressly pelvic myology.

The only breach of logic I noted was minor, and it would only be perceived by paleontologists. Raikow rejects the notion that the presence of a plantar vinculum in the Eurylaimidae is primitive because it "conflicts" with the bulbous stapes and acetabular gap of the iliobibialis lateralis muscle, which are synapomorphic to suboscines. These characters are not necessarily in conflict. Retention of primitive characters in the broadbills does not imply convergence in other characters or lineages, if oscines evolved from an extinct group of suboscines (i.e., fossil and extant suboscines combined are paraphyletic, not monophyletic) and that eurylaims were the first family to diverge from the other extant suboscines (which are definitely monophyletic). There are certain other characters (e.g., the condition of the flexor hallucis brevis shared only by the Eurylaimidae and Philepittidae) that suggest the divergence of the Eurylaimidae was relatively recent among the radiation of suboscines. These do conflict with the interpretation of the plantar vinculum as a primitive character. Thus, Raikow comes to the conclusion that is consistent with his data, but possibly for the wrong reasons.

This is a publication of high quality that will remain significant through the centuries as a descriptive reference. It will be most important to, but liked least by, paleontologists. — P. Houde.
ORNITHOLOGICAL LITERATURE

Voices of All the Mockingbirds, Thrashers, & Their Allies. Family Mimidae. By John William Hardy, Jon C. Barlow, and Ben B. Coffey Jr. ARA 12, ARA Records, P.O. Box 12347, Gainesville, FL 32604-0347, 1987: Monaural tape cassette. $10.—ARA Records continues its highly successful progression through the avifauna of the Western Hemisphere. We have here recordings of all of the 34 members of the family Mimidae. Most species are represented by two or even three examples of recordings obtained by some 21 people besides the three co-authors. The endangered Ramphocinclus brachyurus is represented by the song of an aviary bird. The usual high standards of ARA obtain and all the cuts are good to excellent.

Not only are most of the species in this family accomplished singers, but some are notorious mimics of other sounds. Many of the recordings illustrate this mimicry. The recording of the Northern Mockingbird (Mimus polyglottos) contains at least six imitations. I note with some interest that some of the island forms such as the several Galapagos mockingbirds (Nesomimus) and the Socorro Thrasher (Mimodes graysoni) have simple, rather unmusical songs.

The wrap-around cassette label contains notes on the technical data of the recordings, including the recordist, and a series of comments by Hardy characterizing the songs and pointing out which species are known mimics.—George A. Hall.


Part One is an account of “The Featured Agency,” in this case the Bureau of Land Management. The two earlier volumes had featured the U.S. Fish and Wildlife Service and the U.S. Forest Service. An informative overview of the responsibilities and activities of the Bureau is given with emphasis on current problems.

Part Two discusses 14 other federal programs or agencies in less detail. Included are the Endangered Species Program, the Wetlands Protection Programs, the Animal Damage Control Program, the National Wildlife Refuge System, as well as the Forest Service and the National Park Service. One section discusses International Wildlife Conservation. The emphasis in these accounts is on the current problems and activities of each Program. These accounts are both timely and informative.

Part Three discusses 15 species (7 mammals, 3 birds, 2 fish, 1 butterfly and 2 plants) that are either endangered or of some concern. The three bird species are the Wood Duck (Aix sponsa) written by Frank Bellrose and Robert Heister, the Red-cockaded Woodpecker (Picoides borealis) by Jerome Jackson; and the Piping Plover (Charadrius melodus) by Susan Haig and Lewis Oring. These accounts include an outline of some of the natural history of the species, a Historical Perspective and sections on Current Trends, Management, Prognosis and Recommendations. The selection of forms seems rather odd. Some like the plover and the woodpecker are truly endangered, the running buffalo clover (Trifolium stoloniferum) is known in the wild from only one small population, but others such as the black bear and the elk are popular big-game species in no apparent danger.

A series of 13 Appendices provides a set of directories for the various agencies as well as other useful information including a listing of the Federal Endangered and Threatened Species.

On the whole, this is an attractive publication that contains much of value and interest.
The price is low for a book from this publisher, but even so, the ephemeral nature of most of the material makes this a publication recommended for libraries and not for personal purchase.—George A. Hall.

Bibliography of Ornithological Translations—Reply to Bledsoe.—I am thankful that Bledsoe, for his review of Current Ornithology, vol. 4 (Wilson Bull. 100:149–150, 1988), took the trouble to examine all 1030 of the citations listed in Chap. 7, “A Bibliography of Ornithological Translations.” He found that references to the Rallidae were incorrectly listed. All but one of these references (i.e., 54, 71, 261, 412, 830) unaccountably migrated to the Anseriformes subject listing from their original location in Gruiformes, where they should be replaced, at least until someone undertakes a phylogenetic study of the order. A few other, less egregious, errors crept into the subject indices, in particular ref. 616, which should be listed under Turdidae. Future updates to the Bibliography will report errors as we find them. Bledsoe’s estimate of errors, however, is misleading, but nonetheless does point out the problem with undertakings of this kind, that of bibliographic accuracy.

In his search for typos, Bledsoe seems to have forgotten that this is a bibliography not of original research, but of translation citations. Common names of birds are not well standardized in Eastern Europe, and depending upon the abilities, experience, and background of the translator, can be further obscured when brought into English. Thus, “chemysh” refers to *Tringa ochropus*, *Melanocorypha yeltoniensis*, or *Lyrurus tetrix*—three different families; “chaffinch” has been used to refer to a sylvid, an emberizid, or fringillid, and is often confused with “chiffchaff”; “common sandpiper” may be used for many scorplacidids; and “sparrow” almost any small passerine. Back formation of binomials when they are not given in the article, similar to what Bledsoe did in his review, further compounds the errors. In these cases, the only recourse is to the original article, but this is often not possible; we were able to examine less than one-third of the citations listed. Where possible, we let the subject indices reflect the actual nature of the articles, but did not alter citations. We regret that we were unclear about this. As we indicated in the Bibliography, the subject indices are rough charts to this literature, much like the sailing rutters of medieval Europe. With caution and some imagination, ornithological translations can serve as valuable adjuncts to research and windows upon the ornithology of other countries.—Douglas Siegel-Causey, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045-2454.

BRIEFLY NOTED

**Atlas of Victorian Birds.** By W. B. Emison, C. M. Beardsall, F. I. Norman, and R. H. Loyn. Graphics and Analysis by S. C. Bennett. Victoria Department of Forests and Lands and the Royal Australasian Ornithologists Union, Melbourne, Australia, 1987:271 pp., many maps and graphs. No price given.—Maps for the occurrence of 697 species in the state of Victoria are given. Separate maps indicate the confirmed breeding distribution. American atlasers should note that only an occupied nest or dependent young out of the nest were accepted as criteria for confirmed breeding.—G.A.H.

The Sixty-ninth Annual Meeting of the Wilson Ornithological Society was held Wednesday, 8 June to Sunday, 12 June 1988 at Rosemont College, Rosemont, Pennsylvania and celebrated the centennial year of the Society. The local committee chaired by Dr. Frank Gill was composed of Dawn F. Coughlan, John Guarnaccia, Steven Holt, Robert Ridgely, Mark B. Robbins, Frederick Sheldon, and Douglas Wechsler. The meeting was jointly sponsored by The Academy of Natural Sciences of Philadelphia, Hawk Mountain Sanctuary Association, Cape May Bird Observatory, Delaware Valley Ornithological Club, the Biology Department of The University of Pennsylvania, and Rosemont College.

The Council met from 13:00 to 18:00 on Wednesday, while registration for the 229 guests and members began that afternoon in Heffernan Hall. A bountiful reception for all participants was held in the evening at Alumnae Hall. Of the 17 living past-presidents, 12 were in attendance at this centennial meeting: Clait E. Braun, John T. Emlen, Jr., Abbot S. Gaunt, George A. Hall, Pershing B. Hoflund, Jerome A. Jackson, Douglas A. James, Harold F. Mayfield, Kenneth C. Parkes, Roger T. Peterson, O. S. Pettingill Jr., and Phillips B. Street. The opening session on Thursday was held in McShain Auditorium of the Science Building where the Society was welcomed for all the hosting organizations by Dr. Frank B. Gill. Dr. Mary H. Clench responded for the Wilson Society. The scientific program included paper presentations on Thursday and Saturday in McShain Auditorium and Lawrence Hall Auditorium and a poster session in Alumnae Hall.

Of special note was the Thursday evening bird quiz, featuring slides from the VIREO collection. It was composed of three parts: a North American set of which Steve Sibley identified the most correctly, a world-wide set for which Guy Tudor won first prize, and an especially difficult set that pitted a panel of “old heads” against some younger folks. The final scores for this last competition were inversely proportional to the mean age of the respective panels.

A special Centennial Day celebration was held at The Academy of Natural Sciences of Philadelphia, where the Society was welcomed by Keith Thompson, President of the Academy. The highlight of the program was a symposium on the Paridae developed by Dr. Frank B. Gill and Dr. Millicent S. Ficken. This was followed by workshops on communication and social organization among the parids and presentations by George A. Hall on Alexander Wilson, and overview of the Society’s history by Jerry Jackson, and a panel discussion on the Wilson Society in the year 2000 by Mary Clench, Phillips Street, Elliot Tramer, Stan Senner, and Danny Ingold. There was also the opportunity to take a trolley tour of historic Philadelphia, which included a visit to Old Swede’s Church, the site of Alexander Wilson’s grave. This extraordinary day ended with a gala buffet reception served in the galleries of the Academy.

This was also the year of the George Miksch Sutton bird art competition, arranged by Kenneth C. Parkes. The entries were displayed in the gallery of Lawrence Hall. Those attending on centennial day could also see the work of Guy Tudor from the “Birds of South America,” Don Eckelberry from “Birds of the West Indies,” and John Gwynne from the “Birds of Panama” on display at the Academy.

Early morning field trips on Thursday explored Ridley Creek State Park and on Saturday visited Mill Grove, the home of John James Audubon near Valley Forge. There were well-
planned spouse-guest tours, including a trip to Winterthur in Delaware and another to Lancaster County. On Sunday, all-day field trips were conducted to the Hawk Mountain sanctuary and southern New Jersey, including Cape May.

The annual banquet was held in the cafeteria of Cardinal Hall on Saturday evening. President Clench read greetings from the Hon. Ronald Reagan, President of the United States, offered in recognition of the centennial of the Society. The following awards were presented:

**EDWARDS PRIZE** (for the best major article in volume 99 of *The Wilson Bulletin*):


**LOUIS AGASSIZ FUERTES AWARD**

Daniel R. Petit, “Foraging ecology and habitat selection of migratory neotropical birds during winter in Belize, Central America.”

**PAUL A. STEWART AWARDS**

William L. Benner, “Range expansion and rapid evolution in the House Finch.”
Toni L. DeSanto, “Physiological and ecological factors influencing prey selection in the White Ibis.”
Andrea Dinep, “Post-nesting ecology of White Ibis chicks: the adaptive value of creeping behavior.”
Lawrence D. Igl, “Dickcissel site tenacity and mate fidelity in response to habitat alteration.”
Mark Korodan, “Effect of forest and oldfield fragmentation on neotropical migrants in northwest Arkansas.”
Elmer J. Stewart, “Information center hypothesis in the European Starling: importance of roost formation to food finding.”
Lori A. Willimont, “Sexual dimorphism and foraging ecology of the West Indian Red-bellied Woodpecker, an island species, and the Red-bellied Woodpecker, a continental species.”
Maria E. Zaccagnini, “Patch use of wintering Canada Geese in urban environment.”

**MARGARET MORSE NICE AWARD**

Jeff H. Hardt, “DuPage County bluebirds: behavior, breeding, and population dynamics.”

**GEORGE MIKSCH SUTTON AWARD**

Tracy Pedersen

**ALEXANDER WILSON PRIZE** (for best student paper)

Gonzalo Castro, Academy of Natural Sciences, Philadelphia and the University of Pennsylvania, “Assimilation efficiency of Sanderlings (*Calidris alba*) feeding on horse-shoe crab eggs (*Limulus polyphemus*).”
Selection committees for these awards: Edwards Prize—Keith L. Bildstein, Kathy G. Beal, and Albert Conway; Fuertes, Stewart, and Nice Awards—C. Dwight Cooley, Jon C. Barlow, and T. David Pitts; Sutton Prize—Bob Peck, Charles Blem, and J. William Hardy; Wilson Prize—Jon Barlow, Herb Kale, and Peter Hicklin.

Members and guests then enjoyed an illustrated lecture on the “History of Bird Illustration,” presented by Robert M. Peck, Fellow, Academy of Natural Sciences of Philadelphia.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Clench at 09:30, Thursday, 9 June in McShain Auditorium of the Science Building. Secretary Zimmerman summarized the highlights of Wednesday’s Council meeting. Of special note is a dues increase that will become effective in 1989: $21 regular membership, $15 student membership, $25 family membership, $30 sustaining membership, and $500 life membership. Subscription rates are also to be increased to $40 domestic, $45 foreign. The Council also voted to discontinue the student membership awards, but eliminated the 4-year limit on student membership. As long as a student can validate his (her) status, student rates will apply. The current membership of the Society is 2286, a decrease of 2% from last year. The membership was also informed that Editor Blem had been reelected for another year.

The following amendment to Section 5 of the Constitution was approved for submission to the membership at the next annual meeting:

Section 5. The officers of the Society, all past presidents of the Society, and six additional members who shall be elected by ballot of the Society, shall constitute an Executive Council. The term of office for the six elected members of the Executive Council shall be three years, without re-election, with terms staggered so that the terms of two such members expire each year. The Executive Council shall also constitute the Board of Directors of the Corporation. The business of the Society not otherwise provided for shall be in the hands of the Executive Council, which shall pass upon any urgent matters that cannot be deferred until the next annual meeting. Seven members of the Council shall constitute a quorum.

This change increases the elected members of the Council to 6 and increases the quorum to 7.

Lastly Zimmerman asked those in attendance to stand to honor those members who had died since we last met together—Robert S. Arbib, Jr. (Mamaroneck, NY), Mrs. Herbert (Betty) Carnes (Scottsdale, AZ), William W. Cole, Jr. (Cammilus, NY), Mrs. Esther Coggwell Conboy (Urbana, OH), Joseph M. Heiser, Jr. (Houston, TX), Morgan V. Jones III (Fogelsville, PA), James R. Koplin (Arcata, CA), Carl S. Marvel (Tucson, AZ), Orville O. Rice (Topeka, KS), Ralph W. Schreiber (Los Angeles, CA), Floyd P. Wolfarth (Blairstown, NJ), and Charlie W. Wooten (Elgin, SC).

Gary Ritchison, representing the Nominating Committee (Curtis S. Adkisson, chair, Gary Richison, and James D. Rising), presented the following slate for consideration by the membership: President—Mary Clench, First Vice-president—Jon Barlow, Second Vice-president—Richard Banks, Secretary—John Zimmerman, Treasurer—Robert Burns, Elected Council Member for 1989–1991—Keith Bildstein.

Robert D. Burns gave the treasurer’s report.
REPORT OF THE TREASURER
1 JANUARY 1987 TO 31 DECEMBER 1987

GENERAL FUNDS

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<td>Subscriptions and OSNA Refunds</td>
<td>197.50</td>
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<td>Incorporation Fee</td>
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<td>Deposit to endowment</td>
<td>9,639.91</td>
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ANNUAL REPORT

Bank Charges ........................................ $  32.72
Centennial meeting expenses ......................... $ 1,660.64
Letterhead stationary .................................. $   52.88

TOTAL DISBURSEMENTS—1 January 1987 to 31 December 1987 .......... $ 88,667.38

BALANCE .................................................. $  5,719.10

ENDOWMENT FUNDS

George M. Sutton Color Plate .......................... $51,345.86
Alexander Wilson Prize ................................ 2,182.41
Fuertes/Nice Awards .................................. 10,080.00
Stewart Awards ........................................ 21,316.00
Ernest P. Edwards Prize ............................... 2,350.32

General Endowment .................................... 151,805.95

The Editor's report was presented by Charles R. Blem.

EDITOR'S REPORT—1987

In 1987, 175 manuscripts (64 major papers, 111 short communications) were submitted to The Wilson Bulletin offices. This is a 6% decrease over the number of manuscripts submitted in 1986. Of these, 52% have been accepted, 43% have been rejected, 5% have been returned to authors for revision, and none remain under review. This amounts to an acceptance rate of approximately 58% for manuscripts submitted as major papers and 55% for manuscripts submitted as short communications. These figures are not precise because some papers submitted as major papers were accepted only after being shortened to short communication length. Manuscripts accepted for publication are usually published within 3–8 months of acceptance. Frontispiece articles may require a bit longer because there is only one such paper per issue. Major papers received by the current editor in 1987 were returned to the author within 77 ± 44 days of receipt. Short communications received in 1987 were returned within 60 ± 33 days of receipt.

I am indebted to the staff of Allen Press for their help in initiating a new editor. I particularly thank Arly Allen, Ken Blair, Guy Dresser, Douglas Wasson, and Sharon Kindall. I am extremely grateful to Assistant Editors Leann Blem, A. E. Conway, and Anne Wenner; the Editorial Board Kathy G. Beal, D. F. Caccamise, R. N. Conner, C. H. Stinson, and J. R. Walters; Review Editor George Hall; Color Plate Editor William A. Lunk; Index Editor Kathy G. Beal; numerous members of the WOS, particularly R. Banks, R. Burns, C. Braun, M. Clench, S. Gaunt, J. Barlow, J. Jackson, and the more than 260 volunteer referees who so kindly reviewed manuscripts over the past year. I am also indebted to J. E. Jeffrey, Chairman of the Department of Biology, Virginia Commonwealth University, and Dean Elake and Vice-president Smith for support of my efforts and the editorial office. Karen Blem deserves special acknowledgment for keeping all of the paperwork in order and putting up with her dad's nagging. Finally, I want to express my profound appreciation to the past editor, Keith Bildstein, for his unselfish assistance and kind hospitality. Keith is a dedicated biologist who combines keen insight with a lively personality and he will be hard to follow.

I have enjoyed my first year as editor. I take the responsibility very seriously and am concerned that we maintain the quality of the journal, attract a wider readership, and continue to retain the qualities that make The Wilson Bulletin journal. I know that not all who submit manuscripts to the journal will feel entirely satisfied with the process. However, it is our intention to treat every author fairly, handle each manuscript promptly and carefully, and
to do everything we can do to encourage submission of manuscripts. As the submission rate increases, the rate of rejection also must increase. However, this is one way to improve the quality of the journal, and I hope we are all in favor of that.

In the absence of Doris Watt, President Clench announced that a video tape of next year’s meeting site, St. Mary’s College, Notre Dame, IN, will be made available, and encouraged the membership to reserve the dates of the meeting, 25–28 May 1989.

George Hall moved and A. S. Gaunt seconded that the meeting be adjourned.

SECOND BUSINESS MEETING

President Clench open the second business meeting at 13:25, Saturday, 11 June in McShain Auditorium. The report of the Auditing Committee was received.

We, the undersigned, met on 9 June 1988 to review the financial records presented by the treasurer covering the period from 1 January 1987 to 31 December 1987. Upon checking these records, we are satisfied that they accurately reflect the financial operations of the Society. We believe the balances shown for the general, designated, and endowment funds are accurately stated. Furthermore, they show that the Society is in excellent financial health. The Auditing Committee commends Dr. Burns for his diligent performance in fulfilling the duties of treasurer for 1987.

Hubert P. Zernickow, Chairman
William A. Klamm
Harold Ratcliff
Robert A. Whiting

A motion to accept this report was made by Jerry Jackson and seconded by Chandler Robbins, and passed by the membership.

Treasurer Burns briefly reviewed the rationale for the dues increase. Then President Clench recalled the report of the Nominating Committee to the floor. In the absence of additions, Kathleen Klimkiewicz moved and Chandler Robbins seconded that the nominations be closed, and the motion passed. It was then moved by Peter Stettenheim and seconded by Herb Kale to elect the slate by acclamation. This motion also passed.

Tom Bancroft, chair (other members—Scott Wood, Jon Barlow, and Richard Banks), offered the report of the Resolutions Committee.

REPORT OF THE RESOLUTIONS COMMITTEE

WHEREAS, the ornithological collections of the British Museum (Natural History) are the largest and among the scientifically most important in the world, and

WHEREAS, these collections are viewed by ornithologists from around the world, not only as a national treasure of the United Kingdom, but of international importance, and

WHEREAS, the health of the collection depends upon its growth and use, and

WHEREAS, avian systematics is a vital and important field of research with major impacts on many applied disciplines, and

WHEREAS, ornithological collections are critical to an ever widening array of studies of both systematics and environmental problems,

THEREFORE BE IT RESOLVED, that the Wilson Ornithological Society deplores the reduction in support to the ornithological collections of the British Museum (Natural History) and regretfully predicts that this reduction will lead to the abdication of the United Kingdom from its traditional role of leadership not only in systematic ornithology but in ornithology in general.
Glen Wolfenden moved and Dick Stiehl seconded the motion to accept this resolution, and the motion passed.  
WHEREAS, the Endangered Species Act is one of America's most important laws for protecting plant and animal species, and  
RECOGNIZING that this act focuses public attention on society’s responsibility to balance wildlife preservation with more immediate economic well-being, and  
RECOGNIZING that the proposed amendments provide funding and protection to help avoid endangerment, recover listed populations, and monitor recovery after delisting, and  
RECOGNIZING that the proposed amendments are necessary to establish monitoring programs, provide funding, and hasten effective recovery plans,  
THEREFORE BE IT RESOLVED, that the Wilson Ornithological Society recommends that the United States Senate quickly pass a bill similar to that passed by the House of Representatives and resolve differences between them. All provisions in the proposed Senate bill are important and should be retained and no amendments weakening these provisions should be appended.

David Blockstein moved that this resolution be accepted. George Clark seconded the motion and it passed.

WHEREAS, biological diversity is indispensible to the natural functioning of ecosystems, provides raw material, products, and ideas for human civilizations, and provides aesthetic pleasure, emotional well-being, and spiritual enlightenment, and  
WHEREAS, the Earth’s biological diversity is now being reduced at a rate without precedent in human history and this rate appears certain to increase greatly over the next several decades, and  
WHEREAS, the deterioration of the biological diversity of the planet is a significant concern of scientists and a serious problem for humanity, and  
WHEREAS, present scientific understanding of the components of biological diversity is inadequate for its conservation and sustainable use,  
THEREFORE BE IT RESOLVED that the Wilson Ornithological Society asks the Congress of the United States to approve legislation that will: make the conservation of biological diversity a national goal and a national priority; require biological diversity to be a paramount consideration in Federal land-use planning; and support efforts to understand biological diversity. We ask that this legislation create a National Center for Biological Diversity, a National Scientific Advisory Committee on Biological Diversity, and provide increased financial support for basic scientific research in systematics, organismal biology, and ecology.

Scott Wood moved, Kathleen Klimkiewicz seconded, and the members voted to accept this resolution.

WHEREAS, both terrestrial and aquatic ecosystems provide essential breeding, migratory and wintering habitat for birds, and  
WHEREAS, emissions causing acid precipitation affect a diversity of habitat types and the birds using them, and  
WHEREAS, there is mounting evidence that continuing acidification of the environment has multiple negative effects on birds, both in reduction of the food base and the mobilization of heavy metals and toxins in the food chain, and  
WHEREAS, the National Acid Precipitation Assessment Program omitted any mention of birds in its interim report,  
THEREFORE BE IT RESOLVED that the Wilson Ornithological Society urge NAPAP to include examination of the impact of acid rain on the avifauna of North America in its final report.

Judy McIntyre moved to accept this resolution. Scott Wood seconded the motion. It it was approved.
WHEREAS, National and International Parks are important refuges for resident wildlife and plants, and
WHEREAS, National and International Parks offer important resources for stopover places for migrant birds in transit, and
WHEREAS, National and International Parks have important recreational and educational values for humans throughout the world, and
WHEREAS, National and International Parks contribute to a better world environment and therefore help mankind in general,
THEREFORE BE IT RESOLVED that the Wilson Ornithological Society expresses its appreciation to The Nature Conservancy and to the countries who have allowed The Nature Conservancy to help in setting up numerous Parks and Preserves within their boundaries.
In response to a motion by Jerry Jackson and a second by Chandler Robbins, this resolution was accepted.
WHEREAS, the Deutsche Ornithologische-Gesellschaft has made major and lasting contributions to the body of scientific information about birds, and
WHEREAS, the Deutsche Ornithologische-Gesellschaft is holding its 100th stated meeting during September 1988,
THEREFORE BE IT RESOLVED that on the occasion of our centennial, the Wilson Ornithological Society sends its congratulations to the Deutsche Ornithologische-Gesellschaft for its tradition of highest excellence in promoting ornithology and conservation.
Glen Wolfenden moved and Russ Balda seconded the motion to accept this resolution, and by vote of the Society, it was.
ON THE OCCASION of the Centennial of the Wilson Ornithological Society, the members attending its celebration in Philadelphia, Pennsylvania, send their greetings and good wishes to Robert and Judy Mason, long-time members of the Society and devoted students of the natural world.
FURTHERMORE, those of us fortunate enough to be able to gather for this happy occasion, express our heartfelt thanks to Robert and Judy for their generosity, caring thoughtfulness, and concern for the future by helping to ensure that the Wilson Ornithological Society will be able to continue its strong membership and to support field studies of living birds.
WE WISH Robert and Judy long life and continued joy in the world of birds.
Richard Banks moved that we accept this resolution. Dick Stiehl seconded the motion and it was passed.
ON THE HAPPY OCCASION of Dr. Robert D. Burns’ completing his tenth year of service as treasurer of the Wilson Ornithological Society.
WE, THE MEMBERS gathered for the centennial meeting of the Society, congratulate Bob Burns and express our sincere gratitude for his hard work, his devotion to what (at times) must seem like a thankless task, and his guardianship of our treasury. We have benefited from Bob’s pulling the Society out of a serious financial crisis in 1979, and from his careful stewardship and organization of our funds since he took office. Truly, any society could take a leaf from the Wilson book and find themselves a canny Scot who watches every penny as if it were his own-(although he knows that it isn’t).
BOB, WITH GRATITUDE WE SALUTE YOU. Long may your careful ways profit the Society.
Sandy Gaunt moved that this resolution be accepted. Charles Collins seconded the motion, and the Society approved with a loud hurrah.
WHEREAS, 1988 marks the hundredth anniversary of the founding of The Wilson Ornithological Society, and
WHEREAS, the annual meeting for 1988, the Centennial Celebration, was graciously
sponsored by the Academy of Natural Science of Philadelphia, The Cape May Bird Observatory, The Delaware Valley Ornithological Club, the Hawk Mountain Sanctuary Association, the University of Pennsylvania Biology Department, and Rosemont College, and

WHEREAS, the superb facilities and beautiful campus of Rosemont College enhanced the congenial atmosphere and collegiality of the meeting, and

WHEREAS, the Academy of Natural Sciences contributed a Centennial Celebration day of grand proportions, and

WHEREAS, the Scientific Program Committee arranged a series of informative and interesting lectures, poster sessions, and discussions, and

WHEREAS, Frank B. Gill and Millicent S. Ficken produced a symposium international in breadth and exciting in content, and

WHEREAS, the Committee on Local Arrangements provided a full calendar of social events to entertain and inform participants,

THEREFORE BE IT RESOLVED that the members of the Wilson Ornithological Society express their sincere appreciation to the Committees on Local Arrangements, on Scientific Program and on the Centennial Day Celebration; to the sponsors of the meeting; and especially to Frank Gill and Dawn Coughlin, who all contributed to a most enjoyable and edifying gathering.

Phillips Street moved that this resolution be accepted. Doug James seconded the motion and it was passed by the membership.

A motion was made by George Hall to adjourn the meeting and a second was provided by Scott Wood.

The reports of the standing committees follow.

REPORT OF THE COMMITTEE ON STUDENT MEMBERSHIP

The announcement of the awards was published in the Ornithological Newsletter in August. Three applications were received, and three awards were given: Fred Mikeseill, Kansas State University; Iris Velazquez, University of Puerto Rico; and Abby White, University of Minnesota.

The student membership awards were initially made from funds specified for that purpose in memory of the late Aaron M. Bagg, and thus cost the society "only" the time of the committee members and possibly some costs in soliciting and processing membership applications. It is obvious from our review that the activities of the committee from 1976 to the present involved much time and effort and considerable funds (e.g., in 1985, 230 letters were mailed to selected WOS members who were in positions to identify potential student members, and the WOS paid $364 for the dues of 26 student awardees). We are aware that members of the Council strongly feel that student membership awards recruit continuing members. We wish to point out that any correlation between membership awards and continuing membership does not identify the award as the cause of membership, it merely may indicate the cleverness of the committee in identifying young ornithologists who are not members. (Secretary's note: considerable data were presented by the committee in support of their argument, but I have deleted this for the sake of brevity). We believe that these data constitute compelling evidence that the great majority of the 56 awardees who continue as WOS members would have joined the Society without a membership award. We think that the time and money expended on student membership awards could be invested in a more productive way.

If the Society wishes to aid student members, we offer the following suggestions: (1) Remove the limit of 4 years on student memberships and allow student rates to all students as long as they are students, and (2) Lower the membership fee for students. The WOS
student membership appears to be one of the highest of any society (78% of regular membership, equalled by the AFO and the Ecological Society). COS student fees are only 65% of regular membership, and 63% of regular membership in the Animal Behavior Society, and (3) establish one or more prizes for the best student papers at the annual meeting that award 4 years of free membership. We are not convinced that any of these strategies will increase the number of students who become and remain members of the Society.

Helmut C. Mueller, Chair

LIBRARY COMMITTEE REPORT—1987

If this report seems unusually brief, it is not due to any lull in the Josselyn Van Tyne Library’s activity, but simply because the exigencies of other matters have resulted in rather late and hurried preparation. The year 1987 has been a fairly good one.


From the New Book Fund, 26 books, indices, and reports were purchased for $422.66. The 21 items sold brought a return of $219.15.

Received by the library were 212 journals and other items: 161 titles from 118 direct exchanges; 41 titles as gifts, from 31 members and institutions; and 10 titles from 6 subscriptions.

Our record of loans is up from last year in total items: 306. However, the 70 transactions involving 36 members and libraries is somewhat down. The more our collections are used, the better.

Once more, the committee is appreciative of all the support received.

William A. Lunk, Chair

There were no written reports from the Membership Committee or the Conservation Committee.

The Committee on Scientific Program was chaired by Richard C. Banks. The following members assisted as session moderators: Richard C. Banks, Bruce M. Beehler, Keith L. Bildstein, R. Michael Erwin, Millicent S. Ficken, Mercedes S. Foster, Frank B. Gill, J. William Hardy, M. Kathleen Klimkiewicz, Judy W. McIntyre, Henri Ouellet, Stanley E. Senner, Charles R. Smith, and Kimberly G. Smith.

PAPERS SESSION


T. C. Grubb, Jr., Dept. Zoology, Ohio State Univ., Columbus, OH, “Ptilochronology: Feather growth as an indication of net energy status.”

T. A. Waite, Dept. Zoology, Ohio State Univ., Columbus, OH, “A ptilochronology study of the value of cached food to Gray Jays wintering in Alaska.”

J.-P. L. Savard, Canadian Wildlife Service, Ste Foy, Quebec, and P. Lamothe, Quebec Hydro, Quebec, “Distribution, abundance and ecology of Black Scoters (Melanitta nigra) and Surf Scoters (M. perspicillata) in northern Quebec.”


D. Klem, Jr., Dept. Biology, Muhlenberg College, Allentown, PA, and C. J. Veltri, Tufts Univ. School Veterinary Medicine, Boston, MA, “Avian collision injuries.”


J. C. Bednarz, Hawk Mountain Sanctuary Assoc., Kempton, PA, “Cooperative breeding in the Harris’ Hawk (Parabuteo unicinctus): A test of the habitat saturation hypothesis.”

S. Wiles-Ehmann, Environmental and Forest Biology, SUNY College of Environ. Sci. and Forestry, Syracuse, NY, “The sexy swallow hypothesis: Do high copulation frequencies function to insure paternity?”

H. Landel, Dept. Biological Sci., Purdue Univ., West Lafayette, IN, “Correlates of male mating success in the lek-breeding Sharp-tailed Grouse (Tympanuchus phasianellus).”


B. M. Beehler, Smithsonian Instit., Washington, DC, “Lek behavior of the Raggiana Bird of Paradise (Paradisaea raggiana).”


R. N. Conner and D. C. Rudolph, Southern Forest Experiment Sta., Nacogdoches, TX, “Possible causes for the decline of Red-cockaded Woodpeckers (Picoides borealis) on two national forests in eastern Texas.”


J. R. Sauer and D. K. Dawson, U.S. Fish and Wildlife Service, Patuxent Wildlife Res. Center, Laurel, MD, “Adjusting within-year capture data from migration banding stations to provide an index to the number of migrants.”


R. W. Dexter, Dept. Biological Sci., Kent State Univ., Kent, OH, “Fidelity to mate and nesting site by Chimney Swifts (Chaetura pelagica).”


B. Torres, Dept. Zoology, Ohio State Univ., Columbus, OH, “Can chicks survive on a vegetarian diet?”


A. R. Place, Center of Marine Biotechnology, Univ. Maryland, Baltimore, MD, and E. T. Stiles, Dept. Biology, Rutgers Univ., Piscataway, NJ, “Poor and slow assimilation are not prerequisites for wax digestion.”

W. B. Quay, Napa, CA, “Comparative differences in percent abnormal sperm in North American wood warblers (Parulinae): Geographic, ecologic and etiologic factors.”


L. Clark, Monell Chemical Senses Center, Philadelphia, PA, “Olfactory thresholds of starlings (Sturnus vulgaris), Brown-headed Cowbirds (Molothrus ater) and Tree Swallows (Tachycineta bicolor).”

A. A. Dhondt, Univ. Instelling Antwerpen, Antwerpen (Wilrijk), Belgium, “Ecological and evolutionary effects of interspecific competition in European tits.”
G. Loery, White Memorial Conservation Center, Litchfield, CT, “Possible competition between Parus atricapillus and Parus bicolor.”
M. E. Minock, Univ. Wisconsin, Menasha, WI, and K. L. Dixon, Dept. Biology, Utah State Univ., Logan, UT, “Interactions of sympatric, nesting Mountain (Parus gambeli) and Black-capped (P. atricapillus) chickadees.”
M. Withiam, Albany Medical Center Hospital, Albany, NY, D. Lemmon, SUNY Albany, Albany, NY, and C. Barkan, Smithsonian Environ. Res. Center, Edgewater, MD, “Pair bonds, social behavior, and the use of space in wintering Black-capped Chickadees (Parus atricapillus).”
M. S. Ficken, Dept. Biological Sci. and Field Station, Univ. Wisconsin, Milwaukee, WI, “The vocal repertoire of the Mexican Chickadee (Parus sclateri): A case of extreme vocal divergence.”
R. Weisman and L. Ratcliffe, Dept. Psychology and Biology, Queen’s Univ., Kingston, ONT, “Pitch perception in Black-capped Chickadees (Parus atricapillus).”

A. McCallum, Dept. Biology, Univ. New Mexico, Albuquerque, NM, “Should Mountain Chickadees practice natal philopatry?”

F. C. Rohwer, Appalachian Environmental Lab., Univ. Maryland, Frostburg, MD, “Intraspecific and interspecific variation in clutch size of waterfowl.”

D. M. Finch, Forestry Sci. Lab., Laramie, WY, “Influence of surrounding habitat on nest box use and reproductive outcome in House Wrens and Tree Swallows.”

T. L. Master, Biology Dept., Lehigh Univ., Bethlehem, PA, “Snowy Egret (Egretta thula) participation in mixed species foraging aggregations on southern New Jersey salt marsh pannes.”


M. L. Hebblethwaite, Dept. Environmental and Forest Biology, College of Environ. Sci. and Forestry, SUNY, Syracuse, NY, “Do Barn Swallows (Hirundo rustica) colonies function as information centers?”

E. D. Kennedy, Rutgers Univ., New Brunswick, NJ, “Determinancy of clutch size in House Wrens (Troglodytes aedon) and European Starlings (Sturnus vulgaris).”


W. O. Piper, Dept. Biology, Univ. North Carolina, Chapel Hill, NC, “Correlates of social dominance in the White-throated Sparrow: Age, sex and location.”

H. Wiley, Dept. Biology, Univ. North Carolina, Chapel Hill, NC, “Do subordinate White-throated Sparrows have a special role in finding food for dominants?”


E. O. Willis, Dept. Zoologia, Univ. Estadual Paulista, Rio Claro, S. Paulo, Brazil, “Mimicry in bird flocks of cloud forests in southeastern Brazil.”


C. Hitchcock, Dept. Psychology, Univ. Toronto, Toronto, ONT, “Memory for cache sites in the Black-capped Chickadee (Parus atricapillus).”


ATTENDANCE

ALABAMA: Auburn, Michael P. Losito.
ARKANSAS: Fayetteville, Elizabeth Adam, Douglas James, Kimberly G. Smith.
ARIZONA: Flagstaff, Russell P. Balda.
CALIFORNIA: Albany, Paula K. Kleintjes; Berkeley, Leonard A. Brennan; Hayward, Bess Cogswell, Howard L. Cogswell; Long Beach, Charles Collins; Napa, W. B. Quay.
CONNECTICUT: Litchfield, Gordon Loery; Norwalk, Roland Clement; Old Lyme, Roger T. Peterson, Virginia Peterson; Storrs, George A. Clark, Jr.
DELAWARE: Newark, Craig Berman, Roland R. Roth.
FLORIDA: Gainesville, John William Hardy, John A. Smallwood; Maitland, Herbert W. Kale, II; St. Petersburg, Harold McNaughton, Katherine McNaughton; Venice, Glen E. Woolfenden.
ILLINOIS: Macomb, Ed Franks.
INDIANA: Hanover, J. Daniel Webster; West Lafayette, Hans Landel.
KANSAS: Manhattan, John L. Zimmerman.
KENTUCKY: Richmond, Gary Ritchison.
MAINE: Brunswick, F. Burton Whitman; Richmond, Peter D. Vickery; Wayne, Olin Sewall Pettingill, Jr.
MARYLAND: Annapolis, Mark L. Hoffman; Baltimore, Allen R. Place; Darlington, Sherwood Weisheit; Edgewater, Christopher Barkan; Frostburg, Joan McKearman, Frank C.
The Wilson Bulletin • Vol. 100, No. 4, December 1988

Rohwer; Gaithersburg, Jean Swinebroad, Jeff Swinebroad; Laurel, Deanna Dawson, Michael Erwin, Dennis G. Jorde, Kathleen Klimkiewicz, Chandler S. Robbins, Eleanor Robbins, John R. Sauer.

Massachusetts: Boston, Carl Veltri; Foxboro, William E. Davis, Jr.; Manomet, Jonathan L. Atwood, Barbara Hamilton; South Hadley, Susan M. Smith.

Michigan: Ann Arbor, Janet Hinshaw, Louise Storer, Robert Storer; Grass Lake, Harold Ratcliff, Jackson, Robert A. Whiting; Pleasant Lake, Hubert P. Zernickow.

Minnesota: Duluth, Pershing B. Hofslund, Mrs. P. B. Hofslund; Minneapolis, Kendall Corbin; New Brighton, James L. Howitz.

Mississippi: Mississippi State, Danny J. Ingold, Bette Jackson, Jerome Jackson.

Missouri: Cape Girardeau, Dick Stehl.

New Hampshire: Lebanon, Peter Stettenheim.

New Jersey: Camden, David Dobkin; Collingswood, Lynda Craig; Haddonfield, Kim Laidig; Kendall Park, Charles Leck; Mendham, Susannah K. Graedel; New Brunswick, Ann S. Hoffenberg; Piscataway, Dale Kennedy, Linda Romagana, Douglas White; Princeton, Craig Benkman; Riverton, George B. Reynard; Trenton, Mary E. Doscher; Wenoah, Edward Manners.

New Mexico: Albuquerque, Arch McCallum; Socorro, H. Stephen Logsdon.

New York: Allegheny, Betty Eaton, Stephen Eaton; Ithaca, Carola A. Haas, Lynn A. Mahaffy, Robb Reavlll, Steven C. Sibley, Charles R. Smith; Millbrook, Joerg Boehner, Stephen Nowicki; New York, Walter Bock, Angelo Capparella; Skaneateles, Sarah Wiles-Ehmann; South Salem, Walter Piper, Syracuse, Chris Hebblethwaite, Margaret Hebblethwaite; Utica, John McIntyre, Judith W. McIntyre; West Albany, Ralph Hanano.


Pennsylvania: Allentown, Daniel Klem; Berwick, Douglas Gross; Bemby, Babs Street, Phillips B. Street; Bethlehem, Terry L. Master; Clarion, Roger J. McPherson; Fort Washington, Edward L. Altemus; Harrisonburg, Kathleen H. Finnegan; Hatfield, Harry W. Mankonen; Kempton, Jim Bednarz, Laurie Goodrich, Stanley E. Senner, John Wallace; Lancaster, Paul J. Dubowy; Philadelphia, Larry Clark, Dawn F. Coughlan, Lee Ann Draud, Frank B. Gill, John Guarnaccia, Steven Holt, Alison Mostrom, Robert Peck, Robert Ridgely, Mark B. Robbins, Frederick Sheldon, Douglas Wechsler; Pittsburgh, Kenneth C. Parkes, D. Scott Wood; Sarver, George T. Reese; Scranton, Michael Carey; University Park, Margaret Brittingham.

Rhode Island: Wakefield, Catherine Johnson, Malcolm Jones.

South Carolina: Catawba, Albert E. Conway; Clemson, Jim Belthoff; Rock Hill, Keith Bildstein.

South Dakota: Aberdeen, Dan Tallman, Erika Tallman; Vermillion, Byron Harrell, Mrs. Byron Harrell.

Tennessee: Maryville, Ralph J. Zeuglein.

Texas: Galveston, Mary Clench; Nacogdoches, Richard N. Conner.

Utah: Logan, Keith L. Dixon.

Virginia: Blacksburg, Arlene Blumion, Judi Murray; Castleton, Betsy Trent Thomas;
Richmond, Charles Blem, Leann Blem; Shipman, Allen Hale; Staunton, John F. Mehner; Sweet Briar, Ernest P. Edwards.


WEST VIRGINIA: Great Cacapon, Julia Belton, William Belton; Morgantown, George Hall, Tanya Hall.

WYOMING: Laramie, Deborah M. Finch.

BRITISH COLUMBIA: Burnaby, Nico Verbeek.

NEW BRUNSWICK: Sackville, Carrie Hicklin, Peter Hicklin.

ONTARIO: Kingston, Laurene Ratcliffe, Susan Lemprière; Ottawa, Henri Ouellet; Toronto, Jon Barlow, Tony Lang, Chris Hitchcock, Thomas S. Parsons, David Sherry.

QUEBEC: Ste Foy, Carole Savard, Jean-Pierre Savard.

BELGIUM: Antwerpen, Andre Dhondt.

BRAZIL: Rio Claro, Edwin O. Willis.


NORWAY: Dragvoll, Olav Hogstad; Klaebu, Svein Haftorn.

SWEDEN: Stockholm, Jan Ekman.

CONTRIBUTORS TO THE CENTENNIAL FUND, WOS

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Hubert P. Zernickow
Charles W. S. Ziengenfus
John L. Zimmerman
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by Kathy G. Beal

This index includes references to genera, species, authors, and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text. Common names are as they appear in the volume unless otherwise specified. References is made to books reviewed, and announcements as they appear in the volume.

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