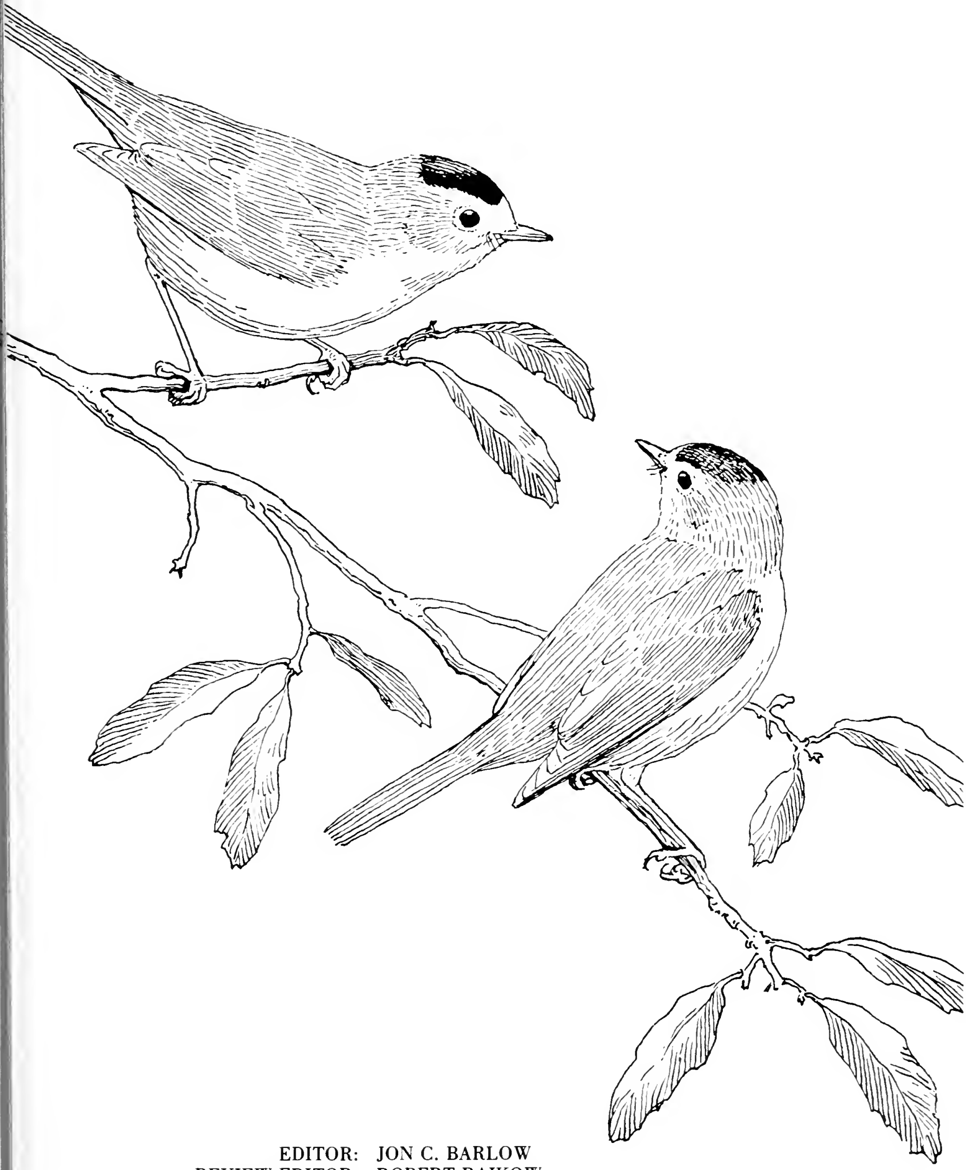
The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOLUME 92 1980 QUARTERLY



President—George A. Hall, Department of Chemistry, West Virginia University, Morgantown, West Virginia 26506.

First Vice-President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

Second Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Clait E. Braun (term expires 1980); Sidney A. Gauthreaux, Jr. (term expires 1981); Richard C. Banks (term expires 1982).

DATES OF ISSUE OF VOLUME 92 OF THE WILSON BULLETIN

NO. 1—8 APRIL 1980
NO. 2—18 JULY 1980
NO. 3—7 OCTOBER 1980
NO. 4—26 FEBRUARY 1981

CONTENTS OF VOLUME 92

NUMBER 1

GENERAL NOTES

NUMBER 2

NUMBER 3

NUMBER 4

GENERAL NOTES

Aj. W

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 92, NO. 1 MARCH 1980 PAGES 1–148

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

Membership dues per calendar year are: Active, $14.00; Student, $10.00; Sustaining, $20.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

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 104 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," 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.

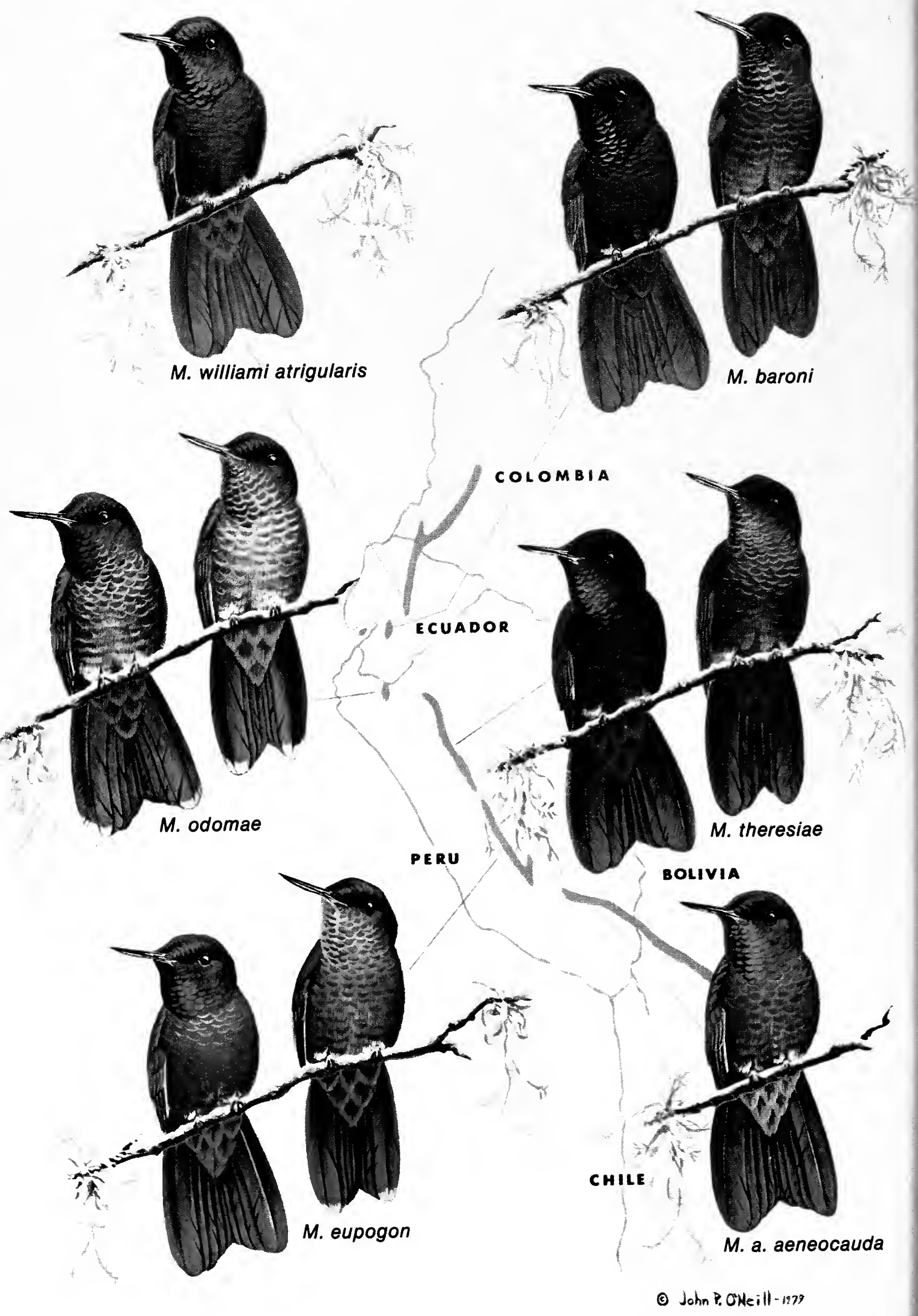
THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan. Known office of publicaton: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.



Hummingbirds of the *Metallura aeneocauda* superspecies (females to right when shown).

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 92, NO. 1 MARCH 1980 PAGES 1–148

Wilson Bull., 92(1), 1980, pp. 1–7

A NEW SPECIES OF METALTAIL HUMMINGBIRD FROM NORTHERN PERU

GARY R. GRAVES

Recent fieldwork in the isolated cordilleras of Peru by personnel of the Louisiana State University Museum of Zoology and other institutions has resulted in the discovery of several new high Andean birds (Blake and Hocking 1974, Weske and Terborgh 1974, Lowery and Tallman 1976, O'Neill and Parker 1976). In October 1977 during a preliminary LSUMZ expedition to the Divisoria de Huancabamba, Department of Piura, Peru, I collected 2 specimens of a previously undescribed metaltail hummingbird. The specimens were stolen in Peru before they could be critically compared with museum material but field sketches of the birds showed sufficient differences from other species of *Metallura* to suggest they represented an undescribed form. A LSUMZ field party returned to the region in 1978 and fortunately obtained 5 skins and 1 complete skeleton of this new form.

In the genus *Metallura*, the related forms *recisa*, *williami*, *primolinus*, *atrigularis*, *baroni*, *theresiae*, *eupogon*, *aeneocauda* and *malagae* form a superspecies group (Fig. 1) of uncertain relationships (*M. tyrianthina* and *M. phoebe* (Black Metaltail) are locally sympatric with members of this group). Peters (1945) merged *primolinus* and *atrigularis* into *M. williami* and reduced *baroni* to an isolated subspecies of *eupogon*. Consequently Zimmer (1952) combined *malagae* and *aeneocauda*, but considered *baroni* to be specifically distinct and states (Zimmer 1952:10): "The remaining three forms (*baroni*, *theresiae*, *eupogon*) are more divergent from the general pattern of the series, and it is probably best to give each of them individual specific status until specific relationships can be more positively demonstrated." Wetmore (1970) considered the newly described *recisa* as a subspecies of *primolinus*, which he raised to specific level on the basis

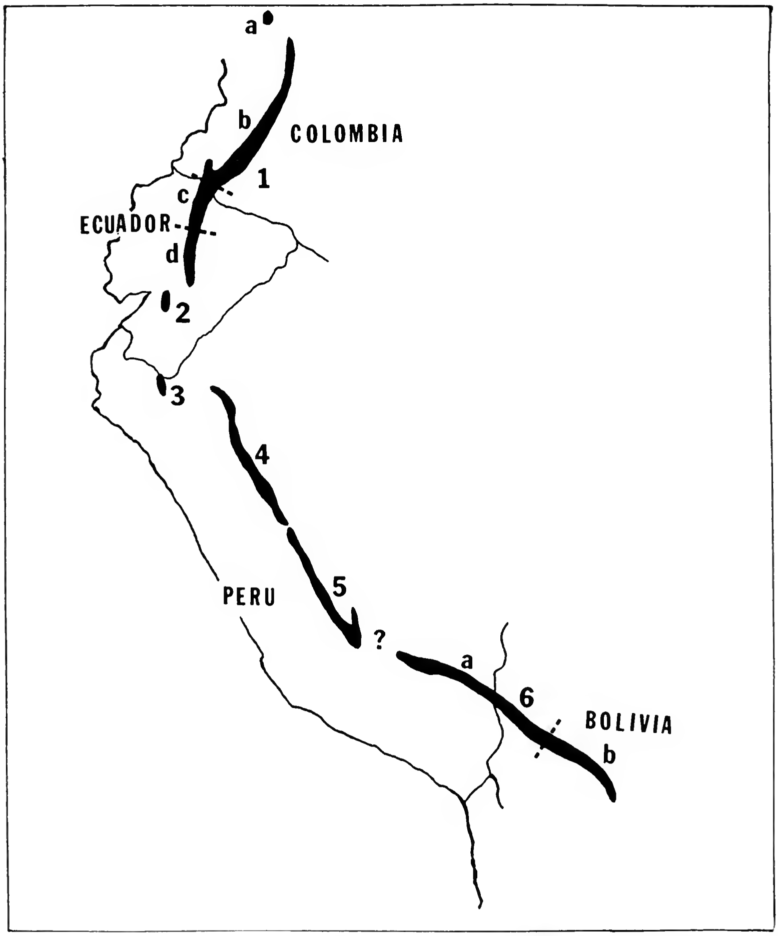


FIG. 1. Distribution of the *aeneocauda* superspecies: (1) *Metallura williami* [including (a) *recisa*, (b) *williami*, (c) *primolinus*, (d) *atrigularis*]; (2) *M. baroni*; (3) *M. odomae*; (4) *M. theresiae*; (5) *M. eupogon*; (6) *M. aeneocauda* [including (a) *Aeneocauda* and (b) *malagae*].

of tail coloration. Since *aeneocauda* (Gould) 1846 has priority, the group can be called the *aeneocauda* superspecies (see Zimmer 1952). The possible relationship of *M. iracunda* (Perija Metaltail) and *M. phoebe* to the *aeneocauda* group should be investigated. The new species clearly belongs to the *aeneocauda* superspecies, and fills what had been an apparent gap in the range of that superspecies (see frontispiece).

Table 1

Ranges and Means (mm) of Selected *Metallura* of the *aeneocauda* Superspecies

	N	Wing (chord)	Tail	Culmen from feathers
baroni	3 ♂♂	56.4–58.0 (57.1)	37.9–38.8 (38.4)	12.7–13.4 (13.2)
	1 ♀	54.8	37.2	13.0
odomae	3 ♂♂	59.2–60.7 (59.7)	40.2–40.9 (40.5)	13.8–14.4 (14.1)
	4 ♀♀	54.6–57.7 (56.3)	38.4–41.0 (40.2)	13.5–14.3 (13.8)
theresiae	4 ♂♂	60.5–65.1 (62.6)	40.7–43.4 (42.3)	12.5–12.8 (12.6)
	3 ♀♀	58.1–60.4 (59.2)	40.3–41.1 (40.8)	12.4–13.3 (12.8)
eupogon	7 ♂♂	62.5–65.4 (64.4)	41.0–43.8 (42.9)	11.6–13.6 (12.8)
	3 ♀♀	59.3–59.4 (59.3)	39.6–40.7 (40.2)	11.9–12.6 (12.3)

Metallura odomae sp. nov.

NEBLINA METALTAIL

HOLOTYPE.—Louisiana State University Museum of Zoology no. 87547; adult male from Cerro Chinguela, ca. 5 km northeast of Sapalache, elevation approximately 2900 m (9500 ft), 05°07′S, 79°23′W; Department of Piura, Peru; 10 June 1978; netted and prepared by Richard D. Semba; original number 535.

DIAGNOSIS.—A medium-sized, sexually dimorphic *Metallura* of the *aeneocauda* superspecies. Gorget in males reddish purple, not green, orange, violet, or black as in other members of the superspecies. In females, chin, throat and upper breast speckled with Scarlet discs (capitalized color names are from Ridgway 1912) not restricted to central throat as in *theresiae* and *eupogon*. Both sexes lighter below than other members of the *aeneocauda* superspecies. Bill of *odomae* longer than those of nearest allopatric of *baroni*, *theresiae* and *eupogon*; not apparently overlapping with respective sexes (Table 1).

DESCRIPTION OF HOLOTYPE.—Crown, hind neck, back, wing coverts and rump iridescent dark green; chin and gorget Amaranth Purple; superorbital and postorbital areas bronzy olive grading to rich coppery bronze on auriculars, lateral throat and sides of neck surrounding gorget; underparts olive-bronze with buffy white subterminal bars giving the lower breast and belly a spotted aspect. Plumes at vent white and fluffy; feathers on lower belly edged terminally with tan; undertail coverts bronzy green, broadly edged with buffy cinnamon. Remiges dark purplish brown; small coverts on carpal region of wing cinnamon-buff. Rectrices seen from above and against the light, dark olive; with the light, shining dark steel-blue. From below rectrices are shining golden green; outermost pair tipped on inner and outer web with pale gray. Soft part colors in life: bill black; iris dark brownish black; feet black.

SPECIMENS EXAMINED.—*M. w. williami* (FMNH) 2♂♂ Purace, Department of Cauca, 1♀ Malvasa, Department of Cauca and (LSUMZ) 1♂ El Crucero, Department of Cauca, Colombia; *M. w. atrigularis* (LSUMZ) 2♂♂ Loma Magdalena, Prov. Morona-Santiago, Ecuador; *M. baroni* (AMNH) 3♂♂, 1♀ Cuenca, Ecuador; *M. odomae* (LSUMZ) 1♂, 4♀♀ Cerro Chinguela (FMNH) 2♂♂ "above Huancabamba," Peru; *M. theresiae* (LSUMZ) 8♂♂, 6♀♀ Cordillera Colon, 1♂, 1♀ above Balsas, Department of Amazonas, 3♂♂, 2♀♀ Zapatagocha, Department of Huánuco, Peru; *M. eupogon* (FMNH) 3♂♂, 3♀♀ Huánuco Mts. (AMNH) 2♂♂ Maraynioc (LSUMZ) 3♂♂ NE Comas, Department of Junin; *M. a. aeneocauda* (LSUMZ) 2♂♂, 1♀ near Ollantaytambo, Department of Cuzco, Peru, *M. a. malagae* (LSUMZ) 1♂, 4♀♀ Chapare, and 1♂ Incachaca, Bolivia.

DISTRIBUTION. —So far, known only from the edge of uppermost forest into paramo from ca. 2600 m–3000 m of the Divisoria de Huancabamba, Department of Piura-Cajamarca, Peru.

ETYMOLOGY.—I take pleasure in naming this new form for Babette M. Odom of Orange, Texas, who has generously supported the LSUMZ field program in Peru as part of her longstanding interest in avian natural history. The proposed English name, Neblina Metaltail, refers to the foggy conditions on the wet, windswept shrublands above timberline on Cerro Chinguela where this hummingbird lives.

REMARKS

M. odomae differs from other members of the *aeneocauda* group in various details consistent at the superspecific level. *M. odomae* females are lighter below than females of *M. w. williami* (Viridian Metaltail), *M. baroni* (Violet-throated Metaltail), *M. theresiae* (Coppery Metaltail), *M. eupogon* (Fire-throated Metaltail), and *M. a. aeneocauda* and *M. a. malagae* (Scaled Metaltail). Females of all forms have buffy throats covered with scattered iridescent discs. The breast and belly feathers, with buff or buffy white subterminal bars, have terminal green discs which are smallest (thus making the underparts lighter) on *M. odomae*, *M. baroni* and *M. a. aeneocauda* progressing on a graded series to wider, darker green discs on *M. theresiae* and *M. eupogon*. Dorsally female *M. odomae* are nearly indistinguishable from examples of *M. a. aeneocauda*, *M. a. malagae* and *M. w. williami*, but lack the olive-bronze highlights of *M. baroni*, the coppery red colors of *M. theresiae* and the bronzy reflections of *M. eupogon*.

Males of *M. odomae* are lighter below than the other allospecies. The subterminal buffy white bars of the underparts give a scaled appearance to *M. odomae* similar to that of *M. a. aeneocauda*. *M. w. williami*, *M. w. atrigularis*, *M. baroni*, *M. theresiae* and *M. eupogon* have uniformly dark green underparts with very little suggestion of barring or scaling. Dorsally, *M. odomae* males are intermediate in color between the bronzy-backed *M. eupogon* and the green-backed *M. w. williami*, *M. w. atrigularis*, *M. a. aeneocauda* and *M. a. malagae*. Gorget colors in males of the *aeneocauda* superspecies vary from green (*recisa*, *williami*, *primolinus*, *theresiae*, *aeneocauda* and *malagae*) to orange (Grenadine Red) in *M. eupogon* (gorget narrower than depicted in frontispiece), reddish purple in *M. odomae*, violet in *M. baroni* and black in *M. w. atrigularis*. Gorget discs in females are not noticeably different in color from gorgets of males except in *M. odomae* (see DIAGNOSIS). Pale tips are present in the outer rectrices of all female *Metallura*, but in males of the *aeneocauda* group, pale tips are conspicuous only in *M. odomae* (faintly present in *M. a. aeneocauda* of Cuzco). The longer bill of *M. odomae* suggests a niche shift relative to its nearest allopatric relatives (*baroni*, *theresiae* and *eupogon*).

HABITAT AND FIELD OBSERVATIONS

Two male specimens in the Field Museum of Natural History identified as "*Metallura eupogon baroni*" proved to be referable to the new form. The collecting locality recorded on the tags by C. Kalinowski in 1954, "Huancabamba, Department of Piura, Peru, 2600 m," probably refers to the crest of the cordillera northeast of Huancabamba along the Huancabamba-Namballe mule trail (=LSUMZ "Cerro Chinguela").

On Cerro Chinguela, *M. odomae* was found in pajonal similar to treeline habitats found in many other locations in Peru along the wet eastern slope of the Andes. The LSUMZ specimens of the type series were captured in a series of nets placed along lanes cut through tongues of stunted forest extending upward along ravines into the paramo and isolated clumps of elfin forest well separated from the forest below (Fig. 2). The *odomae* collected in 1977 were discovered during a wet snowstorm (ca. 5°C with moderately heavy winds). One of the individuals was foraging on the white flowers of storm flattened, dwarf ericaceous shrubs partly concealed by grass. The bird flew low from shrub to shrub, often alighting on prostrate sheaths of grass to probe protruding flowers. During the snowstorm, which lasted for over an hour (most snow melted on contact with the rain drenched slope), I observed *Pterophanes cyanopterus* (Great Sapphirewing), *Coeligena lutetiae* (Buff-winged Starfrontlet), *Eriocnemis vestitus* (Glowing Puffleg), *M. tyrianthina* (Tyrian Metaltail) and *Chalcostigma herrani* (Rainbow-bearded Thornbill) foraging in more sheltered ravines and the leeward sides of elfin forest clumps. No call notes, songs or flight displays of *M. odomae* were noted by any expedition member. No *M. odomae* examined had enlarged gonads (6–24 June, 22 October).

TAXONOMIC RELATIONSHIPS

The relationships of Andean hummingbirds are poorly understood, and the existence of questionably isolated taxa hinders the application of the biological species definition (Mayr 1963). Morphological and behavioral characters and geographical isolation, however, permit inferences concerning species limits between allopatric populations whose potential for interbreeding cannot be determined with certainty.

Members of the *aeneocauda* superspecies are restricted to wet treeline-paramo habitats between 2600? and 4000 m elevation from the Andes of Colombia south to Bolivia (Fig. 2). *M. odomae* is separated geographically by unsuitable habitat from the nearest populations of *baroni* (200 km),

FIG. 2. Isolated grove of elfin cloud forest in páramo on Cerro Chinguela near the type locality of *Metallura odomae* (photograph by Theodore A. Parker, III).

theresiae (120 km) and *eupogon* (640 km). Recent work on the Pleistocene speciation of Andean birds (e.g., Vuilleumier 1969) has shown similar patchy distributions of other high Andean hummingbirds (*Oreotrochilus, Chalcostigma*). Present-day distribution patterns of the *aeneocauda* superspecies may represent relictual interglacial refugia, with much reduced or no gene flow between them. Although the paucity of information on the biology of *Metallura* does not yet permit a thorough systematic revision of the *aeneocauda* superspecies, evidence from central Peru suggests isolating mechanisms have developed between several forms. Specimens of *theresiae* and *eupogon*, from the Cordillera Carpish and the Huánuco Mountains, respectively (separated by the narrow arid intermontane valley of the Río Huallaga, Department of Huánuco, Peru), show no evidence of intergradation. Unfortunately, no specimens have been taken in the area between the known ranges of *eupogon* (Cordillera Vilcabamba) and *aeneocauda* (Urubamba Valley) in the Department of Cuzco, Peru.

Until contradictory information is available, I consider the genetically isolated, morphologically differentiated taxa as allospecies (*M. baroni, M. odomae, M. theresiae, M. eupogon*) and follow Zimmer (1952) in merging *recisa, williami, primolinus* and *atrigularis* (=*M. williami*) and *aeneocauda* and *malagae* (=*M. aeneocauda*). I recommend a north to south linear arrangement of taxa, with *M. odomae* placed between *M. baroni* and *M. theresiae*.

ACKNOWLEDGMENTS

J. W. Eley, T. S. Schulenberg, T. A. Parker, III, R. D. Semba and D. R. Hunter provided moral support and companionship during the 1977 and 1978 expeditions. I appreciate the opinions and discussion freely offered by J. V. Remsen, H. D. Pratt, J. P. O'Neill and G. L. Graham. O'Neill, Pratt, Graham, S. Y. Graves and M. D. Williams commented on several early drafts of this paper. The referees K. C. Parkes and J. W. Fitzpatrick made valuable comments on the manuscript. I thank J. W. Fitzpatrick (Field Museum of Natural History) and J. Farrand, Jr. (American Museum of Natural History) for providing comparative material. I commend John O'Neill for his artistic and scientifically useful frontispiece.

Arturo and Helen Koenig, Manuel and Isabel Plenge and Gustavo del Solar continue their gracious *ayuda* to all LSUMZ personnel during necessary stays in Lima and Chiclayo. I am especially indebted to Manuel Sanchez S. whose help on the 1976, 1977 and 1978 expeditions has been indispensable.

I am grateful to John S. McIlhenny, H. Irving and Laura R. Schweppe, and Babette M. Odom for their support of the LSUMZ fieldwork. Antonio Brack E., Marc Dourojeanni R., Susana Moller H. and Carlos Ponce P. of the Direccion General Forestal y de Fauna of the Ministerio de Agricultura, Lima, Peru, continue their support of the LSUMZ field studies and issued the necessary permits. I also acknowledge the continued collaboration of Aero Peru.

LITERATURE CITED

Blake, E. R. and P. Hocking. 1974. Two new species of tanager from Peru. Wilson Bull. 86:321–516.

Lowery, G. H., Jr. and D. A. Tallman. 1976. A new genus and species of nine-primaried oscine of uncertain affinities from Peru. Auk 93:415–428.

Mayr, E. 1963. Animal species and evolution. Harvard Univ. Belknap Press, Cambridge, Massachusetts.

O'Neill, J. P. and T. A. Parker, III. 1976. New subspecies of *Schizoeaca fuliginosa* and *Uromyias agraphia* from Peru. Bull. Br. Ornithol. Club 96:136–141.

Peters, J. L. 1945. Checklist of birds of the world, Vol. 5. Harvard Univ. Press, Cambridge, Massachusetts.

Ridgway, R. 1912. Color standards and color nomenclature. Washington, D.C. (Published by the author.)

Vuilleumier, F. 1969. Pleistocene speciation in birds living in the high Andes. Nature 223:1179–1180.

Weske, J. S. and J. W. Terborgh. 1974. *Hemispingus parodii*, a new species of tanager from Peru. Wilson Bull. 86:97–103.

Wetmore, A. 1970. Descriptions of additional forms of birds from Panama and Colombia. Proc. Biol. Soc. Wash. 82:767–776.

Zimmer, J. T. 1952. Studies of Peruvian birds, No. 62. The hummingbird genera *Patagona, Sappho, Polyonymus, Ramphomicron, Metallura, Chalcostigma, Taphrolesbia,* and *Aglaiocercus*. Amer. Mus. Novit., No. 1595:1–29.

MUSEUM OF ZOOLOGY, LOUISIANA STATE UNIV., BATON ROUGE, LOUISIANA 70893. ACCEPTED 16 OCT. 1979.

Wilson Bull., 92(1), 1980, pp. 8–20

BI-PARENTAL CARE IN KILLDEER: AN ADAPTIVE HYPOTHESIS

Sarah Lenington

Parental care (here defined as investment made by adults in their young after hatching) occurs in all birds except the Megapodidae. It is to be expected that the amount and proportion of time and energy devoted to parental care will profoundly affect reproductive success. Furthermore, the strategy of parental care (whether young are tended by male, or female, or both) will have far reaching effects on the mating system (Lack 1968, Orians 1969). Participation of both sexes in parental care is widespread among birds and easily understood when the young are fed by their parents (Lack 1968). However, in several monogamous anatids, charadriids, scolopacids and recurvirostrids in which both adults tend precocial, independently foraging young, participation of both sexes in parental care is problematic (Selander 1972).

This paper discusses parental behavior of the monogamous Killdeer (*Charadrius vociferus*), in which broods may be tended by either 1 or 2 adults. To assess advantages of bi-parental care for a species with precocial young, I contrast time budgets for adult behavior with both parents and only 1 adult tending the brood and suggest hypotheses for strategies of parental care in this species.

Killdeer arrive in mid-March at my study area in St. Paul, Minnesota. Males often return to a previously occupied territory and in some instances retain the same mate (Lenington and Mace 1975). Courtship activities and pair formation begin immediately after arrival. Bunni (1959) did the only detailed study of Killdeer breeding biology. He reported a clutch-size of 4 and an incubation period of 24–26 days. Males and females participate equally in incubation. Occasionally Killdeer are double-brooded, with eggs for second nestings laid before the first brood has fledged. The young, never fed by their parents, fledge at about 31 days. If a clutch is destroyed, Killdeer may nest up to 3 times.

METHODS

This study was done in the 1972 breeding season on 150 acres on, and adjacent to, the Minnesota State Fair Grounds, where suitable Killdeer habitat was broken up by busy streets and large complexes of buildings (Fig. 1). Killdeer nested on areas with low or sparse vegetation and foraged regularly on lawns, the margins of ponds and the edges of a drainage ditch.

I watched 8 broods and 13 attendant adults. Five broods were tended by both adults and 3 by 1 adult. Eight adults, including at least 1 from each pair, were trapped and banded with

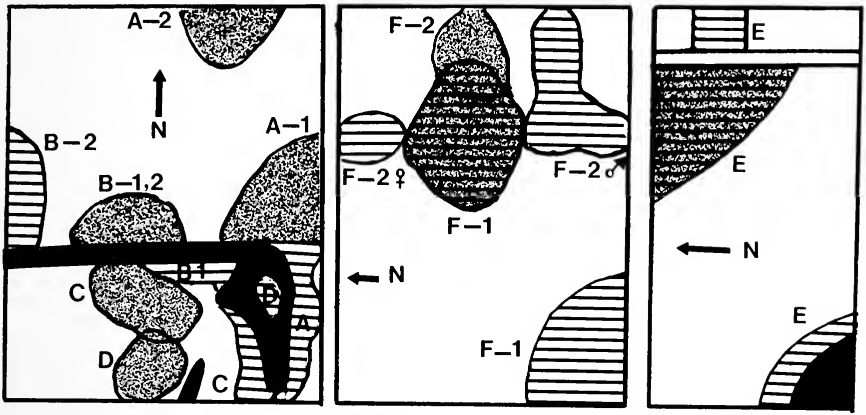


FIG. 1. Scale map of the study area. Scale: 1 in = 75 f. Gray areas are nesting territories, striped areas are feeding territories and solid black areas are standing water. Pairs are labled with letters. In the case of pairs that raised more than 1 brood, locations of individual broods are indicated with numbers (e.g., B-1 = the location of the first brood of pair B).

both colored and numbered Fish and Wildlife Service bands. Sex of adults was determined by the position assumed during copulation. Chicks were color-banded while still in the nest. All observations were made from a car or canvas blind using 7× binoculars and a 25× spotting scope. When recording data, adults in 2-parent broods were classified as either "attentive" or "non-attentive." The attentive adult was either the one that called, led, or brooded chicks, or the bird consistently closest to the chicks. Usually the non-attentive adult was far enough from the chicks to be easily determined. When it was impossible to decide which bird was attentive, both birds were called "attentive."

Estimates of the time budget for parental care were based on 158.3 h of observation, distributed as shown in Table 1. Observation periods for individual broods ranged from 1–5 h/day. The amount of time parents engaged in each of 10 activities was timed to the nearest ½ min. Of these activities, only "standing," "foraging," "anti-predator behavior," "aggression," "brooding" and "incubation" are discussed in this paper. The other 4 activities (calling chicks, preening, courtship and interspecific aggression, e.g., aggression toward Spotted Sandpipers (*Actitis macularia*) comprised less than 5% of the adults' time.

"Standing" consists of all standing, including any pause during preening or feeding of at least 30 sec, but not short pauses during aggressive or courtship activities. "Foraging" comprises all time a bird spent seeking and capturing prey. "Anti-predator behavior" includes giving alarm calls, standing in an alert posture or displaying (see Deane 1944 for a description of Killdeer anti-predator displays) to a potential predator. "Aggression" consists of chasing, fleeing and threat displays between conspecifics (see Phillips 1972 for a description of Killdeer aggressive displays). "Brooding" involves both brooding and shielding chicks from the sun. "Incubation" includes sitting on eggs.

Distances between a chick and the nearest observable chick, and between chicks and the attentive adult were recorded every 10 min. If chicks were in dense vegetation, distances between chicks and the attentive adult were noted whenever a chick became visible. When more than 1 chick emerged, the distance between them was noted. All measurements of distance are estimates based on known distances between landmarks.

TABLE 1
DISTRIBUTION OF OBSERVATION TIME

	Hours	Percent
Age of chicks		
Week 1	49.6	31.3
Week 2	33.9	21.4
Week 3	43.2	27.3
Week 4	17.7	11.2
Week 5	13.9	8.8
Total	158.3	100.0
Time of day		
Dawn–12:00	87.7	55.5
12:00–17:00	45.9	29.0
17:00–sunset	24.7	15.5
Total	158.3	100.0
Roles of adults		
Attentive adult 2-parent broods	98.0	61.9
Non-attentive adult 2-parent broods	35.3	22.2
Attentive adult 1-parent broods	25.0	15.9
Total	158.3	100.0

RESULTS

Hatching and leaving the nest.—Hatching dates on the study area in 1972 ranged from 15 May–22 July. Non-attentive adults were never seen on the territory as eggs were hatching, except during nest relief, or when the nest was threatened by a predator. Attentive adults brooded the chicks continuously during the first few hours after hatching. After chicks were about 6 h old they occasionally emerged from beneath the adult and stood by the nest for up to 15 min. Chicks remained at the nest-site throughout the day of hatching and the following night, after which they were led from the nest by the parents. Both adults accompanied the chicks as they left the nest. Neither adults nor chicks were observed to return to the nest-site.

Movements of the brood.—During courtship and incubation Killdeer defend both a nesting territory and 1 or more feeding territories. Seven of the 8 broods were taken to feeding territories and only 1 pair (pair E, see Fig. 1) remained with its brood on the nesting territory. Availability of cover was an important factor associated with where adults took chicks. Although 3 broods (E, F_1, F_2) used areas which lacked standing water, all

TABLE 2
PERCENTAGE OF OBSERVATION TIME EACH ADULT TENDED CHICKS AND PERCENTAGE OF TIME EACH SPENT TENDING CHICKS IN RELATION TO EGG-LAYING FOR 2 PAIRS

Brood		Minutes of observation	Percent[1] Male	Percent[1] Female
B_1		1075	31.6	68.4
D		717	48.7	53.3
F		1607	44.0	56.0
A	Pre-laying	704	30.4	69.6
	Laying	303	80.5	19.5
	Post-laying	610	45.0	55.0
E	Pre-laying	1146	62.4	37.6
	Laying	405	84.7	43.5
	Post-laying	615	52.5	54.7
	Laying of third clutch	314	64.0	45.1
	Post-laying	1090	54.4	70.5

[1] The percentage totals are more than 100% as a result of instances in which both parents tended chicks.

broods were taken to areas where dense herbaceous vegetation was available; there chicks hid at the approach of a predator. Pair E had nested in an area with heavy herbaceous cover, whereas their 2 feeding territories had sparse vegetation. In this instance, the brood remained on the nesting territory even though the adults used the feeding territories for much of their own foraging.

All pairs continued to defend and occasionally use the original nesting territory until the chicks fledged. One pair (F) returned to the nesting territory to brood chicks at night. Other pairs returned to the nesting territory when the feeding territory was temporarily disrupted by flooding or human construction work. Finally, 5 of 6 clutches for second broods were laid on the original nesting territory.

Attentiveness and formation of 1-parent broods.—Chicks were only unattended when parents responded to a predator, were involved in aggressive encounters with other Killdeer, or were engaged in precopulatory displays or copulation. However, in 2-parent broods, normally only 1 adult at a time remained near the chicks. The non-attentive adult remained at least 23 m from the brood while chicks were young. After chicks were about 2 weeks old, non-attentive adults occasionally spent time near the brood and both parents sometimes tended the chicks. In general, attentive periods lasted 1–1½ h but varied considerably (range 10–327 min).

Females predominated in attentiveness in four 2-parent broods and males in 1 (Table 2). In the 2 (A, E) of 4 (A, B, E, F) second broods for

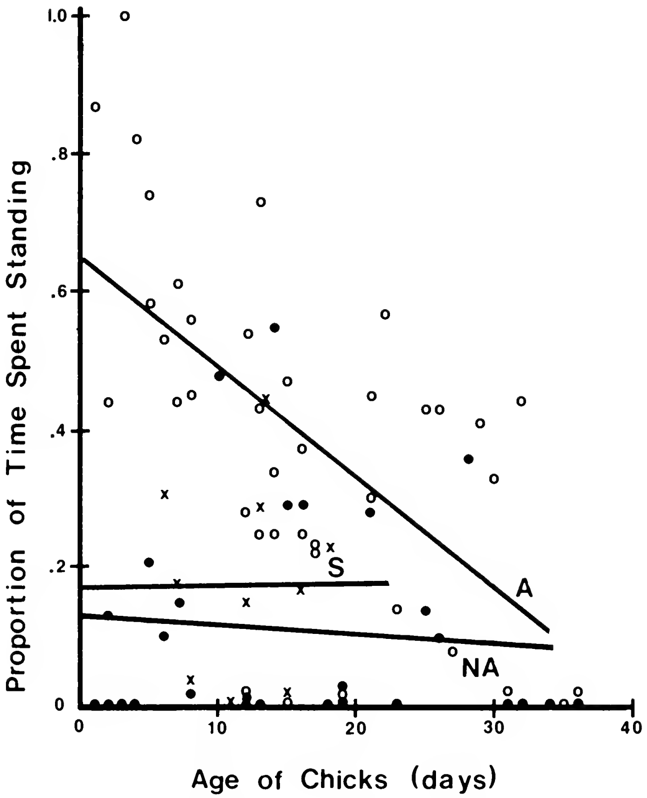


FIG. 2. Relationship between age of chicks and proportion of time adults spend standing. A = attentive adults in 2-parent broods; NA = non-attentive adults in 2-parent broods; S = adult in 1-parent broods. Open circles are observed points for A, closed circles are observed points for NA, and ×'s are observed points for S. Pearson's $r_A = -0.623$, $P < 0.05$; $r_S = +0.023$, NS; $r_{NA} = -0.245$, NS.

which I have adequate data, the proportion of time males tended chicks increased markedly from 1 day before the first egg was laid through the period of egg-laying. After eggs were laid, the proportion of time he tended chicks decreased.

There were no significant differences between attentive and non-attentive adults in the proportion of time spent incubating eggs for second broods ($t = 1.42$, df = 54, $P > 0.05$, N = 56) or in incubation time between males and females ($t = 0.93$, df = 54, $P > 0.05$, N = 56).

All first broods were tended by 2 adults. Two of the 4 clutches for second broods hatched and in each instance the second brood was at-

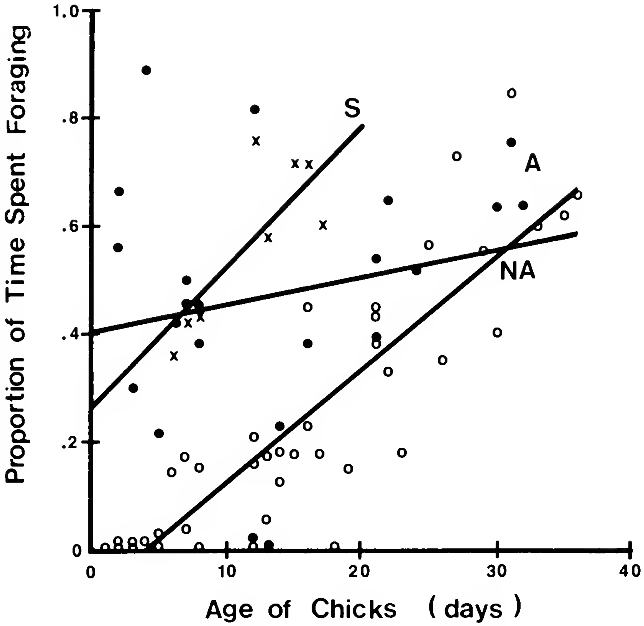


FIG. 3. Relationship between age of chicks and proportion of time adult spent foraging. Symbols are the same as in Fig. 2. Pearson's $r_A = +0.874$, $P < 0.01$; $r_S = +0.777$, $P < 0.05$; $r_{NA} = +0.207$, NS.

tended by only 1 adult. In the first case (B) the female left her second brood when the chicks were 6 days old and the male cared for the chicks until fledging. In the second case (F), the parents divided the brood sometime between 7 and 10 days after hatching. Each adult took 1 chick (the other 2 chicks disappeared during the first 5 days after hatching) and moved about 100 m apart. The brood remained separated day and night and no further interaction between the adults was observed. On the twelfth day after hatching, the banded male developed a lame foot. On the thirteenth day he had frequent aggressive encounters with an unmarked bird; the next day an unmarked bird assumed care of the chick in the area previously defended by the male. The foster parent brooded the chick and behaved in every way like a normal attentive adult.

Time budget.—Standing was the predominant activity of attentive adults in 2-parent broods while chicks were young (Fig. 2). While standing attentive adults usually faced their chicks. As chicks grew older, standing by attentive adults decreased markedly. Non-attentive adults and adults in 1-parent broods spent relatively little time standing; the time spent standing did not appear to change with the age of the chicks.

TABLE 3

THE DISTRIBUTION OF DEFENSE TIME BETWEEN ATTENTIVE (A) AND NON-ATTENTIVE (NA) ADULTS IN 2-PARENT BROODS

Age of chicks (weeks)[1]		Predators		Conspecifics	
		A	NA	A	NA
1	min	66	113	54	74
	%	36.9	63.1	42.1	57.8
2	min	17	20	41	11
	%	46.0	54.0	78.8	21.2
3	min	37.5	0	179	28.5
	%	100.0	0.0	86.5	13.5
4	min	51.5	0	15	0
	%	100.0	0.0	100.0	0
5	min	17	0	42	4.5
	%	100.0	0.0	91.3	8.7

[1] The first 3 weeks of observations are based on 4 broods and the last 2 weeks on 1.

The relationship between foraging time of adults and the age of their chicks is shown in Fig. 3. In 2-adult broods, Killdeer rarely fed while tending young in the first 2 weeks after hatching. Foraging occurred only when adults were non-attentive. Attentive adults and adults in 1-parent broods fed more as their chicks grew older. An analysis of covariance on the regression lines for attentive adults and adults in 1-parent broods showed no significant difference in the slopes ($t = 0.55$, df = 46, $P > 0.05$, N = 48), but there was a significant difference in the intercepts ($t = 17.02$, df = 46, $P < 0.001$, N = 48). Adults in 1-parent broods foraged more than did attentive adults in 2-parent broods, since adults in 1-parent broods can only forage while near their chicks; they have no "off duty" time. Non-attentive adults spent about 40% of their time foraging. The proportion of time they devoted to feeding did not significantly increase as the chicks grew older.

During the first week after hatching non-attentive adults defended the chicks against conspecifics and predators (Table 3), while the attentive adult stood near and faced the brood. When chicks were about 1 week old, attentive adults increasingly defended territory and brood. By the third week after hatching they performed virtually all the defense.

Only 1 adult at a time was ever observed brooding chicks. Chicks were brooded frequently for 2 days after hatching, but much less frequently after that. During rain they were brooded up to 15 days old and at night up to 18 days old.

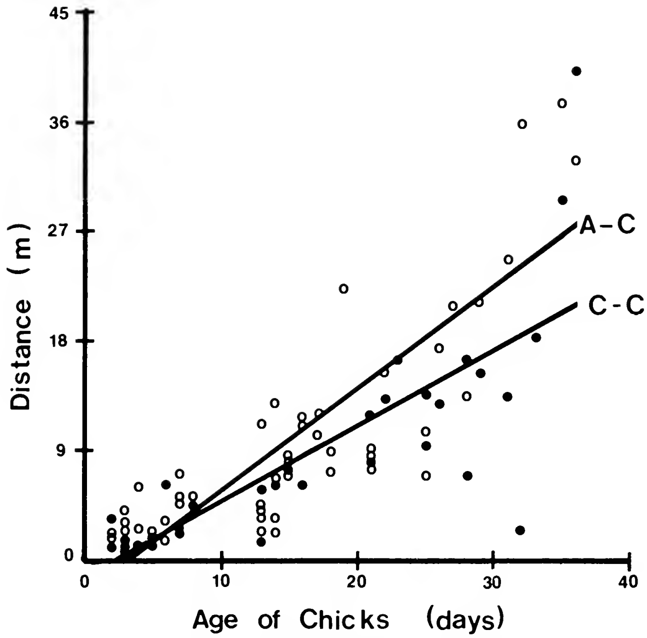


FIG. 4. Relationship between age of chicks and distance between birds. A–C = adult–chick distance, C–C = distance between a chick and the nearest chick. Open circles = observed points for A–C, closed circles = observed points for C–C. Pearson's r_{A-C} = +0.858, $P < 0.01$; r_{C-C} = +0.780, $P < 0.01$.

Distance between birds.—The distance between attentive adults and chicks and between a chick and the nearest chick increased as chicks grew older (Fig. 4). During a 3-week period I noted the activity of attentive adults (whether feeding or standing) when recording distances between adults and chicks. Distances between adults and their chicks did not differ significantly as a function of adult activity.

Fledging period and breeding success.—Chicks fledged 29–34 days after hatching. Adults and fledged chicks stayed together on the feeding area for 3 or 4 days; families then broke up. I occasionally found adults and fledged chicks in flocks of Killdeer that gathered in late summer on the breeding area, but no further interactions between adults and their chicks were observed.

All broods were followed from egg-laying until chicks were lost or fledged. The number of pairs in this study, however, was too small to permit meaningful comparisons of breeding success for 1- and 2-parent broods. Fledging success for 2-parent broods was 1.2 chicks/pair (SD = ±0.98, N = 6), and 1.5 chicks/pair fledged from 1-parent broods (SD =

±0.71, N = 2). Overall fledging success was 1.6 chicks/pair (SD = ±1.03, N = 6).

DISCUSSION

Four hypotheses for the evolution of bi-parental care in species with precocial young are: (1) two adults may be needed to brood chicks, especially as chicks mature; (2) two adults may detect predators sooner than one (Lack 1968); (3) two adults may be needed to defend the brood from predators or the territory from conspecifics (Pitelka et al. 1974); (4) two adults may be needed to prevent chicks from getting lost.

The data obtained in this study do not support the first hypothesis. Only a single adult was ever observed brooding chicks and thus 2 adults are not required for that purpose.

I have no data bearing directly on the second hypothesis, although it seems a likely factor favoring bi-parental care. This hypothesis could be tested by observing which adult gives the first alarm call when a predator approaches. If the first alarm call is most frequently given by the non-attentive adult, or alternatively, randomly distributed between the 2 adults, support would be provided for the predator detection hypothesis.

My data are insufficient to either confirm or reject the third hypothesis. In 2-adult broods most of the defense was performed by 1 adult alone. Two adults, however, were occasionally involved in defending broods against severe threats. Furthermore, it may be advantageous for adults to reduce individual stress by sharing defense.

Although the second and third hypotheses are probable factors favoring the evolution of bi-parental care, they do not account for the behavior of adults in 2-parent broods, particularly the considerable time adults spend standing near the brood. It is possible that the standing adult is watching for predators, but 3 kinds of evidence suggest other factors are also involved in this behavior.

(1) Adults spend less time standing and more time feeding as chicks get older, even though chicks probably remain vulnerable to predators until capable of sustained flight.

(2) When a predator approaches, the attentive adult often stands near the brood, rather than engaging in active defense. This behavior could potentially direct the predator's attention to the location of the chicks.

(3) Attentive adults usually orient toward the chicks. Since predators may approach from any direction, adult orientation should be random with respect to chicks, if the purpose of standing is to watch for predators. Instead, the orientation of adults suggests that the chicks themselves are being watched.

It is possible that highly mobile, precocial chicks need to be closely watched to prevent straying—the fourth hypothesis for parental care. Lost chicks are commonly reported for species with precocial young (Graul 1975, McBride et al. 1969, Parmelee et al. 1968, Ridpath 1971). In this study young chicks frequently wandered from the family group and seemingly did not respond to parental calls until the adult approached closely. One 5-day-old chick in my study did get lost. Both parents were displaying to a dog that had come near the brood. Despite frequent parental alarm calls, the chick got up from where it had been crouching, walked about 60 m from view, and was not seen again.

As chicks grow older they may be less apt to get lost, either because they have learned the boundaries of the adult's territory, or because as their nervous system matures they are better able to attend to parental calls. Few data are available on developmental changes in shorebird chick's responsiveness to parental vocalizations. However, studies of both wild and domestic populations of ducks (*Anas* spp.) and chickens (*Gallus*) have shown considerable individual variation among young chicks in ability to respond to parental calls (Collias and Collias 1956, Gottleib 1961, Jaynes 1956, Slucken 1964), despite the selective advantage of such behavior. In addition, both behavioral (Bateson 1964, Kaufmann and Hinde 1961) and neurological (Corner et al. 1966, Tuge et al. 1960) evidence indicates older galliform chicks sustain avoidance responses longer than younger chicks, suggesting that older Killdeer chicks may "freeze" longer than young chicks when parental alarm calls are given. Finally, both galliform and waterfowl young respond best to a combination of visual and auditory stimuli (Boyd and Fabricus 1965, Evans 1972, Porter and Stettner 1968) suggesting that adults may remain near young chicks to present a combination of visual and auditory cues.

If 2 adults stay with the brood, more time is available for watching chicks, since adults can feed while "off duty." In 1-adult broods all feeding must be done while tending chicks and consequently chicks are watched less. As the danger of chicks straying from the territory decreases, attentive adults in 2-parent broods are increasingly free to forage, or to defend territory and brood. Bi-parental care, however, usually persists until chicks fledge, suggesting that additional advantages, possibly related to defense or predator protection, accrue to 2-adult broods. If the above hypotheses are correct, bi-parental care should have a greater selective advantage than uni-parental care in Killdeer, and thus the existence of 1-parent broods requires explanation.

In Killdeer, uni-parental care has only been observed when second broods are raised (Bunni 1959). Bunni (1959) also reported that females always deserted their second brood, leaving near the time of hatching. In my study 1 of 2 second broods was deserted by the female and the other was split by the adults. Data from other shorebirds suggest that declining food late in the breeding season may be responsible for desertion of 1 adult from second broods. Sandpipers (*Calidris* spp., Holmes and Pitelka 1968) and Ruddy Turnstones (*Arenaria interpres*, Nettleship 1973) time nesting so that young hatch during the period of maximum food availability, and thus late second broods may hatch when food supply is diminishing.

Female desertion has been reported for several monogamous shorebirds, e.g., Lapwing (*Vanellus vanellus*), Green Sandpiper (*Tringa ochrops*), Common Sandpiper (*Actitis hypoleucos*) (Bannerman 1961); Great Knot (*Calidris tenurostris*) (Dement'ev et al. 1969); Stilt Sandpiper (*Micropalama himantopus*) (Jehl 1973); Greenshank (*Tringa nebularia*) (Nethersole-Thompson 1951); Ruddy Turnstone (Nettleship 1973); Dunlin (*Calidris alpina*) (Soikkeli 1967). Trivers (1972) suggests that the sex making the smallest parental investment is most likely to desert the young, since it has the least to lose. However, this argument has recently been criticized on theoretical grounds (Boucher 1977, Dawkins and Carlisle 1976, Maynard Smith 1977). No evidence was obtained in this study to support the hypothesis that females invested less in their young than did males. I found no significant differences between male and female behavior with respect to the first brood, nor in amount of time spent incubating the second clutch. Consequently, females probably invested more than males, since females produce eggs. Graul et al. (1977) and Maynard Smith (1977) have suggested that females will desert their young if they are so physiologically taxed after egg-laying that they are less able to raise the brood than are males. It may be, then, that female Killdeer desert second broods, not because they have invested less than their mates, but rather, because they have invested more.

SUMMARY

In order to assess the advantage of bi-parental care for Killdeer (a species with precocial young) I compared time budgets for adult behavior when both parents tended the brood with the time budget when only 1 adult tended the chicks. In 2-adult broods only 1 parent at a time remained near the brood and adults did most of their foraging while away from the brood. Thus adults in 1-parent broods fed more while near their chicks and watched their chicks less than did adults in 2-parent broods. The data suggest that predator protection and need to prevent chicks from straying from the brood are factors that may select for bi-parental care in this species.

ACKNOWLEDGMENTS

I am grateful to R. E. Phillips for help and advice in planning this research and to L. Abramovitch, R. E. Phillips and J. Walters for their many useful comments on this manuscript.

LITERATURE CITED

BANNERMANN, D. A. 1961. Birds of the British Isles. Oliver and Boyd, London, England.

BATESON, P. P. G. 1964. Changes in chicks' responses to novel moving objects over the sensitive period for imprinting. Anim. Behav. 12:479–489.

BOUCHER, D. H. 1977. On wasting parental investment. Am. Nat. 111:786–788.

BOYD, H. AND E. FABRICUS. 1965. Observations on the incidence of following of visual and auditory stimuli in naive mallard ducklings. Behaviour 25:1–15.

BUNNI, M. K. 1959. The Killdeer in the breeding season. Ph.D. dissert. Univ. Michigan, Ann Arbor, Michigan.

COLLIAS, N. E. AND E. C. COLLIAS. 1956. Some mechanisms of family integration in ducks. Auk 73:378–400.

CORNER, M. A., J. J. PETERS AND P. R. VAN DER LOEFF. 1966. Electrical activity patterns in the cerebral hemisphere of the chick during maturation, correlated with behavior in a test situation. Brain Res. 2:274–292.

DAWKINS, R. AND T. R. CARLISLE. 1976. Parental investment and mate desertion: a fallacy. Nature Lond. 262:131–133.

DEANE, C. D. 1944. The broken-wing behavior of the Killdeer. Auk 61:243–247.

DEMENT'EV, G. P. AND N. A. GLADKOV. 1969. Birds of the Soviet Union. Vol. 3. Publ. for Smithsonian Inst. and N.S.F. Washington, D.C. by Israel Prog. for Sci. Transl. (Jerusalem).

EVANS, R. M. 1972. Development of an auditory discrimination in domestic chicks (*Gallus gallus*). Anim. Behav. 20:77–87.

GOTTLEIB, G. 1961. The following-response and imprinting in wild and domestic ducklings of the same species. Behaviour 18:205–228.

GRAUL, W. D. 1975. The breeding biology of the Mountain Plover. Wilson Bull. 72:6–31.

———, S. R. DERRICKSON AND D. W. MOCK. 1977. The evolution of avian polyandry. Am. Nat. 111:812–816.

HOLMES, R. T. AND F. A. PITELKA. 1968. Food overlap among co-existing sandpipers on northern Alaska tundra. Syst. Zool. 17:305–318.

JAYNES, J. 1956. Imprinting: the interaction of learned and innate behaviour. I. Development and generalization. J. Comp. Physiol. Psychol. 49:201–206.

JEHL, J. R., JR. 1973. Breeding biology and systematic relations of the Stilt Sandpiper. Wilson Bull. 85:115–145.

KAUFMAN, I. C. AND R. A. HINDE. 1961. Factors influencing distress calling in chicks with special reference to temperature changes and social isolation. Anim. Behav. 9:197–204.

LACK, D. 1968. Ecological adaptations for breeding in brids. Methuen, London, England.

LENINGTON, S. AND T. MACE. 1975. Mate-fidelity and nesting-site tenacity in the Killdeer. Auk 92:149–151.

MAYNARD SMITH, J. 1977. Parental investment: a prospective analysis. Anim. Behav. 25:1–9.

MCBRIDE, G., L. P. FARER AND F. FOENANDER. 1969. The social organization and behavior of the feral domestic fowl. Anim. Behav. Monogr. 2:127–181.

NETHERSHOLE-THOMPSON, D. 1951. The Greenshank. Collins, London, England.

NETTLESHIP, D. N. 1973. Breeding ecology of turnstones (*Arenaria interpres*) at Hazen Camp, Ellesmere Island, N.W.T. Ibis 115:202–217.

ORIANS, G. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589–603.

PARMELEE, D. F., D. W. GRENIER AND W. D. GRAUL. 1968. Summer schedule and breeding biology of the White-rumped Sandpiper in the central Canadian arctic. Wilson Bull. 80:5–29.

PHILLIPS, R. E. 1972. Sexual and agonistic behavior of the Killdeer, (*Charadrius vociferus*). Anim. Behav. 20:1–9.

PITELKA, F. A., R. T. HOLMES AND S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in arctic sandpipers. Am. Zool. 14:185–204.

PORTER, R. H. AND L. J. STETTNER. 1968. Visual and auditory influences on following responses in bobwhite quail. J. Comp. Physiol. Psychol. 66:808–811.

RIDPATH, M. G. 1971. The Tasmanian native hen, *Tribonyx mortierii*. 1. Patterns of behaviour. C.S.I.R.O. Wildl. Res. 17:1–51.

SELANDER, R. K. 1972. Sexual selection and sexual dimorphism in birds. Pp. 180–230 *in* Sexual selection and the descent of man 1871–1971 (B. Campbell, ed.), Aldine, Chicago, Illinois.

SLUCKEN, W. 1972. Imprinting and early learning. Methuen, London, England.

SOIKKELI, M. 1967. Breeding cycle and population dynamics of the dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4:158–198.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 *in* Sexual selection and the descent of man 1871–1971 (B. Campbell, ed.), Aldine, Chicago, Illinois.

TUGE, H., Y. KANAYAMA AND C. H. YUEH. 1960. Comparative studies of the development of the EEG. Jap. J. Physiol. 10:211–220.

UNIV. CHICAGO, ALLEE LAB. ANIMAL BEHAVIOR, 5712 S. INGLESIDE, CHICAGO, ILLINOIS 60637. (PRESENT ADDRESS: INSTITUTE OF ANIMALBEHAVIOR, RUTGERS UNIV., 101 WARREN ST., NEWARK, NEW JERSEY 07102.)
ACCEPTED 30 JAN. 1979.

Wilson Bull., 92(1), 1980, pp. 21–32

RESPONSE BY MALE FOX SPARROWS TO BROADCAST OF PARTICULAR CONSPECIFIC SONGS

Dennis J. Martin

Those oscines possessing more than 1 theme, or type of primary song, generally sing a prolonged bout consisting of 1 type of song before switching to another song-type. Fox Sparrows (*Passerella iliaca*), breeding in northern Utah, do not organize their songs, or singing, in such a manner. Typically, these Fox Sparrows possess 3 highly complex song-types (Martin 1976, 1977). Each song-type consists of an introductory portion composed of syllables of a type and sequence usually characteristic of each individual, and a terminal sequence of syllable-types that is stereotyped among birds. Thus, each song uttered could easily encode for messages, such as species (Mulligan 1966, Falls 1969) and individual identity (Brooks and Falls 1975a), population affiliation (Milligan and Verner 1971) and the sex, location, motivation and marital status of the singer (Marler 1956). An individual Fox Sparrow sings each of its song-types only once, until its entire repertoire is exhausted and then begins the sequence again. Sequence of song presentation is usually peculiar to each individual and seems to remain constant through time (Martin 1976).

I have proposed that this organization system, although unlike that of most oscines, functions to reduce the monotony or habituation of songs, or singing, to the singer and/or the receiver. Hypotheses similar to this have been offered to explain the organization of singing in birds that do not exhibit the Fox Sparrow "system" (Falls and Krebs 1975; Hartshorne 1956, 1958, 1973; Hinde 1958; Kroodsma 1977; Mulligan 1966; Isaac and Marler 1963; Dixon 1969; Lemon and Chatfield 1971, 1973). Presentation of song-types in bouts, with ultimate matching of song-types among countersinging individuals, has been suspected also of allowing countersinging rivals to hurl and retaliate with threats more forceful than those immediately being sung (Dixon 1969, Bertram 1970) and, potentially, matching of song themes among neighboring territorial males may facilitate neighbor-neighbor recognition (T. Keeney, pers. comm., abstracted in C.O.S. meeting 1977). An hypothesis quite similar to this has been offered and supported by Lein (1972, 1978). Working with Black-throated Green (*Dendroica virens*) and Chestnut-sided (*D. pensylvanica*) warblers, he has demonstrated that the various song-types sung by some species of warbler can be used to encode for, and transmit, different messages concerning the location of the singer on its territory and its level of aggressiveness. The song-types appear to "form a graded series of signals, increasing the efficiency of male-male communication" more precisely than the use of a single song-type (Lein 1978:1266). Singing in the Yellow-throated Vireo (*Vireo flavifrons*) also may prove to be a complexly ordered graded series of signals (Smith et al. 1978).

It should follow that, if songs are of various valence to the singer and/or receiver, one would expect that particular songs would be sung more frequently than others and that matching of song-themes among countersinging contestants might occur. Further, such a system should result in varying levels of response to broadcast of particular types of conspecific song. Previous study has shown that Fox Sparrows tend not to sing preferentially any particular type of song from within their repertoire more than any other, and that matching of songs between countersinging rivals is virtually precluded by the manner in which Fox Sparrows organize their singing sessions (Martin 1976). However, inasmuch as all males do not share similar song-types, and playback experiments had not been performed previously, discussion as to the valence capabilities (or importance) of the various song-types has been inferential. Thus, in this study, I attempt to determine whether the various songs of Fox Sparrows function similarly in male-male territorial encounters and whether the level of agonistic response to the broadcast of particular types of conspecific song indicates that the valence among various song-types differs.

METHODS

Subjects.—All Fox Sparrows used in playback experiments were located in Logan Canyon, Cache Co., Utah. Arrival on the breeding ground and establishment of territories occurred from late March through mid-May. By early June all birds were paired and well into nest construction, egg-laying, or incubation. Testing was begun on 31 May and ended on 28 June in 1976. Only those data collected from birds which were paired territory-holders throughout the test period were considered. Birds were not captured and individually banded because of the potential trauma they might have associated with the use of conspecific playback to lure them into mist nets. However, birds were easily identified by the composition of their song repertoires (Martin 1976, 1977).

Song repertoire in Fox Sparrows.—Detailed description of song structuring in Fox Sparrows breeding in Logan Canyon is presented in Martin (1976, 1977). Males in the population possess a mean of 3.2 songs (SD = 0.8, N = 133). And, although birds may choose from some 49 complex syllable-types that I have defined to construct their songs, most songs consist of but 8 syllable-types ($\bar{x}$ = 8.15, SD = ±1.2, N of songs analyzed = 416). Typically, the syllable-types and their sequence in the first half of a particular song varies among individuals, whereas the terminal portion tends to be similar in structure within the population (Fig. 1). This uniformity in the endings of songs allows virtually all songs to be grouped into 1 of 5 major song-types: A, B, C, D and E. A complete listing of the syllable-types, comprising the major song-types so far delimited from Fox Sparrows in northern Utah and southern Idaho, is given in Martin (1977 Appendix).

Equipment.—Song-types used as conspecific playback (Fig. 2) were recorded in 1975 using a Uher 517 microphone mounted in a 61 cm parabolic reflector with a Uher 4000 IC type

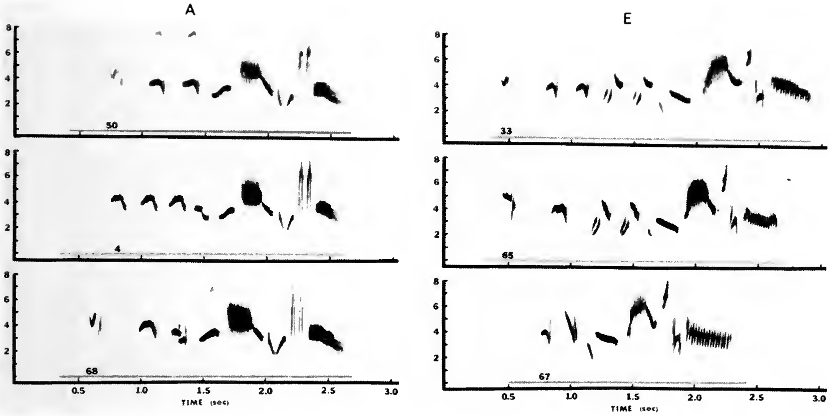


FIG. 1. Sound spectrograms of song-types A and E, each rendition from a different individual.

recorder at 19 cm/sec. These recordings were from individuals in a population breeding in Blacksmith Fork Canyon, 13.6 km south of Logan Canyon. Songs were later re-recorded onto Cousino tape-loops at 19 cm/sec while overall amplitude was maintained at a constant level. A Uher 4000 L tape recorder was used to broadcast song during field tests.

Playback procedure.—Each test session consisted of a 3-min silent observation period (pre-playback) followed immediately by a 3-min broadcast period (playback) and a final 3-min silent observation period (post-playback). A voice description of all overt behavior during each segment of test sessions was tape-recorded and transcribed at a later date. All tests were performed between 08:00 and 14:00 EST; no bird was tested more than once per day.

Only 1 song-type (A, B, C, D or E) was presented during each test day. Each song-type that was tested was presented to all birds on the same or following day. Sequence of presentation of song-types was A, B, C, D, E, A, B, C, D, E. Thus, each bird was tested twice with each song-type. This procedure hopefully lessened the potential affects of intra- and inter-individual variation resulting from weather conditions, phase of breeding cycle, etc. A visual model of a male Fox Sparrow was not present during playback testing.

Response measures.—Song in Fox Sparrows functions as one of a number of species-typical territorial displays. Displays accompanying disputes in which rivals are within a few meters of each other, or an intruder, and are on a resident's territory, tend to be dominated by "chirp" calls, short flights and posturing. After repelling an intruder the victor assumes an exposed perch and sings.

Criteria that were used to quantify the strength of an individual's response to playback of conspecific song were: (1) number of songs sung, (2) latency to utterance of the first song after playback had begun, (3) latency of approach to the speaker after broadcast of the first conspecific song, (4) number of "chirp" calls uttered, and (5) number of flights performed. Due to the rapidity with which Fox Sparrows may change postures while moving through the dense cover on their territories, postural displays and closeness of approach to the speaker were not easily quantified and were not included in the analysis.

Statistical significance was determined by *t*-tests since sample sizes were rather large and data sets were normally distributed. Nonnormality is generally "not too serious" and must be severe to have a marked effect on significance levels (Sokal and Rohlf 1969:377).

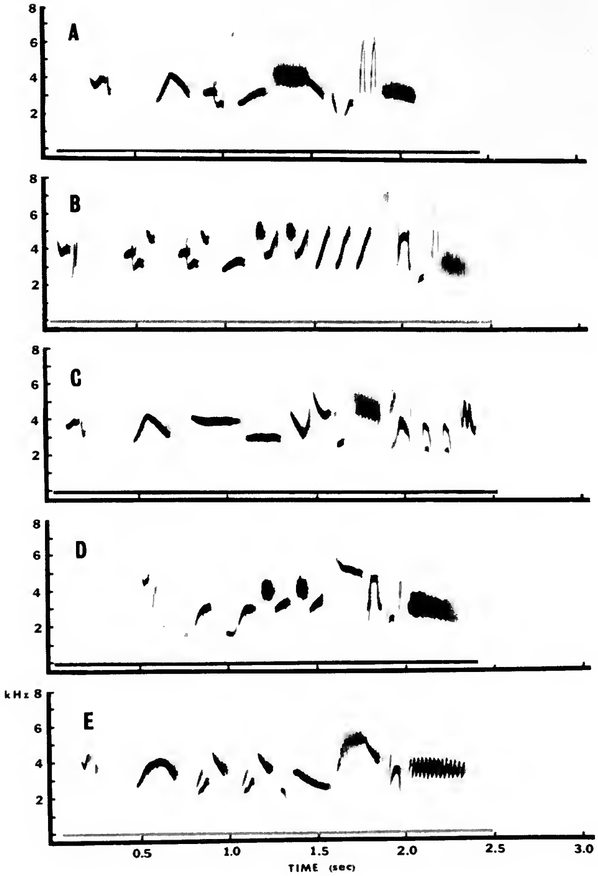


FIG. 2. Sound spectrograms of the song-types used for playback.

RESULTS

Response levels among test sessions.—Table 1 summarizes comparison of the levels of response among test sessions I and II. Throughout the study the level of response remained remarkably constant. Number of chirps and songs, latency of approach and latency of first song were essentially constant. Of the 8 instances of significant variation in the level of response, 6 were attributable to variation in the number of flights performed during the playback (4) and post-playback (2) periods. All instances of significant variation resulted from a decreased level of responsiveness in session II as compared with levels in session I.

TABLE 1

Comparison of the Mean Number of Responses to Playback of Conspecific Song-types Between Test Sessions I and II

		Song broadcast														
		A			B			C			D			E		
Response category	Session	$\bar{x}$	±SD	N	$\bar{x}$	±SD	N	$\bar{x}$	±SD	N	$\bar{x}$	±SD	N	$\bar{x}$	±SD	N
Latency of approach(s)	I	14.8	9.4	8	13.6	16.9		9.5	7.9	10	24.3	17.0	9	20.6	19.1	[b]
	II	15.2	10.9	12	11.0	5.5	9	11.9	7.3	8	7.6	5.0	10	11.9	10.0	
Latency of first song(s)	I	16.1	11.5	7	18.0	17.8		19.4	10.1	9	26.7	26.7		19.2	17.1	
	II	25.5	25.2	12	27.6	24.0	10	16.2	11.7	8	11.4**[a]	10.7	10	13.9	12.5	11
Songs per period																
Pre-playback	I	4.3	6.0	12	6.0	8.3	9	2.2	4.4		4.2	8.3		3.7	5.7	
	II	1.9	6.0	10	1.2	3.5		4.4	7.2		4.6	7.6		3.5	5.1	
Playback	I	15.5	4.1	11	15.4	3.4	9	18.3	3.4		15.8	4.8		13.8	5.0	
	II	16.8	3.3	10	14.5	2.4		14.9	4.2		17.8	1.9		16.8	2.8	
Post-playback	I	25.8	4.1	10	22.9	6.6	9	22.7	2.5		20.9	4.9		19.6	2.5	
	II	26.3	4.8	10	23.5	3.5		23.0	5.7		19.9	5.3		21.8	2.1	
Flights per period																
Pre-playback	I	0.4	0.7	11	0.0	—	9	0.1	0.3	1	0.1	0.3		0.2	0.7	
	II	0.0	—	10	0.4	1.0		0.0	—		0.1	0.3		0.1	0.3	
Playback	I	17.7	3.0	11	12.3	4.2	9	14.8	4.2		11.3	3.2		11.6	2.9	
	II	7.8***	4.2	10	7.8*	4.3		9.5**	3.3		7.3*	3.2		9.0	4.2	
Post-playback	I	3.6	2.4	11	2.4	2.5	9	2.0	1.5		2.3	1.4		1.8	1.9	
	II	0.5***	0.7	10	1.2	1.5		1.0	1.6		0.5**	0.7		1.6	1.1	
Chirps per period																
Pre-playback	I	0.8	2.5	10	0.0	—	9	0.0	—		0.0	—		0.0	—	
	II	0.0	—	10	0.0	—		0.0	—		0.0	—		0.0	—	
Playback	I	21.2	15.7	11	23.4	41.1	9	20.4	13.9		33.0	16.1		17.4	21.5	
	II	9.8	11.1	10	18.6	26.0		20.9	21.9		12.0	17.0		9.6	12.3	
Post-playback	I	0.9	1.6	10	0.4	1.0	9	0.8	2.3		1.4	2.0		2.0	3.8	
	II	0.0	—	10	0.0	—		0.2	0.4		0.0*	—		0.8	1.5	

[a] Response levels between session I and II significantly different at, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

[b] If blank, sample size is equal to the N value first encountered to the left.

Response to particular song-types.—The response of Fox Sparrows to playback of song-types A, B, C, D and E was similar. Analyses of variance tests among the song-types tested for latency of approach, latency of first song and number of songs, number of flights and number of chirps for each of the 3 test periods (pre-playback, playback and post-playback) revealed that the only significant variation ($P < 0.05$) was in the number of songs during post-playback in response to song-type A. Birds did not differ in their response to playback of any of the 5 major song-types.

Broadcast of conspecific song elicited a significant increase in the mean number of songs, flights and chirps from the Fox Sparrows compared with levels during pre-playback (Table 2). The mean number of songs sung during post-playback increased significantly over that of the playback level, whereas the mean number of flights and chirps presented by the birds decreased significantly (Table 2). Correlation tests demonstrated a persistant, albeit weak, inverse relationship between the mean number of songs and the mean number of flights and chirps during both the playback and post-playback periods.

Response by birds with and without the playback song-type.—A comparison among those birds which sang and those which lacked a rendition of the major song-type being broadcast during testing indicated that there was no significant difference in the levels of response for any criteria (Table 3). No comparison was possible using song-type C because all test subjects possessed at least one rendition of that song-type.

DISCUSSION

These results clearly show that male Fox Sparrows react similarly to the major song-types that may be sung by their neighboring conspecifics. Approach, flights, chirp calls and, undoubtedly, other behaviors emerge as the most dominant agonistic displays used in close-quarter confrontations with conspecifics. Song appears to be used primarily as a more distant territorial proclamation. Not surprisingly, then, the amount of song elicited during the playback period, which simulates a proximally located intruder, is less than that given during post-playback, which presents no proximal threat. This is not to say that song is not an effective close-quarters agonistic display. Rather, chirp calls are probably more effective for varying the rate and/or strength of the signal and birds simply cannot sing and chirp simultaneously. Also, visual displays may offer more input than auditory during that phase of male-male interaction.

The use of song in the Fox Sparrow as a distant threat among conspecifics differs somewhat from the use of song by other species in the closely related complex of *Passerella-Melospiza-Zonotrichia* sparrows. Playback of conspecific song to *Zonotrichia* sparrows elicits more song per unit

TABLE 2

MEAN NUMBER OF RESPONSES OF PLAYBACK TO CONSPECIFIC SONG-TYPES

		Response category										
		Latency to approach(s)	Latency to first song(s)	Songs per period[a]			Flights per period			Chirps per period		
Song broadcast				pre-p	p	post-p	pre-p	p	post-p	pre-p	p	post-p
	$\bar{x}$	15.0	22.0	3.3	16.1***[b]	26.2	0.2	13.0***	2.1***	0.3	15.8***	0.5***
A	SD	10.0	21.3	6.1	3.7	4.3	0.5	6.2	2.3	1.7	14.6	1.2
	N	20	19	21	[c]							
	$\bar{x}$	12.2	23.5	3.5	14.9***	23.2***	0.7	9.9***	1.8***	0	20.8***	0.2**
B	SD	12.0	21.6	6.5	2.8	5.0	0.2	4.7	2.1	0	33.1	0.7
	N	17		19								
	$\bar{x}$	10.5	17.8	3.4	16.5***	22.8***	0.2	12.0***	1.5***	0	20.7***	0.6***
C	SD	7.5	10.7	6.0	4.1	4.3	0.05	4.5	1.6	0	18.0	1.6
	N	18		19								
	$\bar{x}$	15.5	18.2	4.4	19.6***	20.4*	0.3	9.2***	1.4***	0	22.0***	0.7*
D	SD	14.7	21.2	7.7	3.6	5.0	0.1	3.8	1.4	0	35.9	1.5
	N	19		19								
	$\bar{x}$	15.8	16.3	3.6	15.3***	21.3***	0.2	10.2***	1.7***	0	13.3***	
E	SD	15.1	14.6	5.2	4.3	2.9	0.5	3.8	1.5	0	17.2	0.9**
	N	20		19								2.1

[a] Pre-playback period (pre-p), playback period (p), post-playback period (post-p).

[b] Asterisks indicate a significant difference between that response level and that which is directly to its left (pre-p and p; p and post-p) (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

[c] If blank, sample size equals the first one located to the left in that row.

time during the actual playback period than during the post-playback period (White-crowned Sparrow [*Z. leucophrys*], Verner and Milligan 1971; White-throated Sparrow [*Z. albicollis*], Brooks and Falls 1975b). Contradictory results for *Z. albicollis*, however, are available (Lemon and Harris 1974; Brooks and Falls 1975 a,b; Falls and Brooks 1976). The Song Sparrow (*Melospiza melodia*) responds to conspecific playback in a manner more similar to that in Fox Sparrows, with the greatest number of songs per unit time occurring during post-playback (Kroodsma 1976a, Harris and Lemon 1976). In contrast to *M. melodia*, however, conspecific playback experiments with Lincoln's Sparrow (*M. lincolnii*) in June and July indicate that this species rarely uses song as an agonistic display during the playback session (Martin, pers. obs.).

The question persists as to why Fox Sparrows and most other oscines possess such elaborate songs and song repertoires. (However, see Lein 1972, 1978, concerning warblers [*Dendroica* spp.]). It appears that, regardless of whether birds possess complex songs (e.g., Indigo Bunting [*Passerina cyanea*] Shiovitz 1975) or rather simple songs (e.g., *Z. albicollis*, Brooks and Falls 1975b), only a small portion of the structuring of song is required for, or used in, species recognition by conspecifics (see also review in Emlen 1972). Singing behavior in Fox Sparrows seems to be highly redundant in conveying species identity. During 1973 1 male possessed only broken song and a much reduced syllable-type repertoire. This bird managed to establish itself in what I considered a "quality" Fox Sparrow territory, mate and fledge 3 young. The present study shows that the type of songs broadcast to males appears to have little effect upon their response, regardless of whether or not they possess a similar song-type. Species specificity apparently is encoded at the level of syllable-types, rather than at the level of entire songs. This fact is not totally unexpected. If other species of birds and humans can differentiate species by hearing only partial or broken songs (thus, for the most, using syllables), why should we not presume, or expect, Fox Sparrows to possess similar abilities?

Detailed study of habituation in Fox Sparrows to song repertoires of various sizes and composition of song-types, although as yet incomplete, indicates that male Fox Sparrows do not habituate faster to repertoires with fewer types of songs when songs are presented at the species-typical rate of singing (Martin, pers. obs.). The only noticeable, but statistically nonsignificant, waning of response to test procedures during the present study was in the number of flights and chirps performed during the playback period (Table 2). However, it is relevant that the behavior of singing itself did not appear to have been markedly affected during the testing.

Thus, with the above information and the knowledge of the equality of

TABLE 3

COMPARISON OF THE MEAN NUMBER OF RESPONSES TO PARTICULAR CONSPECIFIC SONG-TYPES AMONG BIRDS WHICH DID AND DID NOT POSSESS SUCH A SONG-TYPE IN THEIR REPERTOIRE

		Song broadcast											
		A			B			D			E		
Criteria of response	Condition of response	$\bar{x}$ ± SD	df	*t*	$\bar{x}$ ± SD	df	*t*	$\bar{x}$ ± SD	df	*t*	$\bar{x}$ ± SD	df	*t*
Latency of approach(s)	with	16.4 ± 10.2	18	0.670	13.6 ± 13.9	14	0.883	17.8 ± 15.7	15	0.548	14.3 ± 13.7	18	0.488
	lacking	13.1 ± 10.9			7.3 ± 3.9			12.5 ± 11.7			10.9 ± 11.0		
Latency of first song(s)	with	22.4 ± 21.9	16	0.127	26.9 ± 23.3	14	1.499	19.2 ± 22.4	16	0.046	15.7 ± 18.0	18	0.824
	lacking	20.9 ± 24.6			8.9 ± 5.7			18.6 ± 19.4			23.8 ± 20.4		
Songs per													
Playback	with	15.3 ± 3.8	19	1.823	14.8 ± 3.1	17	0.461	17.2 ± 1.3	17	0.214	17.0 ± 2.9	17	0.870
	lacking	18.3 ± 2.2			15.7 ± 0.6			16.8 ± 4.1			14.9 ± 4.4		
Post-playback	with	26.2 ± 4.3	19	0.035	23.5 ± 5.4	17	0.565	18.0 ± 4.7	17	1.255	21.2 ± 2.9	17	0.403
	lacking	26.1 ± 4.5			21.7 ± 1.5			21.2 ± 4.9			20.7 ± 2.5		
Flights per													
Playback	with	12.6 ± 6.8	19	0.366	10.3 ± 4.8	16	1.067	9.4 ± 2.4	17	0.508	8.6 ± 3.6	18	1.121
	lacking	13.7 ± 5.0			7.3 ± 4.9			8.2 ± 3.9			10.7 ± 3.7		
Post-playback	with	1.8 ± 2.1	17	0.023	1.7 ± 1.9	17	0.485	1.8 ± 1.6	17	0.781	2.2 ± 1.9	17	0.749
	lacking	1.8 ± 1.8			2.3 ± 3.2			1.2 ± 1.4			1.6 ± 1.4		
Chirps per													
Playback	with	11.8 ± 12.9	17	1.044	24.1 ± 35.3	17	0.960	11.0 ± 20.7	17	0.792	3.6 ± 6.4	18	1.563
	lacking	18.8 ± 16.2			4.0 ± 3.6			26.0 ± 39.9			16.7 ± 18.0		
Post-playback	with	0.6 ± 1.5	19	0.858	0.2 ± 0.8	17	0.316	0.0 ± —	17	1.177	0.3 ± 0.6	15	0.685
	lacking	0.1 ± 0.4			0.3 ± 0.6			0.9 ± 1.7			1.3 ± 2.3		

response to the various playback tests, the major song-types of Fox Sparrows appear to be of equal valence to the intended male receivers. This contention, however, does not totally negate the possibility that song complexity is important in lessening the singer's habituation to the behavior of singing or, possibly, the female's ability to habituate to male song. This study only measures the response of the male receiver.

Song-types linked together in rather rigid sequences, as they are in Fox Sparrows, may be perceived as but a single behavioral event by the signaler and receiver—singing. However, with regard to the signaler and the female receiver, there may be a critical minimum that must be met, the length and complexity of which is about 2 songs in Fox Sparrows (Martin 1977), below which the extent and rapidity of habituation is much higher and is selected against. Thus, in Fox Sparrows there may be an important difference between habituation to the agonistic function or message of the display by rival males and the act of performing the display or the female's response to song. Although remote, song may even serve the "Beau Geste" function as proposed by Krebs (1976a,b: 1977), in which case habituation may have played but a minor role in the shaping of Fox Sparrow singing behavior. It seems reasonable to consider that natural selection may have molded song in the Fox Sparrow more in line with its epigamic functions rather than with its agonistic functions. Although such an hypothesis seems remote in a monogamous species which attracts only 1 female per breeding season (Krebs 1976b, 1977: Kroodsma 1977) song may be of importance in stimulation of the female and synchronization of the pair's breeding effort (Kroodsma 1976b). Further study designed to measure the times of spring arrival, pairing, nesting and also clutch-size, fledging success and territory quality should help clarify this possibility.

SUMMARY

Agonistic response to tape-recorded playback of particular conspecific song-types was measured in male *Passerella iliaca* breeding in Logan Canyon, Cache Co., Utah, during 1976. Only 1 song-type (either A, B, C, D or E) was presented during each test day; each bird was tested twice with each song-type. Parameters measured during pre-playback, playback and post-playback to indicate level of agonistic response were: number of songs sung, latency to first song and latency of approach after the first song of playback, number of "chirp" calls uttered and number of flights performed.

Response levels of all agonistic behaviors remained remarkably constant throughout the testing. However, a significant decrease in response between the first series of tests and the second series was noted in the mean number of flights performed during some of the playback and post-playback sessions. Except for a significant difference in the mean number of songs uttered during post-playback in response to song-type A, analysis of variance indicated no significant variation among song-types for any of the response criteria. However, mean number of songs, flights and chirps during playback increased significantly over pre-playback levels. Mean number of songs sung during post-playback also increased significantly over that during playback, whereas mean numbers of flights and chirps decreased. Birds which were never heard to sing a particular song-type responded to its broadcast as strongly as those which did sing it.

These results are interpreted as indicating that male *P. iliaca* react similarly to all of the major song-types that may be sung by their neighboring conspecific. Song appears to serve mostly as a distant territorial proclamation, whereas flights, approaches and chirp calls are more important as close-quarter displays. Use of song by *P. iliaca* appears more similar to that observed in *Melospiza melodia* than that in *Zonotrichia* species. Possible reasons for the complex structure of song in *P. iliaca* and the use of more than 1 major song-type by individuals are discussed.

ACKNOWLEDGMENTS

This study was partially financed by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and funds from the Division of Natural Sciences and Department of Biology at Pacific Lutheran University. Criticism of an earlier draft by J. A. Jackson and W. Thompson measurably improved the manuscript. Logistic support, space and equipment were kindly made available by the Department of Biology at Utah State University. My colleagues there are also thanked for engaging me in many profitable discussions concerning avian behavioral ecology. I especially thank L. R. Martin for her understanding during all aspects of this study.

LITERATURE CITED

Bertram, B. 1970. The vocal behaviour of the Indian Hill Myna *Gracula religiosa*. Anim. Behav. Monogr. 3:79–192.

Brooks, R. J. and J. B. Falls. 1975a. Individual recognition by song in White-throated Sparrows. I. Discrimination of songs of neighbors. Can. J. Zool. 53:879–888.

——— and ———. 1975b. Individual recognition by song in White-throated Sparrows. III. Song features used in individual recognition. Can. J. Zool. 53:1749–1761.

Dixon, K. L. 1969. Patterns of singing in a population of the Plain Titmouse. Condor 71:94–101.

Emlen, S. T. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour 41:130–171.

Falls, J. B. 1969. Functions of territorial song in the White-throated Sparrow. Pp. 207–232 *in* Bird vocalizations (R. A. Hinde, ed.), Cambridge Univ. Press, London.

——— and R. J. Brooks. 1976. Individual recognition by song in White-throated Sparrows. II. Effects of location. Can. J. Zool. 53:1412–1420.

——— and J. R. Krebs. 1976. Sequences of songs in repertoires of Western Meadowlarks (*Sturnella neglecta*). Can. J. Zool. 53:1165–1178.

Harris, M. A. and R. E. Lemon. 1976. Responses of male Song Sparrows *Melospiza melodia* to neighboring and non-neighboring individuals. Ibis 118:421–424.

Hartshorne, C. 1956. The monotony threshold in singing birds. Auk 73:176–192.

———. 1958. Some biological principles applicable to song behavior. Wilson Bull. 70:41–56.

———. 1973. Born to sing. Indiana Univ. Press, Bloomington, Indiana.

Hinde, R. A. 1958. Alternative motor patterns in Chaffinch song. Anim. Behav. 6:211–218.

Isaac, D. and P. Marler. 1963. Ordering of sequences and singing behaviour of Mistle Thrushes in relationship to timing. Anim. Behav. 11:179–188.

Krebs, J. R. 1976a. Habituation and song repertoires in the Great Tit. Behav. Ecol. Sociobiol. 1:215–227.

———. 1976b. Bird song and territory defense. New Sci. 70:534–536.

———. 1977. The significance of song repertoires: the Beau Geste hypothesis. Anim. Behav. 25:475–478.

KROODSMA, D. E. 1976a. The effect of large song repertoires on neighbor "recognition" in male Song Sparrows. Condor 78:97–99.

———. 1976b. Reproductive development in a female songbird: differential stimulation by quality of male song. Science 192:574–575.

———. 1977. Correlates of song organization among North American wrens. Am. Nat. 111:995–1008.

LEIN, M. R. 1972. Territorial and courtship songs of birds. Nature 237:48–49.

———. 1978. Song variation in a population of Chestnut-sided Warblers (*Dendroica pensylvanica*): its nature and suggested significance. Can. J. Zool. 56:1266–1283.

LEMON, R. E. AND C. CHATFIELD. 1971. Organization of song in Cardinals. Anim. Behav. 19:1–17.

——— AND ———. 1973. Organization of song of the Rose-breasted Grosbeaks. Anim. Behav. 21:28–44.

——— AND M. A. HARRIS. 1974. The question of dialects in the songs of White-throated Sparrow. Can. J. Zool. 52:83–98.

MARLER, P. 1956. Behaviour of the Chaffinch, *Fringilla coelebs*. Behav. Suppl. 5. 184 p.

MARTIN, D. J. 1976. Structure of songs and the organization of singing in Fox Sparrows breeding in northern Utah and southern Idaho. Ph.D. dissert., Utah State Univ., Logan, Utah.

———. 1977. Songs of the Fox Sparrow. I. Structure of song and its comparison with song in other Emberizidae. Condor 79:209–221.

MILLIGAN, M. M. AND J. VERNER. 1971. Interpopulation discrimination in the White-crowned Sparrow. Condor 73:208–213.

MULLIGAN, J. A. 1966. Singing behavior and its development in the Song Sparrow, *Melospiza melodia*. Univ. Calif. Publ. Zool. 81:1–76.

SHIOVITZ, K. A. 1975. The process of species-specific song recognition by the Indigo Bunting, *Passerina cyanea*, and its relationship to the organization of avian acoustical behavior. Behaviour 55:8–179.

SMITH, W. J., J. PAWLUKIEWICZ AND S. T. SMITH. 1978. Kinds of activities correlated with singing patterns of the Yellow-throated Vireo. Anim. Behav. 26:862–884.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.

VERNER, J. AND M. M. MILLIGAN. 1971. Responses of male White-crowned Sparrows to playback of recorded songs. Condor 73:56–64.

DEPT. BIOLOGY, PACIFIC LUTHERAN UNIV., TACOMA, WASHINGTON 98447.
ACCEPTED 1 APR. 1979.

Wilson Bull., 92(1), 1980, pp. 33–39

THE THERMOREGULATORY SIGNIFICANCE OF THE WINTER ROOST-SITES SELECTED BY ROBINS IN EASTERN WASHINGTON

Glenn E. Walsberg and James R. King

Selection of appropriate microclimates is generally thought to be an important component of avian behavioral thermoregulation. For many species, the winter night is perhaps the most thermally stressful part of the annual cycle, but the effect of winter roost-site selection on a bird's energy expenditure has been estimated quantitatively for only a few species, and the results are variable (e.g., Monk Parakeet [*Myopsitta monachus*], Caccamise and Weathers 1977; Jackdaw [*Corvus monedula*], Gyllin et al. 1977; Starling [*Sturnus vulgaris*], Yom-Tov et al. 1977, Kelty and Lustick 1978; House Sparrow [*Passer domesticus*], Kendeigh 1961).

Flocks of American Robins (*Turdus migratorius*) persistently roost in dense vegetation during winter nights in eastern Washington, as elsewhere in North America, although the flocks that we observed are much smaller than those reported near the center of the winter range (e.g., typically 20–40 birds/flock, compared with a group of 250,000 in Arkansas [Black 1932]). We hypothesized that roosting in dense vegetation is a habit that has evolved as a response to selection for thermoregulatory economy, and we tested this by examination of the microclimatic amelioration afforded by a dense grove of Douglas-fir (*Pseudotsuga menziesii*) that is habitually occupied by flocks of robins in winter near Pullman, Washington.

THEORY

Meteorological data may be used to estimate the power consumption of a roosting bird by application of an equivalent black-body temperature model. The model we use has been fully described and derived in earlier publications (Robinson et al. 1976, Campbell 1977) and tested by Mahoney and King (1977), and we give here only an abbreviated version.

The equivalent black-body temperature (T_e) is an integrated measure of an organism's thermal environment, representing air temperature (T_a) plus a temperature increment reflecting the effect of absorbed radiation:

$$T_e = T_a + (r_e/\rho c_p)(R_{abs} - \varepsilon\sigma T_a{}^4) \qquad (1)$$

Here, ρc_p is a constant equal to 1200 J/m^3–°C, R_{abs} represents radiation absorbed by the animal (W/m^2), ε is the animal surface emissivity, and σ is the Stefan-Boltzmann constant (5.67×10^{-8} W/m^2 – °K^4); r_e is the resistance to heat transfer between the animal surface and the environment. It is calculated as the sum of the parallel resistances to heat transfer by radiation (r_r), and free (r_{fr}) or forced (r_{fo}) convection and thus subsumes, for example, effects due to wind. (See Walsberg and King [1978a] for equations and assumptions used to calculate r_e.) The difference between body temperature (T_b) and the equivalent black-body temperature of the environment defines the thermal gradient operating on the animal and net heat flux is proportional to this gradient divided by the thermal resistance of the system:

$$M - \lambda E = \rho c_p \cdot (T_b - T_e)/(r_b + r_e) \qquad (2)$$

Here, M is metabolic heat production, λE is evaporative heat loss, and r_b is the whole-body thermal resistance.

METHODS

Environmental measurements.—Meteorological data were recorded and averaged over 1-h periods by a Campbell Scientific Co. CR5 recorder. Duplicate measurements were made within the fir grove and 50 m away in an open field. All measurements in the open were made 2 m above the substrate (snow on 13, 14, 16, 17 Jan.; bare soil on 23, 24 Jan. and 9, 11, 12 Feb.). Within the fir grove, radiometers were placed 3–5 m above ground where robins had been roosting. Anemometers and thermocouples were placed 0.5 m below the radiometer. Downward long-wave radiation was measured with a Moll-Gorczynski sensor modified as described in Campbell et al. (1978). Upward long-wave radiation was calculated assuming that emissivity of the vegetation and substrate equaled 0.95 (Gates and Tantraporn 1952, Sellers 1965, Geiger 1965) and assuming that these surfaces were at air temperature. A total of 50 simultaneous measurements of T_a and plant and substrate surface temperature (with a Wahl HSA 120 infrared thermometer) during 5 nights revealed a maximum difference of 3°C. This maximum difference was detected only once and represents a soil surface temperature above T_a immediately after sunset. This difference would produce about a 4% error in the estimate of upward long-wave radiation at the air temperatures measured in this study. Measurements were made only after dark, when short-wave radiation was negligible. Air temperature was measured with 26 ga thermocouples, and wind velocity was measured with sensitive cup anemometers.

Animal characteristics.—Long-wave emissivity of the bird was assumed to equal 0.98 (Hammel 1956). The characteristic dimension used in estimates of convective heat transfer was assumed to be the average horizontal diameter of the torso of 3 robins when held with the long axis of the body in a typical angle (6.5 cm). Latent heat loss (λE) is estimated using equation 56 of Calder and King (1974), and nocturnal T_b was assumed to be 40°C. Body resistance was estimated using the heat transfer coefficient (h) estimated by equation 13 of Calder and King (1974) and assuming an average body mass of 74.9 g (Stewart 1937). This equation predicts $h = 1.97\ W/m^2 - {}^\circ C$ when the external surface area of the bird is estimated as 0.0196 m^2 (Walsberg and King 1978b). This heat transfer coefficient represents a total thermal resistance ($r_b + r_e$) of 611 s/m. Here, r_e is the equivalent resistance operating on a bird under metabolic chamber conditions, in which free convection presumably dominates. Using the equations for r_r and r_{fr} of Robinson et al. (1976), r_e is estimated as ranging from 104 to 118 s/m when $0^\circ < T_a < 25^\circ C$ if the bird's surface temperature under cold conditions remains approximately 13°C above air temperature, as it does in the similar sized Gray Jay

TABLE 1
METEOROLOGICAL DATA AND ESTIMATED HEAT PRODUCTION FOR ROBINS[1]

Date	Location	Air temperature (°C)	Downward long-wave radiation (W/m^2)	Upward long-wave radiation (W/m^2)	Wind velocity (m/s)	T_e (°C)	r_e (s/m)	Metabolic heat production (W/m^2)
13 Jan.	At roost-site:	−16.0	235	251	0.82	−16.4	48	130.1
	Outside of roost-site:	−16.1	183	250	3.62	−16.8	25	136.8
14 Jan.	At roost-site:	−13.3	241	260	0.48	−13.7	60	121.4
	Outside of roost-site:	−13.3	189	260	1.24	−14.5	40	127.7
16 Jan.	At roost-site:	−4.5	287	295	1.62	−4.6	35	105.8
	Outside of roost-site:	−4.4	256	296	6.23	−4.7	19	109.6
17 Jan.	At roost-site:	−6.6	279	289	1.33	−6.7	39	110.0
	Outside of roost-site:	−6.6	263	289	4.29	−6.8	23	113.6
23 Jan.	At roost-site:	+0.6	307	319	0.71	+0.6	50	91.6
	Outside of roost-site:	+0.6	297	319	2.59	+0.6	29	95.2
24 Jan.	At roost-site:	−3.0	283	301	0.61	−3.5	53	100.2
	Outside of roost-site:	−3.1	229	301	1.88	−4.1	33	105.4
25 Jan.	At roost-site:	+1.2	306	321	0.69	+0.7	50	91.4
	Outside of roost-site:	+1.1	250	319	2.46	+0.2	29	96.3
9 Feb.	At roost-site:	+1.7	307	325	1.12	+1.4	41	91.4
	Outside of roost-site:	+1.7	243	325	5.80	+1.0	20	96.0
11 Feb.	At roost-site:	+1.9	317	327	0.67	+1.9	51	88.6
	Outside of roost-site:	+1.9	292	327	2.47	+1.8	29	92.5
12 Feb.	At roost-site:	+2.5	312	328	0.70	+2.4	50	87.7
	Outside of roost-site:	+2.3	294	326	2.55	+2.2	29	91.6

[1] For simplicity of presentation, only average values for the entire night are given. However, all calculations were made using hourly values.

(*Perisoreus canadensis*, Veghte 1964). If the surface-to-air gradient was 5° higher or lower than this, the estimated r_b value would be changed about 1%.

RESULTS

Behavior.—On 7 nights in January and February in which the number of arriving robins was counted, 24–39 ($\bar{x}$ = 28) birds occupied the fir grove. On 4 additional nights, no robins appeared. These 4 nights were not distinctive from those in which the roost was occupied, and the absence of a robin flock may be due to the use of alternative roost-sites. Birds arrived near dusk, between 16:00 and 17:00 PST, and departed at dawn, between 07:00 and 08:00 PST. Thus, the roost was occupied for 14–16 h of a 24 h cycle. Behavior within the fir grove was observed after the birds had settled at dusk on 5 days and prior to departure at dawn on 4 days. Robins typically roosted 3–5 m above ground on a branch 1.5–2 m away from the trunk. Individuals were usually spaced 1–3 m apart and no tendency toward huddling was observed.

Meteorology.—Air temperature differed by an average of 0.1°C or less between inside and outside of the fir grove (Table 1). Wind velocity within the grove in areas typically occupied by robins averaged 28% of that outside of the grove (Table 1). Substantial differences also occurred in downward long-wave radiation. Downward radiative flux was greater within the fir grove by an average of 26% on 4 clear nights (13, 14, 24, 25 Jan. and 9 Feb.), 9% on 2 partially cloudy nights (16, 17 Jan.), and 6% on 3 overcast nights (23 Jan. and 11, 12 Feb.). Within the fir grove, downward flux averaged 5% below the calculated upward flux, thus indicating that the fir trees shielded the sensor or bird almost completely from the night sky.

Black-body equivalent temperature and equivalent resistance.—Reduction of windspeed within the fir grove produced an estimated 50–105% ($\bar{x}$ = 75%) increase in r_e compared to outside the grove (Table 1). Unexpectedly, T_e differed only slightly (0–0.8°C) between the 2 environments (Table 1). The small size of this difference may be attributed to 3 factors. (1) Air temperature is similar in the 2 environments. (2) Since T_a is similar, calculated upward long-wave flux is also similar. (3) Windspeeds are sufficiently high in both environments so that convective heat loss tends to override effects due to the radiative environment.

Power consumption.—Associated with the small differences in T_e, power consumption is estimated as being only 3–5% ($\bar{x}$ = 4.4%) higher for a bird roosting outside the fir grove rather than within it (Table 1). The general conclusion that the roost microclimate has only a slight effect on the thermoregulatory requirement is reinforced by an error analysis (Table 2). If key variables are changed 25%, the difference between the required heat production inside and outside the fir grove remains as only a few percent. Error in estimating r_b is most likely to produce a substantial error in estimates of heat production. If our estimate of r_b as 500 s/m is 100% too large (i.e., r_b = 250 s/m), then energy expenditure for birds in both environments is about 94% greater than predicted; but even in this extreme case the heat production of a robin outside the fir grove is estimated to average only 7% greater than that of a robin inside the grove. The maximum difference (about 9%) in this case occurs on 25 Jan.

Not yet considered in this analysis is the energy potentially saved by radiative exchange between robins or by reduction of wind penetration into the plumage. No net radiative heat transfer from 1 bird to another will

TABLE 2

SENSITIVITY OF ESTIMATES OF AVERAGE NOCTURNAL ENERGY EXPENDITURE TO 25% ERRORS IN KEY VARIABLES

Component of calculation	Percent change in estimated average metabolic rate: At roost-site	Percent change in estimated average metabolic rate: Outside of roost-site	Average percent difference between metabolic rates inside and outside of roost-site[1,2]
Characteristic dimension			
25% increase:	−0.8	−0.4	4.8
25% decrease:	+0.9	+0.5	4.0
r_r			
25% increase:	−1.1	−0.5	5.0
25% decrease:	+0.3	+0.3	4.3
r_{fo}			
25% increase:	−1.9	−1.0	5.3
25% decrease:	+2.0	+1.7	4.1
r_b			
25% increase:	−18.6	−19.2	3.7
25% decrease:	+30.0	+31.1	5.5

[1] Calculated as $100 \times (1 - [M^{\text{outside of roost-site}}/M^{\text{at roost-site}}])$.

[2] Average difference is 4.4% using values described in Methods section.

occur if both maintain the same surface temperature. The significance of this effect is directly proportional, however, to the fraction of an individual's radiative environment that is composed of other robins. This fraction is undoubtedly small. Robins rarely roosted less than 1 m apart. The projected surface area of 1 robin viewed by another must be less than ½ of the bird's total surface area, or less than about 0.0098 m^2 (Walsberg and King 1978b). Thus, if all individuals in the largest observed flock (39 birds) remained at a 1-m radius and oriented themselves so that a maximum proportion of each bird's surface area was viewed by a single, central individual, less than 3% of the central bird's radiative environment would be composed of other robins.

It is not currently possible to estimate reliably heat loss from wind penetrating and disrupting the plumage, as contrasted with convective cooling at the plumage surface. Some investigations have analyzed the effects of wind penetration on swatches of fur (e.g., Lentz and Hart 1960), but little is known about the effect of live birds. Robinson et al. (1976) observed progressive decreases of the r_b of White-crowned Sparrows (*Zonotrichia leucophrys*) associated with increases of windspeed. This suggests penetration of wind into the coat with a consequent decrease of plumage thermal resistance. Values of r_b estimated from the average windspeeds in this investigation and the regression equation of Robinson et al. (1976) for r_b as a function of windspeed at $T_a = 1°C$ are 6–14% less for birds roosting outside the grove rather than within it ($\bar{x} = 9\%$). This would reduce the power consumption of robins inside the grove by an average of about 7% (range, 4–12%) compared with robins outside the grove.

DISCUSSION

The small effect upon power consumption that we estimate is produced by nocturnal roosting in the Douglas-fir grove indicates either that climatic effects not accounted for in conventional heat-budget modeling are of major importance or that our hypothesis is wrong and that factors such as protection from predators may be of greater significance than thermoregulatory economy. The latter seems particularly likely since robins conspicuously did not use what was apparently the thermally most favorable microhabitat available within the fir grove, against the tree trunk. Measurements with a Hastings air meter equipped with an omnidirectional probe revealed that potential roost-sites at the junction of a branch with the leeward side of a tree trunk were generally characterized by windspeeds (0–0.1 m/s) much lower than those at sites occupied by robins. Roosting close to the trunk could thus produce nearly total protection from forced convection. If heat loss under free convection conditions is estimated as described previously, the power consumption of a robin next to a tree trunk is estimated as 20% below that which would be required outside of the grove or about 5 times the reduction that probably is actually achieved. However, the potential advantage of this wind-free site may be offset by increased predation. A bird roosting on a branch 1–2 m from the trunk would be more likely to detect and escape a predator moving up the trunk than would a robin roosting nearer the trunk. Thus, our inability to associate nocturnal roost-site selection with substantial energy conservation refocuses attention on other modes of selection favoring shelter-seeking in birds, and may serve as a caution that either as yet unquantified meteorological effects may be of major importance or that the thermal significance attributed to the nocturnal microclimate in other studies (e.g., Kendeigh 1961, Calder 1973, Kelty and Lustick 1977) may not be transferable to other species and settings.

SUMMARY

Flocks of American Robins habitually roost in dense vegetation during winter nights in eastern Washington. A microclimatic analysis indicates that this behavior produces only a slight thermoregulatory benefit. It thus appears that either nonthermal factors (such as protection from predators) or thermal effects too poorly known to quantify may be of major importance.

ACKNOWLEDGMENTS

This investigation was supported by grants from the National Science Foundation (BMS 75-20338) and the National Institutes of Health (GM 01276).

LITERATURE CITED

Black, J. D. 1932. A winter robin roost in Arkansas. Wilson Bull. 29:13–19.

Caccamise, D. F. and W. W. Weathers. 1977. Winter nest microclimate of Monk Parakeets. Wilson Bull. 89:346–349.

Calder, W. A. 1973. An estimate of the heat balance of a nesting hummingbird in a chilling climate. Comp. Biochem. Physiol. 46A:291–300.

——— and J. R. King. 1974. Thermal and caloric relations of birds. Pp. 259–413 *in* Avian biology, Vol. 4 (D. S. Farner and J. R. King, eds.), Academic Press, New York, New York.

Campbell, G. S. 1977. An introduction to environmental biophysics. Springer-Verlag, New York, New York.

———, J. N. Mugaas and J. R. King. 1978. Measurement of long-wave radiative flux in organismal energy budgets: a comparison of three methods. Ecology 59:1277–1281.

Gates, D. M. and W. Tantraporn. 1952. The reflectivity of deciduous trees and herbaceous plants in the infrared to 25 microns. Science 115:613–616.

Geiger, R. 1965. The climate near the ground. Harvard Univ. Press, Cambridge, Mass.

Gyllin, R., H. Källander and M. Sylven. 1977. The microclimate explanation of town centre roosts of Jackdaws *Corvus monedula*. Ibis 119:358–361.

Hammel, H. T. 1956. Infrared emissivities of some arctic fauna. J. Mammal. 37:375–378.

Kelty, M. P. and S. I. Lustick. 1977. Energetics of the Starling (*Sturnus vulgaris*) in a pine woods. Ecology 58:1181–1185.

Kendeigh, S. C. 1961. Energy of birds conserved by roosting in cavities. Wilson Bull. 73:140–147.

Lentz, C. P. and J. S. Hart. 1960. The effect of wind and moisture on heat loss through the fur of newborn caribou. Can. J. Zool. 38:679–689.

Mahoney, S. A. and J. R. King. 1977. The use of the equivalent black-body temperature in the thermal energetics of small birds. J. Therm. Biol. 2:115–120.

Robinson, D. E., G. S. Campbell and J. R. King. 1976. An evaluation of heat exchange in small birds. J. Comp. Physiol. 105:153–166.

Sellers, W. D. 1965. Physical climatology. Univ. Chicago Press, Chicago, Illinois.

Stewart, P. A. 1937. A preliminary list of bird weights. Auk 54:324–332.

Veghte, J. H. 1964. Thermal and metabolic responses of the Gray Jay to cold stress. Physiol. Zool. 37:316–328.

Walsberg, G. E. and J. R. King. 1978a. The heat budget of incubating Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. Physiol. Zool. 51:92–103.

——— and ———. 1978b. The relationship of the external surface area of birds to skin surface area and body mass. J. Exp. Biol. 76:185–189.

Yom-Tov, Y., A. Imber and J. Otterman. 1977. The microclimate of winter roosts of the Starling *Sturnus vulgaris*. Ibis 119:366–368.

DEPT. ZOOLOGY, WASHINGTON STATE UNIV., PULLMAN, WASHINGTON 99164. (PRESENT ADDRESS GEW: DEPT. ZOOLOGY, ARIZONA STATE UNIV., TEMPE, ARIZONA 85281.) ACCEPTED 20 DEC. 1978.

Wilson Bull., 92(1), 1980, pp. 40–52

FEEDING ECOLOGY OF THE BLACK-WHISKERED VIREO AND ASSOCIATED GLEANING BIRDS IN JAMAICA

Alexander Cruz

Although detailed studies have been conducted on many North American vireos, little information is available on the Black-whiskered Vireo (*Vireo altiloquus*) beyond Bent's (1950) brief description and Wetmore's (1916) account of its food habits in Puerto Rico. The Black-whiskered Vireo breeds from the southern coast of Florida to the Bahamas, Greater and Lesser Antilles to Aruba, and on Curaçao, Bonaire, and Margarita islands off Venezuela. Black-whiskered Vireo populations from southern Florida to the northern Lesser Antilles winter mainly in northern South America, whereas populations in Dominica and islands to the south are permanent residents (Bond 1971).

I studied the Black-whiskered Vireo in Jamaica during the spring and summer of 1970, and the summers of 1971 and 1972. This report considers the feeding ecology of the Black-whiskered Vireo and 4 associated gleaners: Jamaican White-eyed Vireo (*V. modestus*), Blue Mountain Vireo (*V. osburni*), Arrow-headed Warbler (*Dendroica pharetra*) and Bananaquit (*Coereba flaveola*) in a middle elevation forest in Jamaica. These 4 resident species were found to be most similar in their foraging behavior to the Black-whiskered Vireo. For information on the species of birds occurring in this region see Cruz (1972). The objectives of this investigation were to obtain quantitative information on: (1) the distribution and population densities of the Black-whiskered Vireo; (2) the food and foraging ecology of the Black-whiskered Vireo; and (3) ecological interactions between the Black-whiskered Vireo and these other species.

STUDY AREA AND METHODS

The study area.—In order to get as complete a picture as possible of the biology of the Black-whiskered Vireo in Jamaica, I visited many distinct habitats, ranging from limestone scrub forest at sea level, to montane mist forest at an elevation of 1373 m. My principal study area of 40 ha was in Worthy Park (Lluidas Vale), St. Catherine Parish (ave. elev. 460 m). This area contained a mosaic of habitats, ranging from wooded pasture to dense wet limestone forest; the annual precipitation averaged 185 cm (Asprey and Robbins 1953). The canopy in the wet limestone forest is dense and contains trees up to 30 m or more. The dominant trees are broadleaf (*Terminalia latifolia*), Jamaican cedar (*Cedrela odorata*), sweetwoods (*Nectandra* spp.), bulletwoods (*Daphnopsis* spp.), prickly yellow (*Fagara martinicensis*), trumpet tree (*Cecropia peltata*), figs (*Ficus* spp.), cotton tree (*Ceiba pentrandra*) and red birch (*Bursera simaruba*). In the wooded pasture, where some of the original vegetation has been removed, dominant trees also included guango (*Samanea saman*), pimento (*Pimento oficinalis*), logwood (*Haematoxylum campechianum*), and citrus trees (*Citrus* spp.). Many of the trees in the area supported epiphytes and lianas.

I divided the main study area into 523 quadrats, each 30 × 30 m. Each quadrat was inspected for predominant vegetation and assigned to 1 of 3 major vegetation types: (1) wooded pasture (park-like in appearance with little or no understory present); (2) open wet limestone forest (well developed upperstory with little to moderate understory); and (3) dense wet limestone forest (closed canopy forest, understory moderate to dense).

Population analysis.—The population estimates were obtained from a combination of 3 techniques: (1) by the "spot-map" method of Williams (1936) and many others; (2) systematic observations of individual birds; and (3) capture-recapture analysis of netted birds. For each bird observed, its specific position, species identification, movements, etc., were recorded on gridded census maps. All mist-netted birds were examined for sex, age, fat and weight.

Food and foraging ecology.—Detailed observations on habitat use, foraging and feeding methods of the birds were made by adaptions of methods used by MacArthur (1958), Cody (1974) and Cruz (1977, 1978). The total number of feeding observations made on *V. altiloquus, V. modestus, V. osburni, C. flaveola* and *D. phareta* were 1087, 315, 118, 519 and 819, respectively. The specific technique involved walking a predetermined route until a bird was encountered. If the bird was foraging, information was recorded as to the foraging heights, zones and behavior. Each time a feeding bird moved more than 1.5 m these data were recorded. Any observation was terminated if a bird disappeared from view for more than 30 sec. The observation period of each individual was limited to 10 min. The foraging height intervals used were: ground, ground–15 cm, 15 cm–1 m, 1–2 m, 2–3 m, 3–6 m, 6–9 m, 9–12 m, 12–15 m, 15–25 m, greater than 25 m. These foraging height boundaries were chosen to approximate the major change in vegetation profile (ground, grassy areas and low shrubs, shrubs and low trunks, small trees and lower canopy, middle canopy, upper canopy, and emerging canopy, respectively). Ground, shrub, tree and aerial zones were identified. The trees were divided into 3 main feeding zones: trunk, inner branches and outer branches. Each of these main zones was in turn divided into 3 subzones: lower, middle and upper. Feeding behavior patterns of the birds in the study area were categorized as: gleaning (foliage, nectar, fruit, limb), hovering (foliage, fruit, limb), sallying, probing and pecking.

The degree of overlap in resource use for species pairs in various categories of the habitat and foraging matrix (height, zone and behavior) was calculated using the similarity index $o_{ij} = 1.0 = 0.5_h(p_{ih} - p_{jh})$ where o_{ij} is the percent overlap and p_{ih} and p_{jh} are the proportions of species i and j associated with the resource category h. The index is standardized and varies from 0 (no overlap) to 1 (complete overlap). This index was first used as an overlap measure by Schoener (1970) and it was chosen because it is straightforward and easy to interpret mathematically. Frequency data were analyzed using the Chi-square test.

Food analysis.—I collected 17 adult Black-whiskered Vireos in similar habitats near the study area and examined stomach contents. The stomach and intestinal tracts were removed soon after death and preserved in 75% alcohol. Food samples were separated into animal and vegetable material; volume and frequency of occurrence of each food type were determined. Invertebrates that were essentially whole were keyed to the level of family. Fragmented insects could usually be identified to order, and often to family. Similar methods were used to identify fruit and other vegetable material. Stomach contents were directly compared to insects and fruits collected in the study area.

Morphological analysis.—Morphological measurements were obtained by standard mensural methods to see if differences in body structures of possible ecological significance existed among the species. Bill length (exposed culmen) was measured to the nearest 0.1 mm with vernier calipers, and weight was taken to the nearest 0.25 g with a Pesola spring balance. Bill depth and width are measured at the level of the anterior end of the nares. Other measurements (including additional culmen measurements) are from Ridgway 1902 and 1904. All weights and measurements represent mean values.

RESULTS AND DISCUSSION

Distribution, habitat preference and population densities.—In Jamaica, most Black-whiskered Vireos arrived in mid-March and departed in early October. Extreme dates were 5 March 1972, at Rocklands, St. James Parish and 28 November 1972, at Port Henderson, St. Catherine Parish (Black 1972, 1973). The other species are permanent residents, although the Arrow-headed Warbler may move to lower elevations during the winter months (Osburn 1859, pers. obs.).

The Black-whiskered Vireo is a very common summer resident and, in fact, it may be the most common passerine species in certain (see below) habitats (Lack 1976, this study). It occurs from sea level mangrove and scrub forests to montane forests at approximately 1500 m in elevation. The Jamaican White-eyed Vireo and the Bananaquit also have a similar distribution, but the Blue Mountain Vireo and the Arrow-headed Warbler are confined mainly to mid-level and montane mesophytic forests.

The highest Black-whiskered Vireo densities were recorded in dry limestone forest (90/40 ha), and in the main study area, wet limestone forest (95/40 ha). The number of individuals was lowest in the mangrove woodlands (26/40 ha) and montane forests (22/40 ha) indicating that, at least in Jamaica, these areas are suboptimal for Black-whiskered Vireos. The high density figures for the Black-whiskered Vireo in the limestone forests are possibly related to the structural complexity of the forest. These forests have a well developed vertical stratification (more pronounced in the wet limestone forest) and high tree species diversity (including many fruiting trees) all of which increase the total area available for foraging.

Population densities of the Black-whiskered Vireo and associated gleaners in the main study area are shown in Table 1. They ranged from a mean of 13/40 ha for the Blue Mountain Vireo to 95/40 ha for the Black-whiskered Vireo. The number of individuals was reasonably constant from year to year.

Table 2 shows the percent occurrence of the different species in each of the different vegetation types present in the study area. When the percentage of time the bird spent in a vegetation type exceeds the percentage occurrence of that vegetation, some vegetation preference exists. The Blue Mountain Vireo and the Arrow-headed Warbler were found mainly in dense forests (89 and 87%, respectively), and were never found in more open areas. They were also the least common species in the area (Table 1). The Black-whiskered Vireo and the Bananaquit ranged from

TABLE 1

POPULATION DENSITIES (INDIVIDUALS/40 HA) OF THE BLACK-WHISKERED VIREO AND ASSOCIATED GLEANERS IN THE MAIN STUDY AREA

	June 1970	June 1971	June 1972	$\bar{x}$ average
Vireo altiloquus	89	105	91	95 (42%)[1]
Vireo modestus	46	50	49	48 (21%)
Vireo osburni	13	12	15	13 (6%)
Dendroica pharetra	21	24	19	21 (10%)
Coereba flaveola	42	51	48	47 (21%)

[1] Percent of total number of individuals present.

wooded pasture to dense woodlands, but were more common in the open forest (41 and 39%, respectively). The Jamaican White-eyed Vireo was occasionally found in more open forest, but it was usually found in wooded areas with understory present (Table 2).

Foraging ecology.—The average overall overlap values (height, behavior, zone and habitat overlap) for each species pair are shown in Table 3. A more detailed view of the differences in overlap can be obtained by noting the amount of overlap in each specific microhabitat and foraging category (Tables 2, 3).

Fig. 1 summarizes the heights at which birds were seen foraging. Between species differences in foraging heights were significant ($P < 0.01$). Black-whiskered Vireos foraged at a significantly greater height ($P < 0.01$) than the other species, with 86% of its foraging being done in the middle and upper levels of trees (6 m or greater). Both White-eyed and Blue Mountain vireos foraged below 6 m (72% and 58%, respectively) and the

TABLE 2

PERCENTAGE OF OBSERVATIONS OF THE BLACK-WHISKERED VIREO AND ASSOCIATED GLEANERS IN THE MAIN STUDY AREA IN EACH VEGETATION TYPE

Vegetation type	Wet limestone forest		Wooded pasture
Percent occurrence	Open 22.8%	Dense 49.4%	27.8%
Vireo altiloquus	43%	31%	26%
Vireo modestus	33%	53%	14%
Vireo osburni	11%	89%	—
Dendroica pharetra	13%	87%	—
Coereba flaveola	39%	36%	25%

TABLE 3
PERCENTAGE OVERLAP FOR SPECIES PAIRS ALONG VARIOUS ASPECTS OF A FORAGING NICHE AXIS

Species pairs	Foraging height	Foraging zone	Foraging behavior	Habitat overlap	Mean overlap
Vireo altiloquus *Vireo modestus*	0.52	0.72	0.56	0.78	0.65
Vireo altiloquus *Vireo osburni*	0.41	0.31	0.47	0.42	0.40
Vireo altiloquus *Dendroica pharetra*	0.72	0.63	0.46	0.44	0.56
Vireo altiloquus *Coereba flaveola*	0.68	0.68	0.49	0.95	0.70
Vireo modestus *Vireo osburni*	0.83	0.84	0.83	0.64	0.72
Vireo modestus *Dendroica pharetra*	0.79	0.59	0.70	0.66	0.69
Vireo modestus *Coereba flaveola*	0.80	0.55	0.39	0.83	0.64
Vireo osburni *Dendroica pharetra*	0.65	0.45	0.77	0.97	0.71
Vireo osburni *Coereba flaveola*	0.70	0.54	0.45	0.47	0.59
Dendroica pharetra *Coereba flaveola*	0.92	0.73	0.30	0.49	0.61

overlaps in foraging heights with the Black-whiskered Vireo were 0.52 and 0.41, respectively (Table 3). In some cases, the vertical feeding height overlap was high (e.g., 0.72 with the Arrow-headed Warbler and 0.68 with the Bananaquit), but the presence of 2 or more species at a particular height does not necessarily mean competition is occurring, since species may use different foraging zones, foraging behavior, or food items (see below). In addition, the food items may be abundant at certain times, and therefore, not a limited resource (Cruz 1974). For example, feeding assemblages of birds on 2 fruiting trees (*Ficus trigonata* and *Cecropia peltata*) in the same area were investigated (Cruz 1974). A total of 18 species, representing 12 genera and 10 families was recorded. The greatest number of birds observed feeding simultaneously on *Cecropia* was 9, representing 5 species, and on *Ficus* 28, representing 15 species. The large overlap in

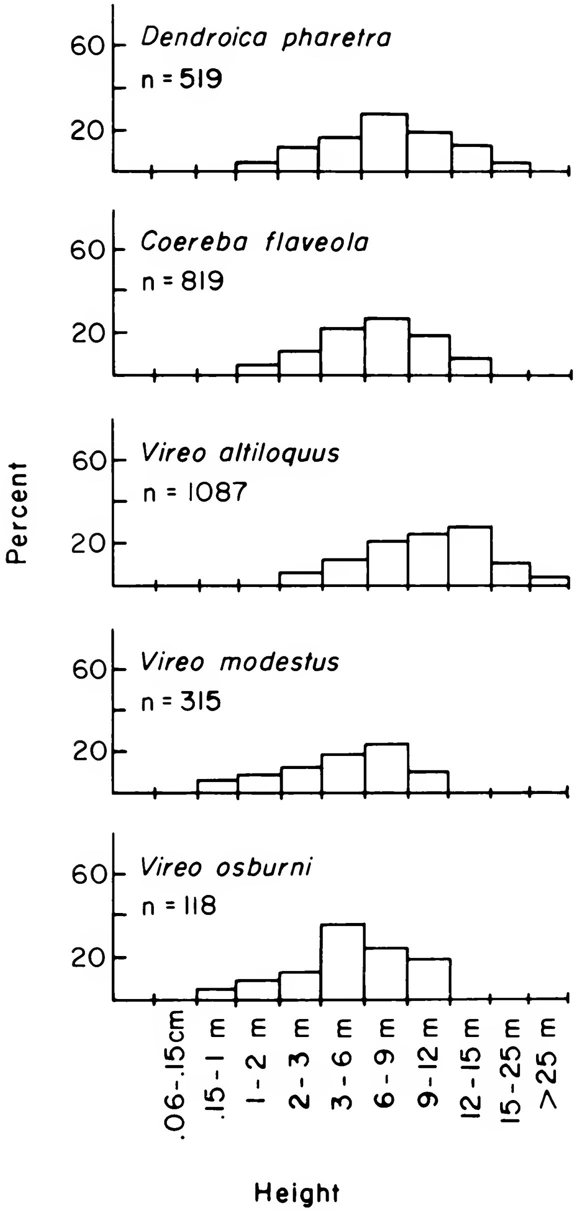


FIG. 1. Distribution of foraging heights of *Vireo altiloquus*, *V. modestus*, *V. osburni*, *Dendroica pharetra* and *Coereba flaveola* in wet limestone forest study area in Jamaica; N = number of observations.

food resource and the minimal degree of interspecific interference observed in that study were probably due to a superabundance of food.

Between species differences in foraging zone usage were significant ($P < 0.01$). The data show that the 5 species did not segregate in an absolute way, but rather, in the frequency with which they used the various foraging zones. The birds differed with respect to the percent of foraging time in foliage (outer branches) and conversely, on stem substrates (inner branches). Thus, the Black-whiskered Vireo, Arrow-headed Warbler and Bananaquit foraged mostly in the middle and upper outer branches, whereas, the Blue Mountain Vireo foraged primarily in the lower and middle branches of trees. The birds also spent very different proportions of their time on shrubby plants, but the Black-whiskered Vireo was never recorded feeding on shrubs and the Arrow-headed Warbler spent only 2% of its time feeding there. Black-whiskered Vireo foraging zone overlap values with other species ranged from 0.31 with the Blue Mountain Vireo to 0.72 with the White-eyed Vireo (Table 3). Highest overlap value was recorded for the White-eyed Vireo and the Blue Mountain Vireo (0.84)—species that foraged mainly in the middle and lower branches of trees and in shrubs.

Between species differences in foraging behavior were also significant ($P < 0.01$). The predominant foraging methods of the Black-whiskered Vireo were gleaning for fruits (50%), foliage gleaning for invertebrates (28%), foliage hovering for invertebrates (7%) and limb gleaning (6%). Hovering for fruits, probing and pecking into limbs and bromeliads accounted for the rest of the foraging procedure (8%).

The variety of fruits eaten by the Black-whiskered Vireo was large; I observed 21 different types of fruits being eaten. Fruits of Moraceae (*Ficus* and *Cecropia*) accounted for nearly 60% of the fruits observed eaten. The majority of fruits were taken from a perched position (gleaning—50%), but occasionally the birds took fruits by hovering (5%). Fruit-eating was also recorded in the other gleaners, ranging from 25% in the Bananaquit to 4% in the Arrow-headed Warbler.

Except for Bananaquits nectar was not a predominant food source. The Bananaquit is primarily a perching nectar feeder (51%), and as such occupies a completely different foraging habitat from the other species in this study. I observed Bananaquits feeding on 16 different species of flowering plants. Ten were large trees, 3 were small trees or shrubs, 2 were herbaceous plants and 1 was a vine. Feeding on fruits accounted for 25% of the total feeding records and these were taken from a perched position. When insect-searching (24%), Bananaquits examine leaves (mainly) and twigs, often hanging upside down to inspect the undersides.

Gleaning for invertebrates accounted for 34% of the total foraging behavior recorded for the Black-whiskered Vireo. This behavior involved

TABLE 4

FOOD ITEMS FOUND IN THE STOMACHS OF THE BLACK-WHISKERED VIREO IN JAMAICA

	Percent			Percent	
Animal taxon	Occurrence	Volume	Plant taxon	Occurrence	Volume
Mollusca	11.7	5.3	Moraceae	94.1	26.4
Gastropoda	11.7	5.3	*Cecropia*	47.1	6.1
Pomatiasidae	11.7	5.3	*Ficus*	70.5	18.3
Arthropoda	88.2	43.3	*Trema*	5.8	2.0
Arachnida	41.1	3.2	Burseraceae	23.5	6.2
Undetermined	41.1	3.2	*Bursera*	23.5	7.3
Insecta	88.2	40.1	Butaceae	23.5	7.3
Orthoptera	47.0	13.1	*Fagara*	23.5	7.3
Blattidae	11.7	3.3	Euphorbiaceae	17.6	4.1
Gryllidae	5.8	4.5	*Sapium*	17.6	4.1
Tettigoniidae	17.6	5.3	Ulmaceae	5.8	2.3
Hemiptera	17.6	2.3	*Trema*	5.8	2.3
Pentatomidae	17.6	1.3	Melastomataceae	17.6	8.2
Undetermined	5.8	1.0	*Miconia*	17.6	8.2
Homoptera	17.6	1.3	Papaveraceae	11.7	1.8
Cicadidae	17.6	1.3	*Bocconia*	11.7	1.8
Coleoptera	47.1	6.2			
Curculionidae	23.5	4.8			
Cerambycidae	17.6	1.4			
Lepidoptera	70.5	17.2			
Noctuidae	35.2	6.5			
Geometridae	47.1	8.9			
Undetermined	11.7	1.8			
Total	88.2	48.6		94.1	51.4

slow and deliberate searching movements along the branches (6%) and foliage (28%) examining the undersides of leaves and branches above it and the uppersides of leaves and branches on its level, and darting forward or fluttering up to snatch its prey. In the 3 vireos, the manner of searching for food was slower-paced and more deliberate than that of the Arrow-headed Warbler and Bananaquit, and bouts of movements were punctuated with periods of searching surfaces of leaves and twigs. Gleaning for invertebrates in the White-eyed Vireo, Blue Mountain Vireo, Arrow-headed Warbler and Bananaquit accounted for 75, 80, 82 and 24% of the total foraging behavior, respectively. Identifiable invertebrates taken by Black-whiskered Vireos included spiders (Araneae) and Orthoptera, Coleoptera and Lepidoptera.

Stomach analysis.—Table 4 presents a list of all food items found in the stomachs of the Black-whiskered Vireo, as well as percent frequency and percent by volume of each prey in the diet. In the Black-whiskered Vireo diet, both animal and vegetable matter are well represented, with an occurrence of 88.2 and 94.1%, respectively, and comprising 48.6 and 51.4%, respectively, of the total volume. These results are in agreement with the findings of Wetmore (1916) in Puerto Rico, where 84 stomachs of the Black-whiskered Vireo were examined and animal food was found to comprise 42.18% and vegetable, 57.82%.

Animal food included 3 classes, 7 orders, 12 families and a number of unidentified fragments. Insecta predominated in the Black-whiskered Vireo's diet, comprising 40.1% by total volume, with Orthoptera, Lepidoptera and Coleoptera, accounting for 13.1, 17.2 and 6.2% of the total volume, respectively. The proportion of the invertebrate prey found in the stomachs (43.7%) is in close agreement with observation of foraging methods, where gleaning, hovering and probing for invertebrates accounted for 45% of the total foraging.

Fruits and seeds of 7 families and 8 genera were identified with Moraceae, accounting for 26.4% of the total volume. *Cecropia* and *Ficus* spp. predominated with 18.3 and 6.1% of the total volume. Also found were Butaceae (7.3%), Burseraceae (6.2%) and Euphorbiaceae (4.1%). The large and diverse numbers of animal and plant species found in the stomachs of Black-whiskered Vireos suggest that it is exceedingly diverse and opportunistic in its feeding habits, taking nearly all the animal and fruit material that it encounters while foraging.

Community coexistence.—The number of species living together in a community depends on several interrelated factors: the range of resources used by each species (its niche width), the tolerable amount of overlap in the use of resources (the limits to similarity) and the total range of resources available to the community (MacArthur 1958, 1972; Hespenheide 1971a). Differences in foraging microhabitat and in diet have been used by other authors as evidence for reduced competition, which makes coexistence possible for closely related species (MacArthur 1958, Crowell 1968, Johnston 1971, and others). Hespenheide (1971b) found that 3 species of eastern flycatchers, which all breed in deciduous forest, actually had different microhabitats. In this study, differences in preferred habitat within a community, in foraging ecology and in the food items consumed are shown, or suggested, to be important factors permitting coexistence.

Hamilton (1962) felt that habitat co-occupancy was seldom found in species of *Vireo*, but when it does occur, the species occupy spatially separated portions of the habitats. That is, 1 species will be primarily a thicket and lower tree branch forager, and another will be primarily an arboreal crown forager of the same habitat. He has further indicated that such species usually are members of different subgenera that occupy different niches and have different combinations of plumage characters. Examples in North America are the arboreal foraging Red-eyed Vireo (*V. olivaceus*, subgenus *Vireosylva*: wingbars and eye-rings absent) and the thicket foraging White-eyed Vireo (*V. griseus*, subgenus *Vireo*: eye-rings and wingbars usually present). In this study, illustrating the above phenomenon, the arboreal foraging Black-whiskered Vireo (subgenus *Vireosylva*) was found with the lower branch and thicket foraging Jamaican White-eyed Vireo and Blue Mountain Vireo (both in subgenus *Vireo*). However, Lack (1976) and I (present study) also found members of the same subgenus (*Vireo*, Jamaican White-eyed Vireo and Blue Mountain Vireo) occupying similar habitats. Barlow (pers. comm.) feels that *V. osburni* and *V. modestus* do not belong to the same subgenus. He notes that "*V. osburni* is probably a very primitive vireo surviving as a relict on Jamaica—from a time when shrike-vireos (*Vireolanius*) and the Vireonidae were separating from early protovireo populations. Or, *V. osburni* is an early, but surviving, *Lanivireo* (i.e., *V. solitarius* and *V. flavifrons*, which have been in their own subgenus, *Lanivireo*, from time to time). Morphology, behavior (vocal and physical), ecology and multivariate phenetic studies all support this latter hypothesis."

In the case of the Blue Mountain and the Jamaican White-eyed vireos, there was a large overall overlap (0.77), but differences in habitat preferences were noted (0.64 overlap). In addition, the difference in body size (48%) and bill size (31%) (Table 5) suggests that these birds could be using food resources differing on the basis of size. Schoener (1965) has shown theoretically that sympatric, congeneric or closely related species of nearly the same body weight, or bill size, would be likely to subdivide food by feeding on similar-sized prey in different microhabitats. When differences in body and bill size are larger it is probable that coexistence (assuming that food is in limited supply) in the same microhabitat is achieved through selection of different sizes of prey. Schoener (1965) compared the ratios of character differences, defined as the ratio of bill lengths of the larger to the smaller species, of groups of species in several families of birds, and he was able to define a zone of transition from small to large ratios, at approximately 1.14, about which it becomes feasible for 2 species to partition food by size, rather than by microhabitats. Schoener's (1965) formulation assumed that body size is correlated with size of prey taken, and that this assumption would likely hold for bill size. Using the data in Table 5, I calculated ratios of character differences for bill dimensions and body weight for the Blue Mountain Vireo and the Jamaican White-

TABLE 5

WEIGHTS AND MEASUREMENTS OF BLACK-WHISKERED VIREO AND OTHER JAMAICAN GLEANERS[a]

Species	Weight (g)	(N)	Exposed culmen (mm)	(N)	Bill depth[b] (mm)	(N)	Bill width[b] (mm)	(N)	Wing (mm)	(N)	Tail (mm)	(N)	Tarsus (mm)	(N)
Vireo altiloquus	17.9	(27)	16.4	(27)	4.9	(7)	4.1	(8)	82.8	(7)	57.6	(7)	18.9	(7)
Vireo modestus	10.1	(6)	9.0	(10)	3.9	(3)	4.0	(3)	56.4	(10)	48.5	(10)	18.7	(10)
Vireo osburni	19.2	(2)	13.0	(1)	6.4	(2)	5.0	(2)	72.0	(1)	58.0	(1)	21.0	(1)
Dendroica pharetra	10.9	(4)	10.8	(6)	3.8	(4)	4.0	(4)	62.5	(6)	52.1	(6)	18.7	(6)
Coereba flaveola	8.1	(10)	12.0	(6)	4.1	(6)	4.2	(6)	58.0	(6)	36.9	(6)	16.4	(6)

[a] The weights and bill measurements are from the author's unpublished data, and represent mean values. Other measurements (including additional culmen measurements) are from Ridgway 1902 and 1904.

[b] Bill depth and width are measured at the level of the anterior end of the nares.

eyed Vireo, following Schoener's method. As predicted by Schoener's model, it is feasible for the Blue Mountain and the Jamaican White-eyed vireos to feed on different sized insects in the same habitats when they occur together because the ratio of bill length (1.4) and body weight (1.9) is larger. Hespenheide (1971b) confirmed Schoener's assumption by demonstrating a strong correlation between size of insect prey and both body size and bill size of their avian predators, although the former is the more strongly correlated of the two in several families of birds, including Vireonidae. However, Hespenheide (1974) in a reanalysis of his data, notes that although mean prey size increases with predator size within each foraging guild, prey size is not as strongly correlated either with body size, or bill size, as it is with foraging method. Foraging differences which affect the choice of prey type and prey size seem the most likely explanation for the close correlation of prey size and prey type in the absence of close correlation of either with bird size.

SUMMARY

This study considers the feeding ecology of the Black-whiskered Vireo and 4 associated gleaners: Jamaican White-eyed Vireo, Blue Mountain Vireo, Arrow-headed Warbler and Bananaquit in a middle elevation forest (460 m) in Jamaica. In Jamaica, the Black-whiskered Vireo is migratory, the majority arriving in mid-March from northern South America and departing in early October. The Black-whiskered Vireo is perhaps the most common passerine in certain habitats. This species occurs from sea level mangrove and scrub forests to montane forests, up to 1500 m.

Differences in foraging ecology of the Black-whiskered Vireo and associated gleaners were observed. The Black-whiskered Vireo foraged at a significantly greater height than the other vireo species, with 86% of its foraging being done in the middle and upper levels of trees. In some cases, the vertical feeding height overlap was high, but differences in the foraging behavior were noted. The Arrow-headed Warbler fed primarily by foliage and stem gleaning and the Bananaquit fed mainly by nectar gleaning, whereas the Black-whiskered Vireo fed largely on fruit and by foliage gleaning. For the Black-whiskered Vireo and associated gleaners, differences in their preferred habitat within a community and differences in their food and foraging ecology were shown, or suggested, to be important factors permitting coexistence.

ACKNOWLEDGMENTS

Support during this investigation came from a National Institute of Health grant awarded to T. H. Patton, Florida State Museum (University of Florida), and a Frank M. Chapman grant and a Ford Foundation fellowship awarded to the author. C. Bock, J. Jackson and an anonymous reviewer read and commented on an earlier version of this paper.

LITERATURE CITED

Asprey, G. F. and R. G. Robbins. 1953. The vegetation of Jamaica. Ecol. Monogr. 23:359–412.

Black, C. 1972. Migrant dates. Gosse Bird Club, Broadsheet No. 19.

———. 1973. Migrant dates. Gosse Bird Club, Broadsheet No. 21.

BENT, A. C. 1950. Life histories of North American wagtails, shrikes, vireos and their allies. U.S. Natl. Mus. Bull. 197.

BOND, J. 1971. Field guide to birds of the West Indies. Houghton Mifflin Co., Boston, Massachusetts.

CODY, M. L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, New Jersey.

CROWELL, K. L. 1968. Competition between two West Indian flycatchers, *Elaenia*. Auk 85:265–286.

CRUZ, A. 1972. Birds of the worthy park (Lluidas vale) region, Jamaica. Quart. J. Flor. Acad. Sci. 35:72–80.

———. 1974. Feeding assemblages of Jamaican birds. Condor 76:104–108.

———. 1977. Ecology and behavior of the Jamaican Woodpecker. Bull. Flor. State Mus. 19:235–300.

———. 1978. Adaptive evolution in the Jamaican Blackbird. Ornis Scandinavica 9:130–137.

HAMILTON, T. H. 1962. Species relationship and adaptations for sympatry in the genus *Vireo*. Condor 64:40–68.

HESPENHEIDE, H. A. 1971a. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. Ibis 113:59–72.

———. 1971b. Flycatcher habitat selection in the eastern deciduous forest. Auk 88:61–74.

———. 1974. Prey characteristics and predator niche width. Pp. 158–180 *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.), Harvard Univ. Press, Massachusetts.

JOHNSTON, D. W. 1971. Niche relationships among some deciduous forest flycatchers. Auk 88:796–804.

LACK, D. 1976. Island biology. Univ. Calif. Press, Berkeley and Los Angeles, California.

MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forest. Ecology 39:599–619.

———. 1972. Geographical ecology—patterns in the distribution of species. Harper and Rowe, New York, New York.

OSBURN, W. 1859. Notes on the mountain birds of Jamaica. Zoologist 6658–6665.

RIDGWAY, R. 1902 and 1904. The birds of North and Middle America. U.S. Natl. Mus. Bull. 50 (Parts 2 & 3).

SCHOENER, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19:189–213.

———. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418.

WETMORE, A. 1916. Birds of Puerto Rico. U.S. Dept. Agric. Bull. 326.

WILLIAMS, A. B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Monogr. 6:317–408.

ENVIRONMENTAL, POPULATION AND ORGANISMIC BIOLOGY DEPARTMENT, UNIV. COLORADO, BOULDER, COLORADO 80309. ACCEPTED 1 FEB. 1979.

Wilson Bull., 92(1), 1980, pp. 53–62

EXPERIMENTS IN FEEDING BEHAVIOR OF THE ANNA HUMMINGBIRD

Thomas G. Wheeler

The reports on hummingbird color preference range from red dominance to blue dominance (Clark 1902; Pickens 1930, 1941; Bene 1941, 1946; Sherman 1913; Poley 1968; Stiles 1976). Such differences in preference may be due to the particular species studied, differing experimental conditions or the bird's ability to learn the most rewarding color (Bene 1941, 1945; Collias and Collias 1968). These reports do have one strong feature in common: each assumes, suggests, or attempts to demonstrate the significance of color preference in the bird's ability to survive. The studies reported herein attempt to answer some basic questions, as well as to elucidate when the bird normally feeds, its ability to learn and its color preference. Unlike most previous studies, my investigation was done on a large population of Anna Hummingbirds (*Calyptie anna*) in the wild. Four separate studies of Anna Hummingbird feeding behavior have been performed: (1) to determine temporal patterns of feeding; (2) to determine if the color or location of a food supply was the controlling factor in attracting the animals to feed; (3) to determine how rapidly the animal could learn the location of a new food supply (or an adversive substance); and (4) to determine if the birds were differentially attracted to various colors.

METHODS

All studies reported here were done at Camp Nelson, California, the High Sierras (elevation 1500 m) during mid-July 1976. The days were warm (23–27°C) with clear skies, unless otherwise noted. The study site was in front of an old cabin where for years hummingbird feeders had been placed and serviced with red colored sugar water. Several species frequented this site.

Temporal feeding schedule.—The feeder used in this experiment, a hanging gravity feed device, with small (1.5 mm) holes in the gray metal base, had been in use for 5 years in the same location. The fluid container (250 ml capacity) was made of clear glass and was filled an average of 3 times per day with a solution of saturated sugar water, using commercial pure cane sugar. All drinks taken by all feeding birds were recorded on a counter, that was read every 15 min throughout the day. Counts taken between 08:00 and 11:00 may be somewhat low; some counts may have been missed due to the high concentration of birds.

Attraction to color or location.—The above experimental setup was varied only by changing the color of the saturated sugar solution in the feeder every 15 min. Sixteen independent test sequences were done and in each sequence 5 colors (red, yellow, green, blue, clear) were presented in random order. Therefore, the color of the solution was changed a total of 80 times providing 16 exposures for each color. Each colored solution contained 15 drops of food color (McCormick brand) per pint of water. For the purpose of experimental repeatability the transmission spectrum was determined for each of the solutions (Fig. 1) with a Cary dual

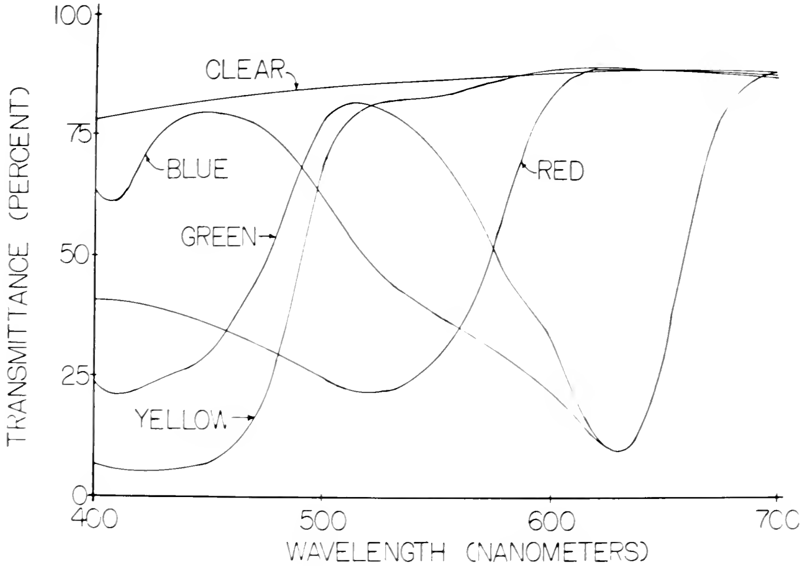


FIG. 1. Spectral transmission curves obtained from samples of the 5 colored sugar solutions used. The sample path length was 1 cm; a proper labeling should therefore be "percent transmittance per linear centimeter" since light scattering was not taken into account.

beam spectrophotometer. The experiment took approximately 26 h and was done between 08:00 and 17:00 on 3 consecutive clear days.

Learning location of a food supply (or adversive substance).— For this experiment the birds were given a choice between 2 identical containers (open-top pint-sized canning jars made of clear glass). One container was filled with water and the other with a saturated sugar solution (both clear). The containers were placed in a location not previously used. Counts were made on birds that approached the container from a distance of at least 1.5 m, and the container from which the bird drank first was recorded. Birds often went from the initial container to the second container (by choice or forced by aggressive birds). Only the bird's first choice was counted.

The experiments designed to determine the bird's response to an unpleasant/adversive substance was done using only a single container at the same location as the previous study. Feeding was permitted to continue until the number of drinks per 5 min period reached steady state. The sugar solution was then replaced with a saturated solution of sodium chloride. The time of replacement was designated time zero (t = 0) and counts were taken of the number of drinks from the container during each 5 min interval thereafter. All counts were taken between 08:00 and 22:30 on 2 consecutive sunny days.

Color preference.—In this study, the same concentrations of sugar and food coloring were used as those described in the experiment on attraction to color or location. All colors were presented simultaneously. Five identical containers were placed side by side in a straight line in a previously unused location to obviate location recall. The color sequence was changed every 15 min. Fifteen sequential arrangements were used, and efforts were made to ensure that each container received equal exposure at the end positions (see Results) and

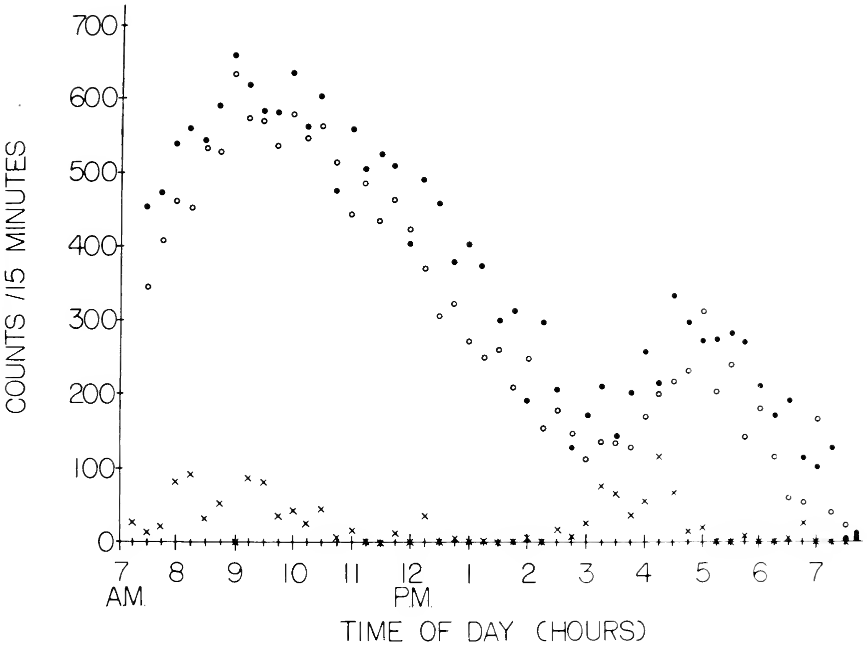


FIG. 2. Concentration of Anna Hummingbirds' feeding on a nectar substitute as a function of time of day. Each data point represents the total number of drinks taken during the preceding 15 min intervals. Data were collected on 3 consecutive days. Day 1 (●) was sunny and warm, the mean number of counts (over the entire day) was 354 ± 179. Day 2 (○) was partly cloudy and had a mean of 301 ± 177. Day 3 (×) was overcast and rainy and displayed a drastic reduction in the total and mean (24 ± 30) number of counts.

that no 2 colors were sequentially adjacent. Counts were made on birds which approached the containers from a distance of at least 1.5 m and scores were kept with respect to the container each bird sampled first. The experiment was conducted between 08:30 and 10:30 on 2 consecutive clear days.

RESULTS

Temporal feeding schedule.—Fig. 2 shows the results obtained from 07:15–20:00 on 3 consecutive days. The day-to-day differences observed in temporal feeding habits were related to the weather conditions. Day 1 was sunny, clear and warm (high 28°C), whereas day 2 was partly cloudy, breezy with a high temperature of 23°C. This difference in weather conditions appears to be reflected in the birds' feeding behavior in that almost every count taken on day 2 was lower than that obtained on day 1. The general shape of the curves for days 1 and 2 were the same. The data taken on day 3, however, were quite different. Day 3 was overcast, light

TABLE 1

NUMBER OF DRINKS PER 15 MIN FROM A SINGLE CONTAINER OF COLORED SOLUTION[a]

Color	Mean counts	SD
Red	292	±138
Yellow	293	±121
Green	296	±117
Blue	293	±141
Clear	275	±142

[a] Color of solution was randomly changed. The mean and SD are presented for 16 presentations of each color. A *t*-test performed on these data produced no significant difference in the birds' feeding behavior for the different colors presented.

to moderate rain fell throughout the day and the high temperature was 17°C. The distinguishing feature of day 3 was the low total count and the different distribution of counts. The increase in counts between 15:00 and 17:00 coincided with a decrease in cloud cover and rainfall. At approximately 17:00 the sky became completely overcast, and the rain increased in intensity. The total number of birds observed in the vicinity was lower on day 3 than on the previous days. However, it was noted that the majority of birds observed on day 3 spent their time around green plants, rather than the feeders, and appeared to be investigating and pecking the underside of the leaves. Sometimes birds would leave the greenery in pursuit of insects. These observations strongly suggest that the Anna Hummingbirds were feeding primarily on insects during this period.

Attraction to color or location.—The second experiment was conducted to determine if color or location of the food supply was the dominant factor in feeding behavior. Eighty independent test intervals are included in these results (Table I). The only solution which appears to have received somewhat less attention than the others was the clear solution. This reduced use may have been due to resemblance of this latter container to an empty container.

The large standard deviation for each color (Table I) reflects the different concentrations of birds feeding at different times of the day. For example, the data collected between 08:00 and 10:00 produced the following results: R = 660, Y = 633, G = 577, B = 618 and C = 567; whereas a color sequence done between 14:30 and 17:00 yielded much lower counts (R = 126, Y = 130, G = 136, B = 113 and C = 136). The difference in counts between the 5 colors in any one test sequence was very small, but the difference in counts for a given color across test sequences was large, reflecting differences in time of day (Fig. 2). In fact, the standard deviations reported in Table I are similar to those reported for the average counts per 15 min in the temporal study.

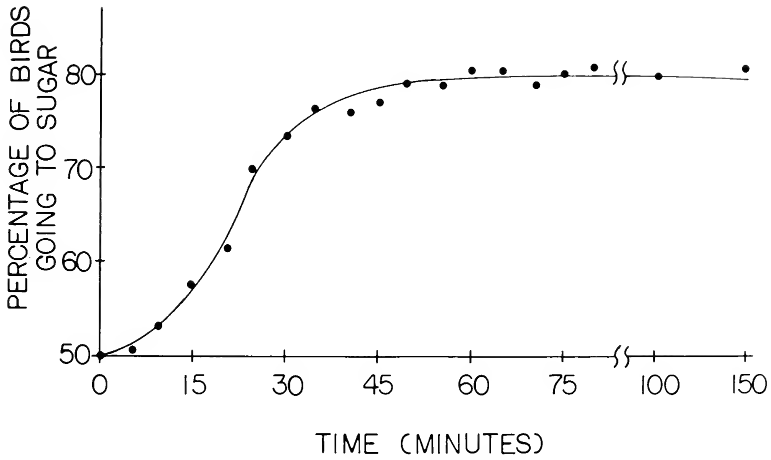


FIG. 3. Learning behavior of birds when given a choice between 2 feeding containers placed side-by-side; one with sugar water and the other with just water. Each data point was computed using the count of birds feeding from the sugar container divided by the total number of birds feeding from both containers during the preceding 5 min intervals.

It is clear that once the animals have located a food supply, its location, not color, was the controlling variable. In fact, one could remove the food supply entirely, including the container, and the birds would continue to come to the location for hours. As the birds discovered that the food supply was no longer at that location, the frequency of investigation decreased. Invariably, however, some dominant males, seemingly protecting their "food supplies," would continue to drive off other birds that came into the vicinity. This was observed to continue for 3 days in 1 case.

Learning location of a food supply (or adversive substance).—In these experiments 2 identical containers were used: 1 contained clear water, and the other clear sugar water. Once the first bird had discovered the location, it was only seconds before large numbers of hummingbirds began approaching the containers. The initial counts I made were evenly distributed between the water and sugar containers. The plot in Fig. 3 reflects how rapidly the investigation period of the birds was replaced with feeding as the birds learned which container was filled with the sugar water. Again, once the birds had discovered a food supply, they patronized the area long after the supply had been removed. After the sugar supply was replaced with water, the ratio of birds which flew to the container which previously contained sugar water remained constant. Even some 6 h later, 80% of the birds that came to feed tested the previous sugar container first.

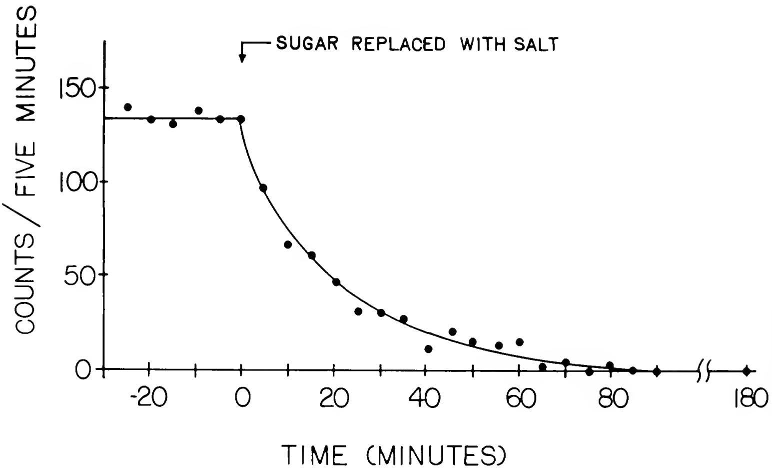


FIG. 4. Response of birds when a food supply was replaced by an adversive substance. Each data point represents the total number of drinks taken during the preceding 5 min intervals.

When the sugar solution was replaced with an adversive solution of salt, the birds quickly began to avoid the area (Fig. 4). Some individually identifiable birds learned to avoid the salt solution after a single trial. Once the bird had tested the salt it would fly away, chirping loudly and shaking its entire body and, on occasion, would even momentarily lose flight control. Some birds returned once or twice to this salt container, investigated it from top to bottom for some time, and then departed without testing the salt solution. After 3 h (t = 180), no birds were observed anywhere in the vicinity. At this time the salt solution was replaced with a clear sugar solution; it was 2 days before the birds began to return and feed from the container.

Color preference.—A distinction must be made between the bird's ability to recall the location of the food supply and the attractiveness of a particular color during a food search (Bene 1946). The second experiment showed that once the location of a food supply had been discovered, the color of that supply was irrelevant to the feeding behavior. Therefore, this experiment was designed to determine which color the birds were most attracted to when in search of food. The birds did respond differently to color of a food source, red being the preferred color (Table 2A). The significance levels calculated for each color combination are shown in Table 2B.

TABLE 2

A AVERAGE NUMBER OF BIRDS APPROACHING AND DRINKING FROM EACH OF 5 CONTAINERS CONTAINING DIFFERENT COLORED SOLUTIONS[a]

Color	Mean counts	SD
Red	33.9	±8.7
Yellow	13.1	±5.0
Green	8.4	±2.7
Blue	4.3	±1.7
Clear	5.3	±1.6

B RESULTS OF STUDENT *t*-TEST ON ABOVE DATA

	Y	G	B	C
R	0.001	0.001	0.001	0.001
Y	—	0.015	0.001	0.01
G	—	—	0.001	0.015
B	—	—	—	0.015

P value

[a] Containers were in a straight line; order was randomly changed every 15 min.

DISCUSSION

A number of authors suggest that nectar is a primary food source for hummingbirds and that the innate attraction for these birds to particular colors is a major factor in their ability to survive. The feeding behavior of hummingbirds would appear to be much more complex when one considers the ability of the birds to rapidly learn the location of a colorless food supply and to recall the location of food for a long period as well as the striking correlation between the number of birds feeding on a nectar substitute and time of day and changes in the weather. Considering the data reported here, the factors controlling the Anna Hummingbirds' feeding on a nectar source may be placed in the following order: (1) time of day, (2) weather, (3) location and (4) color. Obviously, other factors influence feeding behavior and need to be considered as controlling factors. These might include number or type of flowering plants, quantity and quality of nectar and energy expenditure (Stiles 1976).

Given that the weather and time of day are favorable, my studies indicate that location, not color, was the most important parameter in the birds' feeding on a nectar source. Indeed, it would be most efficient in terms of energy expended if the location of food source was known and easily recalled (Stiles 1971). As shown in this series of field experiments hummingbirds are capable of rapidly locating a food source and do not readily forget that location. It was repeatedly noted that the birds in search of a food source investigated (seemingly at random) everything in sight—color, shape, size, or material makeup seemed to make little difference. Once a food supply was located, all attention was directed to it. Therefore, it appears that when a hummingbird is among familiar surroundings, memory of location undoubtedly guides it to a large degree in its feeding. From the color preference study, it is clear that Anna Hummingbird has the ability to locate a red food supply more efficiently, on the average, than green or blue supplies. However, a new food supply of clear sugar solutions placed in unfamiliar locations, was also located rapidly by the birds. As noted above, the time of day and weather appear to be the major controlling factors as to whether the bird feeds on a nectar substitute at all.

Anna Hummingbirds are known to feed on small insects during the warm part of the day and on overcast, rainy days (Gander 1927, Bene 1946). In my study, frequency of feeding from the nectar substitute decreased from 11:00 to 15:00; data obtained on an overcast, rainy day (day 3) showed a tremendous reduction in feeding on the nectar substitute and the birds appear to be in search of other food supplies during this period. This confirms previous observations. The ratio of arthropods to nectar consumed by the Anna Hummingbirds is unknown. Henderson (1927) found that the stomach contents of 111 Anna Hummingbirds comprised: Diptera, 45%; Hymenoptera, 35%; Hemiptera, 17%; spiders, 2%; fruit pulp, a trace. Clark (1902) found that 1 stomach contained 32 treehoppers, 1 spider, 1 fly and other insect parts. The proportion of liquid food in the ordinary diet of the bird cannot be determined by an examination of stomachs, but these data do indicate the bird's need for large quantities of animal protein (Lucas 1893). It has also been reported that Anna Hummingbirds often follow sapsuckers (*Sphyrapicus* sp.) from tree to tree (Woodbury 1938). The hummingbird visits each puncture that the sapsucker makes in the bark and partakes of both sap and small insects that have been attracted to it (Grinnell and Storer 1924). Indeed, attraction to a carbohydrate nectar source may also be for the purpose of feeding on small insects living in flowering plants. The observation that hummingbirds consume a large quantity of food other than nectar is consistent with the known nutritional requirements of other vertebrates. Caution must be taken if nectar is to be considered the hummingbirds' primary food source. Nectar probably serves as a water supply as well as a convenient source of carbohydrates and insect habitat. No alternate source of water has been reported.

A number of questions remain. Why are the birds away from the nectar source for such extended periods during the day? Why does weather play such an important role? Does the Anna Hummingbird frequent different flowers due to nectar quantity, quality or color, or does it do so because insects are more abundant on these plants? Experiments are in progress that may provide answers to some of these basic questions.

SUMMARY

In my studies the Anna Hummingbird fed on a nectar substitute primarily in the early morning. The quantity of nectar consumed increased steadily until 09:30 and decreased thereafter. There was also a short feeding period between 16:00 and 18:00. The quantity of nectar consumed appeared related to weather conditions. Maximum consumption was on clear days, with decreasing consumption with increasing cloud cover. During periods of rainfall, even light drizzle, many birds remained in the vicinity but apparently switched from nectar to feeding on small insects.

C. anna appears to have a keen ability to recall the location of a food source. Sugar containers placed in new locations were rapidly located by the study population. Even when identical containers were placed side-by-side, 1 with and 1 without sugar, the birds learned to distinguish between them. Once a nectar source was located, the color of the source had no effect on the number of birds approaching it, or feeding from it, as demonstrated by repeated changing of the color of the sugar solution. Irrespective of the color of the solution, including clear liquid, the same number of drinks were taken per unit time. The animals did discriminate among colors when 5 colors were presented simultaneously in 5 identical containers placed side-by-side and randomly rearranged in order to avoid location preferences. Anna Hummingbirds approached, and fed from, the red container more frequently than the yellow, green, clear and blue containers (in order of decreasing frequency).

Considering the above observations, the factors controlling the Anna Hummingbirds' feeding behavior, in order of importance, are: (1) time of day, (2) weather, (3) familiarity of the location of the source and (4) color of the source. It is not known what percentage of the bird's diet consists of nectar. Anna Hummingbirds may be attracted to nectar sources in order to feed upon insects that abide there, or, as a source of water.

ACKNOWLEDGMENTS

The constructive scientific reviews by my colleagues are gratefully appreciated. In addition, may I thank Hazel Magill and the Robb family for their gracious hospitality and the use of the mountain cabin. Miss Lillian Robinson provided not only the inspiration, but also intellectual instruction, which ultimately led to the research reported here.

LITERATURE CITED

Bene, F. 1941. Experiments on the color preferences of Black-chinned Hummingbirds. Condor 43:237–323.

———. 1945. The role of learning in the feeding behavior of Black-chinned Hummingbirds. Condor 47:3–22.

———. 1946. The feeding and related behavior of hummingbirds. Mem. Boston Soc. Nat. Hist. 9:403–478.

Chapman, D. 1972. The role of fatty acids in myelin and other important brain structures.

Pp. 31–57 *in* Lipids, malnutrition and the developing brain. Associated Scientific Publishers, New York, New York.

CLARK, F. C. 1902. Food of Anna Hummingbird. Condor 5:18.

COLLIAS, N. E. AND E. C. COLLIAS. 1968. Anna's Hummingbirds trained to select different colors in feeding. Condor 70:273–275.

GANDER, F. F. 1927. The fly-catching habits of Anna Hummingbird. Condor 29:171.

GRINNELL, J. AND T. I. STORER. 1924. Animal life in the Yosemite. Univ. Calif. Press, Berkeley, California.

HENDERSON, J. 1927. The practical value of birds. MacMillan, New York, New York.

LUCAS, F. A. 1893. The food of hummingbirds. Auk 10:311.

PICKENS, A. L. 1930. Favorite colors of hummingbirds. Auk 47:346–352.

———. 1941. A red figwort as the ideal Nearctic bird-flower. Condor 43:100–102.

POLEY, VON D. 1968. Experimentelle Untersuchungen zur Nahrungssuche und Nahrungsaufnahme der Kolibris. Bonn. Zool. Beitr. 19:111.

SHERMAN, A. R. 1913. Experimenting in feeding hummingbirds during seven summers. Wilson Bull. 25:153.

STILES, F. G. 1971. Time, energy and territoriality of the Anna Hummingbird (*Calypte anna*). Science 173:818–821.

———. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. Condor 78:10–26.

WOODBURY, A. M. 1938. Red-naped Sapsucker and Rufous Hummingbird. Condor 40:125.

DEPT. OPHTHALMOLOGY, SCHOOL OF MEDICINE, UNIV. LOUISVILLE, 301 EAST WALNUT ST., LOUISVILLE, KENTUCKY 40202. ACCEPTED 2 NOV. 1978.

Wilson Bull., 92(1), 1980, pp. 63–73

THE SELECTION AND USE OF FRUIT BY BIRDS IN AN EASTERN FOREST

John W. Baird

The fruit crops of a number of temperate forest plants that are eaten by birds ripen in the late summer or early fall and become available just before the main southbound migrations of many facultatively frugivorous birds. The fruit that remains at the end of the migratory period constitutes a major food resource for wintering bird populations. Few studies quantify differential use of fruit (Pulliam and Enders 1971). The research reported here was motivated by many questions. Are all types of fruit harvested simultaneously, or do some types disappear before others? What fraction of the original standing crop remains into the winter for harvest by resident populations? Do the food habits of resident species change as the relative abundances of different fruits vary through the winter?

STUDY AREA AND METHODS

In order to gain insight into the above questions, I studied the feeding habits of birds in a 600 ha tract of woods belonging to the Institute for Advanced Studies in Princeton, Mercer Co., New Jersey in the fall and winter of 1974-75. I found 23 species of fruit-bearing plants in the woods and along its margins. The species composition varied in different successional stages and with different moisture and soil conditions. To take into account the variety of stand types represented in the forest, I chose study sites in 3 different, relatively homogenous areas.

The first study area comprised 235 m² in an area grown in young red maple (*Acer rubrum*) and white oak (*Quercus alba*) with American beech (*Fagus grandifolia*) and some flowering dogwoods (*Cornus florida*); the diverse understory included mapleleaf viburnum (*Viburnum acerifolium*), false Solomon's seal (*Smilacina racemosa*), spicebush (*Lindera bensoin*) and Virginia creeper (*Parthenocissus quinquefolia*). In this plot, only the mapleleaf viburnum and false Solomon's seal produced fruit.

The second plot was 470 m² of white oak, tuliptree (*Liriodendron tulipifera*) and shagbark hickory (*Carva ovata*), with subcanopy of flowering dogwood, blackgum (*Nyssa sylvatica*) and American beech. Understory included mapleleaf viburnum, New York fern (*Thelypteris noveboracencis*), greenbrier (*Smilax rotundifolia*), false Solomon's seal and spicebush. The dogwood and blackgum trees produced fruit, but most of the blackgum berries had already dropped when the study began. The viburnum, false Solomon's seal and spicebush had fruit.

The third plot was 470 m² of floodplain forest near the Stony Brook River. An open canopy of 2 large white oaks with box elders (*Acer negundo*) beneath allowed much sunlight to pass through. Understory was mostly tall, woody spicebush and vine poison ivy (*Rhus radicans*) densely entwined the trunks of the oaks. Both the spicebush and poison ivy produced large crops of berries.

All fruit on each plant in the 3 plots was counted at the outset of the study, as were the berries on 8 spicebushes in different parts of the floodplain study area (Table 1). Fruits (usually 30/species) were dried in an oven to constant weight, and then seeds were removed to give dry weight.

TABLE 1
FRUIT AVAILABLE IN THE STUDY PLOTS

	Study plots					
	Red maple		Oak-Hickory		Floodplain	
Plants	fruits/ha	g/ha	fruits/ha	g/ha	fruits/ha	g/ha
Smilacina	6300	190	320	9.6		—
Viburnum	10000	110	7800	78		—
Lindera	0	0	620	31	74000	3700
Cornus	0	0	3500	350		—
			68000[a]	6800[a]		

[a] *Cornus* in a 36 m^2 area under a gap in the canopy in the study plot.

I continued counting all fruits in the red maple and oak hickory plots until almost all of the fruit had been eaten, or had dropped from the plants. Because of the large crop in the floodplain, subsequent counts were made of berries on 8 spicebushes in different parts of the study area. Counts were also made of a patch of false Solomon's seal berries in a clearing near a path, and of Dogwood berries in another section of the oak-hickory forest, to compare with results from the study plots (Table 2). Poison ivy fruit was too small to count. The fraction of the original crop remaining was estimated by visual inspection and by comparison of photographs of the same patches taken on different days.

Other abundant fruits eaten by birds growing in woodland edge and riparian situations outside the study plots included Asiatic bittersweet (*Celastrus orbiculatus*), Japanese honeysuckle (*Lonicera japonica*), 4 species of grapes (*Vitus* spp.) and greenbrier. Productivity of these plants was difficult to measure because of their patchy distribution, difference in the productivity of different patches, and because many of the fruits were high above the ground. I searched for patches of these species at the outset of the study, and estimated the fractions of the original crops remaining on subsequent dates.

From 25 September 1974, until 28 March 1975, I made 2 or more trips to the woods per week to record feeding observations. On 23 November, at the end of fall migration, I began weekly counts of birds along a 2100 m census route through oak-hickory and red maple forest near the study areas, then through the floodplain forest, and back to my starting point, along an open field at the edge of the woods. All birds heard and seen within 30 m on either side of my route were counted. The total area included in the census was approximately 10 ha. Each bird seen eating 1 or more fruits constituted 1 observation (see Appendix).

RESULTS

Fruit productivity in the forest.—The greatest fruit production occurred in the most open parts of the forest (Table 1). The counts from the study plots and estimates of other crops are incorporated in Fig. 1. Differences in the amount of dropped fruit which was subsequently eaten by birds varied with different species and different habitats, and was exceedingly difficult to quantify. Of fruits dropped mid- to late November, I saw no birds eating the fruit of false Solomon's seal, and only once that of mapleleaf viburnum. Dropped spicebush berries were eaten sparingly, except

TABLE 2

NUMBERS OF BERRIES REMAINING IN STUDY PLOTS ON SUBSEQUENT DATES

Red maple study plot

Date	*Viburnum*	*Smilacina* (in plot)	*Smilacina* (in clearing)
29 Sept.	259	145	—
7 Oct.	259	126	274
19 Oct.	—	65	208
29 Oct.	256	59	156
6 Nov.	225	55	148
22 Nov.	22	40	*

Oak-Hickory study plot

Date	*Viburnum*	*Smilacina*	*Cornus*	*Cornus* (second patch)	*Lindera*
9 Oct.	392	16	398	—	31
17 Oct.	—	12	375	—	12
29 Oct.	339	12	66	273	8
6 Nov.	—	*	36	101	7
14 Nov.	210	—	24	70	—
22 Nov.	—	—	21	51	—
3 Dec.	112	—	—	—	—

Floodplain study plot

Date	*Lindera* (8 selected bushes)
22 Oct.	573
31 Oct.	503
6 Nov.	408
15 Nov.	289
22 Nov.	75

* *Smilacina* stalks were covered by fallen leaves.

by a flock of White-throated Sparrows (*Zonotrichia albicollis*) on 12 December. Although grapes and dogwood berries fell steadily beginning in late September, these plants usually grew in open areas where fallen fruits were visible, and eaten by birds until crops were nearly exhausted.

The use of fruit by fall and winter birds.—Twelve of the 13 commonest migratory species and 11 of the 19 resident species seen between 25 September and 14 November were observed eating fruit, and many of these species were almost wholly frugivorous during this period. Dogwood was the largest and most widely used crop. Large flocks of migratory American Robins (*Turdus migratorius*) and Common Grackles (*Quiscalus quiscula*) fed on dogwood in woodland edge, where fruit production was heaviest. As the berries began dropping, 10 species of birds ate them from the

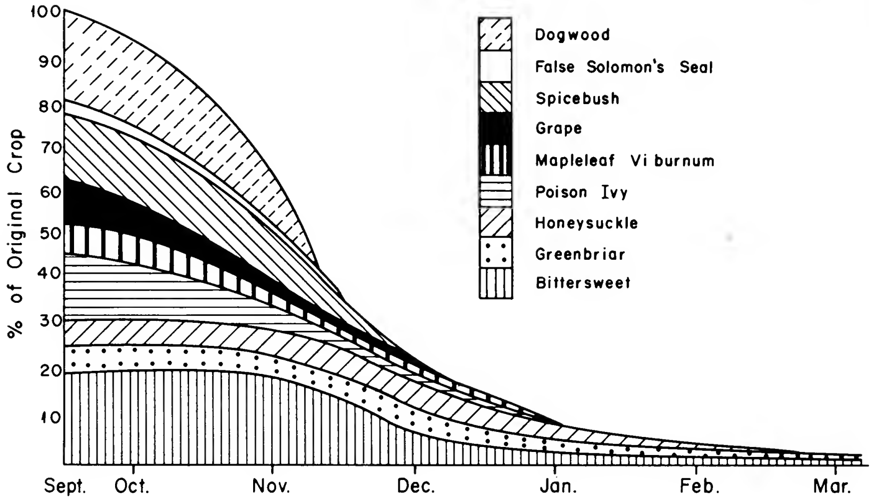


FIG. 1. The times at which different fruits dropped or were consumed by birds. The total height of the curve represents the fraction of the original crop remaining; the widths of the individual sectors show how much of the total is composed of each species. The curve is steepest in late September, October and early November, when bird density in the woods was highest. By the time the last migrants left in mid-November, the crop had been reduced to approximately 30% of the original total.

ground. By mid-October, most of the berries along the woodland margins had been eaten, and the flocks moved into the forest, congregating in small patches and eating all available dogwood berries. The disappearance of patches of dogwood fruit was so abrupt that only 1 dropped berry could be found in the study plot on 6 November (Table 2). By this time, most of the migrants had gone and no more than 10% of the original dogwood crop remained on the branches and the ground to be eaten by winter residents.

Grapes were used extensively by 8 species. Robins and grackles fed on grapes from vines, limbs of nearby trees and the ground in September and October. An estimated 90% of the crop had fallen by 23 November. Cardinals (*Cardinalis cardinalis*) fed on remaining partly-dried grapes until mid-December. Poison ivy berries were eaten by 10 bird species. This fruit grows in conspicuous clusters, is slow to fall, and may have been the most fully used of any of the fruits in the forest.

Bittersweet, a major crop along the forest paths and margins, was the last fruit to ripen (late September to early October), and lasted to late March. The berries began dropping in early November, and were eaten both from the vine and the ground by all frugivorous winter residents. The persistent fruits of Japanese honeysuckle and greenbrier were important

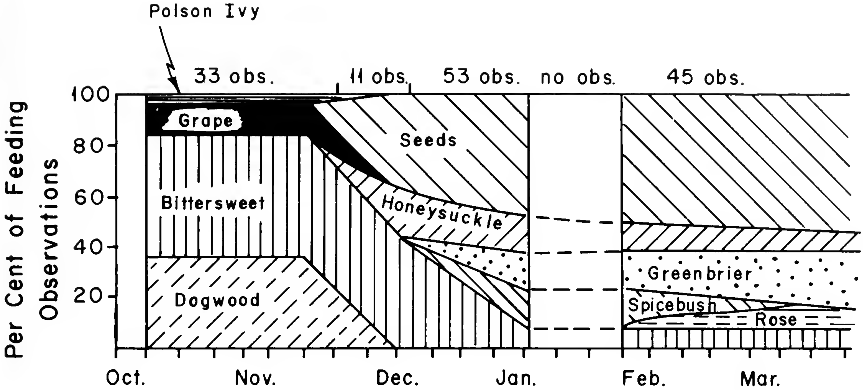


FIG. 2. The foods of the White-throated Sparrow.

late winter and early spring foods for Cardinals and White-throated Sparrows (Fig. 2). Honeysuckle berries lasted until late February, while the firm greenbrier fruits were retained through the winter, until most of them had been eaten.

Feeding ecology of wintering birds.—The depletion of dogwood berries and grapes in late October coincided with the departure of many of the migratory birds. Perhaps a causal relationship exists here. Further study over a period of several years would be required to test this idea.

Later migrants, including robins, Hermit Thrushes (*Catharus guttata*), Rusty Blackbirds (*Euphagus carolinus*) and Yellow-rumped Warblers (*Dendroica coronata*), fed on bittersweet and poison ivy fruits. The last migrant to leave, in mid-November, was the Yellow-rumped Warbler. Between the third week of November and the end of February, the bird species composition and abundances fluctuated very little. During this period the forest interior was inhabitated almost exclusively by bark and twig feeding birds—Black–capped Chickadees (*Parus atricapillus*— Fig. 3), Tufted Titmice (*Parus bicolor*), Downy (*Picoides pubescens*) and Hairy (*P. villosus*) woodpeckers, White-breasted Nuthatches (*Sitta carolinensis*), Brown Creepers (*Certhia familiaris*) and Golden-crowned Kinglets (*Regulus satrapa*). The only other birds observed in this part of the forest during these months were a robin, 2 Hermit Thrushes and an occasional Blue Jay (*Cyanocitta cristata*), or Winter Wren (*Troglodytes troglodytes*).

Frugivorous winter residents.—The frugivorous winter birds foraged almost exclusively along margins and in clearings in the forest, showing marked seasonal changes in their diets and a high degree of overlap in foods eaten (Figs. 2, 3). The most common of these species were White-throated Sparrows, Cardinals and Dark-eyed Juncos (*Junco hyemalis*).

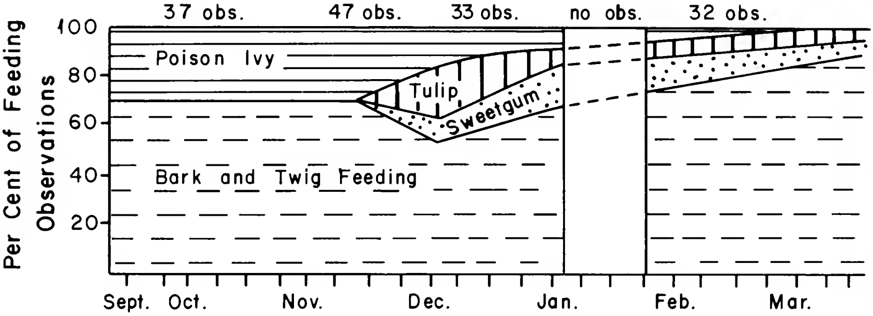


FIG. 3. The foods of the Black-capped Chickadee.

The use of fruit by these species has been noted previously (Martin, Zim and Nelson 1951).

White-throated Sparrows (Fig. 2) arrived for the winter in mid October. They almost always foraged in groups; often in mixed-species flocks. In late March they commonly fed on surficial seeds along edges of fields and in grass and shrubs around a marsh, in association with juncos, Song Sparrows (*Melospiza melodia*) and Mourning Doves (*Zenaidura macroura*). From September until early November, Cardinals were frequently seen and heard in thickets and vines along the banks of streams on the floodplain. Grapes were their primary food during the fall. As the supply of grapes was depleted, Cardinals switched to bittersweet fruit from vines along the fields, dried blackberries (*Rubrus allegheniensis*) and seeds of bur-marigold (*Bidens cernua*) and ailanthus (*A. glandulosa*) from around the marsh. From December until February, Cardinals frequently fed in greenbrier and honeysuckle thickets and foraged on the ground with White-throated Sparrows and juncos. In March they began feeding in fields and on lawns, and on the growing buds of the trees around the marsh. Juncos usually foraged on the ground in small flocks. In the fall they ate fallen berries on the paths, insects from fallen logs and branches, and the seeds of weeds and grasses. During the winter they relied more heavily on seeds, usually feeding in the grass along the edges of the woods.

Relationships among species.—During the fall and winter, birds of different species often used the same foods (see Appendix). Differences in macrohabitat choices minimized competition for food. For example, in early fall, flocks of robins fed on dogwood berries in the margins and clearings, while Hermit and Wood thrushes (*Hylocichla mustelina*) remained deeper in the woods. White-throated Sparrows and juncos arrived later in the fall, and they joined the robins in eating dogwood fruit on the edges of the woods and in the paths. As that was used up, the robins moved deeper into the forest to eat dogwood, but the sparrows and juncos switched to other foods.

Different species were also observed dividing a common resource by using different feeding stations within a habitat. Robins and grackles ate dogwood berries from perches in the larger branches of trees and from the ground, while sparrows fed on smaller branches and thin vines. Juncos were seen eating berries only on the ground. Among the species that ate poison ivy berries, Yellow-rumped Warblers fed on the extreme tips of branches, while Downy, Hairy and Red-bellied (*Melanerpes carolinensis*) woodpeckers, and Common Flickers (*Colaptes auratus auratus*) foraged from larger branches near the trunk.

Mixed species flocking.—Mixed flocks of chickadees, titmice, Downy Woodpeckers and Golden-crowned Kinglets formed during the winter. White-throated Sparrows, Dark-eyed Juncos and Cardinals often foraged in groups on the ground and in low shrubbery. While there was some overlap in the foods eaten, divergent foraging methods and differences in microhabitat use were observed. The frequency of observation of interspecific flocking was greatest from early December until the second week in February, and declined as spring approached.

Mixed flocks of wintering birds have been noted by a number of observers (Short 1961, Morse 1970, Kear 1972). Two main explanations have been hypothesized: (1) flocking enhances feeding efficiency by minimizing duplication of effort in foraging (Cody 1971); (2) flocks aid in predator avoidance (Murton 1971, Lazarus 1972, Morse 1977). Powell (1974) demonstrated that individuals in flocks spend more time searching for food and less time in surveillance than lone individuals (see also Sabine 1949, Turner 1965). Flocking seems particularly advantageous in exploiting foods that are stationary, non-renewing, with patchy distribution, as were the apparent principal winter food resources available in the area studied.

DISCUSSION AND CONCLUSIONS

Basis of food preferences.—In temperate forests, many fruits become ripe in autumn, when arthropods are harder to find and bird populations are largest due to the influx of migrants. The conspicuous colors and high nutritional values of fruits have probably evolved to attract birds to disperse seeds (McAtee 1947, Snow 1971). In this study, birds preferred some fruits over others found in the same parts of the forest. Dry weights of 10 of the most common fruits in the forest were compared. Dogwood and grape, 2 of the most preferred fruits in early fall, also had the heaviest dry pulps.

Differences in the nutritional values of fruits may influence feeding preferences (Morton 1973, Pulliam 1975); they may also be outweighed by other factors. With the exception of spicebush, the most abundant fruits were also the most heavily used (see predictions made in Emlen 1966 and Pulliam 1974). Eugene S. Morton (pers. comm.) noted the relationship between bird species that occur in large, monospecific flocks (e.g., robins and grackles) and their use of abundant concentrated fruit, such as dogwood, and suggested that social behavior, rather than nutrition, may restrict these species to certain foods. Jerome Jackson (pers. comm.) noted that the relative accessibility of fruits may also be a factor (e.g., false Solomon's seal and mapleleaf viburnum, which have berries on stalks that will not support a bird, were rarely used). During the late fall and winter, when food was scarce, the most valuable foods were those retained longest by the plants.

I have shown that the available fruit crops are subject to uneven harvest. Preferred species, such as dogwood, grapes and poison ivy, are avidly consumed by a wide variety of migrant and resident birds. The crops of these fruits were virtually exhausted before the end of the migratory period. Other species, including the less accessible fruits noted above, are eaten infrequently, if at all. Other species, including bittersweet, greenbrier and honeysuckle are persistent and provide a major resource for wintering populations. The total amount of fruit remaining on 7 December was estimated to be 20% of the initial standing crop of all species noted on 25 September.

The diets of the resident species change through the season. As the preferred foods are exhausted or become depleted, new items are added to their diets, including fruits that had previously been ignored. Winter resident frugivores tend to be dietary generalists, although several species consume the available foods in different proportions.

SUMMARY

I estimated the standing fruit crop in a mixed deciduous forest in Princeton, New Jersey at the beginning of fall migration in September 1974 and at frequent intervals until mid-March 1975. I made weekly counts of birds and recorded feeding observations throughout the fall and winter to determine how the fruit crop was used by migratory and resident species. Abundant, concentrated fruits, such as dogwood berries and grapes, were consumed by many bird species and were heavily depleted by the end of the migratory period. Other fruits found in the same parts of the forest fell to the ground uneaten. I estimated that only 20% of the original fruit crop remained on 7 December.

As the preferred fruits were exhausted, the wintering birds added new items to their diets. These included the persistent fruits of several species which had previously been ignored. Mixed-species flocking was common among frugivorous birds during the winter months.

ACKNOWLEDGMENTS

I am grateful to John Terborgh for his guidance and assistance during the study. I thank E. S. Morton, J. A. Jackson and J. C. Barlow for their advice on earlier drafts of the manuscript.

LITERATURE CITED

CODY, M. L. 1971. Finch flocks in the Mohave Desert. Theor. Popul. Biol. 2:142–158.

EMLEN, J. M. 1966. The role of time and energy in food preference. Am. Nat. 100:611–617.

KEAR, J. 1972. Feeding habits of birds. Pp. 471–503 *in* The biology of nutrition (R.N. T-W Fiennes, ed.), Pergamon Press, New York, New York.

LAZARUS, J. 1972. Natural selection and the functions of flocking birds: a reply to Murton. Ibis 114:556–558.

MARTIN, A. C., H. S. ZIM AND A. L. NELSON. 1951. American wildlife and plants. McGraw-Hill, Inc., New York, New York.

McATEE, W. L. 1947. The distribution of seeds by birds. Am. Midl. Nat. 38:214–233.

MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monogr. 40:119–168.

———. 1977. Feeding behavior and predator avoidance in heterospecific groups. Bioscience 27:332–339.

MORTON, E. S. 1973. On the evolutionary advantages: disadvantages of the fruit eating in tropical birds. Am. Nat. 107:8–22.

MURTON, R. K. 1971. Why do some bird species forage in flocks? Ibis 113:534–536.

POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim. Behav. 22:501–505.

PULLIAM, H. R. 1974. On the theory of optimal diets. Am. Nat. 108:59–74.

———. 1975. Diet optimization with nutrient constraints. Am. Nat. 109:765–768.

——— AND F. ENDERS. 1971. The feeding ecology of five sympatric finch species. Ecology 52:557–566.

SABINE, W. S. 1949. Dominance in winter flocks of juncos and Tree Sparrows. Physiol. Zool. 22:64–85.

SHORT, L. L., JR. 1961. Interspecies flocking of birds of montane forest in Oaxaca, Mexico. Wilson Bull. 73:341–357.

SNOW, D. W. 1971. Evolutionary aspects of fruit eating by birds. Ibis 113:194–202.

TURNER, E. R. A. 1965. Social feeding in birds. Behavior 24:1–46.

DARROW SCHOOL, NEW LEBANON, NEW YORK 12125. ACCEPTED 14 AUG. 1978.

APPENDIX

	Flowering Dogwood			Grape			Poison Ivy			Asiatic Bittersweet		
		Date of obs.			Date			Date of obs.			Date of obs.	
Species	No. of obs.	1st	last	No. of obs.	1st	last	No. of obs.	1st	last	No. of obs.	1st	last
Rusty Blackbird										1	27/10	
Cardinal	2	22/10		10	25/9	11/12				13	22/10	2/2
Black-capped Chickadee							16	29/10	11/12			
Mourning Dove				1	25/9							
Purple Finch (*Carpodacus purpureus*)	2	26/10										
Yellow-shafted Flicker	1	26/10					1	29/10				
Common Grackle	90	25/9	17/10	72	25/9	19/10						
Dark-eyed Junco	51	22/10	6/11				10	19/11		28	22/10	21/12
Mockingbird (*Mimus polyglottos*)	1	17/10					1	10/10		4	12/12	2/2
American Robin	110	25/9	3/11	17	25/9	16/11				3	16/11	18/2
Starling (*Sturnus vulgaris*)										3	7/2	
White-throated Sparrow	13	17/10	6/11	4	22/10		1	17/10		32	14/10	7/2
Hermit Thrush	6	22/10	6/11							3	16/11	
Wood Thrush	1	5/10		1	7/10							
Tufted Titmouse	1	17/10		1	14/11		3	17/10	5/11	3	6/11	15/2
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	1	17/10										
Yellow-rumped Warbler							25	10/10	14/11			
Cedar Waxwing (*Bombycilla cedrorum*)										4	27/10	
Downy Woodpecker							8	6/11	4/1			
Hairy Woodpecker							3	29/10	11/12			
Red-bellied Woodpecker				2	16/11	7/2	2	15/11	19/12			
Red-eyed Vireo (*Vireo olivaceus*)												

APPENDIX
CONTINUED

Species	Spicebush			Greenbier			Japanese Honeysuckle		
	No. of obs.	Date of obs.		No. of obs.	Date of obs.		No. of obs.	Date of obs.	
		1st	last		1st	last		1st	last
Rusty Blackbird									
Cardinal	1	12/12		6	12/12	21/2	2	21/12	5/3
Black-capped Chickadee									
Mourning Dove	1	25/9							
Purple Finch (*Carpodacus purpureus*)									
Yellow-shafted Flicker									
Common Grackle									
Dark-eyed Junco							1	26/2	
Mockingbird (*Mimus polyglottos*)				1	12/12				
American Robin	21	25/9	12/12						
Starling (*Sturnus vulgaris*)									
White-throated Sparrow	20	12/12		27	22/11	21/2	24	22/11	21/2
Hermit Thrush	1	26/11							
Wood Thrush									
Tufted Titmouse									
Rufous-sided Towhee (*Pipilo erythrophthalmus*)									
Yellow-rumped Warbler									
Cedar Waxwing (*Bombycilla cedrorum*)									
Downy Woodpecker									
Hairy Woodpecker									
Red-bellied Woodpecker									
Red-eyed Vireo (*Vireo olivaceus*)	1	25/9							

Wilson Bull., 92(1), 1980, pp. 74–87

TERRITORIAL BEHAVIOR IN A PAIR OF WHITE-THROATED SPARROWS

Frederick E. Wasserman

The importance of territorial behavior lies in the survival and reproductive value gained by the animal using it. Not all territories bring the same benefits, but there is good evidence that the survival value is often in the form of the procurement of a food resource (e.g., Lack 1955, 1958, 1964; Stenger 1958; Stenger and Falls 1959; Schoener 1968; Brown 1969; Brown and Orians 1970; Orians 1971; Gill and Wolf 1975; Zach and Falls 1975; Gass et al. 1976; Morse 1976). This is particularly apparent in the case of individual birds holding winter territories far from the breeding grounds (Lederer 1977a, b; Salmonson and Balda 1977). For other birds territorial behavior may be directly related to the procurement of a mate and the protection of the pair from the influence of conspecifics (e.g., Tinbergen 1936; Odum 1941; Conder 1949; Hinde 1952, 1956; Marler 1956; French 1959; Samson 1976). In still other species territoriality may serve as a spacing mechanism, acting to reduce predation or lower mortality due to disease (Hinde 1956).

The possible functions of territoriality are diverse, and simple answers about territorial function are unlikely to be found (Hinde 1956, Schoener 1968, Brown and Orians 1970). Only through concentrated surveillance of individual animals is the ethologist able to unwind the paradigms of territoriality. In this paper I quantify changes in territorial behavior throughout the season in 1 pair of White-throated Sparrows (*Zonotrichia albicollis*). The direct response of the male to his mate's behavior lends support to hypotheses concerning the sexual functions of territoriality, although the possibility that territoriality also serves other functions should not be dismissed.

METHODS

White-throated Sparrows form monogramous pair bonds and activities of the pair occur within the home area during the breeding season (Lowther and Falls 1968, Type A territory as defined by Nice 1937). In Wilmot Co., New Hampshire, males arrive on the breeding grounds in mid-April and females arrive approximately 2 weeks after the males. Here, White-throated Sparrows have their densest breeding populations in semi-open fields where the main vegetation is a low spreading evergreen (*Juniperus communis*) about 1 m tall and often several meters in diameter.

I divided a square area into 400 10-by-10 m quadrats. Within this marked region I observed 1 pair of White-throated Sparrows. Two mated pairs occupied adjacent areas. I distinguished all individuals by color bands or distinctive markings.

The male's behavior was classified into 6 general categories.

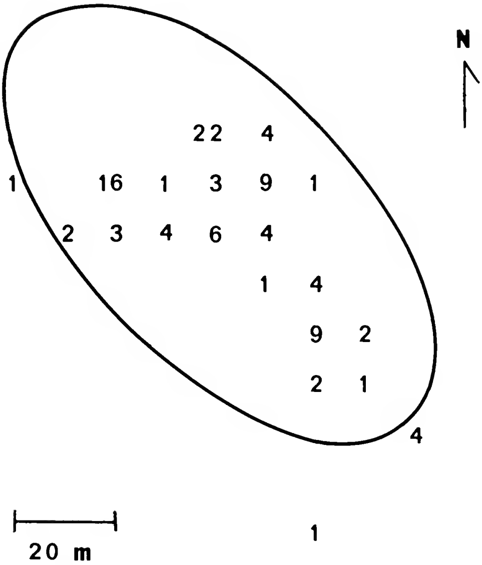


FIG. 1. Ninety-five percent confidence ellipse for the first 100-min sample of male singing during the premating stage. Numbers correspond to the number of minutes the male was observed singing in each quadrat. The area of the ellipse equals 4670 m^2.

(1) *Foraging.*—The male foraged primarily on the ground. In the early spring he fed on spore capsules of the hair cap moss (*Polytrichum* sp.) and later in the season he scratched at the ground and uncovered insects. Occasionally he jumped from the ground and captured flying insects.

(2) *Advertising song.*—The song consists of a series of tonal notes combined in a definite pattern. He sang full loud song from a number of high song perches, typically elevating his head with his beak vertically upward, perhaps allowing optimal spherical spread of the sound.

(3) *Alert defensive posture.*—He performed defensive posture from a perch, directing it toward conspecifics. His head and thorax feathers were fluffed, giving the illusion of increased size. Quite often, chasing or supplanting of the conspecific preceded or followed defensive posture and chipping vocalizations (described by Lowther and Falls 1968 as "pink," "chup-up" and trills) commonly accompanied the behavior.

(4) *Whisper song.*—The pattern of whisper song was identical to that of advertising song, but was of a lower amplitude and was given from the ground.

(5) *Chases.*—Birds flew after conspecific strangers or neighbors.

(6) *Resting.*—The male sat on the ground and showed no overt activity.

In this analysis, I will consider only foraging behavior of the female. She foraged almost exclusively on the ground. I calculated the rate of movement in m per min for both the male and female. This measurement for the male does not include minutes when he was singing, in defensive posture, or in chase.

Between 5 May and 4 August 1974, I observed the male for 197 h and the female for 64

h. Singing of advertising song was categorized into morning (07:00–12:00) and afternoon (12:00–18:00) activity. Behavioral changes accompanying different stages of the breeding cycle influenced the ease with which individuals could be located and followed. The male seemingly habituated to me and occasionally approached to within 1 m of me. The female remained more wary. During each min I recorded the predominant activity and the location of the bird I was observing. Whenever possible I recorded the female's location with respect to the male.

To estimate the area utilized by the birds I used the computer program of Koeppl et al. (1975). The program is advantageous because it: (1) gives a 95% confidence ellipse (Fig. 1); and (2) rotates the axes of the ellipse and gives a measure of area which is independent of the original grid and axes.

For utilized area (male singing, male foraging and female foraging areas) and for the various activities (singing, chases, defensive posture, etc.) successive 100-min observation periods comprised the within-nesting stage replication. To locate differences among stages I used 1-way analysis of variance (ANOVA). I used Dayton's (1970) 2-way ANOVA for unequal cell size on 3 sets of data. In these 3 analyses, nesting stage was 1 independent variable while the other independent variable was sex (male and female foraging area) or activity (male singing and foraging areas) or time (morning and afternoon singing). When an ANOVA indicated a significant difference ($P < 0.05$), I tested differences between subsequent stages using the Least Significance Difference (LSD, 2-tailed test; Snedecor and Cochran 1972). In the results section I use the terms increase or decrease to imply that there was a significant change ($P < 0.05$).

To return area measurements to a linear scale, I applied a square root transformation to the original values ($\sqrt{X} = X'$). To normalize the data when group variances were proportional to the means and some of the observations were 0 (defensive posture, whisper songs, chases and resting) I used a $\sqrt{X + 0.5}$ transformation (Zar 1974). I report back-transformed means ±SE (e.g., the mean plus SE equals $[X' + SE']^2$).

RESULTS

Comparison of the independent variables, nesting stage (Table 1) and activity (male foraging and male singing area), indicated that the area used by the male was different between stages (2-way ANOVA; $F = 2.83$; df = 9, 86; $P < 0.01$). The area in which the male sang (Fig. 2A) was smaller than the area in which he foraged (Fig. 2B; $F = 6.06$; df = 1, 86; $P < 0.001$). The interaction term was non-significant. Considering the means of each stage, male foraging area and male singing area were highly correlated ($r = 0.83$, df = 8, $P < 0.01$). From nest-building to incubation in the first nesting, male foraging area decreased.

Comparison of the independent variables, nesting stage (from mating of the first nesting until fledgling) and sex (male and female foraging area), indicated that the area used for male and female foraging was different between stages (2-way ANOVA; $F = 4.30$; df = 8, 92; $P < 0.001$). The male foraged (Fig. 2B) in a larger area than the female (Fig. 2C; $F = 4.78$; df = 1, 92; $P < 0.05$). The interaction term was non-significant. Considering the mean areas of each of the stages, male foraging area and female foraging area were highly correlated ($r = 0.87$, df = 7, $P < 0.01$). Female

TABLE 1
STAGES IN THE NESTING CYCLE

Stage	Description	Date	
		First nesting	Renesting
Premating (P)	Arrival of the male until the arrival of the female	5–14 May	
Mating (M)	Arrival of the female until nest-building	15–25 May	15–18 June
Nest-building (NB)	Beginning of nest-building until the beginning of incubation	26 May–1 June	19–21 June
Incubation (I)	Female incubating the eggs	2–10 June	22–30 June
Nestling (N)	Eggs have hatched and both parents feed the young	11–14 June	1–10 July
Fledgling (F)	Young leave the nest and the parents feed the fledglings	Predation[1]	11 July–4 August

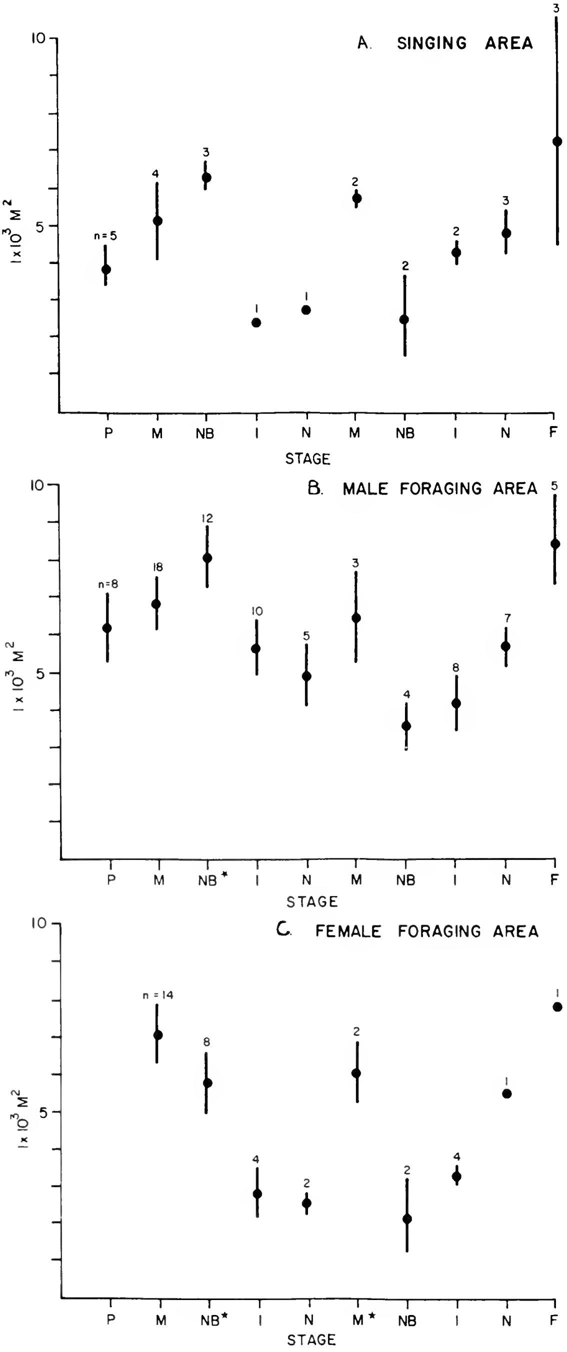
[1] On 14 June the nestlings were taken by a predator.

foraging area decreased when she began incubating eggs during the first nesting. After the predation on the first nest and the mating stage of renesting, female foraging area decreased.

Comparison of the independent variables, nesting stage (premating to incubation of renesting) and time (rate of morning and afternoon singing), indicated that the rate of advertising song was different between stages (2-way ANOVA; $F = 7.72$; $df = 7, 92$; $P < 0.001$). Rate of singing in the morning (Fig. 3A) was greater than the rate of singing in the afternoon (Fig. 3B; $F = 8.82$; $df = 1, 92$; $P < 0.01$). The interaction term was nonsignificant.

Once the female arrived, male singing in the morning decreased. During the mating stage of the renesting (following predation on the first nest), singing increased as the pair established a new area for renesting. In renesting, singing was lower in the afternoon once the female began incubation. Finally, as the young fledged, singing increased in the morning.

The rate of defensive posturing varied between stages (Fig. 4A; 1-way ANOVA; $F = 10.99$; $df = 9, 102$; $P < 0.001$). I first observed it during the mating phase when the female arrived on the breeding grounds. I did not include defensive posture directed toward the female in the calculation of the results so as not to confuse the establishment of the pair bond with a defensive behavior. After mating, defensive posture decreased and did not increase until after the predation on the first nest. Once again, after


A. SINGING AREA
B. MALE FORAGING AREA
C. FEMALE FORAGING AREA
1 x 10^3 M^2
10
5
n=5
4
3
1
1
2
2
2
3
3
n=8
18
12
10
5
3
4
8
7
5
n = 14
8
4
2
2
2
4
1
1
P
M
NB
NB*
I
N
M
M*
NB
I
N
F
STAGE

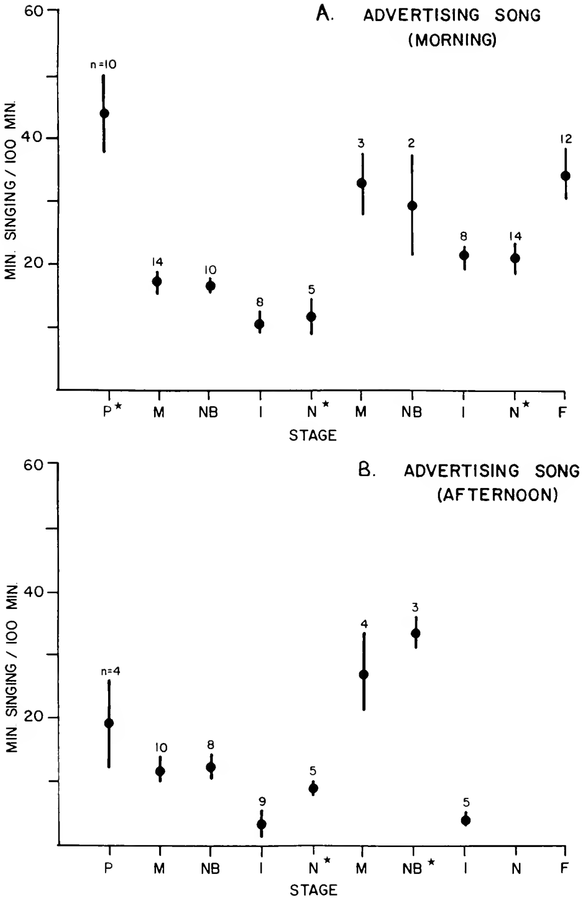


FIG. 3. Average number of min per 100-min of observation (±SE) that the male was involved in advertising song in (A) morning (07:00–12:00) and (B) afternoon (12:00–18:00) in each stage of the nesting cycle. If the male sang at least once during the 1-min interval he was considered singing for that min. N and stars defined as in Fig. 2.

the mating period ended there was a decrease in the number of minutes spent in defensive posture. After the young left the nest defensive posture decreased.

There was no difference between stages in the rate at which chases

---

←

FIG. 2. Average area of the 95% confidence ellipses (±SE) used to determine (A) male singing area, (B) male foraging area and (C) female foraging area for each stage of the nesting cycle. N equals the number of 100-min samples used to estimate area utilized in each stage. A star indicates stages in which mean foraging area was significantly different from the mean area of the stage immediately following.

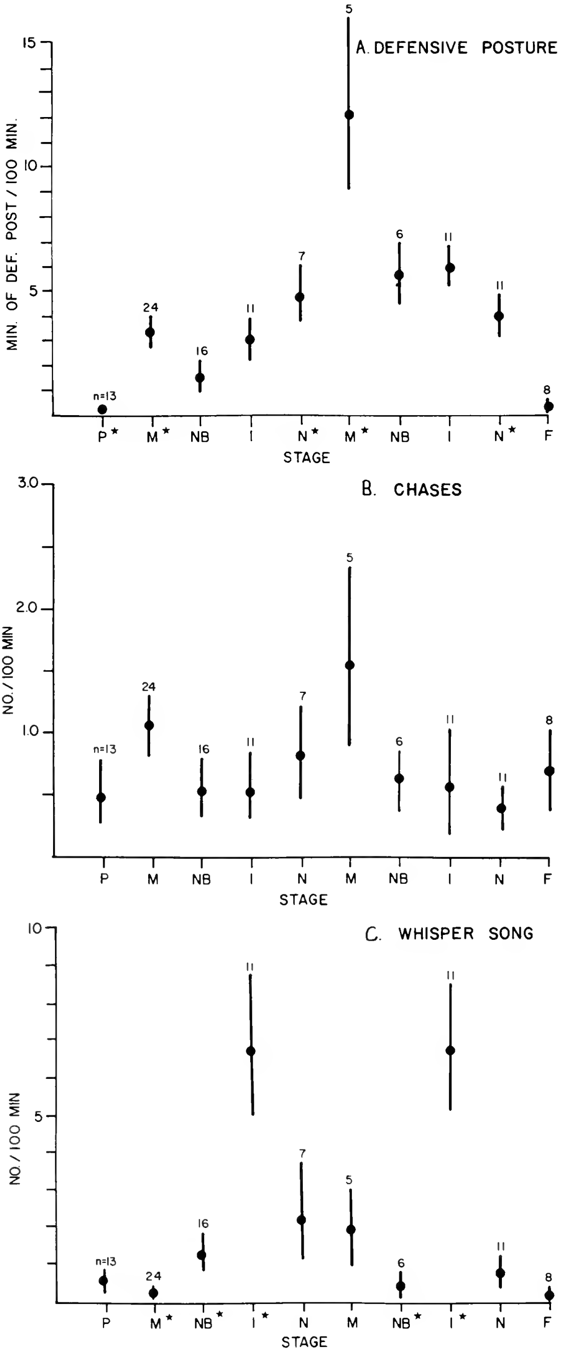

A. DEFENSIVE POSTURE
MIN. OF DEF. POST / 100 MIN.
15
10
5
n=13
24
16
11
7
5
6
11
11
8
P★ M★ NB I N★ M★ NB I N★ F
STAGE
B. CHASES
NO./100 MIN
3.0
2.0
1.0
n=13
24
16
11
7
5
6
11
11
8
P M NB I N M NB I N F
STAGE
C. WHISPER SONG
NO./100 MIN
10
5
n=13
24
16
11
7
5
6
11
11
8
P M★ NB★ I★ N M NB★ I★ N F
STAGE

TABLE 2

FREQUENCY OF WHISPER SONGS GIVEN WHILE THE MALE AND FEMALE WERE IN THE SAME QUADRAT

	No. of whisper songs given when the male and female were in the	
First nesting	Same quadrat	Different quadrats
Observed	20	124
Expected	34.15[1]	109.85
	$\chi^2 = 7.69$, df = 1, $P < 0.01$	
Renesting	Same quadrat	Different quadrats
Observed	12	120
Expected	26.53	105.46
	$\chi^2 = 9.96$, df = 1, $P < 0.01$	

[1] The % of time the male and female were in the same quadrat was calculated only for days in which the male sang whisper song; in the first nesting this was 23.7% (based on 3264 min of observation), and in renesting 20.1% (based on 1995 min).

occurred (Fig. 4B; 1-way ANOVA; F = 0.83; df = 9, 102; $P > 0.05$). The highest rates of chases per min occurred in the mating stages.

There was a difference in the number of whisper songs given per 100 min across stages (Fig. 4C; 1-way ANOVA; F = 11.83; df = 9, 102; $P < 0.001$). After the initial mating period and the establishment of the pair bond there was an increase during incubation. After incubation whisper singing decreased as the parents fed the young. During renesting the highest frequency of whisper singing occurred in the period of incubation. In the nestling period whisper singing decreased.

Whisper songs were given most frequently in the female's absence. This was true during the first nesting as well as during renesting (Table 2).

There was a difference between stages in the rate at which the male rested (1-way ANOVA; f = 3.36; df = 9, 102; $P < 0.01$). I observed the male resting in only 2 stages, incubation and the nestling stage of the first nesting attempt. There was an increase in the rate of resting during incubation and a decrease after the nestling stage. I never saw the female involved in resting behavior off the nest.

←

FIG. 4. Average number (±SE) of (A) min spent in defensive posture, (B) chases and (C) whisper songs per 100 min in each stage of the nesting cycle. N and stars defined as in Fig. 2.

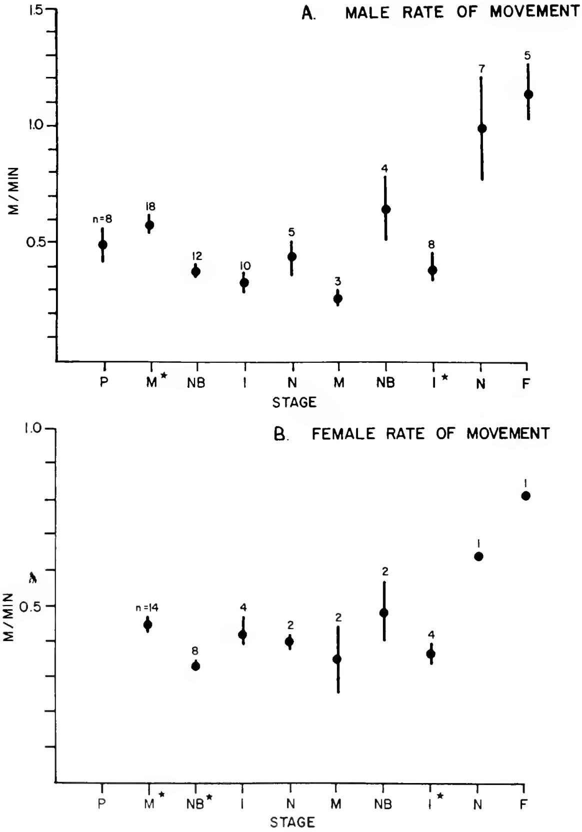


FIG. 5. Average rate of movement (±SE) for the (A) male and (B) female in each stage of the nesting cycle. Calculations of means for the male do not include minutes when he was recorded either singing in defensive posture or in chase. N and stars defined as in Fig. 2.

Rate of male movement (Fig. 5A) was different between stages (1-way ANOVA; F = 8.03; df = 9, 70; $P < 0.001$). It decreased after the mating stage of the first nesting and showed an increase in the nestling stage of the renesting. The female's rate of movement (Fig. 5B) was also different between stages (1-way ANOVA; F = 6.91; df = 8, 29; $P < 0.001$). She demonstrated the same pattern as the male with the additional effect of an increase in rate of movement during the incubation stage of the first nesting attempt. Mean rates of male and female movement in each stage were highly correlated ($r = 0.93$, df = 8, $P < 0.001$).

The likelihood of finding male and female in the same quadrat was different between stages (Fig. 6; 1-way ANOVA; F = 7.25; df = 8, 43; $P < 0.001$). The male spent more than 50% of his time in the same quadrat

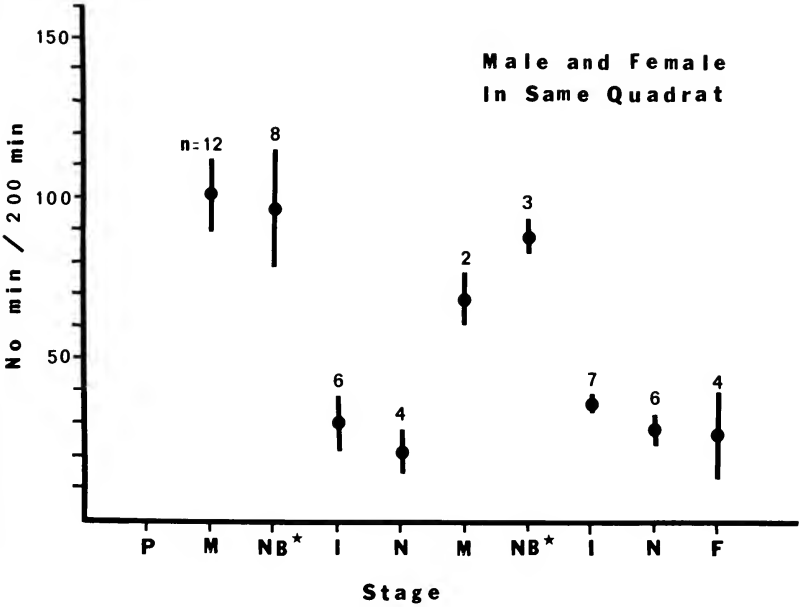


FIG. 6. Average number of min out of 200 (±SE) during which the male and female were in the same quadrat in each stage of the nesting cycle. Stars defined as in Fig. 2. N equals the number of 200-min samples used to determine means.

as the female when she arrived on the breeding grounds. When the female began incubation the amount of time the male and female were together decreased. Following predation of the first nest the male again began a close association with the female until incubation. During incubation male-female association decreased.

DISCUSSION

Upon viewing the overall performance of these 2 birds it is now appropriate to show how the behavior of each complements and interacts with that of the other. The male was continuously chased by conspecifics when he appeared on the breeding grounds. He did not abandon his territory, and after 1 day chases subsided. Singing of advertising song steadily increased, reaching a peak the day before the female appeared and subsequently decreasing (Fig. 3).The decline of singing after female arrival in many species, including the White-throated Sparrow (Wasserman 1977), has suggested to some (e.g. Catchpole 1973, Marshall 1964, Verner 1965) that mate attraction may be one function of song.

When the female arrived the male's activity changed considerably. He increased the size of his foraging and singing areas, began to show defensive behavior and increased his rate of movement. He spent more than 50% of his time in close association with the female. During encounters at territorial boundaries he prevented encroachment upon the female by placing himself between her and a neighboring male. As he accompanied the female into a neighbor's territory he was often chased by the neighbor. In short, the male was in an alert, aggressive state, making territorial alterations to accommodate the female. As Emlen (1957) pointed out, the use of the term "a defended area" is erroneous because there is "no evidence that the area is the object of the aggressive behaviour." Similarly, it should not be said that the male is defending the female; however, it is clear the major objectives of the male are to establish the pair bond and to reduce the chances of being cuckolded. He is accomplishing these objectives with the high energy demand that aggressive behavior requires. At the same time the female is being introduced to his territory. The nest was built on the ground under juniper shrubbery, within 10 m of the center of male activity, before female arrival. During incubation both the male and female decreased their foraging areas. The male sang less and his rate of defensive posturing and chasing remained low. The territorial system appeared to be more stable than before; this stability and the smaller foraging areas were most likely attributable to the female being close to the nest and incubating the eggs. However, it is possible that the smaller territory size during the incubation and nestling stages was due to the availability of a superabundant food supply at this time (Lack 1950; Perrins 1965, 1970).

There are 2 explanations for the preponderance of whisper songs during incubation: (1) pair bond maintenance, and (2) advertising to rival males. These explanations are not mutually exclusive. With the more stable territorial situation during incubation, a lower intensity territorial song is all that may be required to reassert a territorial holder's presence to his neighbors. The low degree of male-female association supports the pair bond maintenance function of whisper song (Table 2).

On 14 June a predator took the 4 nestlings. The female began building the second nest 15 cm off the ground in juniper shrubbery, 35 m west of the first nest. The new nest was situated between the activity centers of 2 adjacent pairs, in a region that had not been frequently used. The male immediately began establishing his exclusive copulatory rights over the female in the new area. Rates of defensive posturing, chasing per min and singing advertising song increased. It was evident that while the male and female re-established the pair bond, the male's territorial behavior changed considerably in response to the female's behavior.

While the female built her second nest the male remained close to her.

He usually sang or foraged within 15 m of the nest-site, and the foraging areas of both adults decreased. Male and female foraging areas increased during renesting and male rate of singing remained at a moderately high level. As the young dispersed during the fledgling stage territorial boundaries seemed to break down. Breakdown of territorial boundaries during the fledgling stage has been noted in a number of species (e.g., Hinde 1952, Stefanski 1967, Yarrow 1970).

Environmental changes, interactions between conspecifics, and/or seasonal gonadal cycles may lead to many territorial alterations. For this pair of White-throated Sparrows, however, my intensive observations reveal that there were proximate changes in male territorial behavior and in the sizes of activity spaces directly related to the behavior and movements of the female and to the stage of the breeding cycle.

SUMMARY

Through detailed observations I examined the territorial and mate guarding behavior in a mated pair of White-throated Sparrows. I recorded the birds' location and behavior each min for a total of 261 h (male for 197 h and female for 64 h). To obtain replicates within each of the stages of the nesting cycle I divided the data into samples of 100 min. Area was measured by using a bivariate home range model which generated a 95% confidence ellipse around each sample. I found that the female and the stage in the breeding cycle were responsible for the proximate changes in the areas used by the male for foraging and singing, as well as for changes in male territorial behavior (the singing of advertising and whisper song, defensive posture, and chases).

ACKNOWLEDGMENTS

I would like to extend grateful thanks to my advisor, W. M. Schleidt, for his continuous support and encouragement during the course of this research. For help of various kinds I would especially like to thank E. R. Buchler, J. B. Falls, D. E. Gill, J. W. Koeppl, L. Machlis, F. McKinney, D. H. Morse, E. S. Morton, H. W. Power and G. D. Schnell and special thanks are given to A. Sharenow for the use of his land and facilities. I appreciate the support of the University of Maryland Computer Center in providing computer time for data analysis. This research was in part supported by a grant from the Harris Foundation.

LITERATURE CITED

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293–329.

——— and G. H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239–262.

Catchpole, C. K. 1973. The functions of advertising song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*). Behaviour 56:300–320.

Conder, P. L. 1949. Individual distance. Ibis 91:649–655.

Dayton, C. M. 1970. The design of educational experiments. McGraw-Hill, New York, New York.

Emlen, J. T., Jr. 1957. Defended area?—A critique of the territory concept and of conventional thinking. Ibis 99:352.

French, N. R. 1959. Life history of the Black Rosy Finch. Auk 76:159–180.

Gass, C. L., G. Angehr and J. Centa. 1976. Regulation of food supply by feeding territoriality in the Rufous Hummingbird. Can. J. Zool. 54:2046–2054.

Gill, F. B. and L. L. Wolf. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. Ecology 56:333–345.

Hinde, R. A. 1952. The behavior of the Great Tit (*Parus major*) and some other related species. Behav. Suppl. 2:1–201.

———. 1956. The biological significance of the territories of birds. Ibis 98:340–369.

Koeppl, J. W., N. A. Slade and R. S. Hoffman. 1975. A bivariate home range model with possible application to ethological data analysis. J. Mamm. 56:81–90.

Lack, D. 1950. The breeding seasons of European birds. Ibis 92: 288–316.

———. 1955. British tits (*Parus* spp.) in nesting boxes. Ardea 43:50–84.

———. 1958. A quantitative breeding study of British tits. Ardea 46:92–124.

———. 1964. A long term study of the Great Tit (*Parus major*). J. Anim. Ecol. 33 (suppl.):159–173.

Lederer, R. J. 1977a. Winter territoriality and foraging behavior of the Townsend's Solitaire. Am. Midl. Nat. 97:101–109.

———. 1977b. Winter feeding territories in the Townsend's Solitaire. Bird-Banding 48:11–18.

Lowther, J. K. and J. B. Falls. 1968. *Zonotrichia albicollis* (Gmelin) White-throated Sparrow. Pp. 1364–1392, in Bent, U.S. Natl. Mus. Bull. 237.

Marler, P. 1956. Territory and individual distance in the Chaffinch *Fringilla coelebs*. Ibis 98:496–501.

Marshall, J. T., Jr. 1964. Voice in communication and relationships among Brown Towhees. Condor 66:345–356.

Morse, D. H. 1976. Variables affecting density and territory size of breeding spruce-wood warblers. Ecology 57:290–301.

Nice, M. M. 1937. Studies in the life history of the Song Sparrow. I. A population study of the Song Sparrow. Trans. Linn. Soc. N.Y. 4:1–247.

Odum, E. P. 1941. Annual cycle of the Black-capped Chickadee—1. Auk 58:314–333.

Orians, G. H. 1971. Ecological aspects of behavior. Pp. 513–546 *in* Avian Biology, Vol. 1. (D. S. Farner and J. R. King, eds.), Academic Press, New York, New York.

Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit (*Parus major*). J. Anim. Ecol. 34:601–647.

———. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

Salomonson, M. G. and R. P. Balda. 1977. Winter territoriality of Townsend's Solitaires (*Myadestes townsendi*) in a pinon-juniper-ponderosa pine ecotone. Condor 79:148–161.

Samson, F. B. 1976. Territory, breeding density, and fall departure in Cassin's Finch. Auk 93:477–497.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123–141.

Snedecor, G. W. and W. G. Cochran. 1972. Statistical methods. Iowa State Univ. Press, Ames, Iowa.

Stefanski, R. A. 1967. Utilization of the breeding territory in the Black-capped Chickadee. Condor 69:259–267.

Stenger, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk 75:335–346.

——— and J. B. Falls. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71:125–140.

Tinbergen, N. 1936. The function of sexual fighting in birds; and the problem of the origin of territory. Bird-Banding 7:1–8.

VERNER, J. 1965. Time budget of the male Long-billed Marsh Wren during the breeding season. Condor 67:125–139.

WASSERMAN, F. E. 1977. Mate attraction function of song in the White-throated Sparrow (*Zonotrichia albicollis*). Condor 79:125–127.

YARROW, R. M. 1970. Changes in Redstart breeding territory. Auk 87:359–361.

ZACH, R. AND J. B. FALLS. 1975. Response of the Ovenbird (Aves: Parulidae) to an outbreak of spruce budworm. Can. J. Zool. 53:1669–1672.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

DEPT. BIOLOGY, BOSTON UNIV., BOSTON, MASSACHUSETTS 02215. ACCEPTED 2 JAN. 1979.

NEW LIFE MEMBER

Jeffrey A. Spendelow, a graduate student in biology at Yale University, is a new Life Member of the Wilson Society. His doctoral research is on genetic variation in egg white proteins of Red-winged Blackbirds (*Agelaius phoenicius*), although he is interested in avian population biology and ecology as well. He is currently working on a colonial bird nesting project but hopes to work on herons in the future. Mr. Spendelow is an active bird bander and is a member of several professional societies. He is married with one child.

Wilson Bull., 92(1), 1980, pp. 88–95

FLOCKING AS A POSSIBLE PREDATOR DEFENSE IN DARK-EYED JUNCOS

PETER GOLDMAN

North temperate birds commonly flock in winter, and many investigators have offered evolutionary hypotheses to explain this behavior. Decreasing predation is central to some hypotheses.

Predators may make flocking advantageous for at least 5 reasons (Powell 1974); 2 may be generally important. Predators may stalk lone individuals more successfully than individuals in flocks because individuals in flocks can collectively assess their surroundings more reliably (Dimond and Lazarus 1974, Lack 1954, Lazarus 1972, Short 1961). Sharing of sentry duty means for the individual less time for vigilance and more time for such tasks as foraging.

Flocking may decrease the threat of predation for another reason. An individual may lower its probability of being captured simply by associating with other equally attractive prey (Hamilton 1971, Vine 1971). Predators most likely attack prey at the flock's edge, so that centrally located individuals should be relatively safe (Hamilton 1971).

According to these ideas both flock size and an individual's location in a flock should influence the individual's behavior. I predict flock size and location have 4 behavioral effects: (1) Birds in large flocks are less vigilant than birds in smaller flocks. (2) Birds in large flocks devote more time to activities other than vigilance. If food is scarce or energy demand high, birds in large flocks devote more time to foraging. (3) If food is scarce and energy demand high, birds in the center of large flocks devote more time to foraging than do peripheral birds. (4) In large flocks high status birds occupy central positions.

Little information exists to test these predictions. Murton, Isaacson and Westwood (1971) observed that Wood Pigeons (*Columba palumbus*) adhere to predictions 2 and 3; White-fronted Geese (*Anser albifrons*) meet prediction 1 (Dimond and Lazarus 1974); Starlings (*Sturnus vulgaris*) adhere to predictions 1 and 2 in an experimental situation (Powell 1974); sometimes Great-tailed Grackles (*Cassidix mexicanus*) meet prediction 1, but apparently not prediction 2 (Smith 1977); and Sanderlings (*Calidris alba*) meet prediction 2 (Silliman et al. 1977). I observed wild Dark-eyed Juncos (*Junco hyemalis*) to evaluate these predictions.

These common winter residents in the central United States form winter flocks stable in membership (Gottfried and Franks 1975, Sabine 1959), and social hierarchies exist in the flocks (Sabine 1959). Flock size varies, and flock size may influence junco survivorship (Fretwell 1969). Accipitrine (*Accipiter* spp.) hawks, small falcons (*Falco* spp.) and shrikes (*Lanius* spp.) hunt juncos (Bent 1968), and perhaps foxes (*Vulpes fulva*), weasels (*Mustela* spp.) and cats (*Felis* spp.) hunt juncos during the day.

Dark-eyed Juncos eat small seeds on, or near, the ground. They may experience energy stress due to low temperatures and snow cover (Ketterson and Nolan 1976), and some favored foods may be depleted during winter (Pulliam and Enders 1971). Hence a mechanism allowing a junco to spend more time foraging should be advantageous.

METHODS

I observed juncos in natural situations and at plots where I provided seeds. Observations were made in central Ohio from 1970 through 1973 and in Adair County, Missouri through 1977.

I quantified vigilance as follows. Juncos searched for seeds by hopping along the ground (95% of 689 observations) with bills pointed downward. Periodically a bird raised its bill to a horizontal position, and I assumed it could see an approaching predator more readily in this position. I also assumed the more alert a junco needed to be, the more frequently it elevated its head and changed orientation of its elevated head. I timed 10 sequential head elevations and reorientations and converted this to head moves/min as a vigilance index. Only birds feeding on small seeds were timed, since birds husking large seeds elevated their heads.

I determined pecking rates to estimate feeding rates. Juncos mandibulated after about 90% of their pecks, so pecking rates probably reflected feeding rates. Even if some pecks were exploratory, or not rewarded, pecking rate still should have reflected the time a junco had to devote to foraging. Sometimes I counted how many hops and short flights juncos made during observation periods to estimate how carefully birds searched small areas during foraging. Most observations were made within 2 h of sunrise and sunset, when juncos should have been highly motivated to feed.

I observed 1 bird for less than 90 sec when studying flocks. I adopted this convention so I would sample the behavior of many birds. At most, 1 individual in a flock contributed a few observations. I changed procedures when observing lone and pairs of juncos because I saw very few lone and pairs of birds (7 and 16, respectively). I repeatedly observed these birds and made more observations of some birds than others. This procedure could make differences between lone and pairs of birds and birds in larger groups hard to interpret. If 1 lone bird was particularly agitated and observed repeatedly, this could bias generalizations about lone birds. To evaluate this potential bias I compared all head movement rates for lone and pairs of birds with only the first head movement rate for each bird. For example, I determined 9 head movement rates for 1 lone bird. Its first rate was 36.1 head moves/min, and the 9 ranged from 34.5–57.6 head moves/min. For this analysis I isolated the first measurement for each bird observed alone, or in a pair,—in this case 36.1 head moves/min—and compared only these with all the measurements for these birds. I found no significant difference ($t = 1.46$, df = 66, $P > 0.10$) between all observations for these birds and just the first observation for each bird. This suggested that my first determination accurately represented a bird's behavior, and also, based on this analysis, I used not only my first observation of lone and pairs of birds, but also all subsequent observations.

I counted all individuals with which a junco foraged to determine flock size. Mostly these

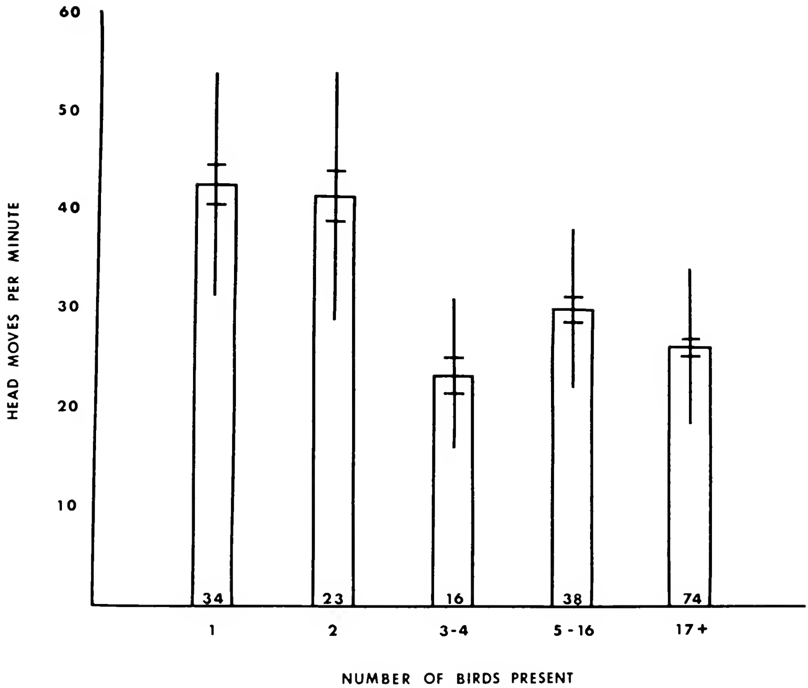


FIG. 1. The vigilance (measured by head movement rates) of Dark-eyed Juncos in different size groups. Bar height indicates mean head movement rate, the vertical line shows 1 standard deviation above and below the mean, and the horizontal line indicates 1 standard error above and below the mean. Number of observations are indicated at the bar base.

were other juncos, but sometimes juncos foraged with other emberizids, like Tree Sparrows (*Spizella arborea*) and Song Sparrows (*Melospiza melodia*).

I provided commerical bird seed on 1.8 m × 1.8 m plots at Sugar Creek State Forest, Adair Co., Missouri, from late December 1976 through mid-February 1977. Every 2 or 3 days I scattered 900 ml of seed evenly over each plot. These plots attracted many juncos because deep snow covered normal feeding sites.

I studied effects of location in a group on a junco's behavior at these plots. Usually 5–20 birds fed simultaneously, and a junco occupied either a central or peripheral position in a group. A bird within an imaginary triangle formed by 3 others was centrally located. I watched central and peripheral birds alternately so that I would have similar sized samples for each location. Central and peripheral birds harvested seeds of about the same density. When many juncos visited a plot, some peripheral birds appeared to be forced off the plot. These were not studied.

I also noted interactions between juncos on seed plots. I counted how many times birds I observed supplanted, or were supplanted, by others.

I analysed results with 1-way ANOVA and simultaneous test procedures, or t-tests, when variances for categories were similar (Sokal and Rohlf 1969). When variances differed substantially I used Mann-Whitney U-Tests (Siegel 1956); χ^2 analysis was also used (Siegel 1956).

RESULTS

Prediction 1.—Birds in large flocks are less vigilant than birds in smaller flocks.

To evaluate this I compared head movement rates of juncos in different size flocks in natural situations (Fig. 1). Lone and pairs of birds elevated and reoriented their heads significantly more frequently than birds in large flocks ($P < 0.001$, Mann-Whitney U-Test). No significant difference existed between lone and pairs of birds ($t = 0.90$, df = 55, $P > 0.40$), and in subsequent analyses I grouped observations of lone and paired birds. No trend existed between head movement rates and flock size for small, medium and large flocks, although head movement rates for most pairs of flock size categories differed significantly ($P < 0.05$, Mann-Whitney U-Test).

Prediction 2.—Birds in larger flocks devote more time to searching for food.

I compared pecking rates of lone and pairs of birds to those of birds in larger flocks to test this. Lone and pairs of birds averaged 34.4 ± 12.4 pecks/min (N = 42), while birds in flocks of 3 or more averaged 44.2 ± 15.5 pecks/min (N = 96). Lone and pairs of birds pecked significantly less frequently than birds in flocks ($t = 2.97$, df = 124, $P < 0.01$).

At least 3 possibilities other than flock size effects could explain behavior differences described so far. Lone and pairs of birds may have foraged in habitats with lower seed densities. I could not compare habitat use by lone and pairs of birds with birds in flocks directly because I observed so few lone and pairs of birds. However, head movement rates of lone birds foraging on lawns (head moves/min, $\bar{x} = 45.1 \pm 8.9$, N = 24) did not differ significantly ($t = 0.87$, df = 32, $P > 0.30$) from their rates in old fields ($\bar{x} = 42.2 \pm 9.2$, N = 10), suggesting habitat did not influence this behavior much.

Possibly juncos foraged alone, or in pairs, late in winter, after birds reduced seed densities. Most lone birds were seen in January. However, advancing season did not influence head movement rates of birds in large flocks. Prior to January, birds in flocks of more than 16 averaged 26.1 ± 7.3 head moves/min (N = 47), not significantly different ($t = 0.30$, df = 72, $P > 0.60$) from the average rate for January, or later (26.7 ± 9.4, N = 27).

Habitat and season also seemed not responsible for differences because they existed within 1 habitat during 1 month. In November, on lawns, birds in flocks averaged 42.2 ± 14.2 pecks/min (N = 55), while lone and pairs of birds averaged 31.0 ± 9.8 pecks/min (N = 14). These rates differed significantly ($P < 0.01$, Mann-Whitney U-Test).

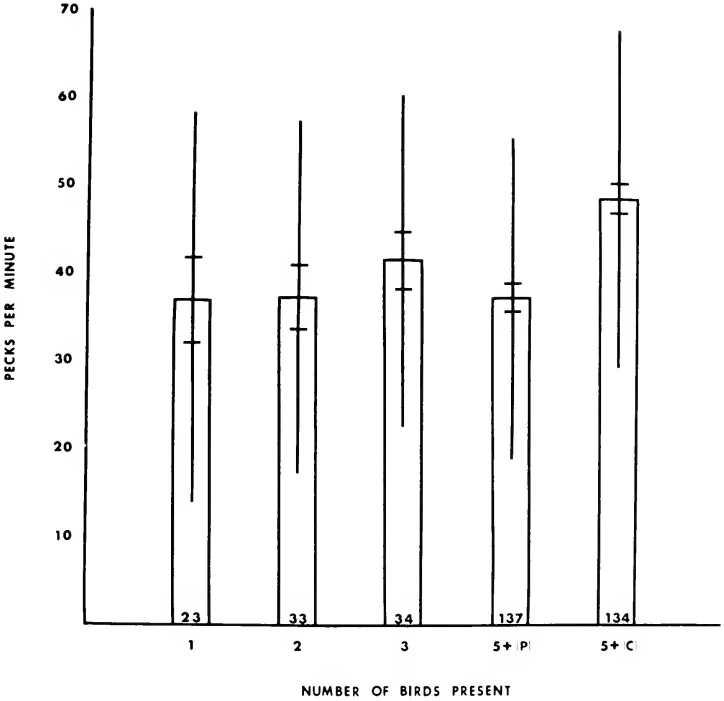


FIG. 2. Feeding rates of Dark-eyed Juncos in different size groups and in different locations in groups at seed plots. (P) designates birds on the periphery of groups; (C) designates birds in central locations. Symbols are the same as in Fig. 1.

Possibly birds in flocks could not forage as slowly because more intense competition among flock birds required rapid movement. However, lone and pairs of birds and those in flocks seemed to progress at about the same rate. Lone and pairs of birds hopped, or flew short distances, an average of 22.6 ± 16.4 times/min (N = 10), not significantly different (Mann-Whitney *U*-Test) from the rate of flock birds ($\bar{x} = 16.6 \pm 19.6$ moves/min, N = 50).

Prediction 3.—Birds in the center of large flocks devote more time to searching for food than peripheral birds do.

I evaluated this by comparing pecking rates of central birds on seed plots to pecking rates of peripheral birds and birds in small groups (Fig. 2). Pecking rates differed significantly ($P < 0.001$, ANOVA) between juncos categorized this way, with central birds in larger groups pecking more frequently than birds in other categories. Peripheral birds in large groups pecked no more frequently than birds in smaller groups. Peripheral birds appeared to spend much time watching birds around them.

Prediction 4.—In large flocks high status birds occupy central positions. To evaluate this I noted how frequently central and peripheral birds on seed plots supplanted others, or were supplanted by others. In 37 interactions involving a peripheral bird, the bird was supplanted 24 times. By contrast, in 48 interactions involving a central bird, the bird was supplanted only 23 times. This difference in outcomes of interactions involving central and peripheral birds was not significant ($\chi^2 = 2.50$, df = 1, $P \geqslant 0.10$), but the difference suggests that central birds probably exceed peripheral birds in status.

DISCUSSION

In natural situations juncos in large flocks fed more rapidly and appeared to spend less time assessing their surroundings than lone and pairs of juncos. These behavioral differences seemed related to flock size and not to ecological factors. These differences are expected if birds in flocks share the task of vigilance. Juncos on the periphery of large groups fed less rapidly than birds in the center, and this could not have reflected differences in food densities available. Slower feeding is expected if marginal predation is more intense than central predation. Birds in central locations tended to displace other juncos more frequently than did peripheral birds, suggesting that high status individuals may occupy central positions.

Advantages to flocking suggest junco flocks should be large. Large flocks allow members to devote much time to foraging. Also, if birds in flocks space themselves evenly, a smaller fraction of birds would have to forage on the periphery in a large than in a small flock. The fraction of birds that occupy peripheral positions will depend on the circumference-area ratio for the flock. As flock size grows, this ratio decreases, and so relatively fewer birds have to forage on the flock's periphery. Tenaza (1971) illustrates this geometric idea for colonial nesting birds.

Despite hypothetical advantages to large flocks, junco flocks I studied averaged 9.6 ± 12.2 birds (N = 46). This implies countervailing disadvantages to large flocks, or advantages that accrue to smaller flocks. Pulliam (1973) points out that the chance of spotting a predator rapidly reaches a high value with increasing flock size, so birds are not much safer in large than in medium-size flocks. The probability that Red-billed Quelea (*Quelea quelea*) detect a novel stimulus varies in the manner suggested by Pulliam (Dimond and Lazarus 1974).

The rate of change in a flock's circumference-area ratio is initially large as flock size increases, but this rate quickly becomes very small. A bird, then, has a good chance of occupying a central position in a medium-size flock; greatly increasing flock size does not lower this chance much.

It is easy to imagine disadvantages associated with large flocks. Excessively large flocks could deplete local resources and force frequent movement to new areas (Goss-Custard 1970, Morse 1970), and make establishment of stable social relations difficult (Wilson 1975:283). Whether or not flock size increases may depend upon a balance between such costs and benefits.

SUMMARY

Four predictions about how flock size and a bird's location in a flock influence behavior were evaluated by observing wild Dard-eyed Juncos. In natural situations, birds in flocks were less vigilant and fed more rapidly than lone and pairs of birds. In areas where I provided evenly distributed food, birds in central locations in flocks fed more rapidly than birds in peripheral locations. Observations weakly suggested that central birds were higher in status than peripheral birds.

These results suggest flocks should be large, although junco flocks averaged fewer than 10 birds. Small flock size may reflect non-linear increase of advantages with increasing flock size and disadvantages associated with large flocks.

ACKNOWLEDGMENTS

I thank Donald Kangas and Daniel Shreeve for helpful criticism of this study.

LITERATURE CITED

Bent, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237.

Dimond, S. and J. Lazarus. 1974. The problem of vigilance in animal life. Brain, Behav. Evol. 9:60–79.

Fretwell, S. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). Bird-Banding 40:1–25.

Goss-Custard, J. D. 1970. Feeding dispersion in some overwintering wading birds. Pp. 3–35 *in* Social behaviour in birds and mammals (J. H. Crook, ed.), Academic Press, London, England.

Gottfried, B. M. and E. C. Franks. 1975. Habitat use and flock activity of Dark-eyed juncos in winter. Wilson Bull. 87:374–383.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31:295–311.

Ketterson, E. D. and V. Nolan, Jr. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis*). Ecology 57:679–693.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, England.

Lazarus, J. 1972. Natural selection and the functions of flocking in birds: a reply to Murton. Ibis 114:556–558.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monogr. 40:119–167.

MURTON, R. K., A. J. ISAACSON AND N. J. WESTWOOD. 1971. The significance of gregarious feeding behaviour and adrenal stress in a population of Wood-pigeons *Columba palumbus*. J. Zool. 165:53–84.

POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking by Starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim. Behav. 27:501–505.

PULLIAM, H. R. 1973. On the advantages of flocking. J. Theor. Biol. 38:419–422.

——— AND F. ENDERS. 1971. The feeding ecology of five sympatric finch species. Ecology 52:557–566.

SABINE, W. S. 1959. The winter society of the Oregon Junco; intolerance, dominance, and the pecking order. Condor 61:110–135.

SHORT, L. L., JR. 1961. Interspecies flocking of birds in montane forest in Oaxaca, Mexico. Wilson Bull. 73:341–347.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York.

SILLIMAN, J., G. S. MILLS AND S. ALDEN. 1977. Effects of flock size on foraging activity in wintering Sanderlings. Wilson Bull. 89: 434–438.

SMITH, J. N. M. 1977. Feeding rates, search paths, and surveillance for predators in Great-tailed Grackle flocks. Can. J. Zool. 55:891–898.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.

TENAZA, R. 1971. Behavior and nesting success relative to nest location in Adelie Penguins (*Pygoscelis adeliae*). Condor 73:81–92.

VINE, I. 1971. Risk of visual detection and pursuit by a predator and the selective value of flocking behaviour. J. Theor. Biol. 30:405–422.

WILSON, E. O. 1975. Sociobiology. Harvard U. Press, Cambridge, Massachusetts.

BIOLOGY DEPT., NORTHEAST MISSOURI STATE UNIV., KIRKSVILLE, MISSOURI 63501. ACCEPTED 25 MAR. 1979.

Wilson Bull., 92(1), 1980, pp. 96–102

SPATIAL AND TEMPORAL DISTRIBUTION OF RAILS IN COLORADO

Herman J. Griese, Ronald A. Ryder and Clait E. Braun

Despite the nearly world wide occurrence of the Rallidae, many species are poorly known and most published data are based on local studies. Regional and statewide studies have been limited; consequently, uniform data concerning the biology of rails over large areas are lacking. Previous published reports of rails in Colorado refer to occurrence (Bailey and Niedrach 1965, Lane and Holt 1975) and censuses in limited areas (Boeker 1954, Glahn 1974).

In early 1975 we began to investigate occurrence, densities and migration of rails in relation to habitats in Colorado. Marshes, apparently suitable for rails, are restricted in size and distribution and occur between 1100 and 3200 m. Colorado marshes resemble those typical of the Great Plains and Intermountain West.

STUDY AREAS AND METHODS

Study areas were selected to represent wetlands in 4 regions of Colorado. Regions, locations of study areas and their elevations were: (1) North Central—Lower Latham Reservoir, Weld Co. (1422 m); (2) Southeastern—Fort Lyons, Bent Co. (1171 m); (3) South Central—Monte Vista National Wildlife Refuge, Rio Grande Co. (2326 m); and (4) Northwestern—Hayden, Routt Co., and Axial, Moffat Co. (1910 m). Water depths averaged 5–6 cm at study areas, except in the northwestern region (20 cm). Spring water level fluctuations were 63, 17, 15 and 130 cm, respectively. Water was uniformly basic (pH = 7.9–9.7) at all study areas.

Vegetation was described based on contribution to cover important to rails. *Typha* spp., *Scirpus acutus*, *Scirpus validus* and *Salix* spp. formed tall robust growth and dominated (74–95%) all but the south central study area (40%). Short fine types, *Eleocharis* spp., Poaceae, *Carex* spp., *Scirpus paludosus* and *Triglochin maritima*, comprised the remaining cover. In mixed stands, the most important contributor of cover was considered dominant.

Study areas were censused by playback of tape-recorded calls of rails at sunrise or sunset, April through October 1975 and 1976 (Tomlinson and Todd 1973, Baird 1974, Glahn 1974, Mangold 1974, Tacha 1975, Holliman 1976). Advertising calls of Virginia Rails (*Rallus limicola*) and Soras (*Porzana carolina*) taped from Peterson's record of western bird songs, were played on a portable Norelco cassette recorder (96 db at 1 m). Listening sites per region numbered 25–32, with 80–130 m between sites. A standardized sequence of alternating calls of both species was used, incorporating 1 min listening periods between each call. Calls of Black (*Laterallus jamaicensis*), Yellow (*Corturnicops noveboracensis*) and King (*Rallus elegans*) rails were occasionally played.

Breeding territory densities were estimated from spot-mapped responses (Glahn 1974) and mean number of responding rails in May and June. Results of the 2 methods were compared by regression analysis and were found to be significantly related ($\hat{Y} = 0.20 + 0.89x$, $r = 0.97$, $P < 0.05$). Compared separately, numbers of responding Soras were more poorly correlated ($\hat{Y} = -0.36 + 1.12x$, $r = 0.93$, $P < 0.10$) with results of spot-mapping than were numbers of responding Virginia Rails ($\hat{Y} = 0.16 + 0.95x$, $r = 0.97$, $P < 0.05$). Results of the averaged censuses for May and June were considered acceptable indices of breeding densities and were used during analysis.

RESULTS AND DISCUSSION

Status.—Virginia Rails and Soras are widely distributed in Colorado from late April through early October in suitable habitats. Occurrence paralleled major drainage systems (i.e., Colorado, South Platte, Arkansas and Rio Grande rivers), water storage impoundments and associated irrigation districts at lower elevations. Rails used wet meadows and irrigated hayfields in lieu of marshes, generally above 2600 m. Elevational extremes of documented breeding were 1120–3140 m and 1120–2730 m, respectively, for Soras and Virginia Rails. Bailey and Niedrach (1965) previously documented Soras breeding to 3231 m and Virginia Rails to 2323 m in Colorado. Binford (1973) recorded Virginia Rails breeding at 2090 m in Mexico. A paucity of suitable habitat above 3200 m in Colorado probably precludes higher elevational records. Of 252 townships (<10% of Colorado) surveyed with seemingly suitable habitats for rails, Soras were detected in 125 (49.6%), Virginia Rails in 100 (39.7%), with at least 1 species being documented in 153 (60.7%). Other apparently unoccupied marshes in the remaining 99 townships may be used periodically. While accurate surveys of the extent of wetlands in Colorado are not available, it is conservatively estimated that over 50% of the townships in Colorado with large (>1 ha) wetlands below 3600 m were examined.

Although positive breeding records are not available for King or Black rails in Colorado, both were noted during this investigation. Single King Rails were recorded at Bonny Reservoir, Yuma Co., on 25 May 1975 (this study), and near Pueblo, Pueblo Co., on 12 June through 3 July 1976 (Griffiths 1976). We found a Black Rail at Ft. Lyons on 11, 18 and 25 June 1975. Black Rails were also reported by birders twice in 1976 in northeastern and north central Colorado. Breeding activities (courtship vocalizations) were exhibited by Black and King rails at Ft. Lyons and Pueblo, respectively. King and Black rails breed at Cheyenne Bottoms, Barton Co., Kansas, 122 km east of Colorado (Parmelee et al. 1970, Baird 1974, Tacha 1975). A Yellow Rail has been recorded in Colorado (Bailey and Niedrach 1965), but breeding is unlikely.

Wintering (30 November–31 March) rails were concentrated primarily in the Arkansas and South Platte drainages below 2100 m, in association with warm water sloughs. We estimated the total rail population for winter 1975–76 to not exceed 200 individuals, of which 80–90% were Virginia Rails.

TABLE 1

INDICES OF BREEDING DENSITIES OF RAILS IN 4 REGIONS OF COLORADO, 1975 AND 1976

		Density (responding rails/ha)[1]					
		1975			1976		
Region	Study area size (ha)	Sora	Virginia Rail	N	Sora	Virginia Rail	N
Southeastern	14.5	0.5 ± 0.6	4.2 ± 1.1	7	0.4 ± 0.3	4.7 ± 0.7	4
North central	13.1	1.1 ± 0.8	3.5 ± 0.8	5	0.9 ± 0.6	3.8 ± 1.0	3
South central	14.3	2.2 ± 0.2	1.9 ± 0.6	3	2.5 ± 1.2	1.6 ± 0.2	3
Northwestern[2]	6.1	1.6 ± 0.7	0.2 ± 0.3	3	0.8 ± 0.5	1.0 ± 0.1	3

[1] Mean of N censuses ± 1 SD.

[2] Additional 4.8 ha marsh averaged into 1976 results.

Breeding densities.—Assuming population normality, Virginia Rails had a higher (parametric t-test, $P < 0.10$) breeding density index (2.6 ± 1.7 SD) than that of Soras (1.3 ± 0.8) (Table 1). Indices for Virginia Rails were higher (parametric t-test, $P < 0.01$) in eastern than in western Colorado. Soras exhibited no difference (parametric t-test, $P > 0.10$) between eastern and western Colorado. Virginia Rails appeared to occur more frequently and at higher elevations in 1976; however, neither species had significant changes in indices between years.

Results of this study are within extremes in average breeding densities reported in other studies. Virginia Rails ranged from 0.9 in Iowa (Tanner and Hendrickson 1954) to 4.3 pairs per ha in Kansas (Tacha 1975). Soras exhibited lowest densities in Kansas with 0.3 pairs per ha (Tacha 1975) and highest densities in Minnesota with 4.1 pairs per ha (Pospichal and Marshall 1954). Glahn (1974) ascertained breeding densities for Virginia Rails and Soras in north central Colorado to be 1.8 and 0.6 pairs per ha, respectively. While we used census methods similar to those of Glahn (1974), we cannot explain the higher densities found in north central Colorado in 1975–1976 (Table 1). Unfortunately, statistical comparisons with other studies are not possible because of differences in census techniques. Obviously, census techniques for rails should and can be standardized.

In this study, species composition of breeding rails appeared related to ambient air temperatures during early migration (Fig. 1). This significant ($\hat{Y} = 7.25e^{-1.96x}$, $r = -0.94$, $P < 0.01$) relationship indicates that Soras occurred most frequently in marshes in regions with mean April air temperatures less than 5.6°C, while Virginia Rails predominated in marshes with air temperatures greater than 5.6°C.

Additional factors such as topography, marsh conditions, such as

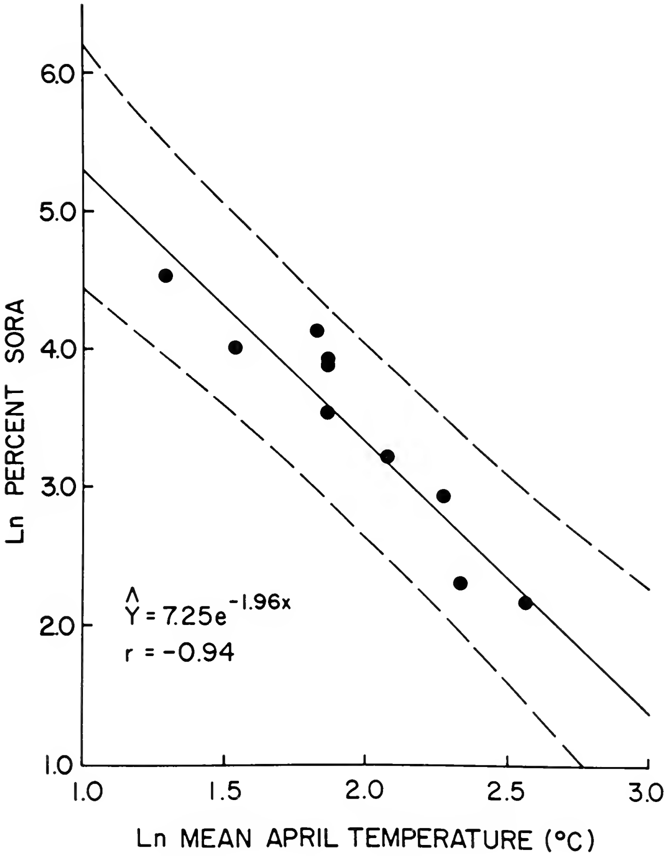


FIG. 1. Relationship between mean April air temperature (°C) near study areas and percent composition of the breeding population, 95% confidence intervals for future Y at given X ($\hat{Y} = 7.25e^{-1.96x}$, $r = -0.94$, $P < 0.01$).

burned or unburned, differential migration dates, or inter-specific competition may further affect composition.

Rapid water level fluctuations disrupted breeding activities. Desertion of 13 of 15 established territories and 1 Sora nest with 7 eggs was observed when water levels rose (rate unknown) more than 20 cm in northwestern Colorado. Decreasing water levels in south central Colorado prevented renesting and apparently caused chick mortality in an extreme case.

Habitat use.—Chi-square analyses of data from 174 marshes revealed no significant ($\chi^2 \geqslant 6.01$, df = 2, $P > 0.05$) relationship between distribution of rails and cattails within and among regions and elevations. While

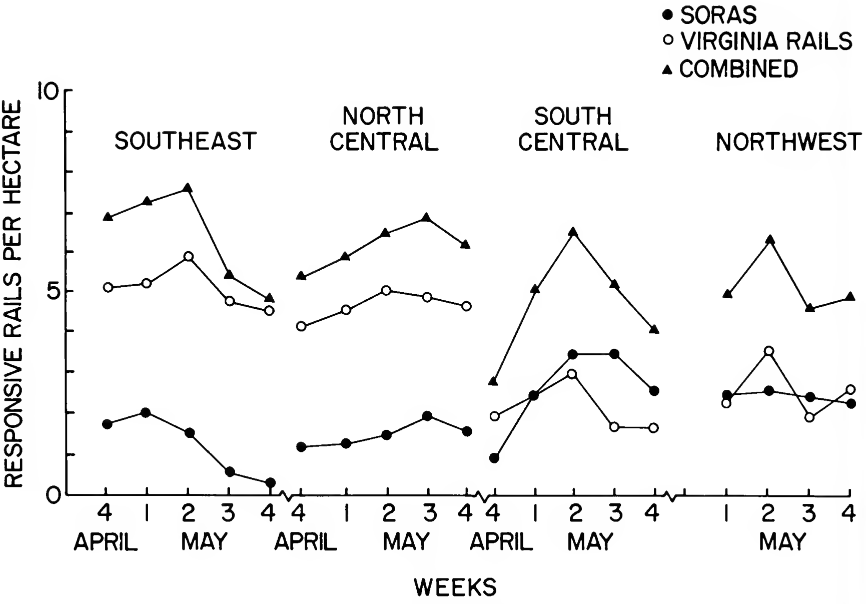


FIG. 2. Densities of rails responding to tape-recorded calls at regional study areas during spring censuses, 1975–1976. (Data from both years were averaged.)

distribution of *Typha*-dominated marshes did not control distribution of rails, both Virginia Rails and Soras appeared to prefer *Typha*-dominated marshes with shallow water (<15 cm in depth) for breeding. Breeding densities were highest in these sites and 20 of 25 nests located were in *Typha*. Water depths at nests of both species averaged 8.2 cm. *Typha* was the cover preferred by chicks of both species prior to fledging. The importance of *Typha* appeared related to its value as cover. Whenever a choice was present within a marsh, rails selected *Typha* for nesting and escape. During fall migration Soras used short emergents such as *Eleocharis*, *Carex* and some species of *Scirpus*, while Virginia Rails generally remained in tall dense vegetation such as *Typha*. These differences are probably related to differences in food habits between the species.

Migration.—Responses to taped calls were used in establishing dates of peak migration or maximum rail concentrations. Migration into Colorado for both species began during the first or second week of April, however, Virginia Rails appeared to be more abundant during early stages of migration. Peak concentrations for Virginia Rails were consistently recorded during the second week of May (Fig. 2). While peak concentrations of

Soras were erratic, they too peaked on, or near, the second week of May. In other studies (Pospichal and Marshall 1954, Tanner and Hendrickson 1954, Baird 1974, Glahn 1974), a 1–3 week period of no vocalization occurred after the arrival of rails. Although a silent period was not obvious during this study, such a period possibly obscured earlier peak concentrations in late April to early May. In either case, spring migration did not appear to differ greatly between plains and intermountain valleys.

Highest rail concentrations (>50 rails/ha) occurred locally in July in Colorado. At the south central study area decreasing water levels reduced the quantity of suitable habitat by 95% in July and early August. As a result, rails became concentrated and were easily observed and trapped. On successive visits noticeable reductions in numbers were apparent. Tracks along adjacent ditches indicated an ambulatory dispersal by flightless individuals. Bent (1926) mentioned a late summer movement of rails to more open marshes and implied that high concentrations resulted from the abundance of food. In Colorado, irrigation practices promoted midsummer drying of wetlands and caused premature concentrations and dispersal.

As responses were difficult to evoke in August and September and due to the masking effect of late summer movement, fall migration was not distinct. Soras appeared to have a more lengthy migration than Virginia Rails, beginning earlier and ending later. Time of peak concentrations of both species ranged from the second week in August in northwestern Colorado to the third week in September in south central Colorado. Responses per ha reached a maximum fall value of 7.1 (3.7 Virginia Rails, 3.4 Soras) on 20 September 1975, in southeastern Colorado.

SUMMARY

Distribution, breeding densities, habitats and timing of migration of rails were investigated in Colorado between May 1975 and October 1976. Major study areas in the Arkansas, South Platte, Rio Grande and Yampa river drainages were censused by playback of taped rail calls.

Soras bred from 1120–3140 m elevation and Virginia Rails from 1120–2730 m. No other rails bred in Colorado. Statewide, Virginia Rails exhibited higher breeding density indices (2.6 responding rails/ha) than Soras (1.3). Indices for Virginia Rails ranged from 4.7 in southeastern Colorado to 0.2 in northwestern Colorado. Indices for Soras ranged from 2.5 in south central to 0.4 in southeastern Colorado. Mean April air temperatures, a function of topography, influenced species composition. Soras were more abundant than Virginia Rails when mean April air temperatures were 5.6°C, or below.

Both species preferred marshes dominated by *Typha* with water depths less than 15 cm. Short emergents attracted Soras during fall migration. Peak concentrations of migrating rails occurred during May and from mid-August through September. Greatest concentrations (>50 rails/ha) occurred locally in late July as the result of irrigation practices. Virginia Rails and Soras wintered in Colorado in small numbers.

ACKNOWLEDGMENTS

This project was funded by the Accelerated Research Program for Migratory Shore and Upland Game Birds, U.S. Fish and Wildlife Service, Contract No. 14-16-0008-2000 administered through Colorado Division of Wildlife Federal Aid in Wildlife Restoration Project W-88-R. Technical assistance was received from G. A. Swanson and R. G. Walter, Colorado State University; C. Bryant, Monte Vista National Wildlife Refuge; and numerous landowners in Colorado. We thank D. Coven, D. Kenvin, D. Miller and J. Wagner, Colorado Division of Wildlife, and numerous work-study students at Colorado State University for field assistance. H. Funk provided administrative support and critically reviewed the manuscript. His assistance is appreciated.

LITERATURE CITED

BAILEY, A. M. AND R. J. NIEDRACH. 1965. Birds of Colorado. Vol. 1. Denver Mus. Nat. Hist., Denver, Colorado.

BAIRD, K. E. 1974. A field study of the King, Sora, and Virginia rails at Cheyenne Bottoms in west central Kansas. M.S. thesis, Fort Hays Kansas State Coll., Hays, Kansas.

BENT, A. C. 1926. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. 135.

BINFORD, L. C. 1973. Virginia Rail and Cape May Warbler in Chiapas, Mexico. Condor 75:350–351.

BOEKER, H. M. 1954. A census of populations of the Wilson's Snipe and Sora Rail in the Yampa River Valley, Colorado. Condor 56:105–106.

GLAHN, J. F. 1974. Study of breeding rails with recorded calls in north central Colorado. Wilson Bull. 86:206–214.

GRIFFITHS, D. 1976. King Rail—first Colorado record. Colo. Field Ornithol. J. 28:17.

HOLLIMAN, D. C. 1976. Clapper Rail (*Rallus longirostrus*) studies in Alabama. U.S. Fish and Wildl. Serv. Accel. Res. Prog. Project Final Rep. Contract No. 14-16-0008-793.

LANE, J. A. AND H. R. HOLT. 1975. A birder's guide to eastern Colorado. L. and P. Press, Denver, Colorado.

MANGOLD, R. E. 1974. 1974 Final report: research on shore and upland migratory birds in New Jersey. Clapper Rail studies. U.S. Fish and Wildl. Serv. Accel. Res. Prog. Contract No. 14-16-0008-937.

PARMELEE, D. F., M. D. SCHWILLING AND H. A. STEPHENS. 1970. Gruiform birds of Cheyenne Bottoms. Kans. Ornithol. Soc. Bull. 21:25–27.

POSPICHAL, L. B. AND W. H. MARSHALL. 1954. A field study of the Sora Rail and Virginia Rail in central Minnesota. Flicker 26:2–32.

TACHA, R. W. 1975. A survey of rail populations in Kansas, with emphasis on Cheyenne Bottoms. M.S. thesis, Fort Hays Kansas State Coll., Hays, Kansas.

TANNER, W. D. AND G. O. HENDRICKSON. 1954. Ecology of the Virginia Rail in Clay County, Iowa. Iowa Bird Life 24:65–70.

TOMLINSON, R. E. AND R. L. TODD. 1973. Distribution of two western Clapper Rail races as determined by responses to taped calls. Condor 75:177–183.

DEPT. FISHERY AND WILDLIFE BIOLOGY, COLORADO STATE UNIV., FORT COLLINS, COLORADO 80523 (HJG AND RAR) AND COLORADO DIV. OF WILDLIFE, RESEARCH CENTER, FORT COLLINS, COLORADO 80526 (CEB). (PRESENT ADDRESS HJG: P.O. BOX 306, APO, SEATTLE, WASHINGTON 98733.) ACCEPTED 22 JAN. 1979.

Wilson Bull., 92(1), 1980, pp. 103–107

GENERAL NOTES

The determination of runt eggs in birds.—Abnormally small eggs occur uniformly rarely in a wide variety of birds (Koenig, in press). However, in at least 1 species, the Acorn Woodpecker (*Melanerpes formicivorus*), the frequency of runt eggs (4.3%) is significantly higher than in other species for which an adequate sample is available (Koenig, op. cit.). Although the reason for this high incidence is unknown, it indicates that significant differences in the frequency of egg dwarfism do exist. Such differences may provide clues about the ecology of the species involved. It is therefore desirable to have an objective set of criteria defining "runt" eggs.

Runt eggs frequently lack a yolk or the normal complement of embryonic membranes (Pearl and Curtis, J. Agric. Res. 6:977–1042, 1916). Nonetheless, internal distinctions between normal and runt eggs are not consistent (Pearl and Curtis 1916), nor do there appear to be electrophoretic differences in the albumins of runt eggs (Baker, Br. Egg Marketing Board Symp. 4:67–108, 1968). Thus, runts must be operationally defined as eggs which are "abnormally" small and which do not hatch because of some internal abnormality. To consistently identify runt eggs, cutoff values based on egg size must be determined.

To test possible criteria I measured maximum length and width of 756 Acorn Woodpecker eggs from 158 sets. Forty-three of these sets were measured in the field at Hastings Reservation, Monterey Co., California. The remainder were from museum collections. In addition, 311 Red-headed Woodpecker (*Melanerpes erythrocephalus*) and 286 Lewis' Woodpecker (*M. lewis*) eggs were measured to provide comparisons with the *M. formicivorus* data.

I compared 2 sets of criteria. The first was based on absolute size. The volume (length × width^2 × $\pi/6$) for each of the 756 Acorn Woodpecker eggs was calculated; these data are combined into 0.33-cc intervals in Fig. 1a. Analogous data for 311 Red-headed Woodpecker eggs, which average slightly smaller than Acorn Woodpecker eggs, are presented in Fig. 1b. A comparison of these 2 histograms clearly shows the relatively large number of unusually small eggs in the Acorn Woodpecker sample; these eggs also result in a significant skewness

TABLE 1
MEASUREMENTS OF ACORN WOODPECKER EGGS

	Mean	SD	Skewness[1]	Kurtosis[1]	K-S D[2]
A. All eggs (N = 756)					
Length (mm)	25.2	±2.00	−1.56[3]	5.26[3]	0.186[3]
Width (mm)	19.2	±1.16	−1.87[3]	6.70[3]	0.245[3]
Volume (cc)	4.91	±0.82	−1.29[3]	3.25[3]	0.089[3]
B. Excluding runts (N = 718)					
Length (mm)	25.5	±1.42	0.04	−0.15	0.159[3]
Width (mm)	19.4	±0.82	−0.21[4]	0.00	0.233[3]
Volume (cc)	5.04	±0.60	0.02	0.14	0.020

---

[1] Tested for significant departure from 0 (Sokal and Rohlf, Biometry, W. H. Freeman, ed., San Francisco, California 1969).

[2] Kolmogorov-Smirnov test for normality (Siegel, Nonparametric Statistics for the Behavioral Sciences, McGraw-Hill, New York 1956).

[3] $P < 0.001$.

[4] $P < 0.05$.

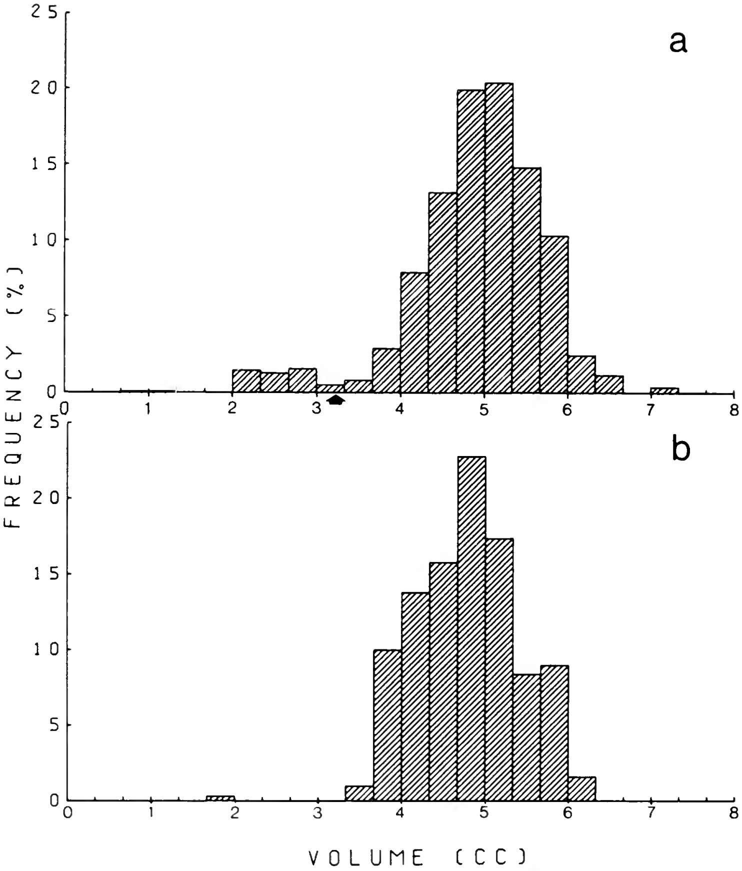


FIG. 1. Frequency distribution of the volume of Acorn Woodpecker eggs (a, N = 756) and Red-headed Woodpecker eggs (b, N = 311). The arrow in a. at 3.20 cc indicates an arbitrary cutoff between normal and runt eggs (see text).

and leptokurtosis in the distribution of egg volumes (Table 1). Comparison also suggests that a cutoff between normal and abnormally small eggs for these species might reasonably be made near the upper end of the 3.00- to 3.33-cc interval, below which only 1 clearly runt Red-headed Woodpecker egg was found. I arbitrarily chose 3.20 cc as the dividing line between the 2 parts of the histogram in Fig. 1a.

A graph of length vs width of Acorn Woodpecker eggs is presented in Fig. 2. The solid line is the isocline separating eggs with volumes greater and smaller than 3.20 cc. Also indicated are 5 eggs whose sizes are near this line and whose subsequent fates are known. Of the 3 above the line, 2 hatched; the volumes of these eggs were 3.87 and 3.56 cc. The 3 eggs which did not hatch had volumes of 3.56, 3.12 and 3.07 cc. Given that runt eggs do not hatch, a cutoff size should be smaller than 3.56 cc and probably near 3.12 cc. The value 3.20 cc provides a cutoff consistent with the division in Fig. 1a, above. A comparable cutoff

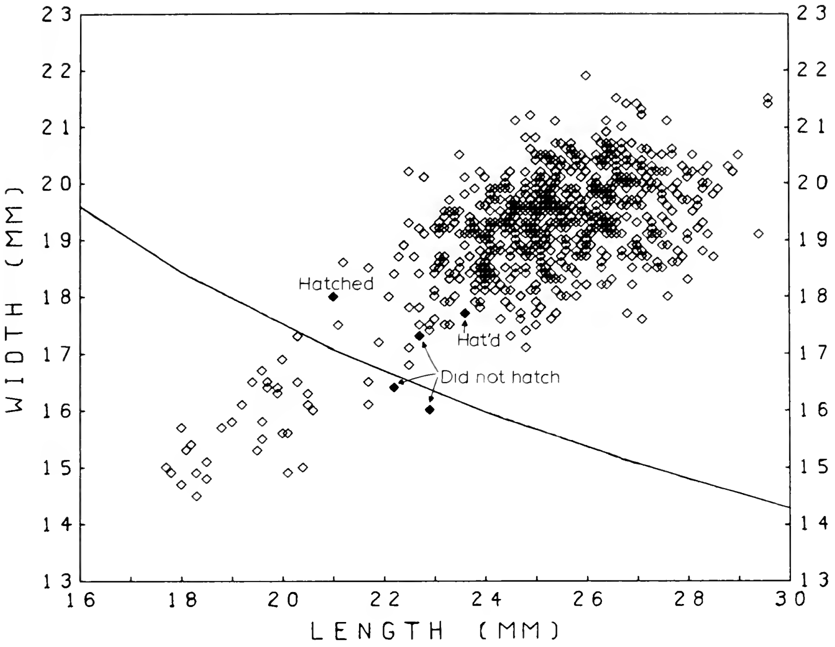


FIG. 2. Scattergram of length vs width of Acorn Woodpecker eggs. The solid line divides eggs whose volumes are smaller than 3.20 cc from those whose volumes are larger. Five eggs with volumes near 3.20 cc whose fates are known are indicated.

value based on absolute size could be determined for any particular species given enough data and a similar series of time consuming analyses.

A second possible set of criteria is based on the relative volume of possible runt eggs compared to others in the same clutch. The method has the advantage of focusing on eggs laid by a small number (usually 1) of females rather than the entire population. To test its viability, the volume of the smallest egg in each of 158 sets of Acorn Woodpecker eggs was divided by the average volume of all remaining eggs in the set to arrive at the relative volume of the smallest egg in each set. The distribution of the resulting values is strikingly bimodal (Fig. 3). (The secondary peak is much larger here than in Fig. 1a because the proportion of sets with a runt is much higher than the percent of runt eggs.)

The division between the 2 principal peaks of the histogram in Fig. 3 lies at about 75%. Two independent lines of evidence suggest that this value may provide a useful criterion for defining runt eggs. First, eggs considered to be runts which are illustrated, or for which weights are given in the literature, vary between 10% and 71.4% of the average volume of the other eggs in their clutch (Ingersoll, Condor 12:15–17, 1910; Kendeigh et al., Auk 73:42–65, 1956; Manning and Carter, Wilson Bull. 89:469, 1977). Second, the relative volumes of the smallest egg in 47 Lewis' Woodpecker and 65 Red-headed Woodpecker sets ranged between 99.2% and 77.2%, except for a 40.3% value for the 1 Red-headed Woodpecker runt egg measured.

By excluding eggs smaller than the 75% relative volume cutoff, the average volume of all

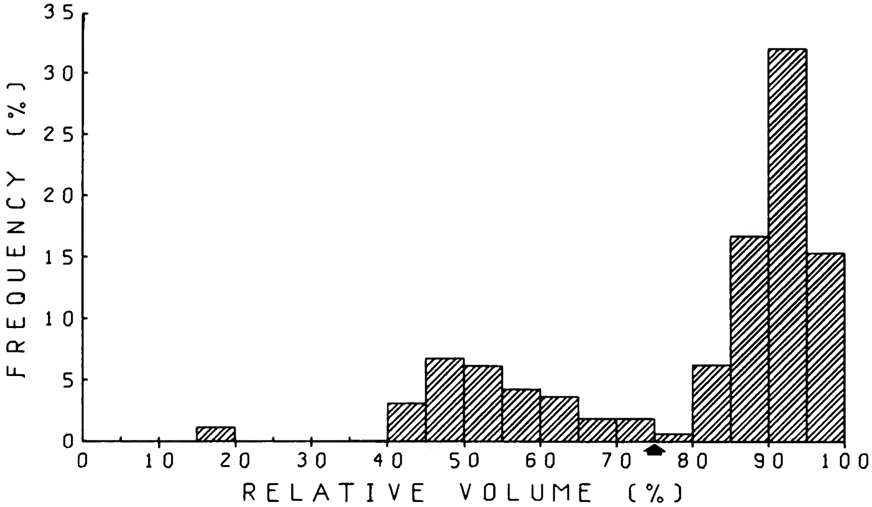


FIG. 3. Frequency distribution of the relative volume of the smallest egg compared to the average of the remaining eggs in 158 Acorn Woodpecker sets. The arrow at 75% indicates an arbitrary cutoff between normal and possibly runt eggs (see text).

Acorn Woodpecker eggs is changed from 4.91 ± 0.82 cc to 5.05 ± 0.60 cc (Table 1). The absolute size cutoff of 3.20 cc arrived at above is then slightly over 3.10 SD below the mean (this is a convenient value because in a normal curve, 0.1% of the values fall $\geqslant$ 3.10 SD below the mean).

A comparison between these 2 criteria for defining runt eggs suggests that the first, based on absolute size, is more conservative. In 37 of the 158 sets, the volume of the smallest egg was less than 3.20 cc. All 37 of these eggs had relative volumes less than 75% of the larger eggs in their clutch. Conversely, the smallest egg in 44 sets had a relative volume less than 75%, of which 37 (84%) were smaller than 3.20 cc. Four of the 6 cases meeting the relative volume criterion, but not the absolute size cutoff, resulted from the occurrence of a large egg (>1.3 SD above the mean of all eggs) in the set, depressing the relative volumes of otherwise normal eggs.

Thus, the method based on absolute size is preferable, but requires extensive data and effort to be used effectively. Fortunately, these 2 methods can be combined to minimize their respective disadvantages and provide a compromise between accuracy and ease of application. First, each egg in a set is weighed or its volume calculated. The relative volume of the second largest egg in the set is then compared to the largest. If the resulting value is more than 75%, the relative volume of the third largest egg is calculated compared to the average of the 2 larger eggs, and so on, to the smallest egg in the set. In practice, usually only the smallest egg in a set need be tested, and then only when it is obviously smaller to the naked eye than other eggs.

Finally, all suspected runt eggs are checked to be smaller than 3.10 SD below the mean volume of eggs not meeting the 75% relative volume cutoff. Eggs larger than this should be considered "normal" even if they meet the first criterion. Unless there are quite a few possible runts with volumes near a cutoff value, measurements of relatively few eggs (25–

50), from as many different sets as possible, should be adequate to determine an upper size limit for runts. An efficient procedure is to measure 1 egg chosen randomly from each available set. Clutches containing only runt eggs, such as have been recorded in several species, must be picked out by eye and tested, using the absolute size criterion alone.

By eliminating the 38 eggs defined as runts by these criteria from the total sample of Acorn Woodpecker eggs, the distributions of length, width and volume change markedly (Table 1). The striking skewness and leptokurtosis of all 3 variables are lost, and the distribution of volume is normalized ($P > 0.50$, Kolmogorov-Smirnov test for normality).

Given the low frequency of runt eggs in most natural populations, samples containing more than, at most, a very few runts are difficult to obtain, and thus differences from species to species are difficult to test using standard statistical methods such as the χ^2 test. The Fisher exact test (Bailey, Statistical Methods in Biology, English Universities Press, London, England, 1959), though usually employed when the total sample size is quite small, can be modified for this problem. This statistic can readily be calculated, regardless of the total sample size, by use of Forsyth's formula for ln n!:

$$\ln n! = \ln \sqrt{2\pi} + \left[(n + \tfrac{1}{2}) \times \ln\left(\frac{\sqrt{n^2 + n + \frac{1}{6}}}{e}\right)\right]$$

Even with the aid of this statistic, however, statistically significant differences in runt egg frequency between species will be testable only on the grossest scale without large sample sizes.

Care must also be taken to insure that samples are comparable. In particular, the bias of museum collectors toward anomalies may result in a higher frequency of runt eggs in collections than in the wild. Furthermore, this bias probably differs among species with different types of nesting habits and of differing degrees of rarity.

I thank the personnel of the Western Foundation of Vertebrate Zoology, the Museum of Vertebrate Zoology, the California Academy of Sciences, and the San Bernardino Co. Museum for allowing me to measure eggs under their care. Special thanks are due to Florence Amamoto and Pam Williams for helping to measure eggs. My work at Hastings Reservation has been supported by an NSF predoctoral grant, the Museum of Vertebrate Zoology, and the Department of Zoology, University of California, Berkeley. The manuscript was improved by the comments of John Davis, Pam Williams and the persistence of the Editor.—WALTER D. KOENIG, *Museum of Vertebrate Zoology and Hastings Reservation, Univ. California, Berkeley, California 94720.* (Mailing address: *Star Route Box 80, Carmel Valley, California 93924.*) *Accepted 10 Aug. 1979.*

Wilson Bull., 92(1), 1980, pp. 107–110

Breeding biology of Eastern Phoebes in northern Wisconsin.— The Eastern Phoebe (*Sayornis phoebe*) breeds widely throughout North America (Bent, U.S. Natl. Mus. Bull. 179, 1942). Despite this, relatively few studies of its breeding biology have been done. Furthermore, only 2 studies (Middleton and Johnston, Jack Pine Warbler 34:63–66, 1956; Cuthbert, Jack Pine Warbler 40:68–83, 1962) have been conducted in the Great Lakes states where the species is fairly common.

During the 1974–76 nesting seasons, I studied several aspects of Eastern Phoebe breeding biology in northern Wisconsin. The main objectives were to determine clutch-size, hatching and fledging success and mortality factors, and to examine the relationship between them and nest placement variables.

Study area and methods.—The study area was in northwestern Wisconsin, in Barron County, which lies in the Central Plain Province (Martin, The Physical Geography of Wisconsin, Wis. Geol. and Nat. Hist. Surv. Bull. 36, 1932). The Red Cedar River and its tributaries comprise the major drainage system. Vegetation was primarily northern deciduous forest (Curtis, Vegetation of Wisconsin, Univ. Wis. Press, 1959), comprised of maple (*Acer* spp.), basswood (*Tilia* spp.) and aspen (*Populus* spp.) subclimax. Willow (*Salix* spp.) and alder (*Alnus rugosa*) were common along stream banks.

I conducted field work in 1974–76, from April to August during the nesting seasons. Nests were located by checking beneath each highway bridge along a predetermined route. All bridges containing an active nest were marked on U.S. Geological Survey topographic maps. An active nest was one in which at least 1 egg was laid.

Initially, the following were recorded on field data sheets for each nest: date, time, general weather conditions, nest placement and height of nest above water; then each nest was visited 1–3 times per week, and its status recorded. Nesting data were later transferred to individual nest cards for analysis. During 1975, nestling Eastern Phoebes were banded with U.S. Fish and Wildlife Service aluminum leg bands. No attempt was made to capture adults. Data were assembled to test for significant differences using Chi-square (with $P \leq 0.05$).

Results and discussion.—Phoebes returned to the study area about 15 April each year. Singing and other territorial displays commenced within a week of arrival.

The mean date of laying the first egg was 7 May (range 5–8 May). This is several weeks later than the findings of Klaas (Occ. Pap., Univ. Kansas Mus. Nat. Hist. 41:1–48, 1975) in Kansas, and later than several Illinois records (Graber et al., Illinois Nat. Hist. Surv. Biol. Notes, No. 86, 1974). Klaas documented the effect of temperature on the initiation of egg-laying in phoebes. A shorter growing season associated with the more northerly latitude of Wisconsin probably explains differences between the later nest initiation I observed, and dates for Kansas and Illinois.

Peak nesting activity, or the maximum number of active nests, for first nesting attempts occurred between 30 May and 10 June. Second nesting attempts (those occurring after successful first attempts) reached a peak during mid-July. Nesting activity ceased by 10 August each year.

All nests examined (N = 71) were found on cross beams under highway bridges constructed primarily of concrete and steel. Height of nests above water varied from 0.9–3.05 m ($\bar{x}$ = 2.04 ± 0.51; N = 71). Bridges are important nest-sites for other phoebe species. Ohlendorf (Wilson Bull. 88:255–271, 1976) found 40.7% of Say's Phoebe (*Sayornis saya*) and 77.3% of Black Phoebe (*Sayornis nigricans*) nests examined, under bridges.

In all instances except one, nests were placed within 2 m of the upstream edge of the bridge. The 1 nest placed within the downstream section was 1 m from the center of the bridge. All nests were placed on the end of the bridge where the deepest water occurred. Coffey (Migrant 34:41–49, 1963) also reported nests on cross beams, with most located on the upstream side of the bridge. He thought that nests placed near deeper water are probably afforded greater protection from terrestrial predators than those placed over shallow water.

I observed 110 nesting attempts, including 39 second nesting attempts. There were 502 eggs laid in the active nests for an average clutch-size of 4.56 ± 0.7. The range was 3–7 eggs, with 5 being the mode. Klaas (1975) reported a clutch-size of 4.33 in nests not parasitized by Brown-headed Cowbirds (*Molothrus ater*) in Kansas. Middleton and Johnston (1956) found an average clutch-size of 5 in 85 nests in Michigan.

The length of time from laying the last egg to the hatching of the last young averaged 16.3

TABLE 1

COMPARISON OF NUMBER, CLUTCH-SIZE, YOUNG FLEDGED AND NESTING SUCCESS BETWEEN FIRST AND SECOND BROODS

Year	Brood number	Active nests	Clutch-size	Young fledged	Successful nests	Percent successful nests
1974	1	24	4.5	71	18	75.0
	2	13	4.5	49	11	84.6
1975	1	23	4.6	69	17	73.9
	2	12	4.6	35	10	83.0
1976	1	24	4.6	73	20	83.0
	2	14	4.6	51	12	85.7

± 0.9 (range 15–17) days in 76 nests. There was no apparent difference in incubation periods between first and second broods. Kendeigh (Illinois Biol. Monogr. 22:1–356, 1952) reported that the average incubation period of Eastern Phoebes was 16 days. Coffey (1963) found the incubation period in Tennessee ranged from 16–20 days, and Cuthbert (1962) cited incubation estimates of 15–21 days.

Three hundred ninety-two of the 502 eggs hatched, for a hatching success of 78.0%, and 348 young fledged, or 69.3% of the total eggs resulted in fledged young. This was greater than fledging success ranging from 38.2–55.8% in nonparasitized nests observed by Klaas (1975). Young fledged from 88 of 110 active nesting attempts, or a nesting success of 79.8%. This was considerably higher than 67.9% reported by Klaas (1975).

Of the 110 nesting attempts I observed, only 1 (0.9%) was parasitized. No young were produced from this nest. A second nesting attempt by this pair produced 4 young. Klaas

TABLE 2

COMPARISON OF EASTERN PHOEBE REPRODUCTIVE SUCCESS, 1974, 1975 AND 1976

	1974	1975	1976	$\bar{x}$	SD
Nesting attempts	37	35	38	36.6	1.52
Second broods	13	12	14	13	1
Eggs laid	166	161	175	167.3	7.09
Clutch-size	4.48	4.6	4.6	4.56	0.07
Eggs hatched	130	122	140	131	9.01
Eggs hatched per nest	3.5	3.48	3.68	3.55	0.11
Percent eggs failed	22.0	24.3	20	22.1	2.15
Young fledged	120	104	124	116	10.5
Young fledged per nest	3.24	2.97	3.26	3.15	0.16
Young fledged per successful nest	4.13	3.85	3.87	3.95	0.16
Successful nests	29	27	32	29.3	2.51
Percent successful nests	78.3	77.1	84.2	79.9	3.8

(1975) reported a very high rate of cowbird parasitism. He found 117 of 321 nests (36.4%) were parasitized. Rates of parasitism from other studies include 1.2% in Tennessee (Coffey 1963), 11.7% in Michigan (Middleton and Johnston 1956) and 14% in Michigan (Cuthbert 1962). The low rate of cowbird parasitism probably contributed to the high rate of reproductive success in my study.

The nestling period ranged from 13–16 days ($\bar{x}$ = 15.2 ± 0.5). Bent (1942) and Coffey (1963) reported fledging at 15–16 days and 15 days, respectively. At a few nests, the return of fledglings made it difficult to determine the length of the nestling period at these nests.

Thirty-nine of the 110 nestlings were second broods, which were always more successful than first broods (Table 1). No significant difference existed between second brood success ($\bar{x}$ = 84.4% ± 1.35) and first brood success ($\bar{x}$ = 77.3% ± 4.96). There was no significant difference in the average number of fledglings per successful nest ($\bar{x}$ = 3.4 ± 0.43) in second broods and ($\bar{x}$ = 3.0 ± 0.04) in first broods.

Annual reproductive success remained essentially constant even though several reproductive parameters varied (Table 2). Chi-square analysis indicated there was no significant difference in yearly reproductive success.

Nest mortality was attributable to infertile eggs, embryonic death, nest abandonment and nest mites. Overall, 22.1% of the eggs laid failed because of all mortality factors combined. Seven nests were abandoned, of which harassment by trout fishermen probably caused 3. The causes of the other 4 abandonments are unknown.

Nest mites observed in 9 nests probably contributed to the deaths of 35 young phoebes. Coffey (1963) reported a low incidence of nest mites, with 3 of 78 nests containing mites. Although the possibility of young being pushed or knocked from the nest seemed high because of the shallow construction, only at 1 site did it appear that nestlings had been pushed out.

During incubation, adult phoebes were passive when I investigated the nest. The incubating adult usually flew from the nest and perched on a nearby branch. Upon my departure, the adult would usually return within 2 min. With young in the nest, the adults became very aggressive when I approached and the brooding adult would give a loud chip call. The mate would usually arrive upon hearing the call note and both adults would fly rapidly among perches continuing to call.—CRAIG A. FAANES, *U.S. Fish and Wildlife Service, Minneapolis, Minnesota 55111.* (Present address: *U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401.*) *Accepted 28 Mar. 1979.*

Wilson Bull., 92(1), 1980, pp. 110–112

Variation in promiscuity among Red-winged Blackbirds.—Promiscuous matings by female Red-winged Blackbirds (*Agelaius phoeniceus*) have been observed by a few investigators (Allen, Proc. Linn. Soc. N.Y. 24–25:43–128, 1914; Beer and Tibbitts, Flicker 22:61–77, 1950; Simmers, M.S. thesis, Univ. Mass., Amherst, Massachusetts, 1961). Bray et al. (Wilson Bull. 87:187–195, 1975) were the first to apply experimental method to the phenomenon by vasectomizing males and using fertile clutches produced on their territories as evidence of promiscuity. They found fertile clutches on marshes in which 100% of the males were sterilized, suggesting that some breeding takes place outside the polygynous "harem."

In 1976, we applied the vasectomy technique at 9 study sites near Amherst, Massachusetts, as part of a study of red-wing promiscuity. Each site contained the territories of a sterilized

TABLE 1
FERTILITY OF CLUTCHES ON TERRITORIES OF VASECTOMIZED MALE RED-WINGS IN 1976 AND 1977

Classification	Phase I[1]			Phase II[2]			Totals	
	1976	1977	total	1976	1977	total	1976	1977
Number of territorial males	2	6	8	7	2	9	9	8
Number of clutches:								
Infertile	0	2	2	7	0	7	7	2
Fertile	4	12	16	4	1	5	8	13
Percent fertile	100	86	89	36	100	42	53	87
Total percent fertile							70	

[1] Males sterilized before arrival of nesting females.
[2] Males sterilized after female began nesting.

male and an adjacent unmarked control male. Within 1 week of establishing territories and before the arrival of breeding females, males were decoy trapped and vasectomized. All sites where males were treated before arrival of females were classified as phase I. In mid-season, after onset of breeding, males were decoy trapped, vasectomized and all nests on their territories were destroyed; these sites were classified as phase II. Preliminary results (see Roberts and Kennelly, Trans. 1977 Northeast Fish and Wildl. Conf., Boston, Massachusetts, 1977:99) supported the conclusions of Bray et al. (1975). All clutches on phase I sites and 36% of phase II clutches were fertile (Table 1).

Behavioral observations were made during 7 h on each of the 9 treated/control territorial pairs, including frequency of territorial singing and display, frequency of pursuit of females or aggressive encounters with other males, and number of territory boundary crossings per female per observation period. These observations failed to show any significant difference between sterilized males and adjacent control males.

Further research in 1977 allowed us to refine and expand our findings. Seven of 9 males sterilized the previous year and 1 sham-operated male returned to their territories, increasing our confidence that the surgical procedure was benign. Oviducts from 13 females of known breeding history were sampled and examined histologically for sperm in utero-vaginal "glands." Proportion of glands containing sperm peaked at 40% on the second day of egg-laying, but declined to 0 by the first day of incubation. Although Bray et al. (1975) reported red-wing sperm persisting in the female tract for longer periods, our data favor promiscuity, rather than sperm retention as the probable cause for fertile clutches.

Clutch fertility over 2 years showed a curious variation (Table 1), with clutch fertility highest in phase I clutches. The sample is too small for valid statistical analysis, and it is difficult at this point to determine whether the disparity arises from the effects of seasonality, year differences or male fertility. It is unlikely that females "remembered" sterile males from year to year, since in our marked sample of females, only 25% were even seen in the study area the following year. A decline in overall male reproductive capacity rather than rate of promiscuous mating could account for declining fertility. However, Payne (Univ. Calif. Publ. Zool. 90:1–115, 1969) found that males maintain a constant fertility throughout the breeding season.

Phase II clutches tended to be initiated later in the nesting season than phase I clutches.

This leads us to propose the following hypothesis as a basis for future research: promiscuity declines as the season advances. This could be true if, for example, food was increasingly available at the nest-site as the season progressed, reducing daily female travel distances and hence the opportunities for mating with other males.

This additional evidence for promiscuity argues against the use of male chemosterilants in blackbird population control, an idea explored by several authors (Davis, Trans. N. Am. Wildl. Nat. Res. Conf. 26:160–167, 1961; Vandenbergh and Davis, J. Wildl. Manage. 26:366–371, 1962; Messersmith, Pest Control 38:35, 40–41, 1971). On a theoretical level, the existence of promiscuity and its possible relationship to an environmental variable raises some questions regarding the reproductive strategies of females. How does optimal mate choice of a female change over the season? Is it a function of change in male behavior, female behavior or some ecological factor such as territory quality? Further research may elucidate some of these options in the behavioral repertoire of this much studied species.

This study was partially supported by the Denver Wildlife Research Center, U.S. Fish and Wildlife Service.—THOMAS A. ROBERTS, *U.S. Forest Service, San Bernardino National Forest, Idyllwild, California 92349,* AND JAMES J. KENNELLY, *Massachusetts Cooperative Wildlife Research Unit, Univ. Mass., Amherst, Massachusetts 01003.* *Accepted 8 Feb. 1979.*

Wilson Bull., 92(1), 1980, pp. 112–113

Notes on parasitism by Bronzed Cowbirds in El Salvador.— Bronzed Cowbirds (*Molothrus aeneus*) are abundant in El Salvador (Dickey and van Rossem, Field Mus. Nat. Hist., Zool. Series 23, 1938; pers. obs.), but there is a notable lack of records of nest parasitism by this species. None was found by van Rossem (loc. cit.) during his sojourn there; his only reference to possible hosts was an undocumented comment that the natives claim the 3 common orioles—Altamira (*Icterus gularis*), Streak-backed (*I. sclateri*) and Spot-breasted (*I. pectoralis*)—are the species most often victimized. During 11 years in El Salvador we have only 3 verified instances of nest parasitism, all within a month's time, and all close together in the narrow canyon of Los Chorros, La Libertad. We have other observations that strongly suggest nest parasitism of other species.

Orange-billed Nightingale-Thrush (*Catharus aurantiirostris*).—A nest found 30 July 1971, at Los Chorros, contained 3 thrush eggs and 1 cowbird egg. On 7 August the nest contained 1 thrush nestling, 1 cowbird nestling and 1 thrush egg. On 10 August the last thrush egg had disappeared. Initially the nestlings closely resembled each other; both were covered with mouse-gray down and were nearly equal in size. However, the cowbird was slightly larger, could stretch its neck a few mm higher and its redder mouth lining contrasted more vividly with its gape.

On 12 August the nest was watched all day from a blind at 6 m; the nestlings received approximately an equal number of feedings. Commonly, after a feeding, a nestling of either species excreted a fecal sac which an adult seized and drew from the cloaca. Occasionally, a sac burst and the adults thoroughly removed the excrement from the nest. Of the few instances when we identified the nestling involved, we noted that 3 burst sacs came from the cowbird and intact sacs were excreted by the thrush.

During the 13 h of continuous observation, and other short observational periods, the nestlings did not vocalize, or if they did, their voices were not audible at 6 m. Both nestlings remained low in the nest throughout the nestling period, crouching when closely approached and, if touched, contracting their bodies.

Both nestlings were in the nest at 15:00 on 17 August. At 06:00 the following morning, after a heavy rain, the nestlings were gone but the nest was dry inside, suggesting that the birds left after the rain. The adults were heard nearby. For the first time feces were seen on the rim of the nest.

Another nest was found at Los Chorros on 17 August 1971. It contained 1 thrush egg and 1 cowbird egg. On 18 August it contained another thrush egg. On 19 August the nest was empty.

Red-crowned Ant-Tanager (*Habia rubica*).—A nest found 17 August 1971, at Los Chorros, contained 1 well-feathered nestling cowbird. We were attracted to the vicinity by the loud vocalizations of the tanagers bringing food, and to the nest by the vocalizations of the cowbird. An egg of unknown origin and not identifiable was found below the nest. The nest was watched for some 4 h over 3 days. The adults usually departed and returned together, calling loudly. The cowbird remained quiet for 5–10 min after being fed, then began to call softly. As the adults approached the nestling stood up, sometimes on the rim of the nest, and called loudly enough to be heard at 20 m. This nestling crouched as we approached, but when touched adopted an upright, "threatening" pose, erecting whitish supraorbital feathers resembling small horns; the cowbird in the successful *Catharus* nest was not seen to erect these feathers.

The nestling cowbird in the *H. rubica* nest defecated semiliquid material over the nest's rim during our observations. No nest sanitation was noted and the interior and rim of the nest and the leaves below were soiled. On 19 August, as we approached, the young cowbird fluttered away and was taken. E. Eisenmann kindly identified the specimen, which is now in the American Museum of Natural History.

The contrast in behavior of the 2 cowbird nestlings described here is notable. Such variability in nestling behavior might have developed to parallel the behavior patterns of different host species.

Streak-backed Oriole (*Icterus sclateri*).—Villeda saw a pair of these orioles drive a female cowbird from a nest at Hacienda Los Pinos, Usulután, on 18 May 1974. At Las Minas de San Cristóbal, Morazán, on 30 May 1976, Thurber saw a female oriole leave an unfinished nest to attack a passing female cowbird, driving her toward a nearby nest from which a second oriole joined the chase, and as the cowbird passed another nest a third pursuer also joined the chase.

At Hacienda Los Pinos, Usulután, we watched the construction of a Streak-backed Oriole nest for several days in early May 1975. At 07:00 on 4 May Villeda saw a female cowbird examine the nest while the female was inside. Between 09:00 and 11:00 on 5 May, we saw a female cowbird near the nest several times, seemingly observing it, and at 10:00, a cowbird flew to the nest during the absence of the orioles and peered inside without entering. At 17:00 on 6 May Thurber saw a female cowbird enter the nest, remaining less than 1 min.

Altamira Oriole (*Icterus gularis*).—At about 07:00 on 12 April 1977, at Las Minas de San Cristóbal, Morazán, Michael Airey, manager of the mines, saw a black bird enter an Altamira Oriole nest where it remained about 30 sec. Mr. Airey, who knows the nest of *I. gularis* but not the cowbird, thought the black bird might be a Melodius Blackbird (*Dives dives*), but it was probably *M. aeneus*.

Yellow-olive Flycatcher (*Tolmomyias sulphurescens*).—While watching a nest of this species on 14 May 1976, at Las Minas de San Cristóbal, Morazán, Thurber noted a female cowbird approaching it stealthily. At about 3 m she launched herself on a course that would have taken her into the vertical tube-like entrance of the nest, but as she neared it, the male, who had been singing nearby, attacked and drove her away.

We thank Lloyd Kiff for his comments on the manuscript.—WALTER A. THURBER, *Cornell Univ. Lab. of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14853* AND AMANDA VILLEDA, *8_a Av. 17-32, Zona 1, Guatemala, Guatemala, C.A.* *Accepted 1 Jan. 1979.*

Wilson Bull., 92(1), 1980, pp. 114–116

Observations of a White-winged Crossbill invasion of southeastern Manitoba.—Crossbills are interesting because of their irruptive tendencies and erratic breeding schedules. The movements and breeding biology of the Red Crossbill (*Loxia curvirostra*) have been studied extensively in Europe (Newton, pp. 337–357 *in* Animal Populations in Relation to Their Food Resources, A. Watson, ed., Blackwell, Oxford, England, 1970) and to a lesser extent in North America (Bailey and Niedrach, Denver Mus. Nat. Hist., Mus. Pict. No. 9, 1953; Tordoff and Dawson, Condor 67:416–422, 1965). The White-winged Crossbill (*L. leucoptera*) has received little attention in this regard, especially in North America. Godfrey (The Birds of Canada, Natl. Mus. Bull., No. 203, 1966) indicates that it winters throughout much of the boreal coniferous forest in Canada, although its local occurrence within this range varies erratically from year to year (Bent, U.S. Natl. Mus. Bull. 237, 1968). In southeastern Manitoba, at Pinawa (50°09′N, 95°55′W), where Christmas bird counts have been conducted since 1967 (Audubon Field Notes, 1967–70; Am. Birds, 1971–1976), White-winged Crossbills have been recorded only 3 times (1968, 1971, 1975). None was seen by Sealy during extensive field work in the winters of 1974 and 1974–75, nor since 1975–76, the period of the invasion under study here.

From late October 1975 to early April 1976, we studied aspects of a White-winged Crossbill invasion in southeastern Manitoba. Only 11 Red Crossbill flocks were seen during this period. Most of our observations were made within a 160 km radius of Hadashville, Manitoba (49°40′N, 95°55′W). Collins' and Sexton's observations were ancillary to Collins' study of the Great Gray Owl (*Strix nebulosa*). Sealy made day-trips every 7–10 days into the study area.

Southeastern Manitoba is forested (see Gill, Forest Serv., Man. Dept. Mines and Resources, Rept. No. 1, 1956) with black spruce (*Picea mariana*, 37%), aspen (*Populus tremuloides*, 21%), jack pine (*Pinus banksiana*, 19%), tamarack (*Larix laricina*, 7%) and white spruce (*Picea glauca*, 3%). All other trees comprise less than 1% of the tree species composition.

Thirty-two White-winged Crossbill specimens (Univ. Man. Zool. Mus. Nos. 386–417) were obtained between 12 November 1975 and 27 March 1976; most of these were killed on roads in the area (see Meade, Auk 59:439, 1942; Baker, Blue Jay 23:79–80, 1965). None of these individuals was molting wing feathers. All birds obtained up to 5 December 1975, were actively molting on the body; by 8 January 1976, when further specimens were obtained, this

TABLE 1

BODY CONDITION OF WHITE-WINGED CROSSBILLS

Date[1]	Age/sex (N)	Body weight (±SD)[2] (g)	Fat[3]	Body molt	Gonad[4]
Nov.–Dec.	ad. ♂♂ (6)	27.1 ± 2.0	1.0	+	≤1.0
Nov.–Dec.	ad. ♀♀ (7)	25.8 ± 1.2	1.4	+	≤1.0
Jan.–Mar.	ad. ♂♂ (10)	28.2 ± 3.6	3.6	–	≤1.0
Jan.–Mar.	ad. ♀♀ (8)	24.8 ± 1.9	2.8	–	≤1.0

[1] Thirteen specimens (UMZM 386–396, 398, 399) obtained between 12 November and 5 December 1975, and 18 (UMZM 400–417) between 8 January and 27 March 1976.

[2] Mean body weight for all males (N = 16), 27.9 ± 1.3 g; for all females (N = 15) 25.3 ± 1.7 g. The juvenile male (UMZM 397) taken on 15 November 1975, weighed 25.8 g.

[3] Subcutaneous fat based on scale 0 (extremely lean) to 4 (extremely fat).

[4] Length (mm) of left testes in males; diameter (mm) of largest follicle in females.

TABLE 2

MEANS OF MEASUREMENTS OF WHITE-WINGED CROSSBILLS FROM SOUTHEASTERN MANITOBA, NOVEMBER 1975 TO MARCH 1976

Characters	Adult		Juvenile
	♂♂ (N = 16)	♀♀ (N = 15)	♂♂ (N = 1)
Exposed culmen	15.4 ± 0.44	15.1 ± 0.44	14.2
Bill height	8.4 ± 0.20	8.1 ± 0.25	8.2
Bill width	9.4 ± 0.30	8.6 ± 0.40	9.2
Wing chord	87.4 ± 1.42	83.9 ± 1.83	85.7
Tarsus	16.4 ± 0.41	15.7 ± 0.34	16.8
Tail	55.5 ± 2.04	54.7 ± 2.24	54.8

molt had ceased (Table 1). The males weighed slightly more (Table 1) and averaged slightly larger than females in all characters measured (Table 2). The reverse was found in Asian White-winged Crossbills (*L. l. bifasciata*) by Kokhanev and Gaev (*in* Pine Crossbills, Nethersole-Thompson, ed., Poyser, Berkhamsted, 1975).

The mean (±SD) flock size we observed was 10.4 ± 9.3 individuals; the median was 14. In 118 flocks, males (pink, red or orange in the plumage) comprised 26.3% of the flocks and females and young (dark with yellow), 73.7%. In White-winged Crossbills, the age composition of flocks which have invaded Scandinavia has varied from adults only (Newton 1970) to predominantly juveniles (G. Notini, *in* Lack, The Natural Regulation of Animal Numbers, Oxford Univ. Press, Oxford, England, 1954; Hildén, Ornis Fenn. 37:51–55, 1960). Wynne-Edwards (Animal Dispersion in Relation to Social Behaviour, Oliver and Boyd, London, England, 1962) reported that adult males migrated later than the females and young. Our small and possibly biased sample of specimens contained 16 males, 15 females and a single juvenile (UMZM 397), the latter obtained on 15 November 1975. The juvenile, a heavily streaked individual, was the only immature we identified positively. Phillips (Bird-Banding 48:110–117, 1977) pointed out that in the Red Crossbill up to 10% of females show some red in their plumage. Therefore we cannot determine with certainty from sight observations the sex and age structure of the invading population we studied.

Our observations of 117 feeding flocks of White-winged Crossbills revealed that 83% fed on tamarack, 12% on black spruce, 3% on white spruce and 1% on white cedar (*Thuja occidentalis*) and forbs. Feeding flocks, very visible in the deciduous tamaracks, were almost invisible in spruce. Therefore we considered that a bias may exist in our observations. The mean (±SD) flock size of White-winged Crossbills seen feeding in tamarack was 10.5 ± 6.5 compared to 5.6 ± 4.1 for the other conifer species. This suggests that we did not see all of the individuals in conifers with needles present. However, to determine whether tamaracks were indeed their preferred feeding trees, we watched 17 flocks fly over predominantly black spruce habitat; 16 flocks settled and foraged on tamarack, the other on black spruce. Furthermore, of 7 flocks seen leaving tamarack stands 5 flew to other tamaracks and 2 to black spruce to feed. From these 2 flocks, 2 or 3 individuals left to feed again in tamarack (which may account for the smaller flocks observed in coniferous trees other than tamarack).

The diverticula and stomachs of 24 White-winged Crossbills all contained tamarack seeds. One specimen contained more white spruce seeds than tamarack and 2 or 3 white spruce seeds were present in 2 other specimens. Arthropod remains and black spruce seeds were present in trace amounts in 3 and 2 birds, respectively.

The White-winged Crossbill consumes conifer seeds, with spruce ranking highest in North America (Gabrielson, U.S. Dept. Agric. Bull. 1249, 1924; Bent, U.S. Natl. Mus. Bull. 237, 1968) and in Europe (Pulliainen, Am. Zool. Fenn. 8:326–329, 1971, Am. Zool. Fenn. 9:28–31, 1972). Newton (1970; Finches, Taplinger, New York, 1973) and Ulfstrand (pp. 780–794 *in* Proc. XIII Int. Ornithol. Congr., 1963) considered it essentially a tamarack seed eater.

Coniferous tree cone production is cyclic with very high crop years occurring in different places in different years (Svärdson, Br. Birds 50:314–343, 1957). Our observations and specimens of White-winged Crossbills examined suggest that tamarack seeds were sufficiently abundant in southeastern Manitoba during the winter of 1975–76 to promote settling by dispersing birds. Also, tamarack cones and hence probably seeds were fed on by Red Crossbills (in small numbers in the area in 1975–76), Common Redpolls (*Carduelis flammea*), Black-capped Chickadees (*Parus atricapillus*), Sharp-tailed Grouse (*Pedioecetes phasianellus*) and Gray Jays (*Perisoreus canadensis*) during the invasion period. Bent (U.S. Natl. Mus. Bull. 162, 1932; U.S. Natl. Mus. Bull. 191, 1946; U.S. Natl. Mus. Bull. 237, 1968) reports that of these species only Red Crossbills are known to feed regularly on tamarack seeds and Sharp-tailed Grouse occasionally feed on these seeds.

We did not obtain evidence of breeding by White-winged Crossbills during our study. None of the specimens examined was in breeding condition (Table 1). We last saw White-winged Crossbills on 10 April 1976, despite continued work by Collins in the area until late June. A gradual increase in body fat from November through March (Table 1) suggests a build up prior to movement in spring. Newton (1970) reports a similar situation in the Red Crossbill in Europe.

We thank Ian Newton, Henri Ouellet and Harrison B. Tordoff for commenting on the manuscript. The field work in 1975–76 was funded by grants to Sealy from the Manitoba Department of Renewable Resources and Transportation Services and the Northern Studies Committee of the University of Manitoba.—SPENCER G. SEALY, DONALD A. SEXTON AND K. MICHAEL COLLINS, *Dept. Zool., Univ. Manitoba, Winnipeg, Manitoba R3T 2N2 Canada.* (Present addresses: [DAS] *Ducks Unlimited [Canada], Box 776, Dauphin, Manitoba R7N 3B3;* [KMC] *96 Noble Ave., Red Deer, Alberta T4P 2H5.) Accepted 2 Jan. 1979.*

Wilson Bull., 92(1), 1980, pp. 116–120

Winter hunting behavior of a Snowy Owl in Michigan.—The Snowy Owl (*Nyctea scandiaca*) has been frequently studied on its breeding grounds (e.g., Pitelka et al., Ecol. Monogr. 25:85–117, 1955a; Pitelka et al., Condor 57:3–18, 1955b; Sutton and Parmelee, Condor 58:273–282, 1956; Watson, Ibis 99:419–462, 1957; Parmelee, Beaver (summer):30–41, 1972; Taylor, Living Bird 12:137–154, 1973) and the literature abounds with diet analyses of this species (e.g., Keith, Wilson Bull. 75:276–277, 1963; Catling, Ont. Field Biol. 27:41–45, 1973; Allan, Jack Pine Warbler 55:42, 1977). Winter studies have been confined to censuses, the periodicity of invasions, food habits and territoriality (Keith, Can. Field-Nat. 74:106–112, 1960; Can. Field-Nat. 78:17–24, 1964; Quilliam, Ont. Field Biol. 19:1–8, 1965). I found no extensive reported examination of hunting behavior of the Snowy Owl in winter.

Study area and methods.—The study area was in slightly rolling terrain consisting of agricultural land (planted mostly to hay, with some rye and corn) with several small cherry orchards and scattered woodlots. The area included eastern Green Lake and western Blair townships in Grand Traverse County, in northwestern lower Michigan. Sunrise and sunset occurred at 07:35 and 18:01 EDST, respectively, on the first day of observations and at 06:39 and 18:44 on the last.

I studied 1 Snowy Owl, recognizable by distinctive plumage, between 11 February and 19 March 1978 for 143 h, including 8 daylong observations (½ h before sunrise to ½ h after sunset). Observations, made from a parked car with 7 × 35 binoculars and a 20–45× scope, were spread evenly throughout the day under varying cloud cover, precipitation and temperature (−29–7°C). An attempt was made to keep the number of observation hours per week equal.

For each observation period I recorded time, weather conditions and all behavior of the owl. Movements were mapped and pellets collected weekly at all perches and loafing sites. Pellets regurgitated as I watched were collected the same day. All pellets were air-dried for 2 weeks then weighed to the nearest 0.01 g. Meadow vole (*Microtus pennsylvanicus*) skeletons were sexed using pelvic characters defined by Guilday (J. Mamm. 32:216–217, 1951) and Dunmire (J. Mamm. 36:356–361, 1955). Specimens of prey species were also captured with snap-traps in the same area.

Weekly snow depth measurements were taken by inserting a meter stick at 10 sample sites (5 in frequent strike areas of the owl, 5 in randomly selected areas) scattered throughout the owl's hunting range. The measurement for each site was the average of 3 measurements made at 2 m intervals.

Winter hunting range.—The winter hunting range was drawn by plotting all observations of the owl on a map and connecting the peripheral locations. Area was measured using the cross-section paper method. The range was roughly oval, with a 1.3 km long axis and an area of 0.8 km^2. Keith (1960, 1964) noted a range of about 1.2 km^2 in Manitoba and 0.5–2.5 km^2 in Wisconsin. Keith (1964) reported that territories were defended against both wild and captive conspecifics.

The size of the winter hunting range was smaller than summer breeding territories, which ranged in size from 1.3–5.2 km^2 on Baffin Island (Watson 1957) and 5.2–10.4 km^2 at Point Barrow, Alaska (Pitelka et al. 1955a). Summer territories must be of a sufficient size to provide food resources adequate to support not only 2 adults, but several growing young as well, while the winter hunting range is used by only 1 individual.

Activity periods.—Three major activity periods were recognized: hunting, loafing and observing. When hunting the owl was acutely responsive to every movement and sound and made frequent assessment movements of the head, bobbing and swaying while staring at a particular location. No preening occurred during hunting.

Loafing was characterized by inactivity and inconspicuousness and consisted of extensive periods of preening and sleeping. The same activities and sounds that would have elicited an immediate response during a hunting period brought no visible response. Loafing usually occurred on the ground next to a fence post, stump or clump of tall weeds, and less commonly on the lee side of a snowbank or next to the center post on a t-bar utility pole. Periods of observing contained behavior common to both hunting and loafing.

Activity periods were easily recognizable by abrupt changes of behavior. Commencement and termination of a loafing period was indicated by a flight to or from the loafing site. Periods of early morning hunting frequently ended with several successful strikes, although if unsuccessful, the transition from hunting to observing was less well defined, but invariably occurred by midmorning.

Mean durations of hunting, loafing and observing periods were 73 min (N = 31), 166 min (N = 15) and 123 min (N = 18), respectively. Hunting times represent minimums since the owl undoubtedly hunted, prior to and after my observation times, when there was too little light for me to see. During a full moon on 21 February the owl was observed hunting 1.5 h after sunset. Long loafing periods (5–7.5 h) occurred twice during very heavy snow falls and twice after the owl had just fed on 3 voles. The shortest observing periods occurred after successful morning hunts, just before the owl began loafing.

The owl's daily behavior appeared to follow a fairly regular routine. The earliest and latest portions of the day were occupied with hunting. A midday loafing period ($\chi^2 = 16.41$, df = 2, $P < 0.005$) followed the early hunting period and preceded the evening hunt.

Approximately one third of each day was spent in each of the 3 general types of behavior. Hunting consumed 30.7% of the daylight hours. This contrasts markedly with the amount of time needed for food-getting during the summer. During 10 observations by Watson (1957) of a male Snowy Owl hunting in July the owl "never failed to catch a lemming after 5 minutes continuous hunting." The owl spent 34.5% and 34.8% of the day loafing and observing, respectively.

The amount of time spent flying was relatively brief. The number of flights per day during daylong observations ranged from 13–57 ($\bar{x} = 27.5$) and covered a total of from 2.7–11.0 km per day ($\bar{x} = 5.1$). The calculations included flights during strikes, as well as between hunting perches and loafing sites. No significant correlation was found between the frequency of the owl's flights and the daily low temperatures. Prey availability and hunting success would appear to be more influential factors.

Hunting methods.—Three hunting methods were employed by the Snowy Owl: still-hunting, ground-hunting and coursing. During still-hunting the owl scanned the surrounding area from a commanding perch on, in decreasing order of frequency: utility poles, fence posts and the tops of hillocks. The owl perched in a tree 5 times ($\bar{x}$ duration = 10 min; range = 3–31 min). One successful strike was launched from a tree.

Still-hunting was used most often (92.5%) and averaged 99 min in duration (range = 67–252 min; N = 21). Twenty-five successful strikes were observed during 35 h of still-hunting, for 0.7 successes per h of effort. Still-hunting minimizes energy expenditure because a large area can be monitored from a single high perch and thus seemed to be the most appropriate during the winter.

Ground-hunting (6.8%) involved walking and/or hopping on the surface and breaking through the snow either with the talons or the beak. The owl pulled vigorously at the ground vegetation exposed by the lunges, tearing open surface runways of voles. Mice under snow are thought to be located by ear by Great Gray Owls (*Strix nebulosa*) (Law, Blue Jay 18:14–16, 1960; Godfrey, Can. Field-Nat. 81:99–101, 1967) and are audible through 25–30 cm of snow to other winter predators such as the red fox (*Vulpes vulpes*) (Kirk, Snow, William Morrow, New York, N.Y., 1977).

Ground-hunting averaged 19 min in duration (range = 7–41; N = 8). One successful strike occurred 9 min after ground-hunting began. This single success, during 152 min of ground-hunting, gave a rate of 0.4 successes per h of effort. No ground-hunting was observed prior to 10:00, further suggesting its secondary importance to still-hunting.

Coursing is a low, search flight over the ground that allows the hunting of a large area with few high perches. According to Watson (1957) systematic quartering over the ground was a common hunting method of breeding owls in the summer. Coursing was observed only twice during this study (0.7% of all hunting time) and was limited to the snow-free areas of the road right-of-way and a barnyard. The 2 search flights lasted 5 and 11 min.

Once, after staring intently at some potential prey, the owl made a low pass over the spot, landing on a nearby stump for a closer examination. After 4 min the owl took flight and hovered for 2 sec over the site before returning to the original perch. Hovering is common during summer (Watson 1957).

Small mammals were usually carried in the talons to a perch for consumption. Occasionally, when the owl landed in the snow during a strike or captured prey while ground-hunting, the prey were consumed on the ground. The owl fed on the remains of a rabbit (*Sylvilagus floridanus*) while on the ground.

Post-capture treatment of prey by the owl appeared to reflect degree of satiation. On 2

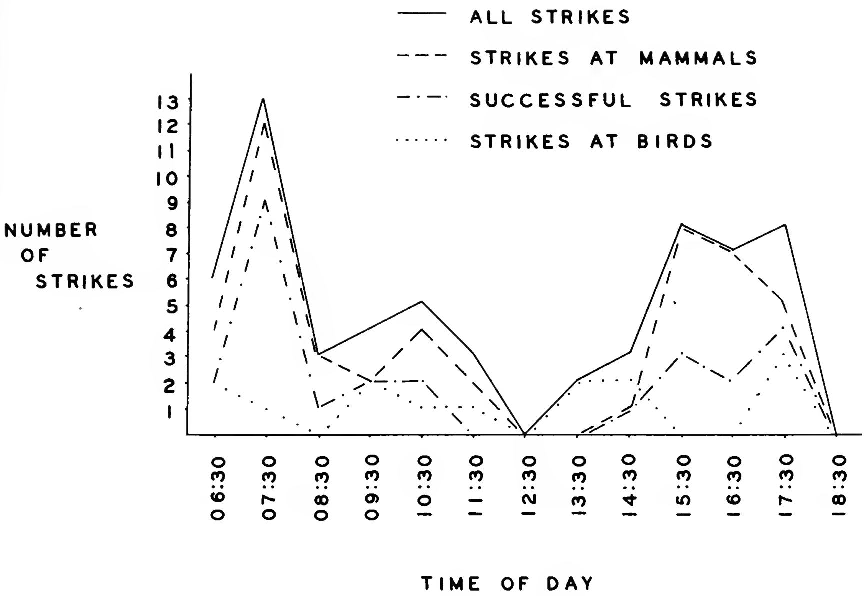


FIG. 1. Number of strikes relative to time of day. Each time block represents 10–11 h of observation.

occasions, when 3 voles were consumed during 1 hunting period, the first voles were totally consumed with 4 quick swallows. Once, the second vole was swallowed immediately, and in the other case held in the talons and mantled before being swallowed whole. The third vole was dismembered and eaten piece by piece. After 1 such bout the owl repeatedly stuck its bill in the snow.

The usual handling time of prey (i.e., the kill, retrieval of prey to a perch, manipulations of prey for consumption) lasted 1–2 min. However, on 1 occasion I saw the owl sit with a freshly caught vole in its talons for 11 min; it regurgitated a pellet, then immediately swallowed its prey.

Hunting success and prey species.—Twenty-six (41.9%) of 62 strikes were successful. The average strike rate per h was 1.7, of which successful strikes averaged 0.7 per h. Excluding 14 unsuccessful strikes at avian prey, the owl's hunting success of mammalian prey was 54.2%. The morning success rate was 59.2% compared with 47.6% during afternoon.

Based on pellet analysis (N = 51) the meadow vole was the most frequent food item, with 159 individuals comprising 86.0% of all prey represented. Of 244 innominates, 85.2% were sufficiently intact to sex, yielding a ratio of 3 females to 1 male. Catling (1973) and Allan (1977) also found this species to be the most common food item of Snowy Owls wintering in southern Ontario and northwestern lower Michigan, respectively.

Other mammalian remains comprised 19 white-footed mice (*Peromyscus* spp., 10.3%) and 6 short-tailed shrews (*Blarina brevicauda*, 3.2%). *Peromyscus* skulls were too fragmentary to differentiate *P. leucopus* from *P. maniculatus bairdi*, however, only *P. leucopus* was trapped in the area. The owl was once observed feeding on a cottontail rabbit. Fur of this species was found in only 1 pellet.

TABLE 1
MEAN SNOW DEPTH RELATIVE TO TIME OF YEAR

Date	Selected sites of frequent strikes (cm)	Random sites (cm)	All sites (cm)
11–19 Feb.	33.4	57.2	45.3
20–26 Feb.	47.8	62.2	55.0
27 Feb.–5 Mar.	41.4	58.6	50.0
6–12 Mar.	30.4	52.2	41.3
13–19 Mar.	27.6	46.8	37.2

All 14 attacks on birds were unsuccessful. Of the 4 species attacked, the Blue Jay (*Cyanocitta cristata*), Starling (*Sturnus vulgaris*) and Snow Bunting (*Plectrophenax nivalis*) have been listed as prey (Gross 1944, Watson 1957, Allan 1977) although, to my knowledge, the Horned Lark (*Eremophila alpestris*) has not. Birds were attacked throughout the day while in flight, perched in a tree or on the snow.

Prey vulnerability.—Peak hunting activity (highest strikes per h) occurred 1 h after sunrise and 1-2 h before sunset (Fig. 1) parallelling peak activity of meadow voles (Hamilton, Ecology 18:255–263, 1937). Hunting success was 75.0% during the first h after sunrise, compared with 47.2% for the remainder of the day. Hamilton (1937) also showed early morning to be the time of greatest vole movement. Craighead and Craighead (Hawks, Owls and Wildlife, Dover, New York, N.Y., 1956) found vole movement increased vole vulnerability to predation. The Snowy Owl appears to be adapted to hunt during these peaks of vole activity and thus successfully take full advantage of localized abundances of this prey species.

A common sign of vole activity was ventilation holes. Mild, stable temperatures under deep snow allow bacterial decay to continue even during the winter (Pruitt, Sci. Am. 202:61–68, 1960; Kirk 1977). Moving away from areas of greatest concentration of the carbon dioxide generated during decomposition, voles tunnel up through the snow, thus constructing ventilation shafts which aerate the subnivean runways. Examination of the snow surface at the sites of successful strikes revealed that voles were very frequently captured at these holes.

Greatest mean snow depth (55.0 cm) occurred during the third week of February, after which snow cover progressively diminished (Table 1). General thawing began the second week in March and continued through the remainder of the month. During mid-March the tops of hillocks and some of the south- and west-facing slopes were bare of snow. These areas were crisscrossed with vole runways. Throughout the winter voles eat subnivean vegetation leaving greatly reduced cover after the snow melts, thus increasing vulnerability to predation (Craighead and Craighead 1956) and as suggested in Table 1. The snow depth of the areas in which prey were captured averaged significantly less than that of randomly selected sites ($t = 4.2$, $P < 0.025$).

Pellet formation.—Pellet regurgitation was seen on 8 occasions (4 observing, 3 loafing, 1 hunting) between 10:00 and 15:30. Twice the owl was under continual surveillance, from prey capture to pellet casting. The owl required 5 h 38 min and 7 h 11 min for pellet formation. Mean length and weight of 51 pellets were 60.6 mm ± 30.5 and 7.7 g ± 6.3, respectively.

Appreciation is extended to L. Susan Ramsay and Alan McKelvy for their assistance in the field and to Peter Colson for his help with the pellet analyses.—MICHAEL L. CHAMBERLIN, *Interlochen Arts Academy, Interlochen, Michigan 49643.* *Accepted 25 Mar. 1979.*

Wilson Bull., 92(1), 1980, p. 121

Warblers feeding from ice.—On 5 May 1970, Philip D. Ould and McNicholl observed approximately 30 Yellow-rumped (Myrtle) Warblers (*Dendroica coronata*) hopping and walking on both fallen cattail (*Typha* sp.) stems and a thin sheet of ice near Hazel Creek in southern Manitoba. The birds were feeding on small black animals on the ice and in the water, these animals appearing to be identical to small dipterans which were flying in abundance over the water.

Goossen observed numerous migrant warblers, including Palm (*Dendroica palmarum*), Yellow-rumped (Myrtle), Yellow (*D. petechia*) and Blackburnian (*D. fusca*) feeding in scattered groups on the ice of Lake Manitoba at Delta Manitoba, during the exceptionally inclement spring of 1974 in which considerable mortality of passerines was recorded in southern Manitoba (Serie and Jones, Prairie Nat. 8:33–39, 1976). An examination of the ice on 22 May showed that Coleoptera, Chironomidae and other Diptera and Araneae were all present on the ice at this time.

Storms and cold spells are not infrequent in late spring on the Canadian prairies. During such periods insects die or become sluggish. Foraging by warblers on lethargic or dead insects on ice surfaces may simply constitute an opportunistic response to a readily obtained food supply in some cases, as at Hazel Creek, but would also have value in times of food shortage. This would be especially important during migration, when energy resources are likely low or depleted. Similar behavior by a Bohemian Waxwing (*Bombycilla garrulus*) has been reported (Kerr, Calgary Field Nat. 7:240, 1976), and may be of regular occurrence in insectivorous species migrating under adverse conditions.

We thank Jon C. Barlow, Spencer G. Sealy and 2 anonymous referees for comments on earlier drafts of this note, and Sealy for the suggestion that we collaborate. This constitutes Publication No. 23 of the University of Manitoba Field Station (Delta Marsh).—MARTIN K. MCNICHOLL, *Beak Consultants Ltd., 3530 11 A St. N.E., Calgary, Alberta T2E 6M7 Canada,* AND J. PAUL GOOSSEN, *Dept. Zoology, Univ. Manitoba, Winnipeg, Manitoba R3T 2N2 Canada.* (Present address JPG: *Regent College, 2130 Wesbrook Mall, Vancouver, British Columbia V6T 1N6 Canada.*) *Accepted 12 Dec. 1978.*

Wilson Bull., 92(1), 1980, pp. 121–122

Rough-winged Swallow feeding on fly larvae.—On 22 May 1977, while driving along the Lake Huron shoreline near Alabaster, Iosco Co., Michigan, I observed a pair of Rough-winged Swallows (*Stelgidopteryx ruficollis*) flying and occasionally landing on the beach near dead fish. Since this species seldom lands on the ground except to procure nesting material or enter a burrow, their actions seemed unusual. The birds were observed from 06:50–07:05 with 7 × 50 binoculars, at approximately 15 m for 5 min and 9 m for 10 min.

Only 1 bird picked material up from the beach or from the dead fish. The other bird circled or landed within 1 m of the feeding bird. The pair flew along the beach for short distances from location to location, but occasionally flew as much as 100 m before returning to the original area. Often the foraging bird walked to several different fish before again taking flight and was then followed by the second bird. I examined the last fish at which the bird stopped and the surrounding area; fly larvae were found in and on both the sand and dead fish (apparently an alewife [*Alosa pseudoharengus*]).

Although members of the order Diptera are a major portion (33%) of the rough-wing's diet (Beal, Food Habits of the Swallows, A Family of Valuable Native Birds, USDA, Bull. 619, 1918; Bent, Life Histories of North American Flycatchers, Larks, Swallows and Their Allies, Dover, New York, N.Y. 1963:429) these insects are taken as adults through aerial foraging by the swallows. This observation seems to represent an opportunistic foraging technique in response to a short-term, high density food source on the part of at least 1 of the observed pair.—RICHARD A. WOLINSKI, *11460 Chamberlain Dr., South Lyon, Michigan 48178.* (Present address: *3143 Braeburn Circle, Ann Arbor, Michigan 48104.) Accepted 20 Jan. 1979.*

Wilson Bull., 92(1), 1980, p. 122

Sandhill Cranes prey on Canada Goose eggs.—Harvey et al. (Wilson Bull. 80:421–425, 1968) reported Lesser Sandhill Cranes (*Grus canadensis canadensis*) feeding on the eggs and hatching young of Blue Geese (*Anser caerulescens*) and Willow Ptarmigan (*Lagopus lagopus*). Littlefield (Wilson Bull. 88:503–504, 1976) saw Greater Sandhill Cranes (*G. c. tabida*) eat young Gadwalls (*Anas strepera*) and Mallards (*A. platyrhynchos*). The literature does not mention Sandhill Cranes eating Canada Goose (*Branta canadensis*) eggs.

On 12 April 1978, I was walking with a biology class along the edge of a marsh in northwestern Washtenaw County, Michigan. With 8 × 40 binoculars, I observed 3 Sandhill Cranes standing approximately 60 m away. Another crane was sitting on a nest about 15 m from these cranes, and a Canada Goose was incubating a clutch of eggs approximately 30 m equidistant from the 3 cranes and the nest. Two of the 3 cranes walked toward the goose nest. When 5 m from the nest the goose flew at the cranes and was joined by another goose in a short, but unsuccessful attempt to chase the cranes away. The cranes then approached the nest and first one, then the other ate the eggs. The geese swam nearby calling repeatedly but they did not attempt to chase the cranes. The cranes also did a great deal of calling while at the goose nest.

I waded out to the goose nest 2 h later and found a few eggshells and some eggwhite in the water next to the nest. A crane was still sitting on its nest and another crane was standing nearby; the other 2 cranes and the geese had gone.

The 2 cranes that ate the goose eggs were undoubtedly nonbreeders, although it is unusual for nesting cranes to allow such nonbreeders in their territory. A nonbreeding pair of cranes was also seen several times before and after 12 April in the marsh, but never again as close to the crane nest.

In the marshes of southern Michigan, Sandhill Cranes and Canada Geese frequently nest close to each other with little interaction. In the past 10 years, while studying 138 Sandhill Crane nests, I have found no evidence of cranes feeding on goose eggs, even when the 2 species had nests in much closer proximity than in the above example of egg predation. Cranes are opportunistic feeders (Mullins and Bizeau, Auk 95:175–178, 1978) and will uncommonly eat Canada Goose eggs.—RONALD H. HOFFMAN, *6142 Territorial Rd., Pleasant Lake, Michigan 49272. Accepted 3 Jan. 1979.*

Wilson Bull., 92(1), 1980, pp. 122–123

Adult Brown Pelican robs Great Blue Heron of fish.—At 11:45 on 7 March 1978, on Little Cumberland Island, Georgia, I watched a Brown Pelican (*Pelecanus occidentalus*) rob a Great Blue Heron (*Ardea herodias*) of a fish. The heron captured a 28–33 cm fish in a 60 × 80 m tidal pond located 150 m from the open ocean and carried it to the ground and there manipulated it. Within 45 sec, 3 of 8 adult pelicans that were fishing over the pond circled in a 7 m radius, 8–10 m above the heron. Each stooped several times within 3–4 m of the fish. After 8–10 circuits 1 of the pelicans landed on the heron's head forcing it to release the fish from its bill, whereupon the pelican dropped to the ground next to the heron, picked up the fish and swallowed it. Simultaneously, the other 2 pelicans landed within 1 m of the first and watched it as it consumed the fish. Neither attempted piracy and all 3 took wing as soon as the fish was eaten and recommenced flying over the pond. The heron did not attempt to recover its dropped prey.

Although they themselves are sometimes victims of piracy (Findley, Condor 9:35, 1907; Meinertzhagen, Pirates and Predators, Oliver and Boyd, Edinburgh, Scotland, 1959; Palmer, Handbook of North American Birds, Vol. 1, 1962), and are known to scavenge and fight with gulls for offal thrown overboard (Gifford, Proc. Cal. Acad. Sci. 4th Ser., Vol. 2, Pt. 1, 1913; Sefton, Condor 52:136–137, 1950), piracy of Great Blue Herons by Brown Pelicans is previously unreported.—KEITH L. BILDSTEIN, *Dept. Biology, Winthrop College, Rock Hill, South Carolina 29733. Accepted 28 Nov. 1978.*

Wilson Bull., 92(1), 1980, pp. 123–125

Food habits of White Pelicans during 1976 and 1977 at Chase Lake National Wildlife Refuge, North Dakota.—Quantitative studies of White Pelican (*Pelecanus erythrorhynchos*) food are lacking; however, lists of prey species taken in North Dakota have been reported by Coues (Govt. Printing Office, Washington, D.C., 1874), Kolstoe (North Dakota Outdoors 29:16–20, 1966) and Anderson et al. (Can. Field-Nat. 83:91–112, 1969). During the summers of 1976 and 1977, we studied prey species consumed by White Pelican chicks at Chase Lake National Wildlife Refuge, North Dakota.

The 1774.6 ha Chase Lake N.W.R. is 13 km north of Crystal Springs, Stutsman Co., North Dakota. Most of the refuge is covered by water (50%) and native and cultivated grasses (45%); the remainder is brush and marsh. It lies in the Missouri Coteau of the glaciated Prairie Pothole region (U.S.D.I., Bur. Sport Fisheries and Wildl., Washington, D.C., 1971) and supports the largest breeding population of White Pelicans in North America, ranging from 8000–10,000 nesting birds (Sloan, I.B.B. News 45:83–86, 1973).

Methods and materials.—Disgorged food samples were collected from chicks of varying ages, and analyzed. From 2 June through 3 August 1976, 84 regurgitated boli were collected and analyzed volumetrically with water displacement recorded as the volume per sample. When several prey species were present in the sample, each item was measured independently and a percent of the total volume was recorded. In addition, 458 boli were qualitatively analyzed, i.e., prey species noted and percent composition per sample calculated.

From 6 June–8 August 1977, 60 boli were volumetrically analyzed and 489 were qualitatively analyzed; 1091 samples were studied during both years. Relative frequency by number (RFN), frequency of occurrence (FO) and relative frequency by volume (RFV) of each prey species were computed (see Table 1 for definitions). RFN and FO were based on both volumetric and qualitative analysis, while RFV was based only on volumetric measurements.

To determine the distance traveled by White Pelicans in search of food 130 adults were marked in June 1977 with picric acid using a modification of the color-marking device described by Moseley and Mueller (Bird-Banding 46:341–342, 1975). A request for information on sightings of marked individuals was sent to all state and federal personnel in North and South Dakota.

TABLE 1
WHITE PELICAN FOOD HABITS ANALYSIS AT CHASE LAKE NATIONAL WILDLIFE REFUGE DURING 1976–1977

Prey species	Relative frequency by numbers[1]		Frequency of occurrence[2]		Relative frequency by volume[3]	
	1976	1977	1976	1977	1976	1977
Adult tiger salamander (*Ambystoma tigrinum*)	1.3	0.8	8.3	30.5	4.2	3.9
Larvae tiger salamander	61.2	26.7	62.1	12.3	60.2	45.8
Combined salamander	62.5	27.5	70.4	42.8	64.4	59.7
Brook stickleback (*Eucalia inconstans*)	16.2	31.3	8.7	5.9	—	2.2
Black bullhead (*Ictalurus melas*)	8.3	2.1	13.3	32.6	13.5	13.6
Fathead minnow (*Pimephales promeias*)	—	19.2	1.0	5.0	0.2	2.3
Carp (*Cyprinus carpio*)	0.8	0.8	13.1	17.0	—	9.9
Yellow perch (*Perca flavescens*)	6.9	7.0	8.3	4.4	1.6	5.4
Crayfish (*Astacus* sp.)	1.7	11.9	7.2	3.5	7.3	2.1
Northern pike (*Esox lucius*)	2.7	0.1	1.3	2.6	0.1	4.2
White sucker (*Catastomus commersoni*)	0.2	0.2	0.8	1.0	—	—
All other species	1.5	0.6	3.2	1.4	12.9	—

[1] RFN = (number of individuals of a species/total number of individuals of all species) × 100. Based on 1408 prey items in 1976 and 1984 prey items in 1977.

[2] FO = (number of samples in which a species occurs/total number of samples) × 100. Based on 542 samples in 1976 and 549 samples in 1977.

[3] RFV = (volume of a species/total volume of all species) × 100. A total of 9220 ml of biomass was analyzed in 1976 and 10,274 ml in 1977.

A United States weather station located in Pettibone (12.8 km NNW of Chase Lake) provided monthly precipitation data. Pothole abundance, recorded at Woodworth Wildlife Research Station (19.2 km NE of Chase Lake), was used as an index for availability of foraging areas.

Results and discussion.—Composition of regurgitated boli in terms of RFN, FO and RFV are summarized in Table 1. The single most important prey item in both years was the larvae of the tiger salamanders (*Ambystoma tigrinum*). Sightings of 13 dyed pelicans in 1977 gave us some idea of foraging areas used by the Chase Lake flock. Six sightings occured at Woodworth Wildlife Research Station. The sighting most distant from Chase Lake (51.2 km) was at Arrowwood National Wildlife Refuge, where an individual was observed in a group of approximately 1000 pelicans. Johnson (M.S. thesis, Mich. Tech. Univ., Houghton, Michigan, 1976) reported round-trip foraging distances of 96–611 km for this colony.

Types of wetlands used by feeding pelicans included seasonal, semi-permanent and permanent ponds and lakes with fresh or slightly brackish water. The vegetative cover of these areas was disjunct or was primarily open water. Pelicans actively fed along the shoreline or in shallow, open water and avoided dense emergent vegetation.

Wetland conditions varied considerably between 1976 and 1977. During May–August 1974–1976, 30–65% of wetland basins occurring on the Woodworth Study Area (19.2 km NE of Chase Lake) contained water. In 1977, only 5% of the basins had water in them, despite similar amounts of precipitation (1974–1976 $\bar{x}$ precipitation = 36 cm, 1977 = 31 cm) (Leo Kirsch, unpubl. data). The natural drawdown phase of the potholes in 1977 allowed exploitation of prey in areas inaccessible the previous year. Black bullheads (*Ictalurus melas*), carp (*Cyprinus carpio*), brook stickleback (*Eucalia inconstans*), and fathead minnows (*Pimephales promeias*) were concentrated in portions of drying sloughs, making them vulnerable to pelican predation. Consequently, these species formed a larger proportion of the pelican's diet in 1977 (Table 1). In 1976, higher water levels inundated shoreline vegetation which provided cover for smaller fish, such as brook stickleback and fathead minnows. Tiger salamander larvae and noetenic forms feed largely on these 2 species (Buchli, M.S. thesis, Univ. North Dakota, Grand Forks, N.D., 1964) and a greater use of salamanders by pelicans occurred in 1976 (Table 1).

Since approximately ¼ of the North American breeding population of White Pelicans nests at Chase Lake, the success of this colony is essential to the maintenance of the continental population. Chase Lake now has additional protection under the 1964 Wilderness Act; however, the foraging areas of the Chase Lake flock suffer under land-use practices which favor drainage, channelization and large reservoirs. This will eventually have an adverse effect, not only upon the pelicans, but also on the multitude of waterfowl and marsh birds nesting there.

We appreciate the logistic support of the Northern Prairie Wildlife Research Center, Jamestown, N.D.; Arrowwood National Wildlife Refuge, Pingree, N.D.; and Woodworth Wildlife Research Station, Woodworth, N.D. A special thanks is extended to Mr. Leo Kirsch and Mr. Kenneth Higgins for their advice and support. This project was part of a graduate study through the Dept. of Forestry, Michigan Technological University, Houghton.—GARY R. LINGLE AND NORMAN F. SLOAN, *Dept. Forestry, Mich. Tech. Univ., Houghton, Michigan 49931.* *Accepted 6 Sept. 1978.*

Wilson Bull., 92(1), 1980, pp. 125–126

Notes on the birds of Honduras.—The study by Monroe (A Distributional Survey of the Birds of Honduras, A.O.U. Monogr. No. 7, 1968) brought together previous information and recorded the results of his own field work in many parts of the country. During a brief visit to Honduras from 23 May–5 June 1973, we obtained a few specimens and sight records that extend the time or area of occurrence of some species recorded by Monroe. Significant records were obtained at Lake Yojoa, elev. 630 m, in the Dept. Cortes in west-central Honduras; at Tela, sea level, in the Dept. Atlantida on the Caribbean coast; and at Choluteca and the Bay of Fonseca area, sea level, in the Dept. Choluteca on the Pacific slope. All specimens obtained have been deposited in the Yale-Peabody Museum collections.

On 30 May, we collected a nonbreeding male Great Egret (*Casmerodius albus*) on the shore of Lake Yojoa. This represents the second specimen for the country of this common species (YPM [Osteo.] 8150).

On 31 May, 4 h were spent exploring the coastal mangrove swamps at Tela. The following 3 species may summer regularly in the mangrove lagoons along the Caribbean coast; the scarcity of records probably reflects the scarcity of visits by ornithologists.

Common Terns (*Sterna hirundo*). A small flock of these terns was seen and 1 immature male was collected (YPM [Osteo.] 8161). This is the second specimen record for Honduras (see Brown and Monroe, Condor 76:348–349, 1974).

Black Terns (*Chlidonias niger*). Several of these terns, in nonbreeding plumage, were present with other terns. The only previous spring record was 13 April.

Black Skimmers (*Rynchops nigra*). Several skimmers were seen, and 1 male was collected (YPM [Osteo.] 8160). This is the first specimen record and the third record for the country.

The afternoon of 3 June and the morning of 4 June were spent exploring the farmland and brackish backwaters around Choluteca and the eastern side of the Bay of Fonseca.

Collared Forest-Falcon (*Micrastur semitorquatus*). On 3 June a light phase adult of this species was seen feeding an immature bird (YPM 88922). This is the first record from the Pacific slope of Honduras, but the occurrence was predicted by Monroe (1968).

American Oystercatchers (*Haematopus palliatus*). On 3 June, 2 oystercatchers were observed as they fed around a small pond. The previous 3 records for Honduras (Brown and Monroe 1974) are all from the Caribbean coast.

A number of shore and marsh birds may summer regularly in the marshy country around the Bay of Fonseca. Again the lack of records probably reflects our limited knowledge of bird life in that area. For example, the following species represent later spring records than any reported by Monroe (1968): Great Blue Heron (*Ardea herodias*), 1; Whimbrel (*Numenius phaeopus*), 10; Lesser Yellowlegs (*Tringa flavipes*), several; Willet (*Catoptrophorus semipalmatus*), several; dowitcher (*Limnodromus* sp.), 8–10; Black-necked Stilt (*Himantopus mexicanus*), 100–150.

We are grateful for the friendly assistance of the officials of the Escuela Agricola Panamericana, and wish to express our special thanks to Miguel Avedillo and Antonio Molina.—Fred C. Sibley, George F. Barrowclough and Charles G. Sibley, *Peabody Museum, Yale Univ., New Haven, Connecticut 06520.* (Present address GFB: *J. F. Bell Museum of Natural History, Univ. Minnesota, Minneapolis, Minnesota 55455.*) *Accepted 10 Jan. 1979.*

Wilson Bull., 92(1), 1980, pp. 126–127

A nest of the Ringed Gnatpipit (*Corythopis torquata*).—The nest of the Ringed Gnatpipit (*Corythopis torquata*) seems not to have been described. While studying Amazonian birds in swampy, mature forest of the Aurá Reserve (Oniki, Acta Amazonica 2:59–79, 1972) near Belém, Brazil, on 30 November 1972, E. O. Willis located, on the ground by a log, an oven-shaped nest of this species.

One singing bird walked near a second individual, which entered the nest. The moss-covered nest, now in the collection of the Museu Goeldi in Belém, has the side entrance somewhat overhung on the upper rim. Other than external mosses, the nest material is mostly leaves, twigs and rachises of Leguminosae; just beneath the lining is a layer of softer decomposed leaves. The lining is of fine rhizomorphs. The nest weighed 45 g when dry, and measured 12 cm high by 13.5 cm long outside; the entrance was 5.5 cm in diameter and the nest chamber 9.5 cm deep from the entrance.

When discovered, the nest contained 2 large pinkish or buffy eggs with very slight mottling of darker buff around the large end. On 8 December, the nest contained 1 young and 1 egg.

On 9 December there were 2 young, which had sparse dusky down on head, wings and back. On 19 December, 2 were still in the nest. On 21 December at 14:20, the single remaining bob-tailed, but well-feathered, young flew from inside the nest, fluttering away close to the ground.

The adults were very timid. Only twice in 15 visits after discovery did an adult fly out of the nest, snapping its beak. In 1 of the 15 visits (17 December) an adult snapped its beak and sang faintly as it walked on the forest floor near the nest.

Oven-shaped nests, pinkish-buffy eggs and downy young are found in many Tyrannidae but seldom in Formicariidae. This may support placement of the genus in the Tyrannidae as suggested by Ames, Heimerdinger and Warter (Postilla 114:1–32, 1968). However the general nest type and egg color of this species do occur in ground-nesting birds of various families.

Fieldwork was possible thanks to Princeton University and to grants GB-32921 from the National Science Foundation and TC no. 6998-71 from the Conselho Nacional de Pesquisas of Brazil.—YOSHIKA ONIKI AND EDWIN O. WILLIS, *P.O. Box 644, Silver Spring, Maryland 20901.* (Present address YO: *Avenida Modesto Fernandes s/no., Bairro Barão Geraldo, 13.100 Campinas, S. Paulo, Brazil*; EW: *Dept. Biology, P.O. Box 249118, Univ. Miami, Coral Gables, Florida 33124.*) *Accepted 4 Dec. 1978.*

Wilson Bull., 92(1), 1980, pp. 127–128

First breeding record of the Double-crested Cormorant in Virginia.—While investigating the breeding avifauna of the lower James River during the summer of 1978, we found active nests of the Double-crested Cormorant (*Phalacrocorax auritus*) in Charles City County, Virginia. As there are no previous records of the nesting of this species in Virginia, and only 1 other breeding locality in this region of the Atlantic seaboard (southeastern North Carolina; Parnell, N.C. State Mus. Nat. Hist. 1977:330–384), we felt that documentation of these nests should be of interest.

The nest-site is located within a heronry on the remains of old, sunken, gravel barges near the middle of the James River approximately 3 km east of Hopewell, Virginia, and is 1.5 km from either shore. Trees and shrubs have become established on the wood of the barges, although there is no soil substrate associated with the "island." The vegetation includes silver maple (*Acer saccharinum*), sycamore (*Platanus occidentalis*), river birch (*Betula nigra*) and at least 4 other woody species of plants. The height of the vegetation is approximately 7 m and the dimensions of the island are 25 × 75 m. A heronry, first noticed in 1977, completely occupies the site. Cormorants might have nested in 1977 as they were seen in the area after the breeding season, but our surveys were too late that year to detect nesting. Censuses during May, June and July, 1978, revealed the presence of the following nests (maximum number): Cattle Egret (*Bubulcus ibis*), 298; Great Egret (*Casmerodius albus*), 6; Snowy Egret (*Egretta thula*), 1; Little Blue Heron (*Florida caerulea*), probably 1 pair, nest not found; Green Heron (*Butorides striatus*), 1; and Double-crested Cormorant, 6. We observed the cormorants sitting on nests on 29 May and these were subsequently observed by F. R. Scott, W. K. Slate and H. Olson (pers. comm.) on 5 June. The cormorant nests began to disappear on-by-one and by 26 June (Scott and Olson, pers. comm.) all were gone. The nests were probably removed by Cattle Egrets which we observed taking material from nearby nests of their own species and of other egrets. Production of young by the cormorants was not substantiated, but 1 or more immature birds were seen within 100 m of the island on 26 June and 4 and 13 July.

The expansion of the range of this species, especially at this inland site more than 100 km from the ocean, is puzzling. It is not known whether these nests represent an expansion of the breeding range of *P. a. floridanus*, which nests only in Florida, Louisiana and at a single site in southeastern North Carolina more than 350 km south of the present locality (see American Ornithologists' Union, Check-list of North American Birds, 5th ed., Baltimore, Maryland, 1957; Parnell 1977), or of *P. a auritus*, which nests about 800 km away in Tennessee and Kentucky (Mengel, The Birds of Kentucky, Ornithol. Monogr. 3, 1965) or 650 km northward in New York (Bull, Birds of New York State, Doubleday Nat. Hist. Press, Garden City, New Jersey, 1974). Both *floridanus* and *auritus* occasionally nest in trees with various herons; the latter is particularly prone to do so in the southern part of its range (Bent, U.S. Natl. Mus. Bull. 121, 1922; Bull 1974). Additionally, the nest-site is very near Bailey Creek, the source of severe Kepone pollution, which has plagued the James River and Chesapeake Bay for the past few years. The sediments in this part of the river are known to remain high in levels of this pollutant. As nearly all fish species in this area have been found to contain Kepone levels detrimental to human health, the taking of fish from the James River has been banned since 1975. Kepone is known to have estrogenic activities in birds and may induce eggwhite protein synthesis (Palmiter and Mulvihill, Science 201:356–358, 1978). However, neurological symptoms appear at dosages lower than those producing the estrogenic effect. Since the cormorants forage extensively in the area of Kepone pollution, the future of this colony would indeed seem to be tenuous.

We are indebted to F. R. Scott for assistance in preparing this note and to C. F. Murray and T. Saunders for help in the field.—CHARLES R. BLEM, WILLIAM H. N. GUTZKE AND CLAIRE FILEMYR, *Dept. Biology, Virginia Commonwealth Univ., Academic Division, Richmond, Virginia 23284.* *Accepted 2 Jan. 1979.*

Wilson Bull., 92(1), 1980, pp. 128–130

Corn cob manipulation in Northern Harriers.—Captive and free-ranging raptors, especially juveniles, often playfully manipulate a variety of inanimate objects, including dead prey, twigs, pieces of wood, pine cones, corncobs, clusters of dead leaves, clumps of grass, stones, cow dung, balls of paper, handkerchiefs and feathers (Ficken, Auk 94:573–582, 1977). Because such behavior is common among predatory birds, and because all manipulated objects appear to be within the size range of the raptors' prey, manipulative play behavior has been suggested as a mechanism whereby young raptors acquire skills in prey capture (Fagen, pp. 189–200 *in* Perspectives in Ethology, Vol. 2, Bateson and Klopfer, eds., Plenum, New York, N.Y., 1976; Ficken 1977). Here I compare the sizes of corn cobs manipulated by Northern Harriers (*Circus cyaneus*) with the size of the harriers' principal prey species, the meadow vole (*Microtus pennsylvanicus*).

During the winters of 1973–1974 through 1975–1976, I watched harriers in south central Ohio (Bildstein, unpubl. Masters thesis, The Ohio State Univ., 1976). On 7 occasions during evening pre-roosting, and twice during morning post-roosting periods, I saw harriers pouncing on and carrying, dropping and catching in midair, and apparently "eating" corn cobs. All of the cobs were without kernels; several were caked with mud. On 6 occasions I saw harriers pounce on, and carry, clumps of dirt and grass as well as pull on, and sometimes uproot vegetation. Adult males were seen playing twice, females 8 times and juveniles of unknown sex 14 times. Although harriers frequently snatch vegetation while pouncing on prey and are known to pounce on, and carry, microtine nests (Rolfe, Nidologist 4:39–41, 1897), the behavior I watched was distinctly different from this since it involved extensive repetition of behavioral sequences, more closely resembling a kitten playing with a ball of yarn than a raptor capturing prey (Ficken 1977).

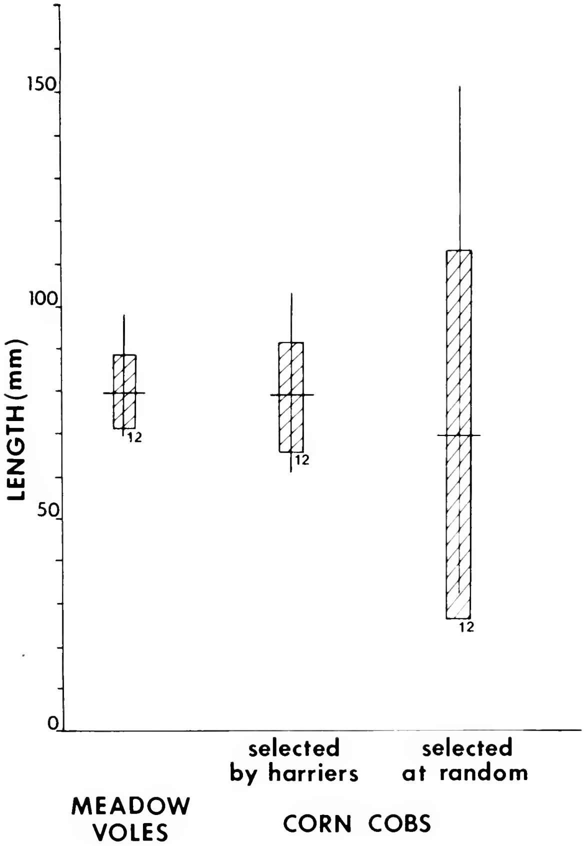


FIG. 1. Lengths of meadow voles, corn cobs selected by harriers and randomly collected corn cobs. Data are presented as the mean ± SD and the range. Sample sizes are shown below the bars.

Harriers were more likely to initiate play if a nearby bird did so, and as many as 3 harriers "played" with corn cobs within 50 m of one another. Whenever possible I noted the location at which a harrier dropped its manipulated object and I attempted to retrieve it. Eighty-five percent (33 of 39) of the objects manipulated were corn cobs, and during the winter of 1975–1976 I was able to collect 12 of them. Three of the retrieved cobs had been manipulated by adult females and 9 by juveniles of unknown sex. All had been carried from an adjacent corn stubble field to the roost field where they were dropped and could be found with certainty. None of the harrier-selected cobs had husks attached. On 11 March 1976, the last day of observation, I used the stick-toss method (Greig-Smith, Quantitative Plant Ecology, Butterworth, London, England, 1964) and randomly collected corn cobs from the same stubble field the harriers had used. As harriers seemed to have selected only huskless cobs, I continued to toss sticks until I had collected 12 cobs without husks. Because it was possible that harriers had differentially depleted the area, I collected cobs only from the side of the field farthest from the roost where harriers had not been seen taking play objects.

Because voles comprised over 85% of these harriers' diet (Bildstein, unpubl. Ph.D. dissert., The Ohio State Univ., 1978), 12 meadow voles were live-trapped and their body lengths measured from photographs.

Since there was no apparent difference in the variance and mean lengths of cobs manipulated by adult females and juveniles of unknown sex, I grouped the cobs ignoring this variable. The lengths of both harrier-selected corn cobs and meadow voles did not differ significantly from randomly collected cobs (approx. t-test, $P > 0.40$, Fig. 1), but variance in the length of the randomly collected cobs was highly significantly different from that of either harrier-selected cobs (F-test, $F = 11.11$, $P < 0.001$) or meadow voles (F-test, $F = 28.70$, $P < 0.001$). Variances in the lengths of harrier-selected corn cobs and meadow voles were not significantly different (F-test, $F = 2.58$, $P > 0.05$). Thus, harriers selected for vole-sized cobs. Harriers did not appear to select corn cobs based on weight. They manipulated both dry, relatively light cobs and completely saturated, relatively heavy cobs.

Although it is possible that physical constraints prevented harriers from manipulating non-vole-sized cobs, this does not appear to be the case. I observed captive harriers manipulate both small fragments of cobs ($<$10 mm) and full length cobs ($>$150 mm), as well as vole-sized cobs. While it is possible that size specificity of harrier play objects results from harriers mistaking corn cobs for voles, I believe this to be highly unlikely. Harriers do not hunt for voles in corn stubble fields (Bildstein 1978), nor do they manipulate their prey to the extent that they manipulate corn cobs. Also, harriers engaged in corn cob manipulation, unlike harriers with voles, interrupted their play frequently, either to fly in tandem with another harrier, or to preen. Therefore, I suggest that harriers do not mistake corn cobs for voles, but rather purposefully select vole-sized play objects. This interpretation supports the hypothesis that play behavior is practice or physical training (Groos, The Play of Animals, Appleton, New York, N.Y., 1898; Bekoff, pp. 165–188 *in* Perspectives in Ethology, Vol. 2, Bateson and Klopfer, eds., Plenum, New York, N.Y., 1976; Fagen 1976), which predicts that play sequences should exercise muscles used in prey capture. By selecting vole-sized play objects harriers improve the coordination necessary to subdue prey.

While the data support the practice or physical training hypothesis they do not negate additional functions. Since juvenile raptors appear to manipulate inanimate objects more frequently than adults (Ficken 1977) raptor play may function in acquisition as well as in maintenance of prey catching skills. Also, raptors often attack and manipulate less "appropriate" nonprey items, including butterflies (Peregrine Falcons [*Falco peregrinus*]) and flowers and leaves (Golden Eagles [*Aquila chrysaetos*]) (Temple, pers. comm.). Why they do so remains unclear.

I thank D. F. Balph, B. Beck, R. Fagen, M. Ficken, T. C. Grubb, Jr., F. N. Hamerstrom, R. L. Orenstein, D. Symons and S. A. Temple for comments on the manuscript. The work was supported in part by the Department of Zoology, The Ohio State University and by the Ohio Biological Survey.—KEITH L. BILDSTEIN, *Dept. Biology, Winthrop College, Rock Hill, South Carolina 29733. Accepted 6 Mar. 1979.*

Wilson Bull., 92(1), 1980, pp. 131–139

ORNITHOLOGICAL LITERATURE

PHILIPPINE BIRDS AND MAMMALS. By Dioscoro S. Rabor. Illus. by Romulo R. Capalad and Porfirio G. Castañeda. University of the Philippines Press, Quezon City (distributed outside the Philippines by the University Press of Hawaii, Honolulu): xi + 284 pp., 131 line drawings. $18.50.—According to the title page, this book is a project of the University of the Philippines Science Center. The Foreward, by J. B. Alvarez, Jr., Assistant Director of the Philippine Bureau of Forest Development, makes it plain that the book is intended to introduce their birds and mammals to the Filipino people, "a great majority" of whom "seem to have a common unconcern" about their native animals. To Americans, the author is undoubtedly the best-known Filipino ornithologist, thanks to his many publications in scientific journals, his several visits to the United States, and the ubiquity in major museum collections of his unmistakable specimens. The provision of such an introductory volume to the people of the Philippines is without question a worthy project: as in any book review, we must examine the question of the author's success in accomplishing this aim. I shall cover only the ornithological portion of the book, thus excluding the 67 pages devoted entirely to mammals.

One hopes, to begin with, that the price of the book in the Philippines is substantially less than the peso equivalent of the $18.50 asked of American purchasers. A book intended for the general populace should obviously be as inexpensive as possible. At $35, duPont's Philippine Birds (1971. Delaware Mus. Nat. Hist. Monograph 2) costs twice as much as Rabor's book, but, if possible, should be in the libraries of Filipino schools and colleges, if only because every species known from the Philippines is illustrated in color. Rabor's book has only line drawings of the 102 species he has chosen as representative of the Philippine avifauna, and these vary from barely adequate to, bluntly, atrocious. It may seem undiplomatic so to characterize the work of the Filipino illustrators, but the drawings are presumably intended to aid in recognition of the species, whereas most are grotesquely distorted, often to the point of being downrightly unrecognizable. Those identifiable as the work of Castañeda (such as *Rallus striatus* and *Dendrocopos maculatus*) tend to be superior to those of Capalad, but are in the minority.

The book begins with a 6-page introduction, which includes a short and over-generalized (to the point of error) account of birds as a group (illustrated by a typical "external topography" diagram and, unaccountably, a half-page drawing of 3 types of tarsal scutellation with no caption explanation or text reference). This is followed by a summary of the Philippine avifauna, explaining very briefly the numbers, endemicity, seasonal status, and extinction or endangerment of native and migrant species. The best part of this introduction is the 2-page section on bird habitats, outlining the typical vegetation at various altitudes, as well as indicating changes effected by man that have altered bird distribution.

Each family of birds is introduced by a generally rather well-done summary of appearance, habits, number of Philippine species, etc. Twenty of the families included by duPont are omitted by Rabor; several of these are seabirds, or rare to accidental in the Philippines, but some of the omissions are surprising. There are 16 species of babblers (Timaliidae of duPont's usage) in the Philippines, but the family is not mentioned. The puzzling creeper-like *Rhabdornis* is omitted, although the 2 species are often given (as by duPont) family status, this being the only endemic family of Philippine birds. During my fieldwork in Luzon in 1956, I found both of the Philippine species of lark (*Alauda gulgula*, *Mirafra javanica*) to be common. The family is not mentioned by Rabor; inexperienced observers of these larks may well believe that they are watching pipits, which Rabor does include (and which are so similar to the larks that I have found specimens of Philippine larks and pipits intermixed in a major U.S. museum).

As indicated earlier, Rabor has made a selection of only 102 of the approximately 500 species of birds recorded from the Philippine Islands. Within such constraints, no 2 authors would choose the same list of species, but some of Rabor's choices and especially some of his omissions are jolting. The species chosen are frequently, but by no means always, those members of a family that are common, widespread in the Philippines, and conspicuous. I was surprised, for example, to find the Pink-bellied Imperial Pigeon (*Ducula poliocephala*) of highland forests and the Nutmeg Imperial Pigeon (*Ducula bicolor*), a bird of islets, included among the Columbidae, but the most conspicuous species in populated areas of Luzon, the Zebra Dove (*Geopelia striata*) omitted. There are 14 resident species of Accipitridae in the Philippines, and 5 regularly wintering species. Rabor has wisely selected the abundant Brahminy Kite (*Haliastur indus* [consistently misspelled "*Haliastus*"]) and the endangered Monkey-eating Eagle (*Pithecophaga jefferyi*) for two of his sample of three of the 19 Philippine species, but for the third, selected the rather uncommon (by his own admission) White-breasted Sea Eagle (*Haliaeetus leucogaster*) rather than, say, one of the 4 *Accipiter* species or the conspicuous Blackwinged Kite (*Elanus caeruleus*).

There is a strong emphasis throughout the book on Negros, the island on which Rabor lived for many years, even though Negros data may not be typical for the archipelago as a whole. The dependence upon the author's own fieldwork for nesting data is almost unavoidable, as there is a deplorable lack of published life history information for even some of the commonest Philippine birds. Rabor must occasionally turn to the literature for data taken from mainland Asia subspecies or even species. According to Rabor, there is no definite breeding information from the Philippines for such well-known species as Cinnamon Least Bittern (*Ixobrychus cinnamomeus*), Little Mangrove Heron (*Butorides striatus*), Little Egret (*Egretta garzetta*), Purple Heron (*Ardea purpurea*), Slaty-breasted Rail (*Rallus striatus*), White-breasted Swamphen (*Amaurornis phoenicurus*), Philippine Hanging Parakeet (*Loriculus philippensis*), Plaintive Cuckoo (*Cacomantis merulinus*), Lesser Coucal (*Centropus bengalensis*), Philippine Trogon (*Harpactes ardens*), Pygmy Woodpecker (*Dendrocopos maculatus*), Pied Triller (*Lalage nigra*), Velvet-fronted Nuthatch (*Sitta frontalis*), and Richard's Pipit (*Anthus novaeseelandiae*). Rabor occasionally relies entirely on gonad data from his specimens, and here he has surely restricted himself too much. For example, for the widespread and well-known Koel (*Eudynamys scolopacea*), Rabor writes: "The nesting [sic—the species is a brood parasite] and breeding of the present form in the Philippines is not definitely known. A female with enlarged gonads was caught in Gubat, Katipunan, Zamboanga Province, Mindanao one May." For a species as common in museum collections as the Koel, there are certainly more label data available than just this single Mindanao record.

One wonders, however, to what extent one can trust Rabor's statements about the lack of breeding data. In some instances he contradicts himself. Of the Gallinule (*Gallinula chloropus*) he states: "Nothing is known of the nesting and breeding of this bird except that the birds are numerous around the edges of Lake Naujan, Mindoro." Two paragraphs later, he writes: "Eggs collected in Samar [a Philippine island] were described as similar to those laid by the European members of this species except for the smaller size and less number of eggs in a clutch." Similarly, of the Black-headed Pitta (*Pitta sordida*) Rabor states: "Nothing definite is known about the nesting and breeding of this bird." The following paragraph is a detailed description of a nest and eggs from Samar. Rabor states that "There are no definite data on the nesting and breeding of [*Alcedo atthis bengalensis*] in the Philippines," which is hardly surprising, as the species is a winter visitor to the archipelago, as he states 2 paragraphs earlier.

There are discrepancies other than those having to do with breeding data. On p. 35, Rabor states that there are still some Monkey-eating Eagles "left in Luzon and are mostly found in the mountains of Nueva Vizcaya, Isabela and Quezon [provinces of Luzon], mainly in the well-forested regions of the Sierra Madre Range." He there gives the population on Mindanao as 25–30 pairs. On p. 4, however, he states that during the last 20 years, "only one specimen has been collected from the wild areas of the Sierra Madre Mountains of eastern Luzon, in the localities of Isabela and Nueva Vizcaya [1 specimen from 2 localities?]," and gives the Mindanao population as "barely 50 pairs." In Fig. 49, the correctly described adult and immature plumages of *Cacomantis merulinus* are captioned as male and female. The white-bellied race of the Shiny Drongo (*Dicrurus balicassius mirabilis*) of the central islands is described, and the figure is so captioned, but the drawing plainly shows one of the black-bellied races of the northern islands. This is a general fault of the book, in that descriptions are given of only a single subspecies even in dramatically geographically variable species, although Rabor lists the names and distributions of all subspecies (generally following duPont) of Philippine birds. Such nominal lists would be meaningless to most readers, to whom the author owes an explanation that, for example, the Philippine Coucals (*Centropus viridis*) of Mindoro and Batan islands (*C. v. mindorensis* and *C. v. carpenteri*) are melanic races that do not fit the description given of the nominate race. Other such instances include the Crimson-breasted Barbet (*Megalaima haemacephala*), in which the description is of the atypically red-faced *intermedia* of some of the central islands, with no mention of the fact that the other three races, inhabiting the largest islands, have a very different head pattern; and the Crimson-backed Woodpecker (*Chrysocolaptes lucidus*), for which the only description is that of the bright red-backed *C. l. xanthocephalus*; no mention is made of the fact that three of the races are yellow-backed, or that this is the only race in which the female has a yellow rather than black or red crown. It is perhaps no coincidence that in such cases, the described race is that found in Negros, even though this form might be atypical for the species as a whole. The book thus loses much of its possible value for the millions of Filipinos living in the vicinity of Manila and elsewhere on the major island of Luzon, and on the largest island, Mindanao.

Also unfortunate in a book addressed to the general public is the frequent use in the text of unfamiliar words that are neither explained nor shown in the "topography" diagram, including, for example, axillars, crissum, gular patch, remiges, and powderdowns.

The section entitled "References" of 97 titles is utterly baffling. There are no citations whatsoever in the text, and the bibliography abounds in papers seemingly randomly chosen from the literature of Philippine birds. Of the 37 of my own papers listed in duPont's bibliography, for example, Rabor lists nine, four of which deal entirely with species omitted from Rabor's book: Four papers by Deignan are listed; of these, two deal with species not mentioned by Rabor, and one, "Birds of Northern Thailand," is not among the 7 Deignan papers listed by duPont. On the other hand, four of the Deignan papers not listed by Rabor do contain information on species covered by Rabor's text.

Rabor's book contains a great deal of good and important life history information on some of the included species, most of it from first-hand observation and published here for the first time. This is obviously the most valuable part of the book to ornithology as a whole, as well as to the Filipino wishing to learn more about his country's birds. It is a pity that the rest of the book is so badly flawed. Some enterprising publisher in the Philippines might do well to obtain permission to produce an offset, paperback edition of Delacour and Mayr's *Birds of the Philippines* (1946, Macmillan, New York), perhaps with a new introduction explaining that it is still decidedly useful and comprehensive, in spite of minor obsolescence in data and nomenclature. Such a paperback would be much cheaper than Rabor's book, and would be more useful to more Filipinos wishing information about Philippine birds, especially their identification (of *all* species and of races not found on Negros). The good but extremely limited life history information presented by Rabor does not make his book a wise investment for most individual Filipinos. Libraries in institutions in other countries in which there are workers on the birds of eastern Asia should have reference copies, again for access to Rabor's field observations, but at $18.50 most of an individual purchaser's money would be wasted.—KENNETH C. PARKES.

PRAIRIE DUCKS. By Lyle K. Sowls. University of Nebraska Press, Lincoln, 1978: 193 pp. $11.50 (cloth), $3.50 (paper).—This is a reprint of a book first published in 1955 by the Wildlife Management Institute.—R.J.R.

BIRDS OF THE GAINSBOROUGH-LYLETON REGION (SASKATCHEWAN AND MANITOBA). By Richard W. Knapton. Special Publication No. 10, Saskatchewan Natural History Society, 1979: 72 pp., paper cover. $3.00.—An avifaunal list with data on distribution, habitats, migration dates, and nesting. Order from the SNHS, Box 1121, Regina, Sask., Canada S4P 3B4.—R.J.R.

A GUIDE TO THE BIRDS OF CEYLON.—By G. M. Henry. Oxford University Press, London, New York, and Melbourne, 1978: 457 pp., 30 half-tone plates (27 in color) and 136 black-and-white drawings. $27.00.—This is not a new book, but an unrevised reissue of the second edition, which was first published in 1971. Though mainly intended as a field guide, the species accounts are fuller than usual for such books, and it will serve well as a general introduction to the ornithology of the island.—R.J.R.

THE BIRDLIFE OF BRITAIN. By Peter Hayman and Philip Burton. Mitchell Beazley Publishers Ltd., London, in association with the Royal Society for the Protection of Birds, 1976:260 pp., many color pl. £8.95.—This attractive volume claims to offer a new approach in field guides, and for once this claim is justified. The book is intended to provide information for both the beginning and the advanced bird-watcher and I would judge that it does this successfully. With a limited experience with British birds I will not comment on the quality and accuracy of the bird descriptions and other aids to identification, but will limit my remarks to a description of the unique format of the book.

The main text treats 253 species, the ones that are most likely to be seen by a bird-watcher during a lifetime in Britain and northern Europe. The species accounts are arranged in groups of similarly-appearing species rather than in the traditional phylogenetic order, and no scientific names are given. (An appendix lists the common name in alphabetical order and the scientific name of all birds included.) In addition to the 253 principal species a total of 31 additional ones is covered in 4 special pages labeled: "Birds of Iberia," "Mountain Birds," "Uncommon Waders," and "Birds of Fenland, Coast, and Marsh."

A full page is usually devoted to each species, but in some cases, i.e., Willow Warbler *Phylloscopus trochilus*-Chiffchaff *P. collybita*, 2 similar species are covered on the same page. Half of the page is taken up with a colored drawing which gives not only a large profile illustration of the bird in the traditional manner, but also from 5–7, and in some cases even 10 additional smaller pictures illustrating other plumages, characteristic poses and behaviors, flight patterns, nests or other informative matters. This extensive illustration follows from the authors' contention that plumage patterns and colors are not the only useful clues to identification and ". . . there is more to birds than feathers—our book is, therefore, about birds in action, the way people really see them." The drawings are excellent and the colors well reproduced.

Besides the pictures and their accompanying captions a great amount of additional information is included. A map (much larger than in most field guides) of northwestern Europe shows the summer and winter ranges. A silhouette diagram compares the bird in profile with a House Sparrow (*Passer domesticus*), and gives a flight pattern. There is a color-coded calendar showing the months of presence, absence and breeding in Britain. At the top of each page a set of diagrams, highly reminiscent of the "hieroglyphic" traffic signs prevalent throughout Europe indicates habitats and general status, i.e., migrant, resident, etc., with a special designation for the 60 most common species in Britain. Finally the page includes approximately 150–200 words of text discussing various matters of interest.

Besides the species treatment there is a brief introduction on bird-watching and a final section called "Biology of the Bird." Interposed in the main text are pages discussing migration and ringing. Also included is a map of Europe showing many important birding sites and a listing of conservation organizations.

I feel that the authors have been very successful in their attempt to provide a good field guide, as well as a wealth of information about the birds. If a resident of the British Isles were to have only 1 book on birds, I can conceive of none that would fill the bill better than this one. Indeed, I urge some enterprising author, artist and publisher to attempt something similar for the eastern United States. Because of the larger number of species this might be more difficult, but such a work would fill a much needed gap in our literature.

Finally, I must add that this book very closely approaches "authorship by committee." No authors are, in fact, actually listed on the title page but Hayman (the artist) and Burton (the text author) are given on the cover. In addition, J. Parslow compiled the maps and R. Morton, J. Davis and B. Delf supplied some of the supplementary drawings.—GEORGE A. HALL.

BIRDS OF SOUTHWESTERN OKLAHOMA. By Jack D. Tyler. Contrib. Stovall Mus., Univ. of Oklahoma, No. 2, 1979:65 pp., 2 maps. $2.25.—This annotated checklist begins with a brief discussion of the history of ornithology in southwestern Oklahoma, and a review of the habitat and the avifauna. Most of the work is devoted to 297 species accounts, giving seasonal, numerical and breeding records. Order from the Stovall Museum of Science and History, Univ. Oklahoma, Norman, Oklahoma 73019.—R.J.R.

BIOLOGY AND EVOLUTION OF THE AVIAN GENUS *ATLAPETES* (EMBERIZINAE). By Raymond A. Paynter, Jr., Bull. Mus. Comp. Zool. 148(7):323–369, 1978.—Twenty-four species of *Atlapetes* occur from Mexico to the southern Andes. Four assemblages are recognized, and the history of speciation in the group is analyzed in relation to Pleistocene climatic events.—R.J.R.

RELATIONSHIPS OF THE SUPERORDERS ALECTOROMORPHAE AND CHARADRIOMORPHAE (AVES): A COMPARATIVE STUDY OF THE AVIAN HAND. By Boris C. Stegmann. Publ. Nuttal Ornithol. Club, No. 17, 1978:119 pp., 37 figs. $13.50. May be obtained from the N.O.C., % Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.—The late Boris C. Stegmann was Professor in the Zoological Institute of the U.S.S.R. Academy of Sciences in Leningrad. This study summarizes and consolidates much of his earlier work and makes it available to the English language audience, his earlier papers having been published in Russian and German. The study is an analysis of relationships among the Tinamiformes, Gruiformes, Galliformes, Cuculiformes, Charadriiformes, Columbiformes, and Psittaciformes. Stegmann studied the muscles, tendons and ligaments of the manus, which have been used very little by previous systematists. He developed a method for extracting the wing from study skins of birds, and of softening the tissues for study. Unfortunately, this useful methodology is not explained in the present work, nor does there appear to be a specific reference to a previous publication where it is documented. Thus, this potentially valuable methodology is not readily available for use by other workers.

The book opens with a forward by Walter J. Bock, who explains Stegmann's purposes and attempts to reconcile Stegmann's concepts and terminology with those more familiar to western readers. Stegmann apparently lacked access to much of the recent literature in systematic theory, and as a result the work has a distinctly dated aura. Yet this is somewhat misleading, as Stegmann's methods share important similarities with cladistics, in that he attempts to determine the primitive and advanced states of various characters, using the condition in reptiles as 1 criterion of primitiveness, and functional specializations for particular types of flying behavior as indicators of derived status. The latter approach also permits him to distinguish between similarities due to ancestry and to convergence. Unfortunately, many of his conclusions regarding relationships are based on what appear to be shared primitive character states.

The bulk of the work is devoted to accounts of the various groups of birds, including detailed anatomical descriptions and discussions of their functional and taxonomic significance. The descriptions are greatly clarified by many excellent line drawings. Unfortunately, the structures in the drawings are not identified by names or abbreviations, but by numbers that refer to a list given on p. 12. It is impossible to remember what the numbers refer to, which makes it necessary to keep referring to the table. I found it useful to copy the list onto an index card for a quick reference to the numbers without having to look back for the table. There is an error in the list that the reader should correct before plunging into the systematic accounts. The tendon labeled (4) in the illustrations (and positively identified by its insertion on the muscular tubercle of metacarpal II in *Gallus*) is extensor metacarpi ulnaris of George & Berger (1966, Avian Myology, Academic Press, N.Y., N.Y., pp. 359–361), or extensor carpi ulnaris of Hudson & Lanzillotti. It is neither flexor metacarpi ulnaris nor flexor digitorum superficialis, as listed under (4). Those are both alternate names for the muscle correctly identified as flexor digitorum sublimis (9), except that superficialis is now the preferred name for sublimis. It is also misnamed flexor carpi ulnaris in the last paragraph of p. 35, and is mislabeled (7) (instead of 4) in Fig. 4A.

The strongest aspect of the study is the mass of detailed and well-illustrated information on the anatomy of the avian manus, far exceeding that in any previous work. Also important are a number of functional/anatomical and evolutionary conclusions relating specific variations to particular types of flying ability. Of special interest is the brief discussion of the loss of muscles in the evolution of the avian wing. Stegmann suggests that muscles are lost because the movements of the wing are simpler than those of the reptilian limb, and that the muscles lost are 1-joint muscles whose function complements that of 2-joint muscles, which are retained.

The systematic conclusions are less satisfying. Stegmann confirms the validity (monophyly?) of the Alectoromorphae, but adds to this group the Cuculiformes and Psittaciformes, and recognizes 2 subgroups, which he terms the superorders Alectoromorphae and Charadriomorphae. Within these superorders the various groups are placed in a confusing discussion of basal and central types, with a welter of side branches. What is needed, but is lacking, is a final classification summarizing the opinions discussed. Also desirable is a phylogeny, but again none is offered. It is therefore difficult to determine how the classification was derived from the phylogeny, if indeed it was. It is not clear, indeed, that Stegmann had in mind an overall picture of the genealogical relationships of the groups studied.

In summary, this study presents an enormous mass of detailed anatomical descriptions of the avian manus, a number of important functional and evolutionary analyses of this system, and a complex but poorly organized application of the data to the analysis of avian systematics.—ROBERT J. RAIKOW.

FEEDING ADAPTATIONS AND EVOLUTION IN THE STARLINGS. By William J. Beecher. Bull. Chicago Acad. Sci. 11(8):269–298, 1978.—This review of the family Sturnidae employs evidence from the skull architecture and the anatomy of the feeding mechanism to better understand the course of evolution in the group. This study recognizes an "island complex" of fruit-eating, arboreal starlings evolving on islands and adjacent continental shores of the Indian Ocean and the Western Pacific, with primitive groups surviving on the periphery. As starlings expanded through southern Asia into Eurasia, it is believed that the nonprying, island-complex species gradually evolved prying, eventually-terrestrial species emphasizing insect diet. The prying adaptation, seen in its perfected state in *Sturnus*, has unquestionably enabled this genus of a predominantly tropical bird family to invade the temperate zone with great success. (From the author's Conclusion.)

BIRDS OF NORTHERN CALIFORNIA: AN ANNOTATED FIELD LIST. By Guy McCaskie, Paul De Benedictis, Richard Erickson and Joseph Morlan. 1979:84 pp., 1 map, paper cover. Order from Golden Gate Audubon Society, 2718 Telegraph Ave., Suite 206, Berkeley, California 94705. $5.80 (incl. postage and tax).—A compilation of information on distribution, habitat preference, relative abundance, seasonal occurrence and comments on field identification and breeding status.—R.J.R.

VANISHING BIRDS. By Tim Halliday. Illustrated by the author. Holt, Rinehart and Winston, New York, New York, 1978:296 pp., 16 color plates, 46 black and white drawings. $16.95.—This is not the usual Vade-mecum of extinct and rare species. "Vanishing Birds" is an examination of some extinct and rare birds, an analysis of extinction and a discussion of man's activities and attitudes as these have influenced extinction. From the developed perspective, consideration is given to preventing extinction of rare species.

A once-over-lightly examination of avian evolution (Chapter 1) resurrects some well known fossil species, stresses that extinction is the natural fate of all species and identifies different strategies for survival evolved by birds. Chapter 2 ("Birds and Man") discusses man's impact on world environments and the attitudes of Western civilization towards animals: abuses of animals are symptomatic of our underlying view of nature—it is our "right" to exploit animals for whatever needs. These deep-seated attitudes are illustrated in "Case Histories of Extinction" (Chapter 3) wherein the Dodo, Great Auk and Pink-headed Duck all, for one reason or another, are accelerated to extinction by man's activities. The next 5 chapters (4–8) discuss extinct and endangered species of North America, New Zealand, islands, Europe and Australia.

How to prevent extinction is the subject of the final chapter. Stressed is the need for research of rare species' biology that we may understand how to relieve human pressures and manage species. But why prevent extinctions? Five classical arguments are presented: ethical, aesthetic, economic, scientific and ecological. Conservationists are convinced of the validity of these arguments, but for those with different attitudes Halliday feels that the ecological argument will be most persuasive: the present rate of extinction is an indication of environmental deterioration—and we are a part of the environment.

"Vanishing Birds" is admirably suited for college undergraduates, advanced high school students, conservationists and the interested biologist. The book is well written and topics are neatly presented. This reviewer found the chapters on Australian and New Zealand extinct and endangered species particularly well done; he would have welcomed similar chapters for Africa and South America.

While I have only praise for what Halliday has presented, the book, I feel, stops short of what could have made it far more instructive. As part of the final chapter on conservation, or as a separate chapter or appendix, it would have been germane to discussions if he had commented on continental and worldwide conservation efforts. In Chapter 7 it is stated that there are many organizations and pressure groups at work in Europe (strangely, no similar comment is made regarding North America) but nothing is said about them. Conservation is generated through human effort and bringing into focus the profiles and strategies of such effort would be edifying to those attracted to this book.

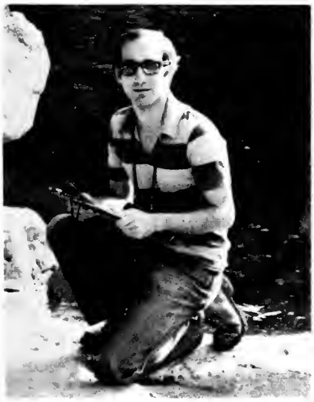
Halliday states that the basic question behind every discussion of conservation is "why should we bother to preserve species?" and he acknowledges that to the "vast majority" of mankind aesthetic and scientific arguments have "no significance whatsoever." Having identified a really boggling dilemma, we could at least expect some address to it. How can we attempt influencing this vast majority? He states at one point that the fact that man is a part of the deteriorating environment may be an effective argument. But this book will be read by the erudite of some developed nations, not by the vast majority of mankind. How may his argument be transmitted to the masses of the undeveloped nations? How are we to convince this vast majority that man must "make the choice between taking more resources and sharing the world with wildlife?" On this vital point the author is silent. Clearly, the planet's future lies in the hands of this majority of mankind. Conservationists must address this problem.

There is no reason to have expected Halliday to have considered this final point, but it is as germane as any consideration about vanishing species. Assuming we achieve a worldwide patchwork of preserves for relict plants and animals, how long will the planet's population be able and, at whatever expenses, willing, to maintain such? And how many of the organisms on these ecological "islands" will ever be "moved back" any significant distance from the precipice of extinction?—OSCAR T. OWRE.

TREES, SHRUBS AND VINES FOR ATTRACTING BIRDS: A MANUAL FOR THE NORTHEAST. By Richard M. DeGraaf and Gretchin M. Witman, illustrated by Abigail Rorer. Univ. Massachusetts Press, Amherst, Massachusetts, 1979:xiv + 194 pp., black and white drawings. $12.50.—This attractively designed and illustrated book is intended for the serious gardener or landscape architect designing and planting a residential area to attract and hold wildlife. After a brief introduction, the text is divided into 3 sections: trees (79 pp.), shrubs (80 pp.) and vines (12 pp.). Each of 162 plant species (or species groups such as crabapples, hawthorns and roses) is given about a page to describe its characteristics, horticultural requirements and propagation, with landscaping notes; a table lists the bird species that use it for food, cover, or nesting. Most of the plants are illustrated by a drawing, often of a fruiting branch. The book ends with an appendix: a plant hardiness zone map, tables of flowering-fruiting periods, lists of plants that will grow in difficult sites (along streets, in dry soils, in cities, in places subject to salt spray), a 5-page bibliography, a short botanical glossary and an index to plant species.

The treatment throughout is competent and professional. The level of presentation, especially in the propagation sections, is to the experienced gardener. The wildlife material is taken almost entirely from other publications. Emphasis is placed on native plants, but exotics such as some of the honeysuckles that are both ornamental and valuable to wildlife are included as well. The novice may have some difficulty in finding certain plants, as they are arranged alphabetically by genus—thus, for example, the cedars (Northern White and Eastern Red) are 38 pages apart, but reference to the index will solve most problems. The authors also point out in the introduction that this is not a complete guide to attracting birds to a garden, and they refer the reader to several good titles for more general coverage. This is a book for the gardener.—MARY H. CLENCH.

NEW LIFE MEMBER



Mr. Robert Craig, a Ph.D. candidate at Rutgers University has recently become a Life Member of The Wilson Ornithological Society. His Ph.D. research involves the comparative ecology of Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes, but he is also interested in evolutionary ecology, competition and coexistence of similar species and conservation and management of non-game wildlife. Mr. Craig has a number of publications to his credit, including one on rare vertebrates of Connecticut. Mr. Craig is also an active outdoorsman and enjoys botany. His wife, Susan, is employed as a naturalist/environmental educator.

Wilson Bull., 92(1), 1980, pp. 140–141

ORNITHOLOGICAL NEWS

SYMPOSIUM ON THE BALD EAGLE IN WASHINGTON

A symposium to review past research on the American Bald Eagle in Washington, and to stimulate further investigation of this threatened species, will be held 14–15 June 1980, at the City of Seattle Aquarium, co-sponsored by the National Wildlife Federation, Seattle Aquarium, Seattle Audubon Society, Seattle City Light, Seattle Woodland Park Zoological Gardens, The Nature Conservancy, U.S. Forest Service, U.S. Fish and Wildlife Service and Washington Department of Game. Preregistration is recommended, as limited space is available. Interested persons should forward $5.00 to cover registration fee to Washington Bald Eagle Symposium, c/o Jeremy Robertson, 2357 N.W. 70th, Seattle, Washington 98117, phone (206) 789-6056, by May 31. A published copy of the symposium proceedings is included in registration fee.

COLONIAL WATERBIRD GROUP

The fourth annual meeting of the Colonial Waterbird Group will be held 9–12 October 1980 in Ottawa, Canada. It will be co-sponsored by the Colonial Waterbird Group and the Canadian Wildlife Service. A symposium on the effects of humans on colonial birds is planned, and a "Proceedings" will be published. For information on contributing papers, please contact J. Burger, Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903. Abstracts due by 1 August 1980. For information on registration, please contact R. Michael Erwin, Migratory Bird and Habitat Research Laboratories, U.S. Fish and Wildlife Service, Laurel, Maryland 20811.

REQUESTS FOR ASSISTANCE

Wanted: recordings of raptor vocalizations.—We are in the process of developing and testing a technique for censusing diurnal and nocturnal raptors, based on responses to recorded raptor vocalizations. We are interested in access to recordings of all North American woodland hawks and owls for which information on the location and behavioral context of the recording is known, and, if possible, age and sex. Direct correspondence to: Dr. James A. Mosher, Appalachian Environmental Laboratory, Univ. Maryland, Frostburg State Coll. Campus, Frostburg, Maryland 21532.

Ring-billed Gull study.—During the fall and winter of 1979–80, as part of a 2 year study on the comparative winter foraging ecology of gulls on southeastern Lake Erie, the wings and tails of Ring-billed Gulls were color marked with green paint. Persons observing these gulls are requested to report the date, time, exact location, plumage or age class, area of wings and tail marked, activity and observer's name, address and telephone number to the Bird Banding Laboratory, Office of Migratory Bird Management, USFWS, Laurel, Maryland 20811. Please send a copy to Betty-Ann Chapman, Biology Dept., State Univ. Coll., Fredonia, New York 14063.

COLOR PLATE

The color plate Frontispiece of hummingbirds of the Metallura aeneocauda superspecies has been made possible by an endowment established by Dr. George M. Sutton.

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in the Wilson Ornithological Society have been made available through funds generously donated in memory of Aaron M. Bagg, a former president of the Society. The Student Membership Committee has designated the award recipients for 1979 as follows: William H. Baltosser, New Mexico State University, Las Cruces; Christopher P. Barkan, SUNY-Albany; Verner P. Bingman, SUNY-Albany; David E. Blockstein, University of Minnesota; Douglas A. Boyce, Humboldt State University, California; Barbara M. Braun, University of California-Irvine; Steven W. Cardiff, Louisiana State University; Penn Richard Chu, University of Maryland; Sharon D. Clawson, University of Nebraska; Janice R. Crook, Livingston College, Rutgers University; Mary A. Fitch, Livingston College, Rutgers University; Robert B. Frederick, Iowa State University; Thomas L. George, University of New Mexico; Mark A. Holmgren, University of Colorado; Kurt A. Johnson, University of Wisconsin; Paul Kerlinger, SUNY-Albany; Mark T. Kopeny, Fostburg State College, Maryland; David S. Maehr, University of Florida; Mark L. McKnight, California State Polytechnic University-Pomona; Kenneth L. Petersen, Iowa State University; Ethan J. Temeles, Louisiana State University; Harvard C. Townsend, Kansas State University; Scott R. Winterstein, New Mexico State University, Las Cruces.

John L. Zimmerman, *Chairman*
Student Membership Committee

NECROLOGY

Mr. Whitney Eastman, a life member of The Wilson Ornithological Society and active ornithologist and conservationist, died in December 1979. He will be remembered, among other things, for his work in the Minneapolis Ornithologists Union and state and national Audubon Society.

Wilson Bull., 92(1), 1980, pp. 142–148

REPORT OF THE CONSERVATION COMMITTEE—1978

Nongame Conservation and Management

If ideas are enlightened by the times, then nongame management is an "idea" whose time has finally come. Nongame management started, in a general sense, with the environmental era of the 1960s (stimulated in large measure by Rachel Carson's *Silent Spring* in 1962) and with the enactment of the Endangered Species Act of 1966 which set the stage for rapid advancements in conservation attitudes.

The National Environmental Policy Act (NEPA) of 1969 and the environmental impact statement process laid the foundation for a broader and more in-depth consideration of wildlife, exposing how little was being done to evaluate proposed developments, how little was known about impacts on living resources, and the inadequacies of project designs to prevent adverse impacts on living resources.

Ornithologists jumped into the mainstream; symposia were held and research pushed forward, e.g., on birds damaged by chlorinated hydrocarbons. Not the least among these advancements was the development—new and renewed—of a conservation ethic by laymen across the land. Membership in the National Audubon Society increased 8-fold in 15 years and the public entered the spirited debate. An example of this was the activist group, Greenpeace; its members literally sallied between whale and harpoon. Clearly, the time was at hand for the conservation and management of nongame.

Historically, ornithologists have taken the lead in promoting conservation, research and management for nongame species. The pioneering work of John James Audubon and Alexander Wilson did not discriminate between the edible and the more aesthetic species.

William Brewster, one of the founders of the American Ornithologists' Union and Curator of Birds and Mammals at Harvard University, aroused the A.O.U. in 1884 to form a Committee for the Protection of Birds (Trefethen 1975) working toward suitable state legislation to protect birds. Early members of this committee included J. A. Allen, George Sennett, William Dutcher and Frank M. Chapman (who also played a leading role in affairs of the National Audubon Society and, in many ways, stimulated public interest in nongame species in the first decades of the twentieth century).

Another pioneer ornithologist, Joseph Grinnell, was instrumental in the campaign against commercialization of wildlife. Through Congressman John Lacey, Grinnell prompted the Lacey Act in 1900 that protected interstate shipment of illegally killed wildlife as well as foreign transport of wildlife (Trefethen 1975).

Committee action within the newly formed American Ornithologists' Union advocated formation of the Division of Economic Ornithology under the U.S. Department of Agriculture, which eventually led to formation of the Fish and Wildlife Service within the U.S. Department of the Interior, with regulatory authority over migratory game and nongame birds (Leedy 1961). Committee action of the A.O.U. also was instrumental in the establishment, in 1903, of Pelican Island, Florida, as the first bird refuge, even paying initial expenses for having the area patrolled (Trefethen 1975).

For nearly a century The Wilson Ornithological Society, American Ornithologists' Union (preceded by the Nuttall Ornithological Club) and The Cooper Ornithological Society have provided outlets for publication of significant papers on nongame species.

It was not state or federal governments that initiated research on rare and endangered species, but ornithologists, such as Carl Koford for the National Audubon Society (California Condor [*Gymnogyps californianus*], 1939–1946), Josselyn Van Tyne of the University of Michigan and Harold Mayfield (Kirtland's Warbler [*Dendroica kirtlandii*], from 1942 on).

Ornithologists at Cornell University's Laboratory of Ornithology have stimulated a variety of new approaches to the study of nongame species, including sound recording and spectrographic analysis of bird vocalizations and the establishment of a nation-wide network for the collection of nest records and a facility for propagation of endangered raptors.

Joseph Hickey's "A Guide to Bird Watching," published in 1943 when he was still an amateur ornithologist, encouraged many other amateurs; similar encouragement and expertise now is provided by various bird observatories, which depend on well-trained amateur help in much of their ornithological research.

Interest in specific lines of endeavor has resulted in the formation of special interest groups (i.e., bird banding associations, the Raptor Research Foundation, Hawk Migration Association of North America, Pacific Seabird Group, Colonial Waterbird Group and the North American Bluebird Society), as well as a vast array of rehabilitation and conservation education groups concerned primarily with nongame species. Sportsmen have also been strong supporters of educational and legislative activities relating to protection of nongame as well as game (Trefethen 1975), and have influenced the broadening of wildlife programs.

In 1975, the Wildlife Management Institute issued a study report entitled, "Current investments, projected needs and potential new sources of income for nongame fish and wildlife programs in the United States" (hereafter cited as the WMI Nongame Report), incisively noting that previous efforts to deal with troubled species have been largely "rescue oriented."

In effect, efforts were a salvage operation designed to recover declining populations from the abuses of development and mismanagement from a multitude of single purpose, land use enterprises, although restrictive laws were often the only means available to conservation agencies for counterattack. Occasionally, the results were positive. Alligator (*Alligator mississipiensis*) populations, once at desperately low numbers, responded within the last decade to the protection and rigorous enforcement of new legislation. Now the species is no longer regarded as threatened in most southern states, and limited harvests are again in effect. Nonetheless, the restoration of alligator, sea otter (*Enhydra lutris*), bison (*Bison bison*) or Atlantic salmon (*Salmo salar*) populations represented action initiated after these species were recognized as threatened. Moreover, these restorations cannot be defined as last-ditch efforts because, literally, no action at all preceded detection of each species' dire status. Too often indifference and ignorance characterized the hapless fund of biological knowledge at hand for nongame.

Clearly, then, the long-term objective of any wildlife program—game or nongame alike—should obviate the need for rescue oriented operations. The WMI Nongame Report thus sounds a clarion call for a scientifically based approach to the management of all wildlife resources.

A Picture of Nongame Funding

The WMI Nongame Report presented a thorough review of revenues devoted to various fish and wildlife programs and activities, including monies invested by more than 30 states or other political units in research, management and enforcement. Analysis of data from the WMI Nongame Report further emphasizes the need for nongame programs for birds. Monetary figures are based on the 1975 dollar value.

Clearly, only a minuscule portion of funds currently available to state and territorial wildlife agencies is spent on identifiable nongame projects. Of funds expressly allocated to nongame, nearly 42% was appropriated for birds, foremost among the groups identified (Table 1). Analysis in Table 1 also reveals that research activities for nongame birds (27%) run a poor third to enforcement (65%) and management (48%) activities.

On a per project basis, 37 projects dealing with the management of nongame birds received

TABLE 1

STATE AND TERRITORIAL EXPENDITURES IN MANAGEMENT, RESEARCH AND LAW ENFORCEMENT FOR NONGAME BIRDS, 1974–1975, ADAPTED FROM WMI NONGAME REPORT (1975)

Activity	All programs[a]	Nongame birds	%	All nongame programs[b]	Nongame birds	%
Management	$ 84,248,176	$ 426,074	0.5	$ 893,459	$ 426,074	47.6
Research	40,550,213	449,305	1.1	1,657,764	449,305	27.1
Enforcement	51,628,385	525,804	1.0	804,815	525,804	65.3
Totals	$176,426,774	$1,401,183	0.8	$3,356,038	$1,401,183	41.7

All figures based on 1975 dollar value.

[a] Includes game and nongame programs.

[b] Includes nongame programs for birds, mammals, fish and other species and their habitats.

an average of $11,516 (vs $12,584 average for each of 71 projects in the management category for all types of nongame); 47 research projects received an average of $9560 (vs $13,053 average for each of all 127 nongame research projects); and 22 law enforcement projects addressing nongame birds averaged $23,900 (vs an average of $16,425 for each of all 49 nongame projects in the enforcement category).

Thus, nongame projects for birds fell far short of the overall average in both management and research at the state level. Law enforcement allocations for nongame birds, however, were well above the average amount for all nongame projects. These data are somewhat surprising. Birds are foremost in abundance among the nongame species in the United States, as shown in Table 2: 600 (46%) of the 1291 vertebrate species classified as nongame are birds, yet research and management expenditures currently fall far short of this representation of birds in nongame biota. Moreover, birds are the most abundant group of vertebrates officially designated as rare or endangered in the United States.

A major point in these and other financial data concerns the source of revenues supporting nongame research programs. Of some 247 nongame projects at the state level identified in the WMI Nongame Report, less than 4% were funded by "other" revenues. That is, hunting and fishing license sales were the mainstay of nearly all nongame research. Similarly, the states' nongame management and enforcement projects derived the bulk of their funds from license sales to sportsmen.

Nevertheless, numerous states have acquired lands to preserve prairie chicken (*Tympanuchus* spp.) and other nongame wildlife habitat by using funds designed for acquisition of public-use areas. In addition, the thousands of acres of refuge and public hunting lands have greatly benefited nongame wildlife. Concerted efforts to raise funds for threatened species have rested primarily on private donors through various organizations, such as the World Wildlife Fund, the National Audubon Society and The Nature Conservancy. A few states have had unsuccessful birding licenses; others are trying them now. Other funding techniques offer promise. Colorado, for example, recently enacted legislation providing a voluntary check-off box on the state's income tax form, dedicating contributions to a nongame wildlife program. Taxpayers in Colorado now can earmark a portion of their tax rebates for specific nongame projects administered by the State's Division of Wildlife.

At the federal level, funding for nongame birds made up 1.8% of the total wildlife budget and nearly 18% of allocations for nongame projects, excluding law enforcement activities (Table 3). On a project basis, 21 nongame bird management projects received an average of

TABLE 2
APPROXIMATE OCCURRENCE OF GAME AND NONGAME SPECIES BY VERTEBRATE GROUPS IN THE UNITED STATES,[a] ADAPTED FROM WING (1951)

Vertebrate group	Total no. species (approx.)	Game			Nongame		
		No.	% of group	% game	No.	% of group	% nongame
Birds	811	69	8.5	29	600	74	46
Mammals	670	82	12.0	34	399	60	31
Fish (freshwater)	600	88	15.0	37	90	15	7
Reptiles	149	0	0.0	0	70	47	5
Amphibians	138	0	0.0	0	132	96	10
Totals	2368	239	10.0	100	1291	54.5	99

[a] Excluded are those species considered as "game-commercial" (e.g., salmon) and those considered as "harmful" (e.g., poisonous snakes). Because of overlapping designations for some species, the total for all categories equals 113%.

$61,689 (vs $55,467 average for 41 management projects in all categories), but research for nongame birds averaged only $19,009 for 36 projects (vs $64,975 average for 135 nongame research projects of all types).

Thus, the funding picture for nongame birds was limited. Research funds, in particular, were less than satisfactory for a resource so widely appreciated in the United States. That either appropriated funds (federal), or those derived from license sales (state), make up the major portion of investments to nongame projects clearly indicates that other sources of revenue are needed to support the research necessary for comprehensive management of nongame birds.

DEVELOPMENT OF THE U.S. NONGAME BILL

Following distribution of its 1975 Nongame Report, the Wildlife Management Institute was invited by the Senate Subcommittee on Resource Protection to draft a nongame conservation

TABLE 3
FEDERAL EXPENDITURES IN MANAGEMENT, RESEARCH AND LAW ENFORCEMENT FOR NONGAME BIRDS, 1974–1975, ADAPTED FROM WMI NONGAME REPORT (1975)

Activity	All programs[a]	Nongame birds	%	All nongame programs[b]	Nongame birds	%
Management	$ 65,845,422	$1,295,460	1.9	$ 2,274,166	$1,295,460	56.9
Research	41,950,320	684,325	1.6	8,771,603	684,325	30.2
Enforcement	9,053,000	—[c]	—	2,264,700	—[c]	—
Totals[d]	$107,795,742	$1,979,785	1.8	$11,045,769	$1,979,785	17.9

[a] Includes game and nongame programs.
[b] Includes nongame programs for birds, mammals, fish and other species and their habitats.
[c] No breakdown available for birds and other groups.
[d] Total shown excludes enforcement funds.

bill, as recommended in the Report. However, the 94th Congress adjourned before the first draft was heard, which was reintroduced in the 95th Congress on 28 March 1977, as S. 1140. A similar bill, H.R. 8606, was introduced in the House on 28 July 1977.

The Senate completed hearings on S. 1140 in early August and the House followed suit with H.R. 8606 in late September. H.R. 8606 was subsequently revised and reintroduced as H.R. 10255.

The Senate proceeded with its version of the bill and S. 1140 was passed 24 May 1978. The House Merchant Marine and Fisheries Committee favorably reported H.R. 10255 and sent the bill to the House Rules Committee.

Both of these bills would establish a nongame fish and wildlife conservation program similar to the long-standing Federal Aid in Fish and Wildlife Resotration Programs that have been successful in restoring and maintaining largely game populations. Strong support for the concepts and proposed nongame program was provided at both Senate and House Committee hearings by a broad spectrum of conservation, environmental and humane organizations, as well as the state fish and wildlife agencies.

Both S. 1140 and H.R. 10255 called for general appropriations to be made available through Congressional actions. Past experiences have shown that such appropriations for wildlife are not dependable, fluctuating widely among years, making it difficult to build or sustain programs.

In February 1978, another nongame bill (H.R. 10915) was introduced, but did not receive hearings in the 95th Congress. It was identical to H.R. 10255 except for the funding mechanism. It called for an 11% manufacturers' excise tax on bird seed, feeders and baths, certain camping equipment, and some binoculars and spotting scopes. That tax could yield from $20–30 million annually to fund nongame research and management.

Although President Carter, in his environmental message in the spring of 1978, pledged to strengthen wildlife programs, the Office of Management and Budget voiced strong opposition to the proposed nongame fish and wildlife conservation act. In June 1978, a coalition of power associations, labor unions and the U.S. Chamber of Commerce swamped House members with letters and telegrams opposing the nongame bill (H.R. 10255), largely on procedural grounds. This opposition, and the negative views of the Office of Management and Budget, stalled action in the Rules Committee and, therefore, in the House.

In mid-August 1978 the conservation community, representing the views of over 100 conservation and environmental leaders, made a direct appeal to President Carter to support the nongame proposal. The bill languished and did not pass before the 95th Congress adjourned in October, 1978. The bills will now have to be reintroduced in the 96th Congress.

THE NONGAME ETHIC

Scheffer (1974, 1976) provided a framework for a modern nongame ethic for wildlife biologists. He believes that 2 new ideas have emerged in the relationship between man and wildlife: (1) man is responsible for the integrity of natural systems—man cannot guide his planet safely or permanently without the proper functioning of Earth's environmental equipment; and (2) there is new awareness and understanding of the values of living organisms.

These ideas, Scheffer predicted, will move wildlife managers into the spectrum of optimal yield, largely replacing the older concept of maximum sustained yield that prevailed for deer, quail and other game species. The natural diversity of ecosystems, not abundance of a select few species, will be the criterion of management. This shift in emphasis will incur changes in the administrative machinery of respective agencies responsible for wildlife management. Hunting will diminish as a dominant influence and instead wildlife agencies will consider more fully the values and benefits of wildlife to nonhunters (Scheffer notes that only 1 in 10 Americans 12 years of age or older was listed as a hunter in 1970).

This climate has brought forth changes in agency names; game departments have become wildlife agencies, or divisions of natural resources. Almost overnight, agencies of game management and biologists trained in game management have inherited the responsibilities for nongame research and management. The states' responses, of course, showed a wide range of involvement and investment. Some states have formed identifiable nongame subunits of several persons, with at least modest budgets. Other states have put forth only limited efforts, further constrained by inadequate funding. Federal response has been somewhat stronger. Several agencies, particularly the Fish and Wildlife Service, were already responsible for nongame species (e.g., Whooping Cranes [*Grus americana*]) prior to enactment of the Endangered Species Act of 1966. Recovery teams comprised of biologists from state, federal and private sectors have been established to deal with designated species; birds figured heavily in these projects.

Universities have also responded favorably. Departments previously oriented toward game species, now emphasize wildlife sciences and natural resources. Crawford (1976) discussed the role of universities in meeting the modern training needs of students in natural resources disciplines. Of the 2 general categories of curricula, he suggested that the "principles method" would best serve today's students. The "life history method" (emphasizing the biology and management of individual species) has a limited perspective in both time and coverage. With the principles method, the ecological role of fire in management can be demonstrated ably with Kirtland's Warbler as an example. This species and its ecological needs would scarcely be mentioned were only the life history approach used in programs that emphasized upland game bird management. Furthermore, the principles method does not preclude instruction in game management, but integrates game and nongame within the perspective of an ecosystem approach.

Missouri's Leadership

Design for Conservation, initiated by a wide audience of concerned Missourians, began with a petition of 164,000 signatures requesting funding for a comprehensive program addressing the natural resources of Missouri. It ended with the enactment of legislation in 1977 dedicating ⅛ of 1% of the existing sales taxes for the program. These revenues are expected to reach $25 million annually.

The first objective has been to acquire conservation lands. Under 4% of Missouri is in public ownership, including state and federal properties. Now with a funding base, the quest is to acquire 121,000 a of upland and wetland sites, natural areas for rare and endangered species, and pristine springs and spring branches. In the first 10 months of the program, $12 million was expended for the purchase of 28,000 a.

Design for Conservation will also support a variety of public services, including wildlife and fisheries management for all species, forest management, conservation education programs, research of several types and a refinement of enforcement operations. The nongame facet of Missouri's program led to a new Natural History Section in the Department of Conservation. The staff includes a section chief, a rare and endangered species coordinator for both plants and animals, a natural area coordinator, an ornithologist, a herpetologist, a naturalist-nature center coordinator and 2 urban wildlife specialists.

The research program includes restoration of Ruffed Grouse (*Bonasa umbellus*) populations (a nongame species in Missouri), shorebird management, management of native prairies for nongame and an evaluation of traditional wildlife management practices and their effects on nongame populations. The program also includes research on prairie chickens and endangered raptors.

A major attempt to avoid land condemnation of vital endangered habitats has been successful to date, and the group hopes never to employ "eminent domain" in the acquisitions process. Fortunately, the large number of willing sellers of habitats has precluded the possibility of legislative backlash if land condemnation had to be employed widely. In all, Design for Conservation is a model deserving national attention.

RECOMMENDATIONS

(1) Through individual and organized efforts, encourage states to develop special sources of revenue dedicated to natural resources research and management with special reference to nongame programs. Sources of state revenue may be derived from the sales of specially imprinted license plates, nongame stamps akin to the well-known duck stamp, dedication of a percentage of state sales or income taxes, rebates or other means to assure revenues independent, but not exclusive, of state appropriations. These funds may be used, in part, as matching funds for federal cost-sharing programs, as described earlier in this report.

(2) Work with existing state conservation agencies to establish viable and comprehensive nongame programs. Formal recommendations establishing nongame research and management priorities, including critical habitat acquisition, originating with local, state or regional ornithological societies or similar conservation groups should be part of this effort.

(3) Direct research findings, whenever possible, to nongame management recommendations (e.g., population and behavioral data as the basis for recommending optimum sized parcels of habitat for acquisition). Funding for nongame projects may be obtained more readily, at least initially, when ornithologists assume mission-oriented research based on previously established priorities.

(4) Vigorously support pending state and federal legislation that can benefit nongame and constructively oppose those with possible negative impacts. Many land and water bills do not contain language addressing wildlife considerations, and such legislation often is patently inimical to the best interests of wildlife resources. Too often, land and water bills may regard wildlife in narrow terms (e.g., game). The ornithological community must guard against such limited interpretations of the ecological impacts of legislation on all wildlife species and populations.

LITERATURE CITED

CRAWFORD, J. A. 1976. Nongame wildlife—the role of the university. Wildl. Soc. Bull. 4:116–119.

LEEDY, D. L. 1961. Some federal contributions to bird conservation during the period 1885 to 1960. Auk 78:167–175.

SCHEFFER, V. B. 1974. A voice for wildlife. Charles Scribner's Sons, New York, New York.

———. 1976. The future of wildlife management. Wildl. Soc. Bull. 4:51–54.

TREFETHEN, J. B. 1975. An American crusade for wildlife. Winchester Press and Boone and Crockett Club, New York, New York.

WILDLIFE MANAGEMENT INSTITUTE. 1975. Current investments, projected needs and potential new sources of income for nongame fish and wildlife programs in the United States. Wildl. Manage. Inst., Washington, D.C.

WING, L. W. 1951. Practice of wildlife conservation. John Wiley and Sons, New York, New York.

Eric G. Bolen, *Chairman*
Marcia M. Wilson
Milton W. Weller
Laurence R. Jahn
Chandler S. Robbins
Brian R. Chapman

This issue of *The Wilson Bulletin* was published on 8 April 1980.

THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "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 (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss 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.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Dr. Robert C. Whitmore, Division of Forestry, West Virginia University, Morgantown, West Virginia 26506.

CONTENTS

GENERAL NOTES

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 92, NO. 2 JUNE 1980 PAGES 149–288

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—George A. Hall, Department of Chemistry, West Virginia University, Morgantown, West Virginia 26506.

First Vice-President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

Second Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Sidney A. Gauthreaux, Jr. (term expires 1981); Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983).

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

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 104 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," 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.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan. Known office of publicaton: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

Adult Magellanic Oystercatcher *(Haematopus leucopodus)*

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 92, NO. 2 JUNE 1980 PAGES 149–288

Wilson Bull., 92(2), 1980, pp. 149–168

DISPLAYS OF THE MAGELLANIC OYSTERCATCHER (*HAEMATOPUS LEUCOPODUS*)

EDWARD H. MILLER AND ALLAN J. BAKER

The Magellanic Oystercatcher (*Haematopus leucopodus*), endemic to southern South America, has a curious combination of features of New and Old World Haematopodidae. It has yellow eyes and pale legs, like the New World Blackish (*H. ater*), Black (*H. bachmani*) and American (*H. palliatus*) oystercatchers, contrasting with the scarlet eyes and pinkish-red legs of other oystercatcher species (Strauch 1976). *H. leucopodus* resembles Old World *Haematopus* spp., however, in lacking a brownish cast to its black dorsal plumage. Moreover, it is unique in having yellow orbital rings, which are orange in other *Haematopus* spp., and in having underwing coverts of a different color than the belly plumage (Strauch 1976). *H. leucopodus* is also unusual ecologically. Most nest inland on the pampas of Argentina, often far from marine littoral habitats. Some populations of the European Oystercatcher (*H. ostralegus*) also nest inland in extensive natural open habitat.

Despite its unusual characteristics *H. leucopodus* is poorly known. We gathered data on its behavior during 1 nesting season, in conjunction with ongoing ecological and systematic studies on the Haematopodidae (Baker 1974, 1975, 1977). We describe some of its visual and vocal displays, particularly piping displays and displays of adults disturbed near the nest or with chicks. We include comparative observations on *H. ater* and on the Patagonian and eastern North American races of the American Oystercatcher (*H. palliatus durnfordi* and *H. p. palliatus*, respectively).

METHODS

We studied *H. leucopodus* about 85 km NW of Rio Gallegos, Argentina, from 1–10 November 1977. We observed *H. ater* and *H. p. durnfordi* at Punta Tombo, Argentina, on 12 and 15 November, and *H. p. durnfordi* at Punta Ninfas, Argentina, on 14 November. Baker also studied a population of color-banded *H. p. palliatus* at Wallops Island, Accomac Co., Virginia, during the 1978 and 1979 nesting seasons.

Motion pictures of *H. leucopodus* and *H. p. palliatus* were taken with a Bolex 16 mm camera at 24 frames/sec. Most tape recordings were made at 19 cm/sec with a Nagra IS tape recorder on Scotch 208 tape, matched to the Nagra, using a Sennheiser MKH 816 microphone with wind sock. Recordings in Virginia were taped at 19 cm/sec on a Uher 4200 Report Stereo IC tape recorder on Scotch 208 tape, using a Uher M517 dynamic microphone mounted in a Dan Gibson parabolic reflector. Sonagrams and amplitude profiles were prepared on a Kay Elemetrics Sonagraph 7029A with amplitude display/scale magnifier unit 6076C. Its frequency calibration was checked against pure frequencies from a signal generator. Time markers are based on the revolution time of the drum (2.55 sec over the range 80–8000 Hz, for the machine used).

We sexed oystercatchers on the basis of the relative sizes of mates and relative bill color. Males average smaller than females in all oystercatcher species, and male *H. ostralegus* in Europe and Australasia are nearly always smaller than their mates (Heppleston and Kerridge 1970; A. J. Baker, unpubl.). Additionally, bill color in breeding males of most or all species is decidedly richer and pinker than in females; their bills seem dull orange by comparison. This sexual difference in bill color was also apparent in 22 copulating pairs of *H. p. palliatus* and in collected specimens of the 4 taxa.

OBSERVATIONS

Tail-flagging.—Adult *H. leucopodus* gave various distraction displays when disturbed near the nest. The most striking display is tail-flagging. A typical display proceeds as follows (Fig. 1A, E): The bird rose from its nest with its neck retracted (note prominence below nape, Fig. 1A, frame 1 [f1]); then turned and walked slowly from the nest with contour feathers sleeked and head and neck low, but with feathers around the vent slightly erected (f46). It then quickly raised its tail (f46–62), exposing the underside of the tail toward us while erecting and spreading the under-tail coverts (f62, 73). It walked slowly or was nearly motionless in this posture. Movement of the wings away from the body began in f46, after which they were conspicuously fluffed and drooped. A similar sequence recurred within seconds, but the bird assumed a low crouched posture with lifted tail (e.g., f173), and it trod quickly on the spot while shuffling its fluffed, drooped wings. Treading usually ceased when an upright posture was assumed (f231, as in f73). The female in Fig. 1E turned toward us and leaned forward with tail up and wings fluffed and drooped (third and fourth sketches). The white chevron at the base of her tail was fully displayed and much of the tail was conspicuously framed by the under-tail coverts (fourth sketch).

False-brooding and other lure displays.—Less striking displays include crouching with sleeked plumage, slight drooping, fanning or rotation of the tail, and lowered wings kept fairly close to the body (note lowered wing tips below tail, Fig. 1B, f1–188). These low intensity postures sometimes

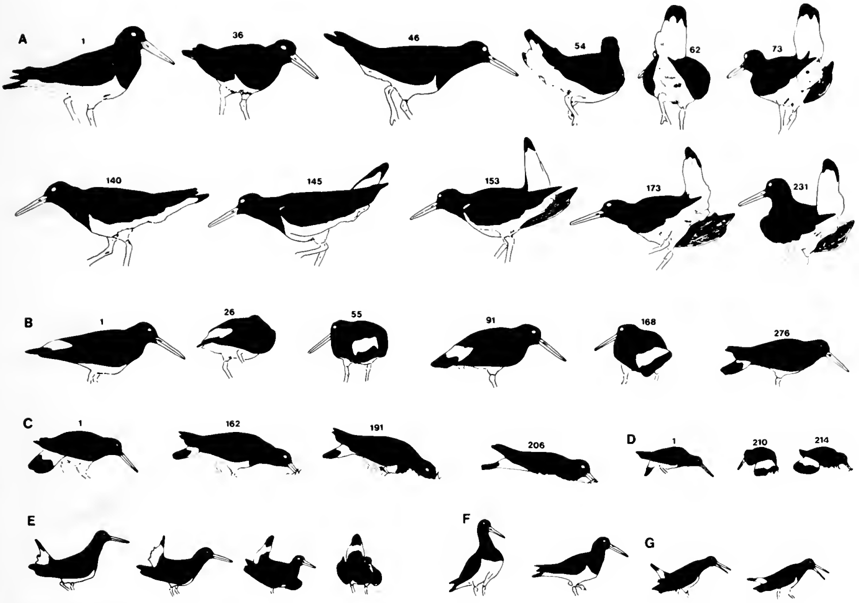


FIG. 1. Postural displays of *H. leucopodus* disturbed near the nest (female throughout). Numbers in A–D refer to frame numbers from movies. Parts E–G are from still photographs. (A) Rising from nest and performing 2 tail-up displays; (B) farther from nest; (C) still later, farther from nest, false-brooding (after f1); (D) still later, farther from nest; (E) another female in display a few seconds after she left nest; (F) this female immediately after landing near nest, then walking toward it; (G) this female near nest, walking slowly, while piping in response to distant piping.

merged into sequences of false-brooding (Fig. 1C, f162–206) or crouches with the tail depressed and fanned (Fig. 1D). Birds like those in Fig. 1B and 1D generally walked slowly and haltingly away from us; the bird in Fig. 1D also stopped and remained motionless for long periods. False-brooding birds remained in place briefly while acting as though settling on a nest.

We saw many *H. ater* and *H. p. durnfordi* near their nests. Most remained nearby while calling loudly, but a few *H. p. durnfordi* false-brooded weakly. Neither species exhibited tail-flagging or other lure displays. False-brooding occurs in *H. bachmani* (J. P. Myers, in litt.). Territorial *H. bachmani* sometimes crouch with depressed tail during aggressive interactions (S. Groves, in litt.).

Piping.—Piping is a common and conspicuous display in all species of oystercatchers. It involves loud calls and striking postures and move-

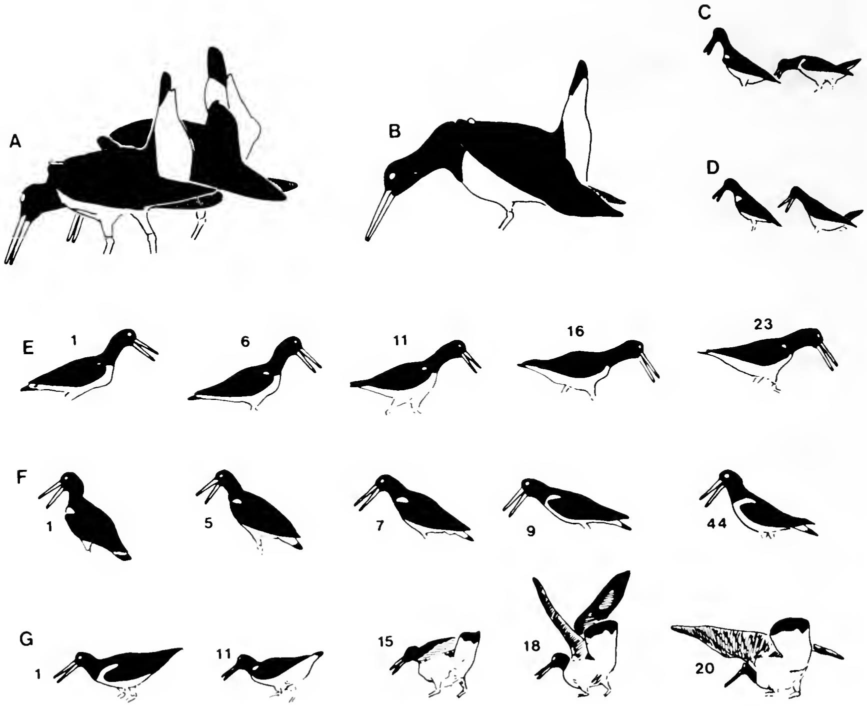


FIG. 2. Postures during piping displays in *H. leucopodus* and *H. p. palliatus*, and displays by a male *H. p. palliatus*. A and B are from still photographs. Numbers in parts E–G refer to frame numbers from movies. (A) Pair of *H. leucopodus* piping with a neighboring pair (not shown); (B) *H. leucopodus* piping with its mate and a neighboring pair (later in the same sequence as A); (C, D) *H. p. palliatus* piping; (E, F) female *H. p. palliatus* piping while walking rapidly toward a neighbor who was circling low over her nesting territory; (G) male *H. p. palliatus* piping while squatting, then raising his wings and tail as a neighboring male swooped down toward him; the intruder apparently struck this male in f27.

ments, and is usually given in aggressive and sexual contexts at close range on the ground. Piping is given less commonly in flight.

Piping in *H. leucopodus* was commonest during territorial demarcation, and involved 1 or both members of neighboring nesting pairs. For example, a nesting pair of *H. leucopodus* engaged their neighbors in piping interactions several times over 2 days of observations. Piping recurred along a stretch of barbed wire fence, with the pairs separated by a few meters on opposite sides. Mates generally remained close together during such encounters (e.g., Fig. 2A). One pair piped when they were reunited with their 2-week-old chick after we released it. Piping also occurred when mates rejoined after an absence, especially if one of them had just engaged in piping elsewhere. Following piping displays with neighbors, birds often piped while flying over their territory or after landing there. One male piped as he flew close to the nest to relieve his mate; the female piped as she flew away after changeover (time elapsed, ca. 8 min). Another pair piped in flight after following a hawk which passed through their territory.

During piping on the ground, *H. leucopodus* lifted the wings slightly out from the body (especially at the carpal flexure), erected the tail until it was roughly vertical, fanned the under-tail coverts and lowered the head and neck. The lifting of the wings at the carpal flexure exposed the white shoulder spots (Fig. 2A, B). The head and neck remained lowered with the bill pointing down throughout high intensity portions of piping interactions (e.g., Fig. 2A, B). Occasionally the head was lifted up quickly with the bill still pointing down, and was held there briefly before being re-lowered. This stiff quick action was often repeated several times in succession, with brief pauses when the head was elevated and longer pauses when it was lowered. The movement strongly resembled feeding, though it was more stereotyped and the bill never touched the ground. Indeed, displacement feeding was common during pauses in aggressive piping performances and was characterized by unusually vigorous insertion of the bill into the ground and twisting movements. It was not observed in piping between mates.

Parallel running with short quick steps also accompanied aggressive piping, and was interspersed with sudden pivoting actions when the piping birds turned about 180° and ran together in the opposite direction. When running, piping birds dropped their tails 20° or more below vertical (Fig. 1G). Mates piping were not observed running and pivoting. They generally walked slowly or stood in one place.

After landing, some birds piped in an erect posture with breast feathers fluffed and the feathers on the belly sleeked (Fig. 1F). This display also occurs in *H. bachmani* (S. Groves, in litt.), and resembles one seen in the Magellanic "Plover" (*Pluvianellus socialis*; Fig. 6 of Jehl 1975).

Piping in *H. leucopodus* was highly contagious. Birds became alert upon hearing piping, and either flew piping toward the source or piped where they were (Fig. 1G). We observed up to 8 *H. leucopodus* piping together on the ground, and at least some of them had nests with eggs. Thus, piping probably has more functions than reaffirming boundaries of nesting territories. Piping lasted up to 11 min between 2 neighboring pairs.

Piping in *H. ater* and *H. palliatus* is similar to that in *H. leucopodus*. One pair of *H. ater* piped in flight after a ground performance with other birds, then piped together after landing at some mussel beds. Paired *H. ater* often piped together on the ground when conspecifics flew over their

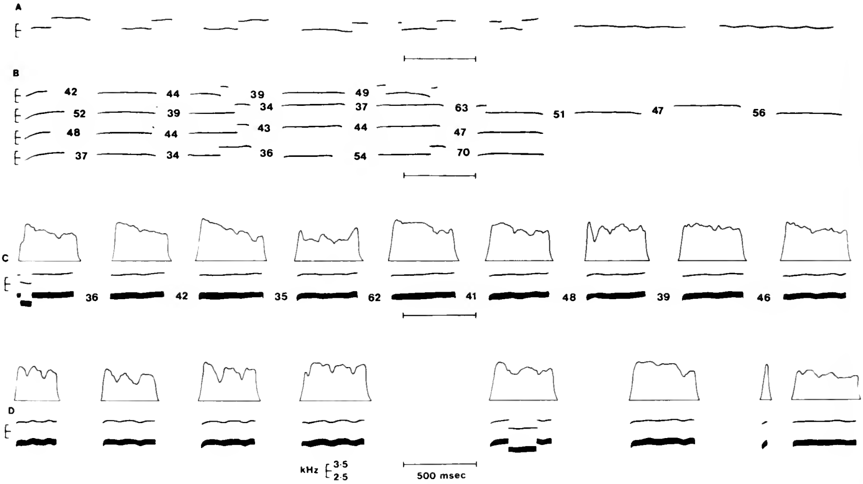


FIG. 3. Calls of *H. leucopodus* disturbed near the nest. (A) Eight calls (not in sequence of occurrence, intervals are arbitrary) from 4 birds flying around us (analyzing filter band width 45 Hz); (B) 4 complete series of ground calls from a lone bird (numbers between calls indicate intervals between them in csec; analyzing filter band width, 45 Hz); (C) flight calls from 1 bird in A (amplitude profiles are above the narrow and wide band representations; numbers between calls indicate intervals between them in csec; analyzing filter band widths, 45 and 300 Hz); (D) flight calls from 1 bird of a pair (amplitude profiles are above the narrow and wide band presentations; call intervals can be estimated by the time marker; analyzing filter band widths, 45 and 300 Hz). Only the fundamental frequency of each call is shown.

nesting territory, and some pairs piped after we moved away from their nests. One male *H. p. durnfordi* started piping when joined in flight by his mate (Fig. 9B). We did not see piping between *H. ater* and *H. p. durnfordi*, though both species were nesting abundantly on Punta Tombo. However, we saw a male *H. ater* chase a passing *H. p. durnfordi* in flight, and saw a nesting bird which appeared to be a hybrid between the 2 species; its mate was a typical *H. p. durnfordi*.

During aggressive piping, *H. p. palliatus* sometimes lifted the tail weakly and briefly (Fig. 2C, D) and held the wings away from the body. Both members of a piping pair occasionally held their tails about 30° above the horizontal for several seconds (see also Kilham 1980). However, this component of piping in *H. palliatus* was less extreme than in *H. leucopodus* (Fig. 2C–F), though Kenyon (1949:198) remarks that "the tail was pointed sharply upward" in a piping *H. p. frazari*. One male *H. p. palliatus* erected and fanned his tail when a neighboring male dove at him (Fig. 2G). We did not see tail erection in *H. ater* but viewed a commercial movie about Punta

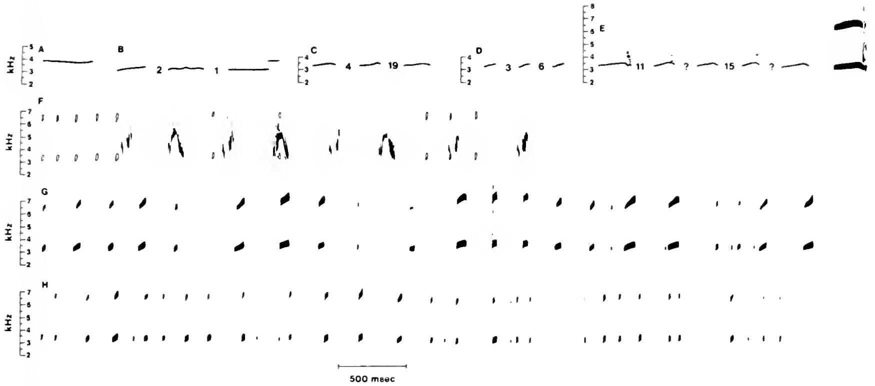


FIG. 4. Calls of *H. leucopodus* disturbed near the nest. (A) Ground call by a lone bird; (B) consecutive calls by a bird on the ground, in takeoff and immediately after takeoff; (C) ground calls by a female of a pair; (D) ground calls by 1 bird of a pair; (E) ground calls by a lone bird; (F) ground calls by a pair (male in outline, female in black): the female was in distraction display (see text); (G, H) later ground calls by the male in F.

The fundamental frequency of each call is shown, except for the wide band representation in E, and all of F–H. Numbers between calls in A–E indicate intervals between them in sec. Intervals between calls in F–H can be estimated by the time marker. Analyzing filter band width for A–E (except last call), 45 Hz, and for E (last call only) and F–H, 300 Hz.

Tombo in which piping oystercatchers purported to be this species held the tail almost vertical. Reynolds (1935) also mentions tail erection in piping *H. ater*. Piping in *H. ater* and *H. palliatus* incorporated head-up/head-down movements as described for *H. leucopodus*.

Butterfly flights.—*H. ater* and *H. p. palliatus* gave occasional "butterfly flights" in which the wings flapped slowly through an exaggerated arc (see Fig. 6 of Glutz von Blotzheim et al. 1975). All butterfly flights by *H. p. palliatus* were lone displays by birds from pairs that were incubating or had recently lost clutches. These flights were given in many circumstances, often away from territories. We do not know the breeding status of the *H. ater* which gave this display. We did not see butterfly flights in *H. leucopodus* or *H. p. durnfordi*, possibly because of the brevity of our study.

Calls by adults disturbed near the nest.—*H. leucopodus* disturbed near the nest gave various calls. Birds which stood attentively or flew near us emitted thin whistle-like alarm calls of nearly constant frequency, which often broke to higher or lower frequency (Fig. 3, 4A–E). Most of these calls were between 3 and 4 kHz, and lasted at least 0.3 sec. These loud calls occurred in fairly rhythmical series with silent intervals lasting ca. 0.5 sec, and their durations varied little (Fig. 3B–D). One bird gave several call series, each starting with a brief call rising gently in frequency (Fig. 3B). These were followed by nearly constant frequency calls (twice with brief high frequency endings), then calls which broke to higher frequency partway through. The beginning frequency of a call is seemingly related to the terminal frequency of the preceding call. For example, in the second sequence in Fig. 1B, the third call ended at high frequency, the fourth and fifth calls continued at the same level, the sixth call started there, then shifted to a lower frequency, and the seventh call remained there.

Amplitude profiles of calls varied among individuals. One bird's alarm calls generally declined in amplitude throughout, and another bird's calls showed 3 amplitude peaks (Fig. 3C, D). These trends were not affected strongly by breaks in frequency (e.g., first call in Fig. 3C, and fifth call in Fig. 3D).

One bird ended its flight calls in wide band noise (Fig. 4E). Slow rhythmic frequency modulation (FM) coupled with amplitude modulation characterized some individuals (e.g., Fig. 3D), and occurred in certain very long flight calls (e.g., last 2 calls in Fig. 3A). Frequency modulation also occurred in calls emitted during takeoff (e.g., second call in Fig. 4B) and in calls associated with changeovers at the nest (see below). Other variants also occurred commonly, including descending frequency calls (Fig. 4A) and brief calls of rising frequency (Fig. 4C, D). The latter resemble early calls in piping series.

H. leucopodus has several other distinct types of calls. One female emitted complex noisy calls (Fig. 4F) while crouching in weak distraction display with her tail elevated to about 45°, and occasionally while false-brooding. The 2 call types she uttered were alternated; if we refer to her first and second call types in Fig. 4F as A and B, then A followed A once, B never followed B, B followed A 16 times, and A followed B 13 times. During this sequence the male stood upright and gave very brief soft "chip" calls, which were brief when delivered rapidly and lengthened when the cadence slowed (Fig. 4F, H). Some of the long chip calls resembled calls from a parent answering a chick calling in distress after we captured it (Fig. 6B). Finally, both sexes occasionally gave a "growl" call near the nest, usually while partly crouched with weak or no tail erection. Growls are wide band calls which were sometimes emitted in rapid rhythm (e.g., Fig. 5A, male in Fig. 5C), but at other times were longer, louder and less rhythmic (e.g., Fig. 5B, female in Fig. 5C).

H. ater, disturbed near the nest, gave variable loud calls (Fig. 7A, G). Some of the compound calls are comprised of rapidly delivered simple calls (e.g., second call in Fig. 7A–C, last 5 calls in Fig. 7D), and some seem to result from coalescence of simple calls (e.g., last call in Fig. 7F). Intermediate states are common (e.g., third call in Fig. 7A, second call in

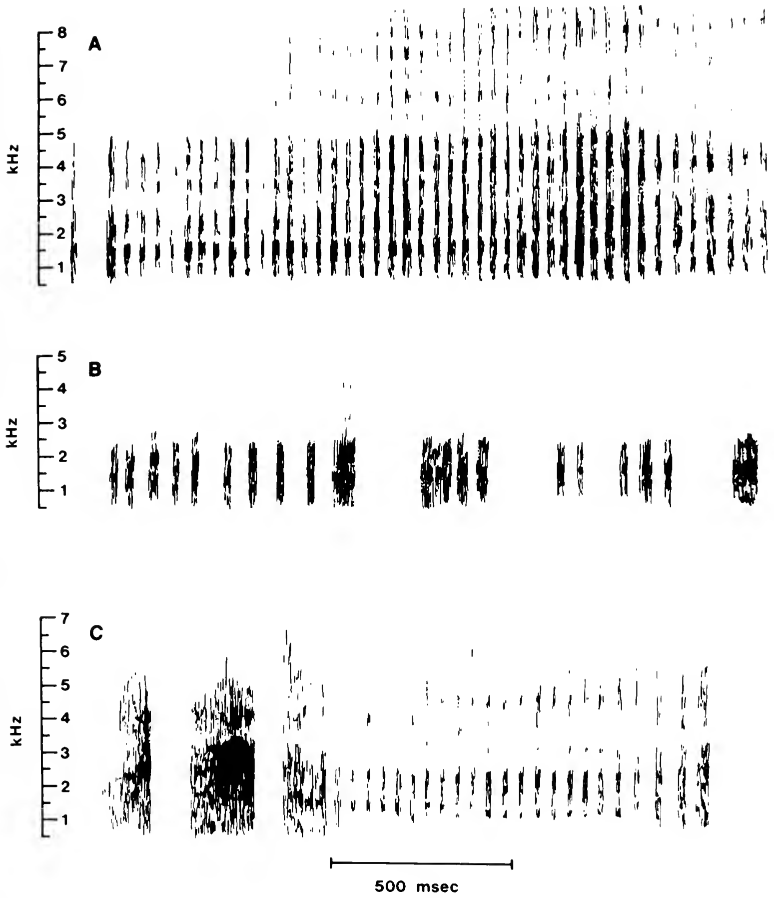


FIG. 5. "Growling" calls of *H. leucopodus*. (A) female standing upright near her nest, with tail erected about 45°; (B) different female near her mate, crouched with tail erected about 20°; (C) 3 loud bursts by the female in B, the last of which overlaps the start of a softer growling sequence by her mate, who was standing upright nearby. Analyzing filter band width, 300 Hz.

Fig. 7C). Even some simple calls show suggestions of being bi-peaked possibly through fusion or elaboration of a simple call (e.g., in Fig. 7D, E).

Calls of *H. palliatus* disturbed near the nest were similar to those of *H. ater* (Fig. 7H–P). Sonagrams for *H. palliatus* show few intermediates between simple and compound calls, in contrast to *H. ater*.

Sonagrams of calls of *H. ater* and *H. palliatus* show a sudden upward

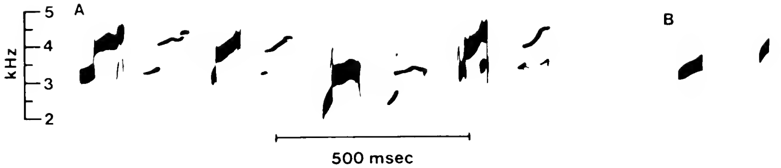


FIG. 6. Distress calls of a 2-week-old chick of *H. leucopodus* and answering calls by 1 parent. (A) Four cries by the chick while hand-held (each call shown in wide, and narrow band representation; analyzing filter band widths, 300 and 45 Hz); (B) 2 isolated ground calls by a parent of the chick, each given in immediate response to single loud calls by the chick before we released it (analyzing filter band width, 300 Hz). Only the fundamental frequency of each call is shown.

shift to a lower or higher frequency component, reminiscent of *H. leucopodus* (Fig. 7E, fourth and fifth calls in Fig. 7F, third to fifth calls in Fig. 7I, Fig. 7K–M).

Piping.—It was usually impossible to distinguish among calling birds in a piping display, for they all assumed piping postures. However, sequences of calls from piping interactions involving several birds often included sequences from only 1 or 2 birds at a time.

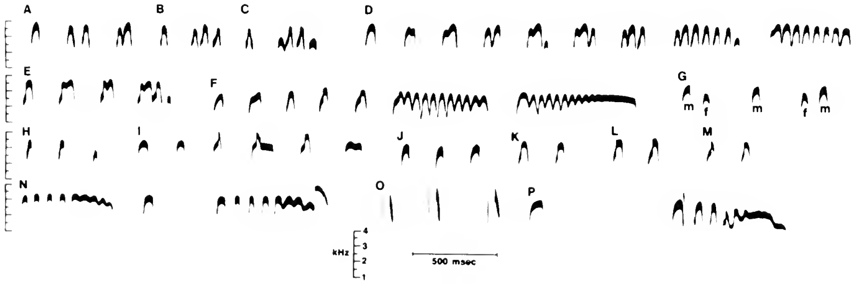


FIG. 7. Ground calls of *H. ater* and *H. palliatus* disturbed near the nest. Intervals between calls are arbitrary except where noted. Only I and N are from the same bird. (A, B, C) Three, 2 and 2 calls of *H. ater*, respectively; (D) 9 calls of *H. ater* arranged to show variation from single to bi-peaked and compound-repetitive forms; (E) 4 calls of *H. ater*, arranged as last; (F) 7 calls by a female *H. ater*; (G) calls by a pair of *H. ater* in the sequence they were given (m = male, f = female) (intervals between the first 5 calls can be judged from the time marker; the interval between the last 2 calls is arbitrary); (H–M) calls of *H. p. durnfordi*; (N) calls of *H. p. durnfordi* (the interval between the single central call and the last compound call can be judged from the time marker; the preceding interval is arbitrary); (O) 3 calls of *H. p. palliatus*; (P) 2 calls of *H. p. palliatus* (the interval between them can be judged from the time marker). Only the fundamental frequency of each call is shown. Analyzing filter band width, 300 Hz.

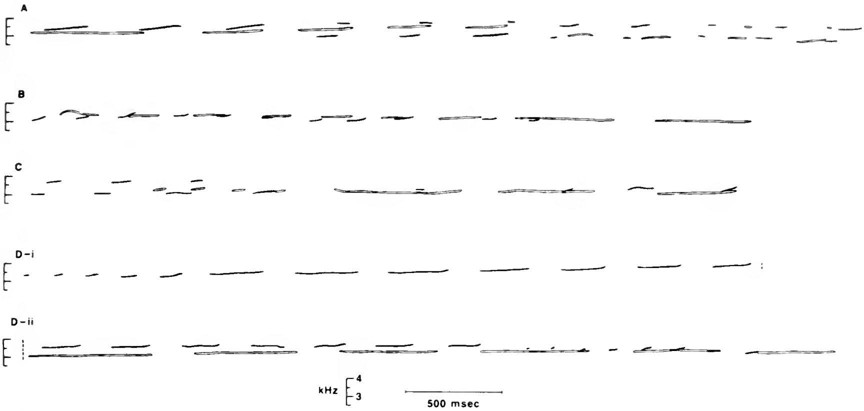


FIG. 8. Ground piping vocalizations of *H. leucopodus*. (A–C) Parts of a long piping interaction by a pair after they were joined by their chick we released (see Fig. 6) (calls of the 2 adults are distinguished in each part, but may not be represented the same in all parts); (D) part of a long piping interaction among 5 birds (vertical dashed line indicates where the 2 segments of the sequence are joined; 2 calling birds are distinguished, though at the end of part D-ii other birds started calling; their calls are not shown). Only the fundamental frequency of each call is shown. Analyzing filter band width, 45 Hz.

Piping in *H. leucopodus* began with brief calls which rose slightly in frequency and became progressively longer (e.g., Fig. 8D-i). Sometimes the calls shortened later in the series, then led into another series of brief calls (e.g., Fig. 8D-ii), or changed to a series of calls with rapid frequency shifts (e.g., both callers in Fig. 8A). Numerous other variants occurred.

Piping in *H. ater* and *H. palliatus* also began with rapid, brief calls which became progressively longer (Fig. 9–11), a trend which occasionally recurred in a single piping sequence (last part of Fig. 11E-ii). Piping in *H. p. durnfordi* and *H. p. palliatus* was similar in all respects (Fig. 9, 10). In this species the longer calls later in a sequence tended to occur in couplets (e.g., black calls in Fig. 9 near end of A-ii, B, and D–ii; outlined calls in Fig. 10C–E). This was even more pronounced in *H. ater,* and sonagrams show some calls that are fused, bi-peaked (Fig. 11A–E) and even multi-peaked (Fig. 11C-i). Long calls occurred in piping interactions in *H. ater* and *H. palliatus,* often near the beginning and end of complete sequences (Fig. 9A-i, B, C, and D-ii; Fig. 10A, E; Fig. 11E-i), though none was as long as comparable calls of *H. leucopodus.* Many brief piping calls in *H. ater* and *H. palliatus* showed sudden changes in frequency suggestive of those seen in *H. leucopodus* (e.g., most of the black calls in Fig. 9A-i;

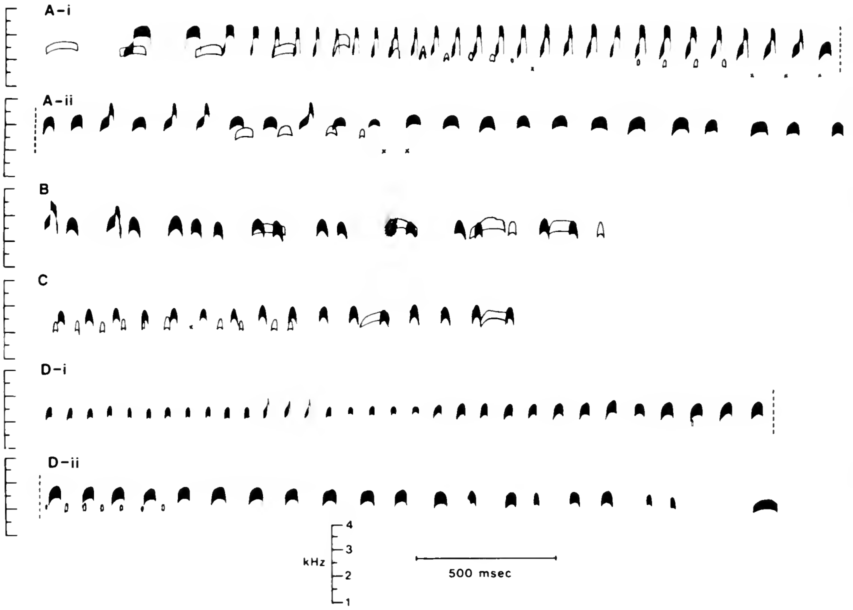


FIG. 9. Piping vocalizations of *H. palliatus durnfordi*. An 'x' or hatching indicates that a call was too faint or distorted to reproduce. (A) Nearly complete piping sequence by a male in flight (in black) and an unknown bird (only the first few calls are not shown; vertical dashed line indicates where the 2 segments of the sequence are joined); (B) segment of a piping sequence by a male in flight (in black) upon being joined by its mate (this segment starts about 500 msec after the start of calling); (C) later segment in the same piping sequence as in B, with the male's calls still shown in black (vocal component of this interaction ended about 2.5 sec after the end of this segment); (D) nearly complete piping sequence by a pair on the ground (only the first few calls are not shown). Only the fundamental frequency of each call is shown. Analyzing filter band width, 300 Hz.

third, fifth, sixth and ninth calls in Fig. 9A-ii, first and third calls in Fig. 9B; first 5 calls in Fig. 10A, etc; most of the black calls in Fig. 11E-ii, etc.).

Many calls from piping series are very similar to alarm calls (e.g., compare calls of *H. ater* in Fig. 11A–D with those in Fig. 7A–G, and calls of *H. leucopodus* in Fig. 8 with those in Fig. 3 and 4A–E).

Other calls.—A hand-held 2-week-old chick of *H. leucopodus* gave brief calls (Fig. 6A). These involved sudden frequency shifts closely resembling those described for adult *H. ater* and *H. palliatus*, though longer.

H. ater and *H. palliatus* gave long *hueep* calls which gently rose, then fell in frequency (Fig. 11F–J), usually associated with flight (see legend to

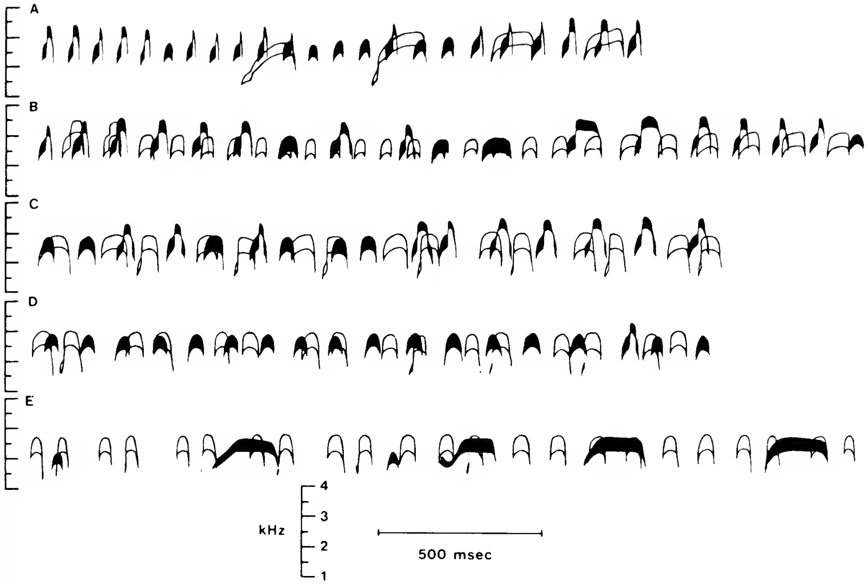


FIG. 10. Ground piping vocalizations from a piping interaction involving about 4 *H. p. palliatus*. (A) and (E) show beginning and end of a single unbroken calling sequence lasting about 23 sec; and (B–D) are segments from in between, shown in the order they occurred. Two calling birds are distinguished in each part but they may not be represented the same in all parts. Only the fundamental frequency of each call is shown. Analyzing filter band width, 300 Hz.

Fig. 11F–J). In both species, these long calls were given when 1 or 2 paired birds flew over foreign territories. We do not know if *H. leucopodus* possesses an analogous call, although undisturbed paired birds of this species flying together called often.

H. leucopodus gave many calls before or after changeover at the nest. For example, relieving birds sometimes called before and after landing, and the relieved bird often called before flying off or during its flight away. These calls all seemed to be of constant frequency and many were relatively soft. One female gave flight calls with slow rhythmic FM before and after nest relief.

H. ater, in butterfly flight, uttered a continuous series of simple notes. Our tape recordings of this call are poor, but its fundamental frequency is around 2.5–3 kHz, and its mean duration ± SD is 23.8 ± 2.98 msec (N = 14). The intervals between calls are around 84.8 ± 13.34 msec (N = 11). Similar notes have been heard during butterfly flights of *H. palliatus*.

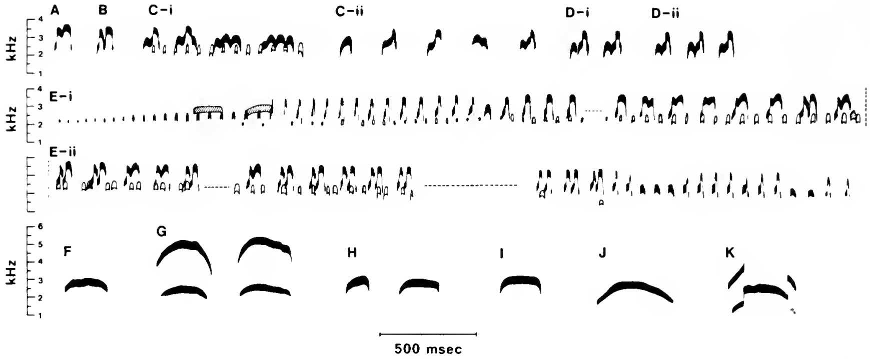


FIG. 11. Ground piping vocalizations of *H. ater* and long calls of *H. ater* and *H. p. palliatus.* (A, B) Piping calls of *H. ater*; (C) partial piping sequence of *H. ater* (i) and single calls from later in that sequence (ii) (intervals shown in C-i can be judged from the time marker; those shown in C-ii are arbitrary); (D) piping calls of 1 *H. ater* (intervals between calls can be judged from the time marker); (E) complete piping sequence of 3 *H. ater* (illegible parts are replaced by horizontal dashes; vertical dashed line indicates where the 2 segments of the sequence are joined); (F) flight call from a pair of *H. ater* after they left a piping interaction; (G) ground calls of a male *H. ater* far from us, when we were near his nest (interval between calls is arbitrary); (H, I) ground (H) and flight (I) calls of a pair of *H. ater* after piping with other birds; they flew to a feeding area (interval between the calls in H is arbitrary); (J) call from a lone *H. p. palliatus*, in an unknown context; (K) call from a pair of *H. p. palliatus* as they flew high over other territories. Only the fundamental frequency of each call is shown, except in G, where the second harmonic contains the most energy and in K (the central part of this call had a weak second harmonic, which is not shown). Analyzing filter band width, 300 Hz.

DISCUSSION

Behavior of adults disturbed near the nest.—Diversionary displays of *H. leucopodus* near the nest include false-brooding, tail-flagging and crouching with the tail slightly erected or depressed and fanned. False-brooding is widespread in waders, and needs little comment (Hall 1959; MacLean 1972; Simmons 1955; Williamson 1943, 1952). Tail-flagging is the most striking display, and occasionally grades with false-brooding, when the tail may be lifted to various degrees (see Fig. 10 of MacLean 1972). Tail-flagging resembles piping in that the tail is erected and the under-tail coverts are erected and spread, the wings are lifted away from the body, and there is occasional rapid treading of the feet, suggestive of the rapid running that occurs in aggressive piping. It differs in the erect carriage of the head and neck, and in the fluffing and drooping of the wings. The wing component also occurs in a display of nesting Killdeer (*Charadrius vociferus*), when approached by man (see Fig. 2 in Plate III of Simmons 1955), and strongly resembles the use of wings during brooding in waders. Tail-flagging in *H. leucopodus* may therefore include components of threat display (aggressive piping) and brooding tendency, now ritualized as an anti-predator display.

Crouching with the tail depressed resembles a widespread distraction display in waders (Simmons 1955). This display is weakly developed in *H. leucopodus*, in contrast to some populations of European *H. ostralegus* (Williamson 1943, 1952) and the Chatham Islands (*H. chathamensis*) and Variable (*H. unicolor*) oystercatchers (A. J. Baker, unpubl.). These trends are not related simply to predation intensity. There are no natural mammalian predators on the Faeroes, where distraction display of *H. ostralegus* is very strongly developed, or in the range of *H. chathamensis* or *H. unicolor*. This display is shown weakly by *H. bachmani*, *H. leucopodus* and the South African Black Oystercatcher (*H. moquini*), all of which are exposed to nest predation by mammals (Hall 1959, Webster 1941).

Calls of *H. leucopodus* alarmed near the nest are very different from analogous calls of *H. ater* and *H. palliatus*. These differences are like those between piping vocalizations of the same species, and are discussed below. Calls of *H. ater* and *H. palliatus* are quite similar, and vary from simple short notes to long compound calls. Alarm calls by *H. ater* seem to be more graduated than those of *H. palliatus*, possibly because *H. ater* nests in very high densities (at least at Punta Tombo), a situation allowing information in graded signals to be transmitted (see below). Grading in alarm calls of 1 female *H. ater* is discussed by Miller (1979).

Piping.—Piping probably has similar functions in all oystercatcher species. In European *H. ostralegus* it is predominantly hostile behavior between birds with adjacent nesting territories, but also occurs in many other circumstances, such as when mates meet or in response to fledged young begging for food (Glutz von Blotzheim et al. 1975, Heppleston 1970, Huxley and Montague 1925, Lind 1965, Makkink 1942, Vines 1979). These contexts are similar to those for piping in *H. leucopodus* and *H. ater*. Males of *H. ostralegus* may pipe more than females (Buxton 1939, Glutz von Blotzheim et al. 1975), which may explain why only a few birds vocalize during piping interactions (Huxley and Montague 1925, this study); could these be males most frequently? S. Groves (in litt.) suggests that this is so for *H. bachmani*. Piping clearly functions within the pair-bond (and family?) as well as in territorial demarcation. (Detailed study of piping in at least 1 species is needed for meaningful interpretations.)

Piping in *H. leucopodus* includes several striking visual components, including: wings held slightly out from the body, especially at the carpel flexure; parallel running; vertical tail position with spreading and fluffing of the under-tail coverts; and vertical movements of the head and neck. Many species of birds hold the folded wings away from the body in visual threat (Tinbergen 1953, many others). In pied *Haematopus* spp. this action also displays the white shoulder bay just above the carpal joint, an important component of visual display in some taxa (Lumsden 1970). Within the Charadriiformes, parallel locomotion appears to be most highly ritualized in the Haematopodidae (Glutz von Blotzheim et al. 1975, Hall 1959, Huxley and Montague 1925).

H. palliatus and *H. ater* occasionally raise the tail for a few seconds during piping, but not vertically, in contrast to *H. leucopodus*. Prolonged vertical erection of the tail also occurs in threat and courtship of calidridine sandpipers (Drury 1961, Holmes 1973, Holmes and Pitelka 1964). In the Least Sandpiper (*Calidris minutilla*) this display further resembles that of *H. leucopodus* in the spreading of the under-tail coverts (E. H. Miller, unpubl.). Erection of the under-tail coverts in *H. leucopodus* may be a ritualized expression of defecation, which occurs commonly in stressed vertebrates (Eisenberg and Kleiman 1972, Simmons 1955:143).

Vigorous false-feeding is common in aggressive piping. This displacement reaction may have become ritualized as the vertical movements of the head and neck of piping birds (Heppleston 1970). Both characteristics of piping appear to be widespread in oystercatchers.

Piping in *H. leucopodus* differs from that of *H. ater* and *H. palliatus* mainly in the prolonged upright erection of the tail and fluffing of the under-tail coverts. The tail is not lifted, or is lifted weakly, in *H. bachmani* (rarely reaching a vertical position, S. Groves in litt., but see Kenyon [1949]), European *H. ostralegus* (Huxley and Montague 1925, Makkink 1942), *H. fuliginosus* and Australian *H. ostralegus* (A. J. Baker, unpubl.), *H. chathamensis, H. o. finschi* and *H. unicolor* (Baker 1974).

Vocal components of piping in *H. leucopodus* are even more distinctive. Most, or all other species emit brief piping calls which are relatively wide band: *H. ater* and *H. palliatus*; *H. bachmani* (Webster 1941); European *H. ostralegus* (Glutz von Blotzheim et al. 1975, Huxley and Montague, 1925); *H. fuliginosus* and Australian *H. ostralegus* (A. J. Baker, unpubl.); *H. chathamensis, H. o. finschi* and *H. unicolor* (Baker 1974). Nevertheless, individual piping vocalizations of the 3 species we studied are similar in an important respect: all are strikingly similar to alarm calls in the same species. Piping seems to be a highly ritualized form of these calls in its rapid delivery, rhythm and strong grading across adjacent elements. Further support for this interpretation lies in the relationship between grading of vocalizations and nesting density in *H. ater* and *H. palliatus*. Alarm calls of *H. ater* vary from single calls to couplets, triplets, etc., according to level of excitement. This species nests at high densities, which should favor highly aggressive displays with high information content (e.g., through grading). Both characteristics are more pronounced in *H. ater* than *H.*

palliatus: conspicuous call couplets occur in piping of *H. ater*, and these show extensive gradation.

H. leucopodus responds to piping over long distances, and the extremely narrow band width of its vocalizations may be an adaptation for long distance propagation. The allocation of all sound energy to a narrow band width may be most economical evolutionarily (Marten, Quine and Marler 1977, Morton 1975, Wiley 1976), and the spectrum of a narrow band call changes very little over distance, as compared to a wide band call with the same center frequency (Konishi 1970, Smith 1977). In addition, the long duration of piping and alarm calls of *H. leucopodus* provides redundancy which improves chance of accurate reception by listeners. Similar long-range vocal displays occur in other waders: Knot, *Calidris canutus*, (Salomonsen 1950) and *Numenius* spp. (Forsythe 1967, 1970; Skeel 1976, 1978). These species nest at low densities in extensive open habitat, like *H. leucopodus*, and their calls are uttered during high flight displays, which further enhances long-distance transmission. The convergences in length and simple spectral structure of these calls probably arose because frequency characteristics degrade much less over distance than do amplitude characteristics and patterns of frequency and amplitude modulation (Wiley 1976, Wiley and Richards 1978). Such calls should therefore have simple temporal structure because of the unstable attenuation characteristics of open habitats (Marten, Quine and Marler 1977), and should have simple spectral structure if they are used over various or great distances, or both.

Systematic comments.—Piping may be an effective isolating mechanism. *H. palliatus* and *H. ater* have similar piping displays which differ markedly from that of *H. leucopodus*. *H. palliatus* and *H. ater* hybridize frequently where they are sympatric (Jehl, Rumboll and Winter 1973; A. J. Baker, unpubl.), whereas only 1 putative hybrid between *H. ater* and *H. leucopodus* has been reported (Jehl 1978). Interbreeding between *H. palliatus* and *H. leucopodus* has not been reported. Likewise, *H. bachmani* and *H. p. frazari* have very similar "behavior and vocal expressions," engage frequently in piping and hybridize extensively (Kenyon 1949:198).

The systematic position of *H. leucopodus* has not been resolved by morphological studies (Baker 1977; Jehl 1968; Strauch 1976, 1978). Some displays of the species are probably unique, but these just strengthen the view that *H. leucopodus* is aberrant within its family. The systematic value of other displays cannot be judged until a detailed comparative study is done.

SUMMARY

The display behavior of the Magellanic Oystercatcher was studied in southern Patagonia and is described comparatively here. Original observations on *H. ater*, *H. palliatus durnfordi* and *H. p. palliatus* are also included.

Behaviorally, *H. leucopodus* is an aberrant species within the Haematopodidae. Nesting adults have a unique tail-flagging display near the nest, when disturbed by man. Piping birds hold the tail upright and fluff the under-tail coverts, display components which are absent or only weakly developed in other oystercatcher species. Vocalizations of alarmed or piping *H. leucopodus* may also be unique. Most or all other Haematopodidae emit short, wide band calls in both contexts. Analogous calls of *H. leucopodus* are extremely narrow band and often of nearly constant frequency, and are much longer. These characteristics also occur in long-distance epigamic acoustic displays of some other waders which nest at fairly low densities in open habitat.

ACKNOWLEDGMENTS

We were assisted by many people in making arrangements for field work in Argentina and in carrying it out. We particularly wish to thank Mr. R. Meadows (Dept. of External Affairs, Government of Canada), Mrs. M. de Escardo (Canadian Embassy, Buenos Aires), Dr. J. M. Gallardo (Director, Museo Argentino de Ciencias Naturales), Vcom (R) C. E. I. Julio (Secretario de Estado de Agricultura y Ganaderia), Sr. A. Lynch, Sr. A. Clifton, Sr. Luis Gomez, Sr. J. Jamieson, Dr. J. G. Strauch, Jr. and Sr. Z. Kovacs. We are indebted to Dr. J. R. Jehl, Jr., for generously providing the photograph for the frontispiece. Ms. S. Groves, Dr. J. R. Jehl, Jr., Dr. J. P. Myers, Dr. F. A. Pitelka and Dr. J. G. Strauch, Jr., kindly reviewed manuscript drafts. Field work and data analysis were supported by the Royal Ontario Museum, the Faculty of Science of York University and individual operating grants to A. J. Baker and E. H. Miller from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

BAKER, A. J. 1974. Ecological and behavioural evidence for the systematic status of New Zealand oystercatchers (Charadriiformes: Haematopodidae). Life Sci. Contrib., Roy. Ont. Mus. 96, Toronto, Canada.

———. 1975. Morphological variation, hybridization and systematics of New Zealand oystercatchers (Charadriiformes: Haematopodidae). J. Zool., London 161:357–390.

———. 1977. Multivariate assessment of the phenetic affinities of Australasian oystercatchers. Bijdragen Tot De Dierkunde 47:156–164.

BUXTON, E. J. M. 1939. The breeding of the oystercatcher. Br. Birds 33:184–193.

DRURY, W. H., JR. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. Auk 78:176–219.

EISENBERG, J. F. AND D. G. KLEIMAN. 1972. Olfactory communication in mammals. Ann. Rev. Ecol. Syst. 3:1–32.

FORSYTHE, D. M. 1967. Vocalizations of the Long-billed Curlew. M.S. thesis, Utah State Univ., Provo, Utah.

———. 1970. Vocalizations of the Long-billed Curlew. Condor 72:213–224.

GLUTZ VON BLOTZHEIM, U. N., K. M. BAUER AND E. BEZZEL. (eds.). 1975. Handbuch der Vögel Mitteleuropas. Band 6. Charadriiformes. Akademische Verlagsgesellschaft, Wiesbaden.

HALL, K. R. L. 1959. Observations on the nest-sites and nesting behaviour of the Black Oystercatcher *Haematopus moquini* in the Cape Peninsula. Ostrich 30:143–154.

HEPPLESTON, P. B. 1970. The function of oystercatcher piping behaviour. Br. Birds 63:133–135.

——— AND D. F. KERRIDGE. 1970. Sexing oystercatchers from bill measurements. Bird Study 17:40–49.

HOLMES, R. T. 1973. Social behaviour of breeding Western Sandpipers. Ibis 115:107–123.

——— AND F. A. PITELKA. 1964. Breeding behavior and taxonomic relationships of the Curlew Sandpiper. Auk 81:362–379.

HUXLEY, J. S. AND F. A. MONTAGUE. 1925. Studies on the courtship and sexual life of birds. V. The oyster-catcher (*Haematopus ostralegus* L.). Ibis 1925:868–897.

JEHL, J. R., JR. 1968. Relationships in the Charadrii (shorebirds): a taxonomic study based on color patterns of the downy young. Mem. San Diego Soc. Nat. Hist. 3.

———. 1975. *Pluvianellus socialis*: biology, ecology and relationships of an enigmatic Patagonian shorebird. Trans. San Diego Soc. Nat. Hist. 18:25–74.

———. 1978. A new hybrid oystercatcher from South America, *Haematopus leucopodus* × *H. ater*. Condor 80:344–346.

———, M. A. E. RUMBOLL AND J. P. WINTER. 1973. Winter bird populations of Golfo San Jose, Argentina. Bull. Br. Ornithol. Club 93:56–63.

KENYON, K. W. 1949. Observations on behavior and populations of oyster-catchers in lower California. Condor 51:193–199.

KILHAM, L. 1980. Cocked-tail display and evasive behavior of American Oystercatchers. Auk 97:205.

KONISHI, M. 1970. Evolution of design features in the coding of species specificity. Am. Zool. 10:67–72.

LIND, H. 1965. Parental feeding in the oystercatcher (*Haematopus o. ostralegus* [L.]). Dansk orn. Foren. Tidsskr. 59:1–31.

LUMSDEN, H. G. 1970. The shoulder-spot display of grouse. Living Bird 9:65–74.

MACLEAN, G. L. 1972. Problems of display postures in the Charadrii (Aves: Charadriiformes). Zool. Afr. 7:57–74.

MAKKINK, G. F. 1942. Contribution to the knowledge of the behaviour of the oyster-catcher (*Haematopus ostralegus* L.). Ardea 31:23–74.

MARTEN, K., D. QUINE AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization II. Tropical forest habitats. Behav. Ecol. Sociobiol. 2:291–302.

MILLER, E. H. 1979. An approach to the analysis of graded vocalizations of birds. Behav. Neural Biol. 27:25–38.

MORTON, E. S. 1975. Ecological sources of selection on avian sounds. Am. Nat. 109:17–34.

REYNOLDS, P. W. 1935. Notes on the birds of Cape Horn. Ibis 5 (ser. 3):65–101.

SALOMONSEN, F. 1950. The birds of Greenland. Munksgaard, Copenhagen, Denmark.

SIMMONS, K. E. L. 1955. The nature of the predator-reactions of waders towards humans; with special reference to the role of the aggressive-, escape- and brooding-drives. Behaviour 8:130–173.

SKEEL, M. A. 1976. Nesting strategies and other aspects of the breeding biology of the Whimbrel (*Numenius phaeopus*) at Churchill, Manitoba. M.Sc. thesis, Univ. Toronto, Toronto, Ontario, Canada.

———. 1978. Vocalizations of the Whimbrel on its breeding grounds. Condor 80:194–202.

SMITH, W. J. 1977. The behavior of communicating. An ethological approach. Harvard, Cambridge, Massachusetts.

STRAUCH, J. G., JR. 1976. The cladistic relationships of the Charadriiformes. Ph.D. diss., Univ. Michigan, Ann Arbor, Michigan.

———. 1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. Trans. Zool. Soc. London 34:263–345.

TINBERGEN, N. 1953. The Herring Gull's world. Collins, London, England.

VINES, G. 1979. Spatial distributions of territorial aggressiveness in oystercatchers, *Haematopus ostralegus* L. Anim. Behav. 27:300–308.

WEBSTER, J. D. 1941. The breeding of the Black Oyster-catcher. Wilson Bull. 53:141–156.

WILEY, R. H. 1976. Communication and spatial relationships in a colony of Common Grackles. Anim. Behav. 24:570–584.

——— AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav. Ecol. Sociobiol. 3:69–94.

WILLIAMSON, K. 1943. The behaviour pattern of the Western Oyster-catcher (*Haematopus ostralegus occidentalis* Neumann) in defence of nests and young. Ibis 85:486–490.

———. 1952. Regional variation in the distraction displays of the oyster-catcher. Ibis 94:85–96.

BIOLOGY DEPT., YORK UNIV., DOWNSVIEW, ONTARIO M3J 1P3 CANADA (EHM) AND DEPT. ORNITHOLOGY, ROYAL ONTARIO MUSEUM, TORONTO, ONTARIO, M5S 2C6 CANADA (AJB). (PRESENT ADDRESS EHM: VERT. ZOOL. DIV., B.C. PROVINCIAL MUSEUM, 667 BELLEVILLE, VICTORIA, BRITISH COLUMBIA, V8V 1X4 CANADA.) ACCEPTED 21 FEB. 1980.

COLOR PLATE

The color plate Frontispiece of the Magellanic Oystercatcher (*Haematopus leucopodus*) has been made possible by an endowment established by Dr. George M. Sutton.

Wilson Bull., 92(2), 1980, pp. 169–176

THE INCIDENCE OF RUNT EGGS IN WOODPECKERS

WALTER D. KOENIG

Little is known about "runt" or "dwarf" eggs in birds. Physiologically, runt eggs are often produced by a temporary disturbance to the reproductive organs; a minority are laid by birds with permanent abnormalities (Pearl and Curtis 1916). Runt eggs do not develop; their yolks are generally abnormal or missing. Although reported in many species, runt eggs are of uniformly low incidence (Table 1). This suggests that the disturbances responsible for the production of a runt egg are accidental, occur rarely in most or all species, and are not affected by nutritional or behavioral factors.

As part of a study of the ecology of the Acorn Woodpecker (*Melanerpes formicivorus*), I discovered a high occurrence of runt eggs in this species. The purpose of this paper is thus twofold: (1) to compare the incidence of runt eggs among North American picids, and (2) to examine hypotheses which may explain the frequency of egg dwarfism in the Acorn Woodpecker.

METHODS

Data were collected in 3 ways. (1) Museum egg sets were examined for unusually small, possibly runt eggs. Maximum length and width for a large sample of Acorn, Red-headed (*M. erythrocephalus*) and Lewis' (*M. lewis*) woodpeckers' eggs were measured. Sets of other species were measured only when inspection revealed 1 or more eggs which might be a runt. When possible, the original data cards were examined for Acorn Woodpecker sets and the stage of incubation noted. (2) Information on the presence of runt eggs in Acorn, Red-headed and Lewis' woodpeckers was requested from curators of several major oological collections. (3) Sets of Acorn Woodpecker eggs were measured in the field at Hastings Reservation, Monterey Co., California, between 1976 and 1978.

Runt eggs are those whose relative volume (length × width^2 × $\pi/6$) is: (1) $<75\%$ of the average of all larger eggs in the set and (2) smaller than 3.10 SD below the mean of eggs not meeting criterion (1) of that species. For rationale of these criteria see Koenig (1980).

A comparison of the 3 sets of data for Acorn Woodpeckers indicates a bias towards a higher frequency of runts in museum collections (Table 2). However, these differences are not significant. Thus, data from all sources are lumped when possible.

In total, data were collected on 1845 sets (9136 eggs) of 18 species of woodpeckers. Statistical testing was made by either the 2-tailed Fisher exact test (Bailey 1959, Koenig 1980) or a χ^2 test of independence with Yates' correction (Siegel 1956); difference at the $P \leq 0.05$ level were considered significant.

RESULTS AND DISCUSSION

Frequency of occurrence of runt eggs in North American woodpeckers.—Table 3 lists the frequency of runt eggs and the frequency of sets with

TABLE 1

FREQUENCY OF OCCURRENCE OF RUNT EGGS REPORTED IN THE LITERATURE[a]

Species	Eggs examined	Runts	% runts	Source
Canada Goose (*Branta canadensis*)	500	3	0.60	Manning and Carter 1977
Domestic fowl (*Gallus domesticus*)	199,137	103	0.05	Warner and Kirkpatrick 1916
	151,736	131	0.09	Pearl and Curtis 1916
Gulls (*Larus*, 4 spp.)	4559	1	0.02	Barth 1967
Anis (*Crotophaga*, 2 spp.)	438	1	0.23	this study (museum)
Picidae (17 spp., not incl. *M. formicivorus*)	7979	38	0.48	this study (museum)
Acorn Woodpecker (*Melanerpes formicivorus*)	1157	50	4.32	this study (museum and field)
House Wren (*Troglodytes aedon*)	1347	2	0.15	Kendeigh et al. 1956
Starling (*Sturnus vulgaris*)	2000	2	0.10	Ricklefs 1975
Red-winged Blackbird (*Agelaius phoeniceus*)	1100	2	0.18	Rothstein 1973 (museum)
Common Grackle (*Quiscalus quiscula*)	1277	1	0.08	Rothstein 1973 (field)
	560	3	0.54	Rothstein 1973 (museum)

[a] Field data except where noted; studies based on fewer than 250 eggs are excluded.

runts for 18 species of North American picids. The results of statistical comparisons between species are the same using either of these measures. None of the 136 two-way comparisons between species other than the Acorn Woodpecker is significant. Compared to the Acorn Woodpecker, however,

TABLE 2

FREQUENCY OF OCCURRENCE OF RUNT EGGS IN FIELD AND MUSEUM SETS OF ACORN WOODPECKER EGGS

	Eggs examined	Sets examined	Runts	Sets with runts	% runts[a]	% sets with runts[a]
Museum (examined)	767	147	37	36	4.82	24.5
Museum (solicited data)	193	37	7	7	3.63	18.9
Field	203	43	6	5	2.96	11.6

[a] All 2- and 3-way comparisons non-significant.

TABLE 3

FREQUENCY OF OCCURRENCE OF RUNT EGGS IN NORTH AMERICAN WOODPECKERS

Species	Eggs examined	Sets examined	Runts	Sets with runts	% runt eggs	% sets with runts	Comparison with *M. formicivorus*[a]
Colaptes auratus (Common Flicker)	2574	422	15	13	0.583	3.08	***
Dryocopus pileatus (Pileated Woodpecker)	236	63	0	0	0.000	0.00	***
Melanerpes carolinus (Red-bellied Woodpecker	239	57	1	1	0.418	1.75	**
M. aurifrons (Golden-fronted Woodpecker)	416	86	1	1	0.240	1.16	***
M. uropygialis (Gila Woodpecker)	175	48	0	0	0.000	0.00	**
M. erythrocephalus (Red-headed Woodpecker)	731	155	5	5	0.684	3.23	***
M. formicivorus	1157	227	50	48	4.322	21.15	—
M. lewis	619	110	3	3	0.485	2.73	***
Sphyrapicus varius (Yellow-bellied Sapsucker)	417	87	1	1	0.240	1.15	***
S. thyroideus (Williamson's Sapsucker)	235	44	1	1	0.426	2.27	**
Picoides villosus (Hairy Woodpecker)	502	129	4	4	0.797	3.10	***
P. pubescens (Downy Woodpecker)	743	154	1	1	0.135	0.65	***
P. scalaris (Hadder-backed Woodpecker)	203	51	0	0	0.000	0.00	***
P. nuttallii (Nuttall's Woodpecker)	271	64	1	1	0.369	1.56	***
P. borealis	75	20	1	1	1.333	5.00	
P. albolarvatus (White-headed Woodpecker)	449	104	3	3	0.668	2.89	***
P. arcticus	64	17	1	1	1.563	5.88	
P. tridactylus	30	7	0	0	0.000	0.00	

[a] All other 2-way comparisons non-significant.

* $P < 0.01$.

*** $P < 0.001$.

the frequency of runts is significantly different in 14 of the 17 species (82%). The 3 species not significantly different are those with such small sample sizes (Arctic Three-toed [*Picoides arcticus*], Northern Three-toed [*P. tridactylus*] and Red-cockaded [*P. borealis*] woodpeckers), that they are statistically indistinguishable from any of the other species examined.

TABLE 4
FREQUENCY OF OCCURRENCE OF RUNT EGGS IN SMALL AND LARGE SETS OF ACORN WOODPECKER EGGS

	All sets		Incubated sets only	
	2–5	6–13	2–5	6–13
Number of runts	26	24	4	12
Normal eggs	676	431	237	175
Total	702	455	241	187
% runts	3.70	5.27	1.66	6.42
χ^2 (df = 1)	1.29^{NS}		5.37*	

* $P < 0.05$.

Combining data, the frequency of runt eggs in Acorn Woodpeckers is highly significantly greater ($P < 0.001$) than in the other picids (Table 1). No other departures from the low incidence of runt eggs emerge for any of the species or genera examined.

Why do Acorn Woodpeckers lay so many runt eggs?—Pearl and Curtis (1916), in a comprehensive study of egg dwarfism in the domestic fowl (*Gallus domesticus*), concluded that runts are laid by hens in active laying condition, that they are not associated with sexual immaturity, that they are an isolated event in the life of a hen, and that there is no obvious genetic basis underlying their production. These conclusions suggest no factor which might differ significantly from 1 species to another, thereby resulting in a higher or lower than normal frequency of runt eggs.

In the Acorn Woodpecker, a high frequency of runt eggs is present in samples from both California (4.2%, N = 927) and the southwest (5.0%, N = 84). What unique aspect of the biology of this species might be conducive to the production of runt eggs? One clearly unusual feature is the group living habit of this woodpecker—birds live in bisexual groups of up to 15 individuals of all ages (MacRoberts and MacRoberts 1976, Koenig 1978). Within these groups the precise mating system is not known, but I have recently found that under some circumstances more than 1 female may lay eggs in a nest (Koenig 1978). These communal nests are usually distinguishable because they contain more eggs than nests of single females. If runt egg production in Acorn Woodpeckers is related to communal nesting, larger clutches should contain disproportionately more runts. This is tested in Table 4 for (1) all sets and (2) those known to have been incubated (i.e., complete). In both cases the proportion of runt eggs is higher in the larger sets; this difference is not significant for the complete sample but is for those sets known to be complete.

TABLE 5

FREQUENCY OF SETS OF ACORN WOODPECKER EGGS WITH RUNTS ACCORDING TO INCUBATION STATUS

	Incubated	Incubation uncertain
Number of sets with runts	14	34
Number of sets with no runt	67	112
Total sets	81	146
% sets with runts	17.3	23.3
χ^2 (df = 1)	0.79^{NS}	

Data from groups of woodpeckers of known composition at Hastings Reservation provide more direct support for a relation between runt eggs and communal nesting. Four of the 5 sets with at least 1 runt egg occurred in sets of 7 eggs produced by groups in which 2 females are believed to have been nesting. A fifth set contained only 3 eggs when discovered and the nest subsequently failed. However, the group associated with the failed nest also contained 2 females who nested together the following year. A final runt, the sole egg of its "clutch," was discovered in an abandoned nest used by a group also with 2 probable breeding females. However, 7 other sets to which 2 females were suspected, or known to have contributed, did not contain runt eggs.

The actual time during the laying cycle when Acorn Woodpeckers lay runt eggs may be critical in explaining their occurrence. Table 5 compares the proportion of sets with runts among those known to have been incubated vs those whose incubation status is uncertain. If runts are usually laid last, sets collected prior to their completion should not contain runts, and a higher fraction of incubated sets should contain runts than sets whose status is unknown. If runts are laid first, or at any time in the clutch sequence, incubated and uncertain sets should contain about the same proportion of runt eggs. The result (Table 5), is that the proportion of sets with runts is slightly, but insignificantly, lower among incubated sets. This supports the hypothesis that runt eggs are laid either early, or at no particular time in a clutch. There is no satisfactory way to decide between these hypotheses with the available data.

I suspect that, as in the domestic fowl (Pearl and Curtis 1916), Acorn Woodpeckers lay runt eggs at any time during the laying cycle. If this is true, it is likely that these eggs are accidental (and, since they do not hatch, maladaptive), regardless of how common they may be. Why, however, should accidents resulting in runt eggs be especially common in

Acorn Woodpeckers? One possibility is that there is greater inter-individual contact within the social groups of this species than between the pairs of other species, especially between females nesting together. An increased number of interactions, particularly those involving maneuvers within the limited space provided by nest holes, might result in collisions or other physical accidents which would throw off the normal sequence of events during egg production and result in a runt egg.

Two predictions of this hypothesis are: (1) there should be a higher incidence of runt eggs among hole nesters in general than open-nesting birds, and (2) there should be a higher incidence of runt eggs among communal nesting species than those with other breeding systems. The first of these predictions is only marginally supported by data comparing the rate of runt egg production in all species of woodpeckers combined except the Acorn Woodpecker with that of the other species in Table 1. The frequency in woodpeckers is significantly higher than that reported for gulls (*Larus* spp.), the field sample of the Common Grackle (*Quiscalus quiscula*), and the 2 domestic fowl samples. However, the incidence in woodpeckers is also greater than in Starlings (*Sturnus vulgaris*) ($P < 0.05$) and the House Wren (*Troglodytes aedon*) ($P < 0.12$), both hole nesting species.

The second of the above predictions can be tested with data from the Groove-billed (*Crotophaga sulcirostris*) and Smooth-billed (*C. ani*) anis, both communal nesters. However, the frequency of runt eggs in these 2 species is significantly less than in the Acorn Woodpecker (Table 1), contrary to the prediction. Thus, neither the effects of hole nesting nor communal nesting alone can explain a high frequency of runt eggs. Possibly both must be combined in order to produce this anomaly.

If runt eggs are maladaptive in the Acorn Woodpecker, then to the extent that their incidence is a function of communal nesting they may be considered a disadvantage of group living (Alexander 1974). Nearly 5% of the energy put into egg production by females is wasted in producing unviable runt eggs. However, my data do not preclude an adaptive basis for runt eggs. They might, for example, be consistently laid first, or even several days before the rest of the clutch, and serve as a synchronizing "signal" indicating when and where the other female(s) in the group should lay her (their) eggs. The occurrence of a runt in only 4 of the 11 nests in which 2 females are believed to have been nesting at Hastings Reservation, however, suggests that other less energetically wasteful, behavioral cues are adequate for reproductive synchronization in most instances. Alternatively, runt eggs could be a result not of reproductive cooperation but rather of reproductive competition between communally nesting females. Fights between such females for dominance, access to nests, males, or other resources during the breeding season might result in a high frequency of abnormal eggs, especially by subordinate individuals.

Though the function of runt eggs, if any, is unclear, their incidence appears to be related to communal nesting and possibly hole nesting, at least in the Acorn Woodpecker. Other factors influencing runt egg production clearly exist—perhaps any feature of the ecology of a species affecting the probability of physical contact and temporary injury during the laying cycle affects the incidence of runt eggs.

SUMMARY

The incidence of runt eggs among most North American woodpeckers and all other species for which data are available is uniformly low (average 0.54%). In the Acorn Woodpecker, however, over 4% of all eggs are runts, and over 20% of all sets contain at least 1 runt. Both museum and field data support the hypothesis that this high frequency is related to communal nesting. I suggest that an unusual amount of inter-individual contact as a result of females nesting together within the confined space of a nest hole may be responsible for this high frequency of runt eggs. However, predictions from this hypothesis that hole nesters and other communal nesters should by themselves have high frequencies of runt eggs are not supported by the data presently available. Other data will be necessary before meaningful interpretations of the significance of interspecific variation in the frequency of runt eggs can be made.

ACKNOWLEDGMENTS

I would like to thank the curators who compiled data on the frequency of runt eggs in collections under their care and permitted me to measure eggs: J. C. Barber (National Museum of Natural History), L. C. Binford (California Academy of Sciences), R. A. Bradley (Florida State Museum), E. Cardiff (San Bernardino County Museum), J. A. Hamber (Santa Barbara Museum of Natural History), N. K. Johnson and V. Dziadosz (Museum of Vertebrate Zoology), L. F. Kiff (Western Foundation of Vertebrate Zoology), D. Maurer (Field Museum of Natural History), D. M. Niles (Delaware Museum of Natural History), H. W. Pelzl (American Museum of Natural History) and R. W. Schreiber (Los Angeles County Museum). Florence Amamoto and Pam Williams helped to measure eggs. C. R. Grau, F. W. Lorenz and F. A. Pitelka contributed their knowledge of egg physiology and ecology. The latter suggested reasons for the high incidence of runt eggs in the Acorn Woodpecker and has been a continuing source of assistance and information during my work. The study was supported by an NSF pre-doctoral grant, an NSF fellowship, the Museum of Vertebrate Zoology and the Department of Zoology, University of California, Berkeley. The manuscript was helped by the comments of John Davis, Pam Williams and Jon C. Barlow.

LITERATURE CITED

Alexander, R. D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5:325–383.

Barth, E. K. 1967. Egg dimensions and laying dates of *Larus marinus*, *L. argentatus*, *L. fuscus*, and *L. canus*. Meddr. Zool. Mus., Oslo 81:5–34.

Bailey, N. T. J. 1959. Statistical methods in biology. English Universities Press, Ltd., London, England.

Ingersoll, A. M. 1910. Abnormal birds' eggs. Condor 12:15–17.

KENDEIGH, S. C., T. C. KRAMER AND F. HAMERSTROM. 1956. Variations in egg characteristics of the House Wren. Auk 73:42–65.

KOENIG, W. D. 1978. Ecological and evolutionary aspects of cooperative breeding in Acorn Woodpeckers of central coastal California. Ph.D. thesis, Univ. Calif., Berkeley, California.

———. 1980. The determination of runt eggs in birds. Wilson Bull. 92:103–107.

MACROBERTS, M. H. AND B. R. MACROBERTS. 1976. Social organization and behavior of the Acorn Woodpecker in central coastal California. Ornithol. Monogr. 21:1–115.

MANNING, T. H. AND B. CARTER. 1977. Incidence of runt eggs in the Canada Goose and Semipalmated Sandpiper. Wilson Bull. 89:469.

M'WILLIAM, J. M. 1927. Some abnormal eggs of wild birds. Scott. Nat. 166:108–110.

PEARL, R. AND M. R. CURTIS. 1916. Studies on the physiology of reproduction in the domestic fowl—XV. Dwarf eggs. J. Agric. Res. 6:977–1042.

RICKLEFS, R. E. 1975. Dwarf eggs laid by a Starling. Bird-Banding 46:169.

ROTHSTEIN, S. I. 1973. The occurrence of unusually small eggs in three species of songbirds. Wilson Bull. 85:340–342.

SIEGEL, S. 1956. Non-parametric statistics for the behavioral sciences. McGraw Hill, New York, New York.

WARNER, D. E. AND W. F. KIRKPATRICK. 1916. What the size of an egg means. J. Hered. 7:128–131.

MUSEUM OF VERTEBRATE ZOOLOGY AND HASTINGS RESERVATION, UNIV. CALIFORNIA, BERKELEY, CALIFORNIA 94720. (MAILING ADDRESS: STAR ROUTE BOX 80, CARMEL VALLEY, CALIFORNIA 93924.) ACCEPTED 15 FEB. 1979.

Wilson Bull., 92(2), 1980, pp. 177–187

HABITAT STRUCTURE IN RELATION TO POPULATION DENSITY AND TIMING OF BREEDING IN PRAIRIE WARBLERS

Michael C. Moore

Brown (1964) argued that territoriality results when it is economically feasible to defend a limiting resource. Perrins (1970) and Slagsvold (1976) reviewed evidence that timing of breeding is also related to resource availability. However, studies in which the limiting resource is identified are few (see Wilson 1975:263–264), largely because environmental complexities make interpretations difficult.

Any study of resource relationships is greatly facilitated by a simple environment, and the pine barrens of Plymouth County, Massachusetts, offer an ideal situation in this respect. This habitat has fewer than 6 principal plant species. Frequent fires have created a patchwork of uniform tracts in various stages of regeneration, each differing in structure, but not composition, of its vegetation. Prairie Warblers (*Dendroica discolor*) are one of the commonest breeding birds of these barrens, and in this study I examined the role that vegetation and related resources play in territory size, breeding density and timing of breeding of this species.

METHODS

Description and vegetation of study plots.—I selected two 7.5-ha plots less than 2 km apart, each marked with a 50-m grid and representing different stages of regeneration after fire. Fires are common in these barrens, and Prairie Warbler breeding densities apparently differ according to stage of regeneration (Lloyd-Evans 1973). Plots selected were those that appeared to promise the greatest contrast in Prairie Warbler densities. One (hereafter called REGN) was regenerating from a fire in 1963, and the other (hereafter called BURN) had burned in 1974. Care was taken to insure within-plot uniformity by selecting level ground and by avoiding edges between tracts in different stages of regeneration. However, REGN did contain a small area, less than 18% of the plot, that had been bulldozed in an effort to stop the fire. It differed from the rest of the plot in having no trees, but the presence of this small area had no discernible effect on the results reported herein. Data for the following descriptions of the vegetation were collected in 1973 for REGN and in 1975 for BURN, but because regeneration in the pine barrens is slow the data are believed to be adequate to depict conditions of the plots in 1976, the year that I studied the Prairie Warblers.

Much of the vegetation of Plymouth County is a coastal pine barrens growing on sandy soil comprised largely of glacial till. Older forest is characterized by 3, essentially monospecific, vegetative layers: (1) a tree layer, largely pitch pine (*Pinus rigida*) more than 3 m high; (2) a shrub layer, mostly scrub oak (*Quercus ilicifolia*) 1–3 m high; and (3) an herb layer, mostly black huckleberry (*Gaylussacia baccata*), low blueberry (*Vaccinium vacillans*) and dwarf blueberry (*V. angustifolium*), all less than 1 m tall (all botanical names from Gleason 1968). I have used these 3 natural layers to describe the vegetative structure of the plots, even though the heights of the layers in the more recently burned plots are less than those in the older forest.

For purposes of describing the vegetation, a map of each study plot was divided into 125 numbered 25-m squares. Using a random number table, 5 squares were selected to be described. For each of these, species composition and vegetation density, height and percentage cover were measured in the following manner: tree layer species composition and density were measured for the entire 25-m square, but tree height and percentage cover were taken only in a 10-m square in the SW corner of the 25-m square. All shrub layer measurements were taken in the smaller square just described and all herb layer measurements were made in each of 5 randomly thrown 1-m squares within it. Percentages of cover are estimates of the amount of area covered as if looking down from above, so layers could overlap and total more than 100% cover. *Q. ilicifolia* densities are expressed in clumps per unit area, a clump being all stems growing from the original root stock.

Prairie Warblers.—Except during settlement, when both plots were visited daily, visits were on alternate days from 6 May to 3 July 1976, between 05:00 and 11:00. Behavior of randomly selected males was recorded for 30–90 min per bird. Individuals were recognized by song during the first three weeks. Thereafter songs became more variable (Nolan 1978, pers. obs.) and less recognizable, but by that time stages of reproduction of the various males were less in phase than at the beginning of the season and territories were well delineated. Therefore, individuals could be identified by location and continuity of behaviors other than song.

Male densities were determined on the basis of the number of territories or parts of territories in each plot after pair bond formation was completed (ca. 20 June). Territories were mapped by a method adapted from Odum and Kuenzler (1955). At the end of each observation period the male's activity space was plotted, and plotting was repeated until a further observation period added no appreciable new area to the total. The resulting area, excluding obvious encroachments into neighboring territories, represents at least 4 h of observation per male and constitutes the seasonal activity space. Areas were calculated by tracing territories on graph paper and counting the squares or parts of squares covered. (For a few males, enough defense was observed to permit mapping a defended area; these areas were identical to their respective activity spaces.) Stage specific variations in territory size during the breeding cycle, known for some species (Odum and Kuenzler 1955, Stenger and Falls 1959, Stefanski 1967), have not been found in Prairie Warblers (Nolan 1978). None were noted in the present study and, in any event, since territories were small, fluctuations in daily activity were probably not important (Weeden 1965).

A pair is defined as a male and female whose association led to nest-building, and the date of pair bond formation is defined as the date of the first persistent association between a male and a female. While individual females were not marked, a male found courting a female and in the company of a female on subsequent days was assumed to have paired on the day he first was observed courting.

RESULTS

Vegetation.—The tree layer of REGN consisted entirely of *P. rigida* (N = 404). The density of live trees was 1293/ha with a mean height of 3.0 m (range 2.0–6.0 m) and 25.8% cover. The density of standing dead trees was 141/ha. In BURN all sampled trees were standing dead (N = 249), so that species differences (71% *P. rigida*, 29% seven other species) were unimportant for this study. The density of these dead trees was 794/ha and the mean height was 6.4 m (range 3.0–11.0 m). The shrub layer of

FIG. 1. The REGN study plot at the time of the study (13 years after the fire). Note that both oak and pine layers have regenerated (compare Fig. 2).

REGN was also monospecific and contained only *Q. ilicifolia* (N = 470) with a mean height of 1.10 m, a density of 9400 clumps/ha and 53.0% cover. In addition, the BURN's shrub layer was slightly more diverse (85% *Q. ilicifolia*, 15% six other species; N = 541). This layer had a mean height of 0.72 m, a density of 10820 clumps/ha and 40.6% cover. Herb layers in both plots were essentially identical. Fewer than 6 species accounted for over 90% of the total herb cover (principally *G. baccata*, *V. vacillans*, *V. angustifolium* and spring wintergreen, *Galtheria procumbens*) and only 19 herb species were found in the sample squares.

The preceding data show that the 2 plots were very similar in that: (1) both had the same 6 principal plant species; (2) each was internally homogeneous because all vegetation had burned at the same time; (3) herb layers were nearly identical; and (4) *Q. ilicifolia* densities were similar (suggesting similar *Q. ilicifolia* layers previous to the fire, since these oaks regenerate from the old root stock). Differences between the plots were few: (1) *Q. ilicifolia* was slightly taller in REGN, and (2) the presence of live *P. rigida* in REGN gave it a more closed tree canopy (Fig. 1), whereas the more open tree canopy of BURN consisted entirely of dead *P. rigida* (Fig. 2).

FIG. 2. The BURN study plot at the time of the study (2 years after the fire). Note that only the oak layer has regenerated and that the tree layer consists entirely of dead trees (compare Fig. 1).

Additionally, the plots differed in that: (1) the unusually dry spring of 1976 delayed the emergence of *Q. ilicifolia* in BURN by nearly a month (some leaves emerged from buds as early as 10 June, but most emerged between 15 and 22 June), whereas oak in REGN emerged at the normal time (20–28 May), presumably because it was protected by the shade of the live pines; and (2) the proximity (50–150 m) of the BURN to the edge of the unburned forest (Fig. 3), which consisted of large live *P. rigida* and *Q. velutina*, may have been an important factor to Prairie Warblers breeding in BURN. Oak leaves in this forest emerged normally, *Q. velutina* in early May and *Q. ilicifolia* in late May, and Prairie Warblers often foraged there.

Settlement of study areas by Prairie Warblers.—As shown below, settlement dates of the study plots were strikingly different. REGN was settled early and quickly, while BURN was settled later and more slowly.

The first Prairie Warbler was seen on 3 May, and many appeared on 4–5 May (T. L. Lloyd-Evans, pers. comm.). I first visited both plots on 6 May. On 6 May I did not count males in REGN, but the frequent singing there by many individuals suggested that territory establishment had be-

FIG. 3. The edge between recently burned forest (shown in Fig. 2) and more mature forest (ca. 25 years after the most recent fire).

gun (Nolan 1978). On 11 May I estimated that 30–35 males were singing in REGN; many seemed to be individuals that had first been seen on 6 May and had occupied the same locations every day since. By 13 May I estimated 20–25 singing males, a figure which approximated the final breeding density (see below).

BURN, in contrast, on 6 May held no males, but 2 or 3 sang infrequently in the adjacent unburned forest. (This older forest has been shown by Lloyd-Evans [1973] to support a high density of Prairie Warblers.) On 7 May, 6–8 males sang infrequently and ranged widely over the plot itself, but on 9 May the plot was deserted. Not until 13 May, with the arrival of 2 birds, did any males settle. An additional 5 males established territories in the next few days, the last on 22 May.

Timing of pair bond formation.—Although the first female arrived on 8 May, no others were found until 16 May (compare Nolan 1978). Thereafter I saw them regularly.

Visibility of females was poor in the thick vegetation of REGN and I relied on various kinds of observations to establish timing of pair bond formation: direct observation of the first persistent association with a female by 5 males; discovery of first nesting for 3 males (in these laying

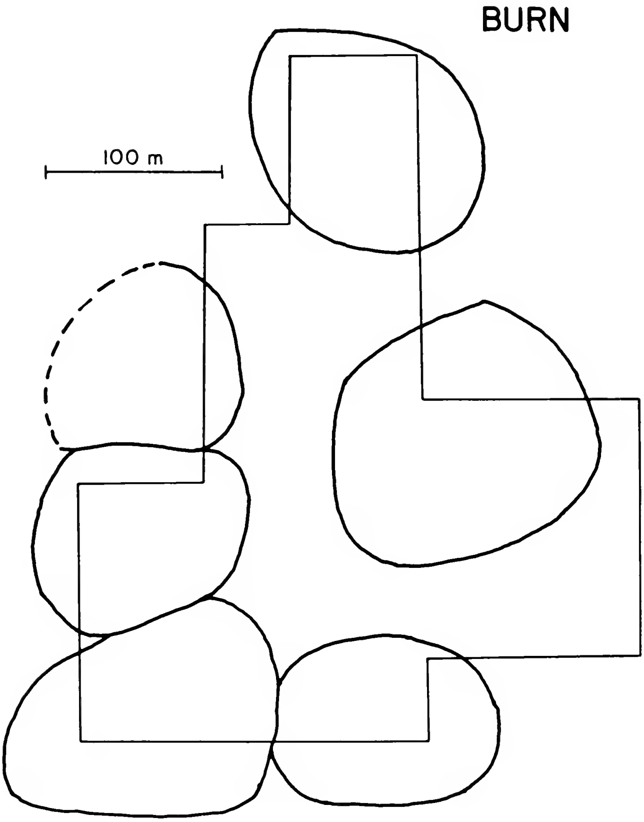


FIG. 4. Map of BURN indicating boundaries of territories of the male Prairie Warblers that bred there in 1976.

began on 2, 3 and 11 June), and extrapolation using the average lengths of breeding stages determined by Nolan (1978); and determination of the day of first occurrence of certain behaviors associated with pairing, e.g., changes in male vocal behavior (Nolan 1978). All these lines of evidence coincided well, indicating that pair bonds were formed in REGN from 18 May to 5 June.

Pair bond formation occurred much later in BURN, between 11 June and 21 June. Here visibility was not a problem and all first associations of male and female were observed on the day the association began. Prior to 11 June there were only 2 brief observations of females in BURN, whereas in REGN I had seen them regularly since 16 May in spite of the

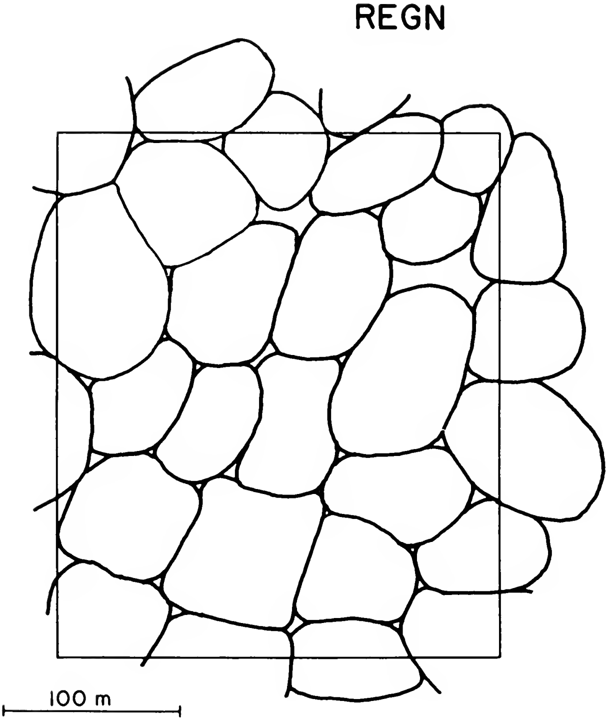


FIG. 5. Map of REGN indicating boundaries of territories of the male Prairie Warblers that bred there in 1976.

poorer visibility. BURN females apparently nested late, as well, and in the 2 nests discovered laying began on 26 and 28 June.

Breeding density and territory.—Breeding density was much lower in BURN than in REGN (Figs. 4 and 5). Only about 54% of the area in BURN was included in a Prairie Warbler territory, while in REGN about 98% was occupied. Most territory boundaries in REGN were contiguous, whereas in BURN large unoccupied areas often separated territories.

None of the 6 males in BURN confined his whole territory to the plot. Therefore, the 7.5 ha held only 3.8 territories, a density of 0.51 territories/ha. In REGN there were 20.1 territories, representing 26 males, a density of 2.68 territories/ha.

Mean territory size of males in BURN was 1.38 ± 0.30 ha (N = 5, range 1.06–1.78 ha), almost 4 times greater than the mean in REGN, which was 0.36 ± 0.12 ha (N = 22, range 0.18–0.64 ha). In a test of significance: $t = 7.29$, df = 25, $P = <0.005$.

All males in BURN foraged frequently in the portions of their territories in the unburned forest outside the plot, especially before *Q. ilicifolia* emerged. One male initially stayed entirely within BURN until his neighbor of the preceding 3 weeks disappeared. He then shifted his boundaries to take in most of the latter's territory, including the portions in unburned forest. Before this shift I had occasionally seen him fly 75–150 m to forage in unoccupied portions of the unburned forest.

Food for young.—Fifteen of 16 food items brought to young were the small caterpillars that are abundant on *Q. ilicifolia*. Similarly, 82% of food items brought to young Indiana Prairie Warblers were caterpillars (Nolan 1978).

DISCUSSION

Considering the proximity of the 2 plots and the considerable similarity of their plant species, the few distinct differences in their vegetation structure almost certainly account for the different breeding densities of their Prairie Warbler populations.

Q. ilicifolia leaves emerged 2 weeks after male arrival, and therefore the minor differences in this layer were probably of little importance to arriving males and are unlikely to account for density differences. The herb layers were nearly identical and, in any event, were rarely used by Prairie Warblers. Therefore, considering that: (1) *P. rigida* was the only arboreal foliage present when males arrived and (2) the plots differed substantially only in the *P. rigida* layer, it appears that the presence of live pines in REGN and their absence in BURN most likely accounts for density differences.

That Prairie Warbler breeding densities can respond to food abundance is suggested by the fact that they were twice as dense in unsprayed as in sprayed orchards (Springer and Stewart 1948, DeGarmo 1949). Other studies have cited food as an important variable in breeding density and territory size (Stenger 1958, Morse 1976, reviews by Lack 1966, Brown 1969). Male Prairie Warblers arrive as soon as there is enough food on the breeding grounds to support them (Nolan 1978) and, in Indiana, often concentrate on pines as a foraging substrate before deciduous leaves become available (Nolan 1978). Therefore, the absence of food available on live pines in BURN during this critical period may have been responsible for the low density of settling males, even though food supplies in the 2 plots are probably very similar after *Q. ilicifolia* leaves emerge (and therefore while nestlings are being fed). Though it is possible that the dead trees could have supplied sufficient food, a shortage of food in BURN is also suggested by the facts that: (1) males settling in BURN usually foraged in the adjacent unburned forest (where pines were abundant); (2) nearly all males included portions of unburned forest in their territories and the sole exception soon shifted his territory to include a portion of unburned forest; and (3) males settled later in BURN than in REGN. However, it must be considered that in addition to providing an early food supply, *P. rigida* also protects *Q. ilicifolia* from drought by lowering evapo-transpiration rates, thus ensuring a more dependable food supply for the entire season. Prairie Warblers may favor evergreen-covered habitats for this reason, especially in regions susceptible to drought.

Another factor that may have contributed to the greater attractiveness of the plot bearing *P. rigida* is the concealment of nesting activities from Brown-headed Cowbirds (*Molothrus ater*), which were common on my plots (compare Nolan 1978), and from neighboring male Prairie Warblers, whose interference in efficient pair formation and nest-building is discussed by Nolan (1978).

In order to explain the difference in time of female settlement on the 2 plots, factors of importance to females must be considered. While females prospecting for breeding locations may have been influenced by the same factors as males (i.e., pines), it appears more likely that the delay in pairing in BURN was caused by the delay in leafing of *Q. ilicifolia*. The importance of this event to females is suggested by the fact that most females in 1976 (and probably other years as well) arrived from 16–20 May, just prior to the normal time of leafing of *Q. ilicifolia*. That the dealy in leafing caused the BURN pairing delay is strongly suggested by the correlation between dates of pairing and leafing (even though delayed by nearly a month in BURN).

Harmeson (1974) and Wittenberger (1976) have argued that food available on the territory affects pairing success and it is known that a certain threshold of food abundance is necessary for the female to synthesize eggs (Lack 1963, Perrins 1970, Ankney and MacInnes 1978). Caterpillars are abundant on *Q. ilicifolia* leaves and the importance of *Q. ilicifolia* as a factor in influencing female settlement may be as a source of food required for egg-laying. These caterpillars are also an important source of food for young (see above). However, Zimmerman (1966, 1971) has shown that the amount of vegetative cover, independent of food, can influence pairing success, probably because greater cover provides better nest concealment. In my study area, all nests were placed in forks of *Q. ilicifolia* (Lloyd-Evans, pers. comm.; pers. obs.). These sites are very exposed before the leaves emerge, and therefore are probably unsuitable. The timing of nest-site availability may be important to the timing of pairing, and the lack of suitable nest-sites in BURN prior to leafing may have caused the pairing delay.

In either case, the delay in pairing indicates that females found the territories unsuitable and would not settle until *Q. ilicifolia* leaves emerged. Lack (1966) and Slagsvold (1976) have reviewed evidence that timing of egg-laying (not pair formation) is related to vegetation phenology, but this paper is the first to present evidence that timing of female settlement is also dependent on vegetation phenology. While it is also possible that the males in BURN were in some way less suitable, the fact remains that they all acquired mates once oak leaves emerged. These facts are consistent with the predictions of Orians (1969) and Wittenberger (1976) that some sort of evaluation of the territory by the female is important during female settlement.

SUMMARY

The breeding Prairie Warbler populations of 2 uniform tracts of pitch pine forest in different stages of regeneration from fire were contrasted. One plot (BURN) had burned too recently for the tree layer to have regenerated, and it supported a much lower density of males compared to the second plot (REGN) which had burned less recently, and in which the tree layer had partially regenerated. Males in REGN also had much smaller territories. Reasons for these differences are suggested.

A drought during the study caused a delay in leafing of the oak shrub layer (whose leaves are the primary foraging substrate for Prairie Warblers during the breeding season) in BURN, but not in REGN where oaks were protected in the shade of live pines. While male settlement was unaffected (it was completed even before normal leafing time), pairing by males in BURN was delayed by almost a month (until after the oak leaves emerged) relative to males in REGN. The significance of this delay is discussed.

ACKNOWLEDGMENTS

I am greatly indebted to Val Nolan, Jr., Brian A. Harrington and Trevor L. Lloyd-Evans for the amount of time they invested in helping me during all phases of this study and especially for their useful comments on this manuscript. I am also grateful to T. L. Lloyd-Evans for allowing me access to his vegetation data. In addition, I would like to thank the entire staff of the Manomet Bird Observatory for their invaluable assistance in the fieldwork and for constantly providing me with encouragement.

LITERATURE CITED

ANKNEY, C. D. AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of Lesser Snow Geese. Auk 95:459–471.

BROWN, J. L. 1964. Evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

———. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293–329.

DEGARMO, W. R. 1949. Apple orchard. Audubon Field Notes 3:255.

GLEASON, H. A. 1968. The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. Hafner Publishing Co., Inc., New York, New York.

HARMESON, J. P. 1974. Breeding ecology of the Dickcissel. Auk 91:348–359.

LACK, D. 1963. Cuckoo hosts in England. Bird Study 10:185–201.

———. 1966. Population studies of birds. Oxford Univ. Press, Oxford, England.

LLOYD-EVANS, T. L. 1973. Pitch pine-scrub oak forest I–III. Am. Birds 27:975–977.

MORSE, D. A. 1976. Variables affecting the density and territory size of breeding sprucewoods warblers. Ecology 57:290–301.

NOLAN, V., JR., 1978. Ecology and behavior of the Prairie Warbler, *Dendroica discolor.* Ornithol. Monogr. No. 26.

ODUM, E. P. AND E. J. KUENZLER. 1955. Measurement of territory and home range in birds. Auk 72:128–137.

ORIANS, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589–603.

PERRINS, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

SLAGSVOLD, T. 1976. Annual and geographic variation in the breeding of the Great Tit (*Parus major*) and the Pied Flycatcher (*Ficedula hypoleuca*) in relation to environmental phenology and spring temperature. Ornis Scand. 7:127–145.

SPRINGER, P. F. AND R. E. STEWART. 1948. Apple orchards. Audubon Field Notes 2:227–229.

STEFANSKI, R. A. 1967. Utilization of breeding territory in the Black-capped Chickadee. Condor 69:259–267.

STENGER, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk 75:335–346.

——— and J. B. Falls. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71:125–140.

WEEDEN, S. 1965. Territorial behavior of the Tree Sparrow. Condor 67:193–209.

WILSON, E. O. 1975. Sociobiology. Harvard Univ. Press, Cambridge, Massachusetts.

WITTENBERGER, J. F. 1976. The ecological factors selecting for polygyny in altricial birds. Am. Nat. 110:779–799.

ZIMMERMAN, J. L. 1966. Polygyny in the Dickcissel. Auk 83:534–546.

———. 1971. The territory and its density dependent effect in *Spiza americana.* Auk 88:591–612.

MANOMET BIRD OBSERVATORY, BOX 936, MANOMET, MASSACHUSETTS 02345. (PRESENT ADDRESS: DEPT. ZOOLOGY, UNIV. WASHINGTON, SEATTLE, WASHINGTON 98195.) ACCEPTED 15 FEB. 1979.

Wilson Bull., 92(2), 1980, pp. 188–199

REPRODUCTION AND NEST-SITE SELECTION BY WHITE-TAILED PTARMIGAN IN COLORADO

Kenneth M. Giesen, Clait E. Braun and Terry A. May

White-tailed Ptarmigan (*Lagopus leucurus*) are widely distributed in alpine regions of western North America and are locally abundant in suitable habitats (Braun and Rogers 1971). Prior to 1966 little intensive research had been conducted on this species. Notable exceptions are the work of Weeden (1959) and Choate (1960, 1963). Most other references to the species provide limited information on distribution or some aspect of its natural history. Only 14 of 30 literature references of nests or clutches provide original data, and most describe only 1 or 2 nests.

Intensive research on the ecology of White-tailed Ptarmigan was initiated in Colorado in 1966. Results of these studies have been published in a series of papers (Braun and Rogers 1971; Braun and Schmidt 1971; May and Braun 1972; Stabler et al. 1974; Hoffman and Braun 1975, 1977; Braun et al. 1976). This paper summarizes data from 62 nests and hatch dates of 673 chicks observed during 12 years (1966–1977) of research on the southern White-tailed Ptarmigan (*L. l. altipetens*).

STUDY AREA AND METHODS

Nests were located at study areas in Colorado along the Front Range (Crown Point, Rocky Mountain National Park, Niwot Ridge, Loveland Pass, Guanella Pass, Mt. Evans), Collegiate Range (Independence Pass) and in the San Juan Mountains in southwestern Colorado (Mesa Seco) (Fig. 1). These areas have been described elsewhere (Braun 1969, Braun and Rogers 1971, May 1975, Braun et al. 1976).

Most nests were located by following hens. Two in 1968, and 1 in 1972 were located by radio telemetry. Several were found incidental to other activities, or reported to us.

Rock and vegetative cover were visually described and color photographs were taken for permanent records. Slope at nest-sites was measured with a clinometer except for a few instances when it was estimated. Elevation was determined from topographic maps. Eggs were measured with vernier calipers. Nests were checked at irregular intervals to determine their fates.

Field techniques are described by Braun and Rogers (1971). Timing of reproductive events was based on observations of marked birds and by back-dating age of chicks to estimate hatch dates (Giesen and Braun 1979a).

RESULTS

Chronology of nesting events.—Timing of White-tailed Ptarmigan breeding and nesting events in Colorado is controlled by climatic conditions (Braun and Rogers 1971). Adult males usually begin defending breeding territories in early to mid-April, with females arriving in late April or early

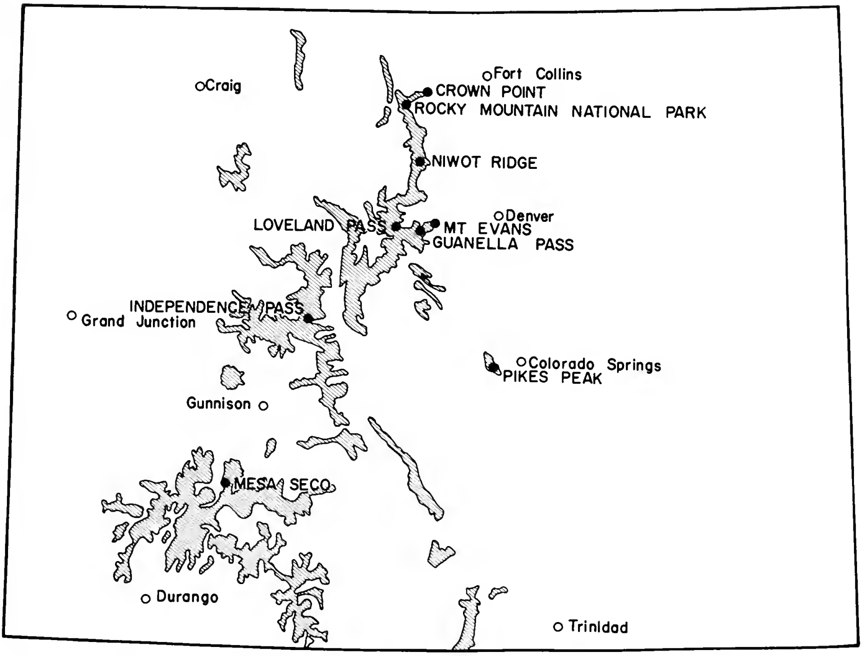


FIG. 1. Study areas (solid circles) and alpine habitats within Colorado.

May. In early years mated pairs are often seen in late April, while in normal or late years pairing begins in early to mid-May. Severe snowstorms may result in temporary separation of mated pairs as females retreat downslope to more protected areas (Schmidt 1969, Braun and Rogers 1971). Peters (1963) reported similar findings for Willow Ptarmigan (*Lagopus lagopus*) in Newfoundland.

Copulation and egg deposition began after females were in alternate (nuptial) plumage, usually in early June. Timing of prealternate (prenuptial) molt is controlled ultimately by day length (Host 1942) and appears to be further affected by amount of snow cover and resulting light intensity (Braun and Rogers 1971).

The temporal relationship between copulation and egg deposition is not known. Schmidt (1969) observed copulation in White-tailed Ptarmigan prior to egg deposition, but also observed 2 instances of copulation involving females that were apparently incubating. We assume that timing of copulation in White-tailed Ptarmigan is similar to that reported for Ruffed Grouse (*Bonasa umbellus*), approximately 3–7 days prior to egg deposition (Bump et al. 1947). Zwickel (1977) estimated a 4-day interval between copulation and laying for Blue Grouse (*Dendragapus obscurus*). White-tailed Ptarmigan are monogamous and the pair bond remains intact until late in incubation; thus copulation may occur several times before and during laying.

Timing of egg deposition was determined from intensive observations of 12 hens. These hens approached their nests for laying between 08:30 and 16:30 MDT. Hens deposited an egg soon after arriving at the nest, although they often remained on the nest for several hours, especially as clutches neared completion. There is no evidence that egg deposition occurred after dark.

The interval between deposition of successive eggs was estimated to be 26–30 h when eggs were laid on successive days. On some days no eggs were deposited. Three hens each laid 3 eggs in 4 days; another laid 4 eggs in 6 days. Hens deposited eggs later during the day on successive days and skipped every third or fourth day. Maxson (1977) observed a similar pattern in Ruffed Grouse.

Females spent increasing amounts of time on the nest as clutches approached completion, but incubation did not begin until the last egg was deposited. This differs from the report of Choate (1960) who reported incubation began 3 days (2 eggs) before clutch completion. We define incubation period as the interval between deposition of the last egg and hatching of the clutch (eggs within clutches usually hatched within a 2–6-h period). Incubation length was 23 days for 5 hens and 22–23 days for another. Pipping of eggs was observed 24–48 h prior to hatching.

In most years hatching did not begin until the first or second week in July (Fig. 2). The 12-year median hatch date was 15 July when varied from 6 July in 1977 to 23 July in both 1969 and 1973. Except for 1969 most of the hatch (>65%) occurred within a 2-week period. Zwickel (1977) reported a similar pattern of hatch for Blue Grouse on Vancouver Island. The long period of hatch in some years was the result of renesting (Giesen and Braun 1979c).

Peak of hatch varied predictably between areas within years. The hatch at Mesa Seco, Mt. Evans, Guanella Pass and Pikes Peak occurred 1–2 weeks earlier than at Rocky Mountain National Park. This may have been the result of different snowfall and solar radiation patterns as these areas were also earlier phenologically. Hatch dates at Crown Point and Independence Pass were similar to those in Rocky Mountain National Park.

Clutch-size.—Few clutches were located in any year so data for all years were pooled. Clutch-size varied from 2–8 eggs in 56 clutches examined. Four clutches were incomplete and 4 represented known renests. The remaining 48 clutches averaged 5.9 eggs (range 4–8). Reported clutch-sizes for 40 additional nests were found in the literature (Brewer 1874;

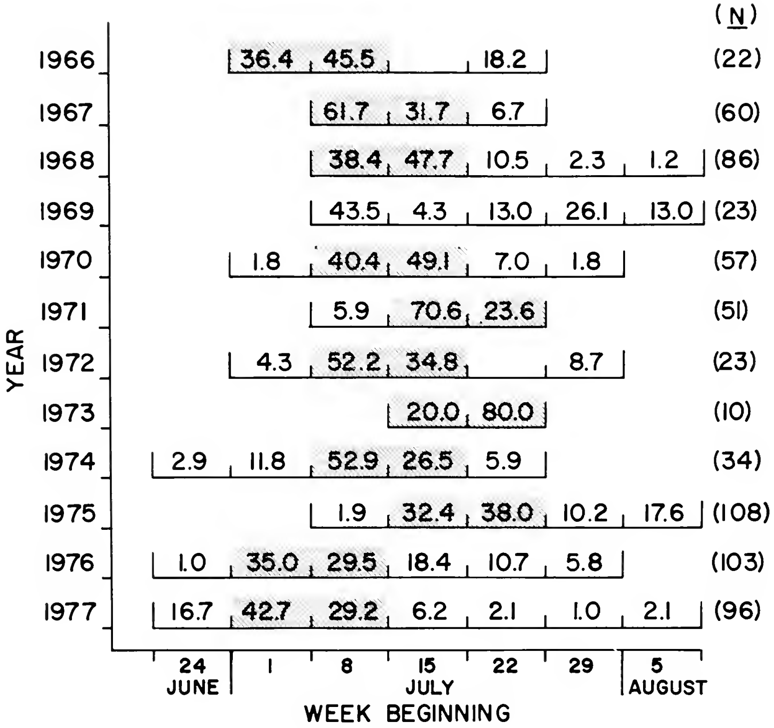


FIG. 2. Timing of White-tailed Ptarmigan hatching in Rocky Mountain National Park, 1966–1977. Percentage of chicks hatching in each weekly period is given for each year. Peak hatching periods are shaded. Sample sizes are in parentheses.

Lewis 1904; Sclater 1912; Bradbury 1915; Taylor 1920; Taylor and Shaw 1927; Weydemeyer 1931; Jewett et al. 1953; Thatcher 1954; Edwards 1957; Evans and Fisher 1958; Choate 1960, 1963; Bailey and Niedrach 1965). Clutch-sizes for these nests ranged from 2–8, excluding 1 of 9 eggs to which 2 hens contributed (Choate 1960). The average size of these clutches was 5.2 eggs. It is possible that some incomplete clutches, or renests, were among those reported. Clutches resulting from renesting have fewer eggs (Giesen and Braun 1979c). Other workers estimated clutch-size to range from 4–16 eggs (Bent 1932, Gabrielson and Lincoln 1959) and Batty (1874) reported that White-tailed Ptarmigan never lay more than 4 eggs.

We calculated average clutch-sizes separately for yearling (N = 17) and adult (N = 25) females. Those of adults were significantly ($P < 0.01$) larger than those of yearlings (6.2 vs 5.5 eggs). Clutch-size of yearlings ranged

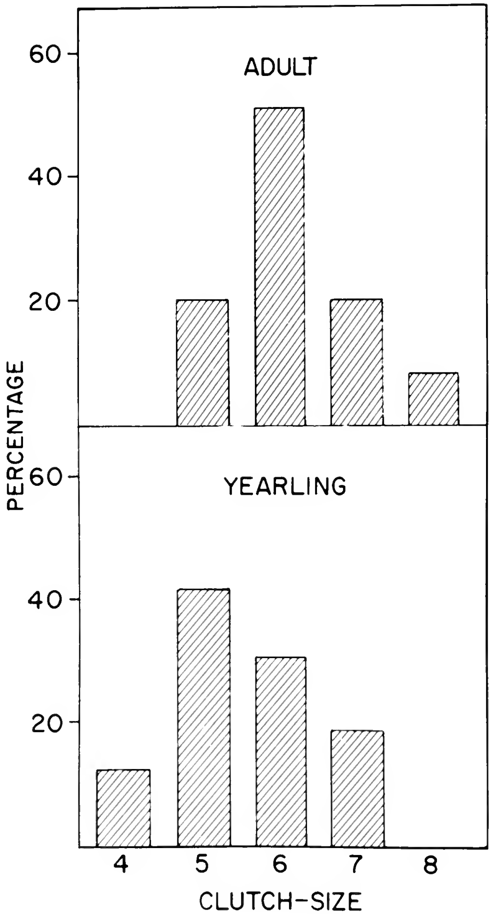


FIG. 3. Frequency distribution of clutch-size of yearling (N = 17) and adult (N = 25) female White-tailed Ptarmigan.

from 4–7, those of adults from 5–8 (Fig. 3). Zwickel (1975) described a similar relationship for Blue Grouse. Since the yearling to adult female ratio varies annually in White-tailed Ptarmigan, production of young is influenced by age structure of females in the population.

Egg size and coloration.—We examined 227 eggs for size and coloration between 1968 and 1977. These eggs represented 43 partial or complete clutches from 39 hens (eggs from 4 hens were sampled in 2 different years). Eggs were oval in appearance and averaged 43.74 ± 1.70 mm × 29.71 ±

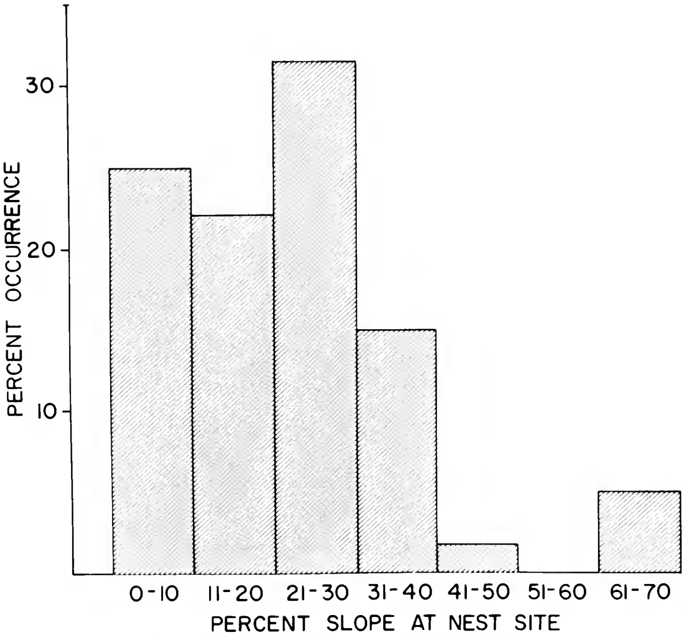


FIG. 4. Distribution of White-tailed Ptarmigan nest-sites (N = 60) by percent slope, 1966–1977.

0.68 mm ($\bar{x}$ ± SD). Extreme measurements were 48.9 × 29.3 mm, 39.2 × 29.6 mm, 43.1 × 31.4 mm and 39.6 × 27.2 mm. Bent (1932) summarized measurements of 31 eggs, which likely included those reported by Bradbury (1915), Brewer (1874) and Sclater (1912). Choate (1960) reported measurements of 14 White-tailed Ptarmigan eggs from Montana. Measurements reported were within the range observed in this study.

Eggs were lightly to heavily blotched, or spotted reddish-brown on a creamy brown background. Blotches measured up to 6 mm in diameter, although most were less than 2 mm. Blotches on newly deposited eggs were deep red; those on eggs incubated for several days were dull reddish-brown. Fading of blotches has been reported for eggs of Willow Ptarmigan (Dement'ev and Gladkov 1952).

Nest-site characteristics.—Slope was measured at 60 of 62 nest-sites. The median was 20% ($\bar{x}$ = 21.4%) with a range from 0–70%. Slopes of less than 40% were selected by 93.3% (N = 56) of the nesting females, with nest-sites evenly distributed within this range (Fig. 4). Steep slopes were avoided, as only 4 nests were located on slopes over 40% and none was located on slopes over 70%.

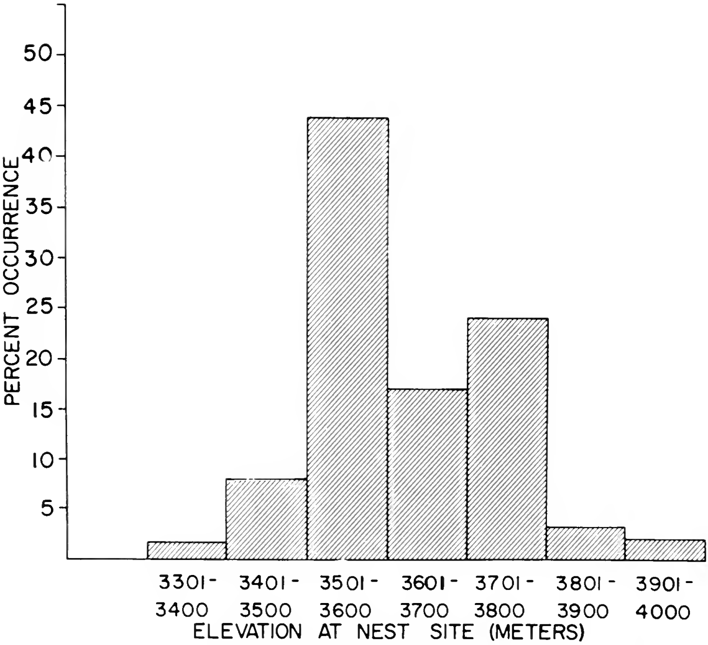


FIG. 5. Elevations of nests of White-tailed Ptarmigan (N = 59), 1966–1977.

Of 60 nest-sites examined, more (N = 19) were on south-facing than on north- (N = 15), west- (N = 14), or east-facing (N = 12) slopes. Chi-square analysis for preference of aspect indicated there was no selection. This was expected since hens nest within the territory of the male (Braun and Rogers 1971) and usually have limited choice of aspect. Although our searches for nests were not random, we did search territories at many locations within the study areas.

Nest-sites (N = 59) ranged in elevation from 3383–3901 m with a mean of 3618 m (median = 3597 m) (Fig. 5). Treeline depends on latitude, slope and aspect, and averaged about 3505 m on the study areas. Few nests (N = 7) were below treeline. Most were located in the krummholz, or within 250 m of treeline. Although some breeding territories extended to 3962 m, no nests were found this high. While this may reflect lack of search effort at these elevations, we believe most females nested on the lower periphery of their mate's territory.

Twenty-five of 62 nests (40.3%) were in rock or boulder fields, 20 (32.3%) in various turf situations, 11 (17.7%) in evergreen krummholz (usually *Picea engelmannii*) and 6 (9.7%) in willow (*Salix* spp.) krummholz. The importance of rocks was apparent as 12 of 20 nests in turf areas were near rocks or boulders.

Krummholz, both willow and spruce, served to protect incubating birds from the wind. In addition, the vegetation served to conceal the female. Most nests in krummholz were at the edge of a shrub clump or near an opening. This characteristic likely facilitated departure from the nest.

Five of 8 nests in turf situations were protected from wind by clumps or hummocks of sedge (*Carex* spp.) or grasses (*Deschampsia* spp. or *Poa* spp.). Two nests were in small natural depressions, possibly enlarged somewhat by the female. Only 1 of 62 nests had no obvious protection from the wind; it failed. Nest-sites described by Choate (1960) and Bent (1932) are similar to those described here. Lewis (1904) concluded, erroneously, that White-tailed Ptarmigan do not nest near willow. However, he searched primarily above the krummholz.

Based on our observations, suitable nesting sites are abundant on the alpine. This observation is supported by lack of reuse of old nest-sites, even when females returned to the same territories (Schmidt 1969, this study).

Nest construction.—Most nests were in natural depressions, which may have been slightly enlarged by the females. Average size of 38 nest bowls was 151 × 130 × 36 mm. Materials used in nest construction reflected the vegetation at the site, as materials were gathered within 40 cm. Depending upon site, dead leaves and stems of willow, spruce, grass or sedge were used. Lichens (principally *Dactylina madroporiformis*, *Thamnolia vermicularis* and *Cetaria* spp.) were commonly used as nesting material. Most nests contained several small white feathers.

Nesting success.—Success was determined for 60 of 62 nests. Thirty-four hens hatched all, or part of their clutches (56.7%). Only 2 nests were deserted, 1 after 30 days of incubation. Coyotes (*Canis latrans*) and weasels (*Mustela* spp.) were the primary predators, although 1 nest was depredated by corvids. Nests were not marked and observer interference was not thought to affect success, even though some were visited almost daily. Several nests in Rocky Mountain National Park, located near areas of high use by Park visitors, hatched. Yearly samples were too small to compare annual variation in success. Nesting success estimated from surveys of hens with and without broods was generally similar to that obtained from nest examination.

Hatchability of 177 eggs incubated to completion was 88.1% (156 of 177 eggs). All eggs hatched in 23 of 31 nests. Minimum egg fertility for 55 eggs from 10 successful nests in 1975 and 1976 was 94.5%. Of the 6 eggs that failed to hatch, 3 contained well developed embryos. The other 3 eggs were either infertile or failed to develop.

DISCUSSION

Timing of nesting is critical for avian species living in arctic-alpine environments. Climatic factors determine timing of resource availability and set the temporal boundaries within which a species mates, reproduces and rears young. White-tailed Ptarmigan in Colorado demonstrate behavioral and physiological adaptations for completing their reproductive cycle during the few months of favorable weather in summer.

Males acquire and defend territories prior to arrival of females (Schmidt 1969). Females return to their territory (and mate) of the previous year, eliminating the need for elaborate pair-formation and courtship displays. Territorial defense is entirely accomplished by males (Schmidt 1969) allowing females to devote their time to feeding. As a consequence, females have sufficient energy intake to undertake a prealternate molt and to complete ovarian development within 30 days. Of the North American Tetraonidae, White-tailed Ptarmigan have the smallest clutch-size (Johnsgard 1973), permitting a shorter egg-laying period.

Nests are located within the pair's territory, effectively limiting female choice of elevation and aspect. Within the territory females select snow-free nest-sites on areas of moderate slope. Depending on snow conditions, about 10–50% of the territory may be suitable for nesting.

Rock and vegetative cover is important for protection from inclement weather and less important as concealment. Although quantitative measurements of concealment and protection were not systematically recorded, detailed descriptions of nest-sites reveal most (61 of 62) were protected from the prevailing winds. Since females spend over 95% of the time on the nest during the incubation period (Giesen and Braun 1979b) it is energetically advantageous to have protection from the weather. In contrast, the concealment value of rocks and vegetation was judged to be of minor importance as most incubating females were exposed. The cryptic plumage of incubating females lessens visual detectability at least for human observers (Lewis 1904). Keppie and Herzog (1978) concluded that concealment from predators was more important than protection from weather in determining nest success of Spruce Grouse (*Canachites canadensis*).

SUMMARY

Nesting events of White-tailed Ptarmigan in Colorado began in early June after females completed their prealternate molt. Average clutch-size was 6.2 for adults and 5.5 for yearlings. Eggs were oval and averaged 43.74 × 29.71 mm in size. Incubation began after clutches were complete and lasted 23 days. Hatching usually occurred in mid-July, but varied annually due to spring weather. Predation by coyotes and weasels was the major cause of nest failure. Egg hatchability (88.1%) and fertility (94.5%) were high. Data from 62 nests indicated that most (93.3%) were on moderate slopes of less than 40% at elevations between 3501 and 3800 m. There was no selection for aspect. Nests were typically located adjacent to rocks or

boulders or in krummholz vegetation which protected them from the wind. Nests were usually shallow scrapes lined with dead vegetation collected at the nest-site.

ACKNOWLEDGMENTS

We acknowledge the assistance of R. K. Schmidt, Jr., who initially conceived ideas for locating nests. P. Gilbert, R. W. Hoffman, W. Mautz, D. Pattie, B. Poley, G. E. Rogers, personnel of Rocky Mountain National Park and conferees of the National Wildlife Federation Conservation Summit all contributed in helping find nests. We are grateful for their interest and cooperation. Funding was received from the National Science Foundation (traineeship to Braun), Tundra Biome and the Colorado Division of Wildlife. R. A. Ryder, Colorado State University, helped direct early phases of the study and, along with H. D. Funk, Colorado Division of Wildlife, provided encouragement, administrative support and critically reviewed an early draft of the manuscript. This is a contribution from Colorado Federal Aid to Wildlife Restoration Project W-37-R.

LITERATURE CITED

BAILEY, A. M. AND R. J. NIEDRACH. 1965. Birds of Colorado. Denver Mus. Nat. Hist., Vol. 1., Denver, Colorado.

BATTY, J. H. 1874. The White-tailed Ptarmigan, *Lagopus leucurus.* Forest and Stream 1:390.

BENT, A. C. 1932. Life histories of North American gallinaceous birds. U.S. Natl. Mus. Bull. 162.

BRADBURY, W. C. 1915. Notes on the nesting of the White-tailed Ptarmigan in Colorado. Condor 17:214–222.

BRAUN, C. E. 1969. Population dynamics, habitat, and movements of White-tailed Ptarmigan in Colorado. Ph.D. diss., Colorado State Univ., Fort Collins, Colorado.

——— AND G. E. ROGERS. 1971. The White-tailed Ptarmigan in Colorado. Colorado Div. Game, Fish and Parks Tech. Publ. 27.

——— AND R. K. SCHMIDT, JR. 1971. Effects of snow and wind on wintering populations of White-tailed Ptarmigan in Colorado. Pp. 238–250 *in* Proc. Snow and Ice Symp., (A. O. Haugen, ed.). Iowa Coop. Wildl. Res. Unit, Iowa State Univ., Ames, Iowa.

———, R. W. HOFFMAN AND G. E. ROGERS. 1976. Wintering areas and winter ecology of White-tailed Ptarmigan in Colorado. Colorado Div. Wildl. Spec. Rep. No. 38.

BREWER, T. M. 1874. Note on the nesting and eggs of *Lagopus leucurus.* Proc. Boston Soc. Nat. Hist. 16:348–349.

BUMP, G., R. W. DARROW, F. C. EDMINSTER AND W. P. CRISSEY. 1947. The Ruffed Grouse: life history, propagation, management. N.Y. Conserv. Dept., Hilling Press, Inc., Buffalo, New York.

CHOATE, T. S. 1960. Observations on the reproductive activities of White-tailed Ptarmigan (*Lagopus leucurus*) in Glacier Park, Montana. M.A. thesis, Univ. Montana, Missoula, Montana.

———. 1963. Ecology and population dynamics of White-tailed Ptarmigan (*Lagopus leucurus*) in Glacier National Park, Montana. Ph.D. diss., Univ. Montana, Missoula, Montana.

DEMENT'EV, G. P. AND N. A. GLADKOV. 1952. Birds of the Soviet Union, Vol. 4. Publ. for Smithson. Inst. and N.S.F. Washington, D.C. by Israel Prog. for Sci. Transl. (Jerusalem).

EDWARDS, J. G. 1957. The Ptarmigan of Glacier National Park. Audubon Mag. 59:252–255.

Evans, F. H. and R. L. Fisher. 1958. Observations of White-tailed Ptarmigan. Unpubl. Rep. Zool. Dept., Univ. Montana, Missoula, Montana.

Gabrielson, I. N. and F. C. Lincoln. 1959. The birds of Alaska. Stackpole Co., Harrisburg, Pennsylvania.

Giesen, K. M. and C. E. Braun. 1979a. A technique for age determination of juvenile White-tailed Ptarmigan. J. Wildl. Manage. 43:508–511.

——— and ———. 1979b. Nesting behavior of female White-tailed Ptarmigan in Colorado. Condor 81:215–217.

——— and ———. 1979c. Renesting of White-tailed Ptarmigan in Colorado. Condor 81:217–218.

Hoffman, R. W. and C. E. Braun. 1975. Migration of a wintering population of White-tailed Ptarmigan in Colorado. J. Wildl. Manage. 39:485–490.

——— and ———. 1977. Characteristics of a wintering population of White-tailed Ptarmigan in Colorado. Wilson Bull. 89:107–115.

Host, P. 1942. Effects of light on the moults and sequences of plumage in Willow Ptarmigan. Auk 59:388–403.

Jewett, S. G., W. P. Taylor, W. T. Shaw and J. W. Aldrich. 1953. Birds of Washington State. Univ. Wash. Press, Seattle, Washington.

Johnsgard, P. A. 1973. Grouse and quails of North America. Univ. Nebraska Press, Lincoln, Nebraska.

Keppie, D. M. and P. W. Herzog. 1978. Nest site characteristics and nest success of Spruce Grouse. J. Wildl. Manage. 42:628–632.

Lewis, E. 1904. The nesting habits of the White-tailed Ptarmigan in Colorado. Bird-Lore 6:117–121.

Maxson, S. J. 1977. Activity patterns of female Ruffed Grouse during the breeding season. Wilson Bull. 89:439–455.

May, T. A. 1975. Physiological ecology of White-tailed Ptarmigan in Colorado. Ph.D. diss., Univ. Colorado, Boulder, Colorado.

——— and C. E. Braun. 1972. Seasonal foods of adult White-tailed Ptarmigan in Colorado. J. Wildl. Manage. 36:1180–1186.

Peters, S. S. 1963. Population dynamics of the Newfoundland Willow Ptarmigan on the Avalon Peninsula. Ph.D. diss., Cornell Univ., Ithaca, New York.

Schmidt, R. K., Jr. 1969. Behavior of White-tailed Ptarmigan in Colorado. M.S. thesis, Colorado State Univ., Fort Collins, Colorado.

Sclater, W. L. 1912. A history of the birds of Colorado. Witherby and Co., London, England.

Stabler, R. M., N. J. Kitzmiller and C. E. Braun. 1974. Hematozoa from Colorado birds. IV. Galliformes. J. Parasitol. 60:536–537.

Taylor, W. P. 1920. A new ptarmigan from Mount Rainier. Condor 22:146–152.

——— and W. T. Shaw. 1927. Mammals and birds of Mount Rainier National Park. U.S. Natl. Park Serv., Washington, D.C.

Thatcher, D. M. 1954. Birds of the season. Colorado Bird Notes 2:6–7.

Weeden, R. B. 1959. The ecology and distribution of ptarmigan in western North America. Ph.D. diss., Univ. British Columbia, Vancouver, British Columbia.

Weydemeyer, W. 1931. A day with the birds of Glacier National Park. Bird-Lore 33:169–175.

Zwickel, F. C. 1975. Nesting parameters of Blue Grouse and their relevance to populations. Condor 77:423–430.

———. 1977. Local variations in the time of breeding of female Blue Grouse. Condor 79:185–191.

COOPERATIVE WILDLIFE RESEARCH UNIT, COLORADO STATE UNIV., FORT COLLINS, COLORADO 80523 (KMG); COLORADO DIV. WILDLIFE, WILDLIFE RESEARCH CENTER, 317 WEST PROSPECT, FORT COLLINS, COLORADO 80526 (CEB); SCHOOL OF FOREST RESOURCES, UNIV. MAINE, ORONO, MAINE 04473 (TAM). (PRESENT ADDRESS KMG: COLORADO DIV. WILDLIFE, WILDLIFE RESEARCH CENTER, 317 WEST PROSPECT, FORT COLLINS, COLORADO 80526.) ACCEPTED 1 MAR. 1979.

Wilson Bull., 92(2), 1980, pp. 200–220

NEST-SITE AND COLONY CHARACTERISTICS OF WADING BIRDS IN SELECTED ATLANTIC COAST COLONIES

Donald L. Beaver, Ronald G. Osborn and Thomas W. Custer

Along the Atlantic Coast colonies of herons, egrets and ibises nest in diverse habitats ranging from small shrubs to tall trees (Bent 1926, Custer and Osborn 1977). Often colonies occur where there appear to be large amounts of similar, unused habitat (Bent 1926, Jenni 1969, McCrimmon 1978) suggesting that social factors predominate in the selection of a colony site (see Krebs 1974, for review).

The role of social factors in the dispersion of species and their nests within a colony is not so well known. Usually nests of the same species are built in a variety of sites in colonies with differing vegetation. Several authors have provided qualitative assessments of nesting sites (Eyles 1938, Gersbacher 1939, Patten 1952, Meanley 1955, Ralph and Ralph 1958, Dusi 1966, Lowe-McConnell 1967, Dusi and Dusi 1968, Maxwell and Kale 1977), but it seems clear that their descriptions apply to the specific colony sites where they worked, and considerable variation exists between studies.

Within a colony, nests of various species are not easily differentiated, even by experienced observers (Bent 1926, pers. obs.). However, quantitative methods and detailed behavioral observations suggest that slight, but significant differences in nest-site characteristics do exist. Jenni (1969) and Maxwell and Kale (1977) reported differences in vertical and horizontal placement by wading birds in a Florida heronry. Burger (1978) noted similar patterns in a number of heronries on the Atlantic Coast and in tropical areas. Using multivariate statistical analyses of nest-site variables, McCrimmon (1978) demonstrated a fine vertical and horizontal separation in a heronry in North Carolina. Burger (1978) has inferred the mechanism of nest-site separation is dominance: larger species nest higher in the vegetation than subordinate smaller ones.

These observations suggest that both social and vegetation factors influence the placement of the nest. This paper examines characteristics of nest placement and dispersion in relation to vegetation in the colony. Social interactions were not directly examined, but we discuss their possible role in spacing of nests and choice of nesting sites. Six colonies and 5 species were examined in detail. This project was a part of a larger study of the value of herons and their allies as indicators of the environmental conditions in Atlantic coast estuaries (Custer and Osborn 1977).

COLONY LOCATION AND DESCRIPTION

Study sites were selected from the heron colonies located earlier in the year where nests had been marked for demographic investigation (Custer and Osborn 1977). Colonies on Spectacle and Clark's islands, Massachusetts, 2 colonies in Swash Bay, Virginia, and 2 colonies in Middle Marsh, North Carolina, were chosen because they represent various combinations of heron species and vegetation types (Table 1).

Spectacle Island (42°19.5′N, 70°59.2′W) was formerly the site of the Boston city dump. The center of the island is filled with compacted trash. The edges drop steeply into the bay from a height of 20 m. Herons nest mostly in small, closely spaced apple (*Pyrus malus*), cherry (*Prunus* spp.), buckthorn (*Rhamnus* spp.), poplar (*Populus heterophylla*) and sumac (*Rhus typhina*) trees (5–6 m in height). Where trees are dense there is little ground vegetation and much of the soil contains broken glass and rusting pieces of metal.

Clark's Island (42°0.7′N, 70°38.2′W, elev. 10 m) is thickly covered with shrubs and trees. Common types of vegetation (2–5 m) used by nesting herons include arrow wood (*Viburnum* spp.), high bush blueberry (*Vaccinium corymbosum*), shad bush (*Amelanchier* spp.) and juniper (*Juniperus* spp.). One side of the island is inhabited, but apparently there is very little disturbance to nesting herons.

The 2 Swash Bay colonies (37°32.0′N, 75°40.5′W) are located on a large sand flat island of a dredge spoil (elev. 1 m). We named these colonies south-south west (SSW) and north-north east (NNE) according to their positions. The vegetation is still in an early stage of succession, probably because of the continuous dumping of spoils on the island. Highwater shrub (*Iva frutescens*) is the dominant plant on both islands.

Middle Marsh colonies (elev. 1 m) are located on 2 islands in a large estuary near Beaufort, North Carolina. A survey marker dated 1933 was found on Middle Marsh Island (34°41.6′N, 76°36.9′W) suggesting it is at least 42 years old. Vegetation is mostly a dense growth of shrub and small trees (1–5 m) of yaupon (*Ilex vomitoria*), live oak (*Quercus virginiana*), highwater shrub and poison ivy (*Rhus radicans*). The Lower Middle Marsh colony (34°41.3′N, 76°36.8′W), 0.5 km southwest of the Middle Marsh colony, is much smaller than the more northern colony.

METHODS AND MATERIALS

The site characteristics of each nest, its position relative to other nests, and vegetative patterns within the colony were quantified. Eleven characteristics of nest-sites were measured (Table 2). The set of measurements reflects nest-site conditions that were mostly independent of the seasonal growth of the vegetation. The variables OPEN and EXIT are the weakest in this regard. Four (GRD, TOP, CTR, OUT) are related to the vertical and horizontal location of the nest in the supporting vegetation. Two represent measures of nest stability (DEF) and exposure (OPEN). Other information included the time of nest initiation (TIM), nest success (SUC), the probable direction of entrance into, or exit from, the nest (EXIT), species (PSP) and condition (PCON) of the vegetation which supported the nest. These last 3 variables were used in the study of nest dispersion and colony characteristics, but not the analysis of nest-site characters. This was because no suitable transformation of radial measures (EXIT) was available in the statistical package and because plant species (PSP) is a nominal variable which yields no useful numerical result. PCON was omitted because it could not be consistently applied in all colonies.

Variables were measured in metric units or converted to metric units before analysis. GRD, TOP and CTR were transformed ($\log_e$) to product homogeneous variances and to reduce skewness and kurtosis.

The variable set was subjected to a factor analysis (subprogram FACTOR, SPSS, Nie et

TABLE 1

SUMMARY OF COLONIES STUDIED, THEIR SPECIES COMPOSITION AND ABUNDANCE AND INVESTIGATORS INVOLVED WITH MARKING NESTS

Colony	Species[b]	Number of nests[a]		Investigator
		Active	Measured[c]	
Spectacle Island, Massachusetts	SNEG	66	47	J. J. Hatch Dept. Biology Univ. Massachusetts, Harbor Campus, Boston, Massachusetts
	BNHE	161	43	
	GLIB	5	—	
Clark's Island, Massachusetts	GREG	5	—	B. A. Harrington Manomet Bird Observatory Manomet, Massachusetts
	SNEG	150	34	
	LBHE	5	—	
	BNHE	350	30	
	GLIB	45	21	
	CAEG	3	—	
			SSW/NNE	
Swash Bay, Virginia[d]	GREG	1	—	M. A. Byrd, T. F. Wieboldt and J. W. Bill Akers Dept. Biology Coll. of William and Mary Williamsburg, Virginia
	SNEG	150	51/103	
	LOHE	180	18/23	
	LBHE	2	—	
	GLIB	8	0/8	
Middle Marsh, North Carolina	GREG	44	53	J. O. Fussell, III Box 520 Morehead City, North Carolina
	SNEG	29	11	
	LOHE	10	8	
	BNHE	7	8	
Lower Middle Marsh, North Carolina	GREG	23	28	J. O. Fussell, III
	SNEG	24	30	
	LOHE	49	55	
	LBHE	16	17	
	BNHE	2	—	
	GLIB	5	—	
	CAEG	1	—	

[a] Estimate of nests represents the maximum number active at any 1 time (see Osborn and Custer 1978). The number of nests measured may exceed the estimated number because of this.

[b] Species abbreviations are: GREG—Great Egret; SNEG—Snowy Egret; LOHE—Louisiana Heron; LBHE—Little Blue Heron; BNHE—Black-crowned Night Heron; GLIB—Glossy Ibis; CAEG—Cattle Egret.

[c] Measured by us.

[d] Information for 3 Swash Bay colonies are combined; we were able to measure nests in only 2 colonies.

al. 1970). The procedure produces a correlation matrix among the measured variables which is then used to create linear combinations of the original variables called factors (or principal components), that are uncorrelated with each other (orthogonal). These factors account for all of the variation in the original data. The number of factors produced by the procedure is equal to the number of variables in the original data set. However, usually the first few factors explain a very large proportion of the total variation in the data. Herein rests the

TABLE 2
LIST OF VARIABLES MEASURED TO DESCRIBE THE NEST-SITES OF WADING BIRDS

Measurements	Description
GRD (nest height)	distance from the ground to the top edge of the nest
TOP (height above the nest)	distance from the top of the nest to the top of the vegetation (in an imaginary 15 cm diameter cylinder projected vertically above the nest)
CTR (distance to center)	distance from the center of the nest to the center(s) of the main supporting structures (measured from the nest to a vertically projected line in the center of the supporting structure)
OUT (distance to the outside)	distance from the center of the nest to the outside of the supporting structure on the axis through the nest and support center (in an imaginary 15 cm diameter cylinder projected horizontally from the nest)
DEF (nest deflection)	amount of displacement vertically when a standard 1200 g weight was placed in the nest (geometric scale)
OPEN (nest angle)	the degree of exposure of the nest to the sky, measured by compass as the arc of a circle to the nearest 10°
EXIT[a] (nest opening)	the probable direction of entrance and exit used by the nesting bird, measured as the compass bearing to the nearest 10°
TIM (month eggs laid)	categories: March, April, May, June, July
SUC (reproductive success of nest)	categories: never active, eggs laid but not hatched, and eggs hatched
PSP[b] (support species)	species of plant(s) supporting the nest
PCON[b] (condition of support)	categories: dead, live, partially dead

[a] This variable was used only in relation to nest dispersion.
[b] Nominal variables were not used in the multivariate analysis.

power of factor analysis where a large set of variables can potentially be reduced to a manageable few. A further refinement of the factors can be obtained by rotation in matrix space. This produces a better fit to the data for the derived factors (see Nie et al. 1970 for a graphical treatment). We used the option VARIMAX rotation in the SPSS package to emphasize the difference between factors.

Factors by themselves do not reveal nest-site patterns for individual species of wading birds. For this analysis, which is of interest because of possible resource division, a procedure was used to calculate a mean factor score (or mean vector) for each species of bird along each factor (FACSCORE procedure in SPSS package). It was then possible to view each species' position on every factor generated in the analysis of the data.

We also examined the extent to which physical characteristics of nesting sites were correlated with time of nest initiation and nesting success. Canonical correlation, which is akin to regression, but more general, was used to answer this question. By this technique pairs of factors are extracted simultaneously from a variable matrix composed of an independent variable set (in this case vegetation characters) and a dependent set (time and success) (Cooley and Lohnes 1971). The criterion is that the first pair of factors has maximum correlation between the 2 sets of data. A second independent (orthogonal) pair of factors is constructed next and so on until all the common variation in the data sets is explained. The maximum number of pairs of factors is equal to the number of variables in the smaller set. In practice, however, pairs of factors are extracted until the canonical correlation between them is no longer significant. The analysis was conducted using the subprogram CANCORR of the SPSS package (Nie et al. 1970).

Nests were mapped in the 2 Swash Bay colonies by determining their angle and distance from a fixed point with a Keuffel and Esser alidade. In the Middle Marsh colonies mapping was done by triangulation with a Keuffel and Esser transit. Repeated measurements and comparisons with m tape readings showed that both techniques were accurate within 1 dm of the true nest location. Two-way radios (Johnson, Messenger 109) were also used by the person at the nest and the alidade or transit operator. Angle and distance of nest location were converted to X and Y coordinates with a pocket calculator and plotted on a map in the field. In this manner, a continuous check of nest positions was possible.

Height and density of vegetation and size of the colony prevented accurate mapping on Spectacle and Clark's islands. However, cooperators measured nearest neighbor nest distances with a meter tape in portions of each colony.

Dispersion patterns were assessed by the nearest neighbor analysis of Clark and Evans (1954). Spectacle and Clark's islands were excluded because data were incomplete.

The dominant plants were recorded for each colony. For the Virginia and North Carolina colonies, the dominant plant forms were mapped as outlines of individual bushes and/or trees, or as groups of plants with continuous canopy on a 5-m grid. The vegetation height was estimated by a 3-m stick, with marked dm intervals, held vertically. In bushes of uneven height an average height was calculated. A continuous check of the position of plants on the maps was made possible by reference to nests previously placed on the map. (Maps are available on request.)

The height and density of vegetation and the size of the colony again prevented the use of similar methods on Spectacle and Clark's islands. Simple line transects were used to estimate plant cover on Spectacle Island. Plant cover was not estimated at all for Clark's Island because of the abundance of poison ivy.

The study was undertaken during late July and August 1975, after the nests had already been located, identified and marked by cooperators monitoring reproductive success in early summer. Except for a few nests in Swash Bay, none were active at the time of our fieldwork, so at the time of measuring nest variables, we rarely knew the species that had occupied the nest, thereby reducing a possible bias. Our field crew varied from 3–8 persons.

In the Virginia and North Carolina colonies all marked nests were measured (Table 1). On Spectacle Island all Snowy Egret (*Egretta thula*) nests and a random sample of about one-third of all Black-crowned Night Heron (*Nycticorax nycticorax*) nests were measured (Table 1). On Clark's Island all nests (mainly Snowy Egrets and Glossy Ibises [*Plegadis falcinellus*]), within a ¼-ha plot were measured. In addition, 30 randomly sampled nests of the more dispersed Black-crowned Night Heron were measured. The number of nests measured was often greater than maximum-number-estimated-to-be-active-at-peak-nesting (see Osborn and

TABLE 3

CORRELATION OF VARIABLES ON THE FIRST 4 PRINCIPAL FACTORS AFTER VARIMAX ROTATION OF THE FACTOR MATRIX

Variable[b]	Factors[a] I	II	III	IV
CRD	0.33	0.23	−0.12	−0.10
TOP	0.37	−0.16	0.11	−0.07
CTR	0.60	0.55	−0.04	−0.04
OUT	0.32	0.02	−0.21	−0.07
DEF	0.19	0.80	0.14	0.04
OPEN	−0.17	0.76	−0.12	−0.10
TIM	−0.15	−0.06	0.01	0.98
SUC	−0.13	0.01	0.97	0.01
Percent of total variance	37.1	18.1	12.4	11.4
Cumulative percent of total variance	37.1	55.2	67.6	79.0

[a] Factors are interpreted to be vegetation size (I), nest stability (II), nesting success (III) and time of nest initiation (IV).
[b] Abbreviations of variable neames are defined in Table 2.

Custer 1978) shown in Table 1, because nests from the entire nesting season were measured.

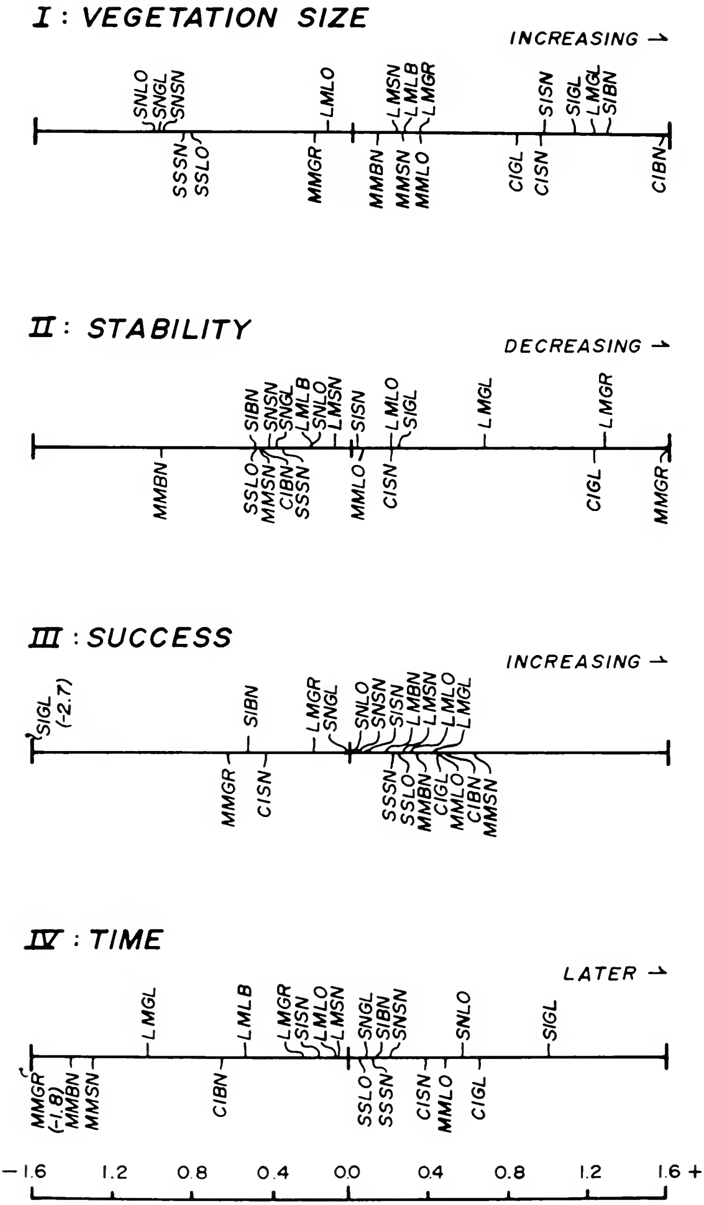
Data analysis was accomplished on a CDC 6500 computer at Michigan State University and with facilities at Patuxent Wildlife Research Center.

RESULTS

Factor analysis.—The factor analysis basically defined 3 aspects of wading bird nesting: vegetative characteristics, time of nest initiation, and nesting success. Of the 8 axes (factors) derived, 4 account for 79% of the variation. The loadings of the 8 variables on these 4 factors are shown in Table 3. The remaining 4 axes, accounting for only 21% of the variation, were omitted because of eigenvalues less than 1 (Cooley and Lohnes 1971). They were also not included in the final VARIMAX rotation.

The first axis is best termed a "vegetation size" factor since highest correlations are with GRD, TOP, CTR and OUT. The second axis reflects nest stability because of high correlations of CTR, DEF and OPEN. The highest correlations on the third axis are with SUC; TIM is the most highly correlated on the fourth. All other variables have very low correlations with these last 2 axes, designated the nest success factors and time of nest initiation, respectively.

Mean factor scores by species and colony are plotted for each factor in


I : VEGETATION SIZE

II : STABILITY

III : SUCCESS

IV : TIME

FIG. 1. Ordination of mean factor scores for each species in each colony for the 4 main factors. Abbreviations are for colony and species. The first 2 letters abbreviate the colony, the second 2 the species. Colonies are SN—Swash Bay NNE, SS—Swash Bay SSW, MM—Middle Marsh, LM—Lower Middle Marsh, CI—Clark's Island, SI—Spectacle Island. Species are: SN—Snowy Egret, LO—Louisiana Heron, LB—Little Blue Heron, BN—Black-crowned Night Heron, GR—Great Egret, GL—Glossy Ibis.

Fig. 1. By examining how means are grouped it is possible to determine if the factor is important as a possible characteristic of the wading bird species or whether it is the result of a colony's physical characteristics.

The vegetation size factor (Fig. 1) shows that species-colony means tend to be grouped by colonies. Thus the greatest amount of the variation accounted for by the statistical model appears to reflect directly the variation in plant size in nesting colonies, i.e., a colony's physical characteristics.

Species groups, rather than colonies as in the first factor, tend to sort out along the stability factor (Fig. 1 [II]). The most stable nests are of the Black-crowned Night Heron regardless of colony. The least stable nests are of the Great Egret (*Casmerodius albus*) in both colonies and the Glossy Ibis on Clark's Island and Lower Middle Marsh. The remaining species show a trend toward decreasing nest stability with colonies containing larger vegetation. An exception is the Snowy Egret with a slightly more stable nest at Middle Marsh than at either Swash Bay colony.

Patterns along the nesting success factor (Fig. 1 [III]) are less clearcut than for the previous factors. In general, Snowy Egrets, Louisiana Herons (*Hydranassa tricolor*), Little Blue Herons (*Florida caerulea*) and Glossy Ibises all have similar nesting success in colonies where they nest together. Two exceptions occur in the north where Glossy Ibises are noticeably more successful than Snowy Egrets—on Clark's Island and on Spectacle Island where the reverse is true.

For the last factor, time of nest initiation, no apparent pattern can be seen (Fig. 1 [IV]). Even the expected relationship of time of nest initiation to the latitude of a colony is not consistent.

Two-dimensional plots may also be examined for combinations of these factors since the statistical model derives them orthogonally. Because of the large amount of variability explained by the first 2 factors (55.2%), only vegetation size will be examined with nest stability (Fig. 2).

In the Swash Bay colonies Snowy Egrets, Louisiana Herons and Glossy Ibises nest in vegetation of very similar size and the nests are equally stable. Birds in the Middle Marsh colonies show large differences in stability of nest-sites they choose. Here, the Black-crowned Night Heron has very stable nests and the Great Egret very unstable nests (Fig. 2). Black-crowned Night Heron nests are more stable than the nests of all other species, but in Massachusetts their nest stability has decreased to a level comparable to that observed in the Swash Bay colonies for Snowy Egrets and Louisiana Herons. Great Egret nests are considerably less stable than other species even though other species in the Middle Marsh colonies nest in similar sized vegetation. In the Swash Bay colonies Snowy Egrets and Louisiana Herons have nests in similar sized vegetation and vary only slightly in stability. Little Blue Heron nests are found only in the Lower

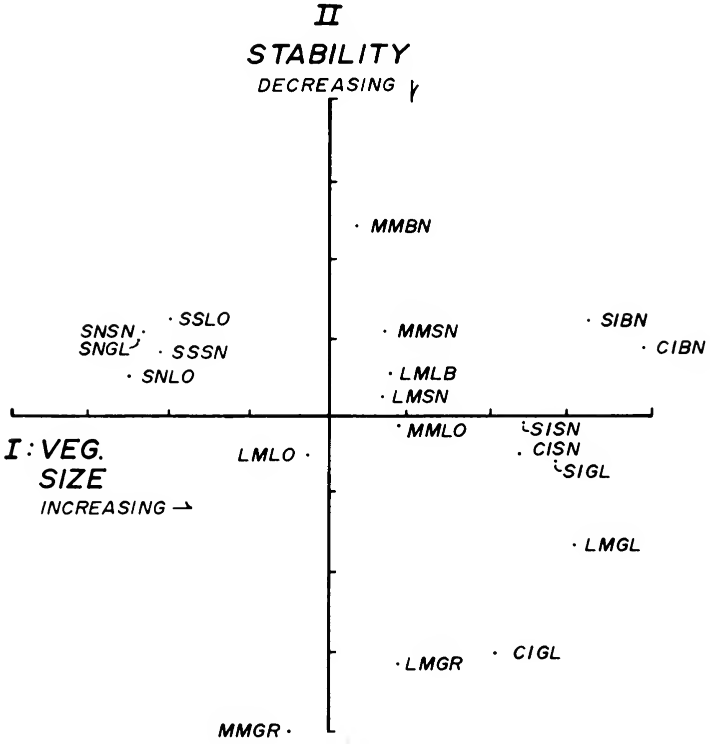


FIG. 2. Plot of mean factor scores for each species and colony of Factor I against Factor II. Abbreviations as in Fig. 1.

Middle Marsh colony where they are similar to Snowy Egret nests in both their stability and the size of vegetation in which they are placed.

The Glossy Ibis shows a marked decrease in nest stability in Lower Middle Marsh compared to Swash Bay (Fig. 2). Nests of this species are placed in the largest vegetation present on Lower Middle Marsh, which is similar in size with those in the Massachusetts colonies. However, Glossy Ibis are also often found nesting on the ground, even when there is vegetation present (Burger and Miller 1977). Their versatility in this respect may indicate that factors other than nest stability are important in choice of a nesting site.

Snowy Egrets on Clark's and Spectacle islands have lower stability in their nest-sites than in Swash Bay and Middle Marsh colonies. The overall pattern of each species is a consistent, but decreasing, stability of nest-

TABLE 4

THE STRUCTURE OF THE FIRST CANONICAL VARIATE

Variable sets[a]	Correlation with first canonical variate
Vegetation characters (independent)	
GRD	−0.89
TOP	−0.42
CTR	−0.61
OUT	−0.82
DEF	−0.12
OPEN	−0.12
Time and success (dependent)	
TIM	0.63
SUC	0.81

[a] Variable explanations Table 2.

sites with increasing vegetation size from the Swash Bay to Middle Marsh to Massachusetts colonies.

Vegetation characters and time and success of nests.—Factor analysis demonstrated that TIM and SUC are highly correlated with factors III and IV, respectively (Table 3), and therefore vary independently of each other. However, possible relationships between these variables and characteristics of the vegetation were suggested for at least the Great Egret. This was examined using canonical correlation. Table 4 shows the loading of variables on the only significant pair of canonical variates (canonical r = 0.35, $\chi^2 = 47.6$, df = 12). The canonical variate from the first (independent) variable set describes, as with the first factor in the factor analysis, the size of vegetation in which the nest is placed. GRD, TOP, CTR and OUT have large, negative correlation values. Both variables of the second (dependent) set are positively correlated with the other canonical variates suggesting that part of both time of nest initiation and nest success are related to the size of vegetation supporting the nest.

At least a part of the correlation is due to the poor nesting success shown by the Great Egret (Fig. 2) which tended to choose nest-sites that are exposed and unstable relative to the nests of other species. Also, the Great Egret nested very early in Middle Marsh. It should be noted that in the canonical model only 12% of the variation in nest placement is explained by timing and success of nest. We therefore feel that while the result is interesting, it is not general. We would not expect to see the same

TABLE 5
DISPERSION PATTERNS OF NESTS IN WADING BIRD COLONIES

Colony	Parameters[a]						
	N	A	ρ	$\bar{r}_A$	$\sigma_{\bar{r}_E}$	c	P
Swash Bay, SSW	96	256	0.375	0.431	0.043	−8.95	<0.001
Swash Bay, NNE[b]	211	2473 (406)	0.085 (0.520)	0.966	0.062 (0.025)	−12.11 (10.92)	<0.001 (<0.001)
Middle Marsh	120	3675	0.033	1.629	0.132	−8.63	<0.001
Lower Middle Marsh	193	1400	0.138	1.106	0.051	−4.75	<0.001

[a] Parameters are: N = number of nests in colony; A = area of colony, in m^2; ρ = observed density of nest per m^2; $\bar{r}_A$ = mean nearest neighbor nest distance in meters; $\sigma_{\bar{r}_E}$ = the standard error of mean nearest neighbor nest distance when nests are randomly distributed; c = standard variate of the normal curve; P = probability of getting a deviation this great from random dispersion.

[b] Values in parentheses represent the exclusions of an unusable central portion of the colony in the calculations.

relationship in other wading bird colonies without specific qualifying conditions.

Summarizing, the factor analysis clearly distinguishes colonies based on the size of the vegetation used for nesting. Secondly, nest stability in the form of our measure of deflection, distance to the center and openness show consistent trends for a species regardless of the colony location. It is this factor that we feel characterizes how and where these wading birds choose their nesting sites. We will return to this important point in the discussion.

Dispersion of nest-sites.—Dispersion of nests within colonies was examined by nearest neighbor analysis (Clark and Evans 1954). All 4 colonies tested show significant aggregation of nests (Table 5), however, the test appears to be sensitive to what is defined as the area of a colony. In Swash Bay NNE, bushes with nests were nearly continuous around the perimeter of the colony. The center was occupied by grasses, forbs and a few dead bushes. If this central area is excluded the result shows a uniform dispersion of nests (Table 5, data in parentheses). All deviations from randomness are in the direction of clumping. An analysis of variance indicated that differences in the degree of departure from randomness were highly significant (F = 336, df = 3/616, $P < 0.001$).

The spacing of nests by species in relation to the nearest nest of any species shows a pattern that appears to be related to the average size of the vegetation in the colony (Table 6). In general, larger inter-nest distances occur in the colonies with larger vegetation.

The angle of exit from the nest was measured for all species in every colony to see if it was related to the spacing pattern or some other factor,

TABLE 6

DISTANCE ($\bar{x}$ ± SE[N]) (N) BETWEEN A SPECIES NEST AND THE NEAREST NEST OR ANY WADING BIRD[a]

	Species[a]					
Colony	GREG	SNEG	LOHE	LBHE	BNHE	GLIB
Swash Bay, SSW		0.44 ± 0.38 (51)	0.5 ± 0.06 (17)			
Swash Bay, NNE		1.0 ± 0.07 (99)	0.9 ± 0.10 (25)			0.9 ± 0.19 (8)
Middle Marsh	1.2 ± 0.10 (55)	0.5 ± 0.06 (11)	3.0 ± 0.80 (8)		3.4 ± 1.80 (9)	
Lower Middle Marsh	1.0 ± 0.07 (25)	1.0 ± 0.10 (32)	1.2 ± 0.10 (53)	0.9 ± 0.08 (12)	1.1 ± 0.51 (2)	1.1 ± 0.10 (9)
Clark's Island		1.6 ± 0.41 (10)			7.8 ± 3.40 (7)	0.9 ± 0.12 (10)
Spectacle Island		1.7 ± 0.52 (6)			1.6 ± 0.71 (5)	

[a] Species abbreviations are given in Table 1.

TABLE 7

ANGLE ($\bar{x}$ ± SE[N]) (°) AS MEASURED ACCORDING TO THE COMPASS BEARING OF THE EXIT FROM THE NEST FOR SPECIES OF WADING BIRDS IN 6 ATLANTIC COAST COLONIES

Species[a]	Swash Bay SSW	Swash Bay NNE	Middle Marsh	Lower Middle Marsh	Clark's Island	Spectacle Island
GREG			299 ± 113 (25)	129 ± 103 (19)		
SNEG	207 ± 152 (35)	326 ± 126 (79)	235 ± 91 (3)	124 ± 109 (23)	92 ± 114 (26)	258 ± 88 (38)
LOHE	213 ± 76 (13)	54 ± 122 (17)	281 ± 60 (4)	143 ± 90 (26)		
LBHE				103 ± 112 (14)		
BNHE			315 ± 25 (2)		29 ± 106 (24)	75 ± 124 (39)
GLIB		105 ± 68 (4)		299 ± 62 (5)	323 ± 118 (15)	129 ± 81 (6)

[a] Species abbreviations Table 1.

TABLE 8

PERCENT COVER OF PLANT SPECIES SUPPORTING WADING BIRD NESTS AND THEIR USE BY WADING BIRDS IN 6 COLONIES ALONG THE ATLANTIC COAST

Colony	Plant species supporting nests	Relative cover in colony	Percent nests found in plant species						
			All nests[a]	GREG	SNEG	LOHE	LBHE	BNHE	GLIB
Swash Bay, SSW	highwater shrub (live)	77			94	90			100
	highwater shrub (dead)	<1			6	10			0
	other[b]	23			0	0			0
					(55)[c]	(20)			
Swash Bay, NNE	highwater shrub (live)	37			51	74			33
	highwater shrub (dead)	11			49	26			67
	other	52			0	0			0
					(103)	(23)			(8)
Middle Marsh	highwater shrub (live)	18	4	2	0			0	
	oak	8	43	56	34	88		43	
	yaupon	10	31	20	58	0		57	
	juniper	1	16	22	8	12		0	
	other	63	6	0	0	(8)		0	
			(115)	(55)	(12)			(7)	
Lower Middle Marsh	ground	8	2	3	0	0	0	0	0
	highwater shrub (live)	26	16	0	6	18	0	0	0
	palmetto (*Serenoa* spp.)	10	1	0	3	0	0	0	0
	pokeberry	10	1	0	6	0	0	0	0
	poison ivy	10	2	0	0	0	0	0	0
	bay (*Myrica* spp.)	1	0	12	0	0	6	0	0
	oak	27	44	31	50	40	83	100	44
	yaupon	10	25	31	25	29	11	0	23
	juniper	10	9	23	10	0	0	0	33
	other	20	0	0	0	0	0	0	0
			(308)	(26)	(32)	(53)	(18)	(2)	(9)
Clark's Island	Virginia creeper (*Parthenocissus* spp.)				0			0	4
	arrow wood				26			19	70
	shadbush				10			2	4
	highbush blueberry				30			7	9
	staghorn sumac				4			2	4
	cherry				4			10	9
	pine (*Pinus* spp.)				0			2	0
	juniper				26			58	0
					(23)			(43)	(23)
Spectacle Island	ground[d]				0			1	0
	raspberry (*Rubus* spp.)	3			23			2	0
	rose (*Rosa* spp.)	2			4			0	0
	staghorn	77			18			15	0

TABLE 8
CONTINUED

Colony	Plant species supporting nests	Relative cover in colony	Percent nests found in plant species						
			All nests[a]	GREG	SNEG	LOHE	LBHE	BNHE	GLIB
Spectacle Island (continued)	buckthorn	3			15			34	71
	apple	1			2			10	0
	pear (*Pyrus communis*)[e]	0			0			1	0
	cherry	2			36			30	29
	poplar	4			0			5	0
	linden (*Tilia* spp.)	0			2			0	0
	tree-of-heaven (*Ailanthus* spp.)	5			0			2	0
	other	3			0			0	0
					(47)			(122)	(7)

[a] Included all species and nests not identified to species. Clark's and Spectacle islands have no figure for this category because only a sample of nests was made.

[b] Other includes grass, composites, etc., that were judged not suitable as nesting supports.

[c] In parentheses are the number of nests measured for the category.

[d] Not measured—little ground cover at all.

[e] Zero percent cover estimated by line transect; plants were present in the colony and some were used by birds.

such as shading from the sun. We predicted that nests would be opening to the north if shading was important. However, the nest exit angles of all species in every colony were random (Table 7, test of angular dispersion, Zar 1974:310). If the nest exit angle was a function of interactions with the nearest neighbor, one would expect them to be oriented in different directions. No significant relationship between exit angles emerged that would suggest that openings were selected to avoid leaving or entering in the path of the nearest nest.

In the Swash Bay colonies, the vegetation used for nesting was highwater shrub, comprising the major part of both of these colonies (Table 8). The birds nested exclusively in either dead or living shrubs, but preferred living ones. These colonies appeared to be "full," that is, very little additional nesting space appeared to be available. In the 2 Middle Marsh colonies, where there is a higher diversity of plants, the waders nested in the higher nesting sites offered by oak, yaupon and juniper, rather than in highwater and other shorter shrubs. This may have been in response to tidal or storm flooding, or predation by mammals such as rats (*Rattus* sp.) and raccoons (*Procyon lotor*). Middle Marsh appeared to have considerable unused nesting sites, whereas Lower Middle Marsh had fewer unused sites. A greater diversity of supporting plant species occurred in the Massachusetts colonies, although this was not accompanied by an increase in wading bird species. Our impression was that many potential nesting sites were unused in both colonies.

Using percent cover as an estimate of the availability of nest-sites of all species combined in the Middle Marsh colonies, a Chi-square test yielded significant deviations (all $P < 0.005$) from the expected pattern (i.e., random). The same result is obtained for each species in these colonies, although the smaller sample size makes the result less reliable. The same trend was found for Spectacle Island, with cherry, buckthorn and staghorn sumac being the most frequently used nesting supports. Staghorn sumac appears to be avoided, whereas the other 2 support species are selected above their proportion of the cover. Wading bird species occurring on Spectacle Island were not tested for their nest support preference because we took subsamples within the colonies.

DISCUSSION

Nest-site characteristics.—The general applicability of our results is difficult to assess because only a few studies are available for comparison. McCrimmon (1978) studied a colony of egrets and herons in 1974 on Phillip's Island, only a few km north of our Middle Marsh colonies. He used a principal component analysis to examine 12 nest-site characters for 5 species of wading birds (Great Egret, Snowy Egret, Little Blue Heron, Cattle Egret [*Bubulcus ibis*] and Louisiana Heron). Six of his variables closely resemble those used in this study; those relating to position of the nest in the vegetation and vegetation size (nest height, height of vegetation above the nest, distance from center, degree of openness above the nest, diameter of nest branch and diameter of the nest tree 1 m above the ground). He found that 4 components accounted for 69% of the variation in the model. Two of his components (factors I and IV) are basically similar to our vegetation size (factor I) and nest stability (factor II). McCrimmon did not use a measure of nest deflection as we did, but the variables of distance to the nest from the center, diameter of nest branch and the degree of openness above the nest were measured and are the basis for the similarity of his fourth and our second factor in the statistical model. McCrimmon's remaining 2 factors (II and III) involve "accessibility" and "protection" of the nest by the surrounding vegetation and they appear to be specific to the Phillip's Island colony. We do not have comparable data for these factors.

Comparing our factor I with McCrimmon's factor I (vegetation size) shows little similarity in the magnitude or order of individual species' factor scores along the axis in the Middle Marsh colonies. Either the variables measured are different enough in the 2 studies to produce this effect or the size of the vegetation used for nesting is not a consistent feature for

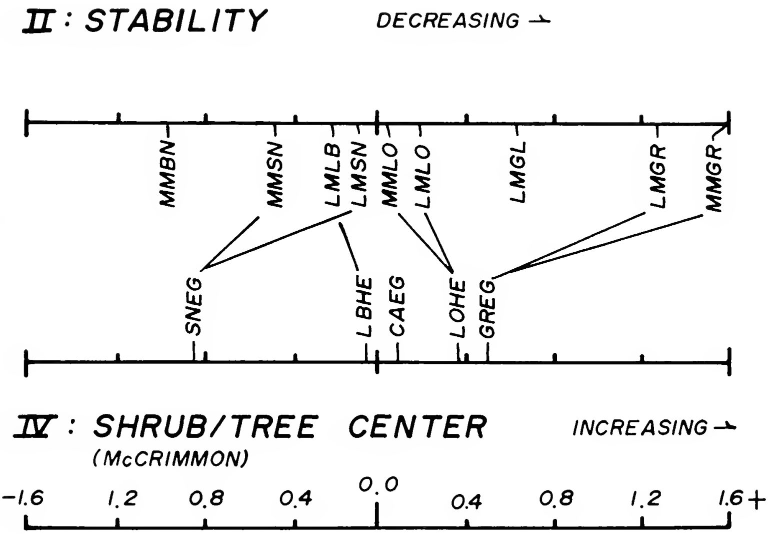


FIG. 3. A comparison of Factor II in our study for the species nesting in the 2 Middle Marsh colonies to McCrimmon's (1978) Factor IV. Lines connect the species. Abbreviations for the stability factor are the same as those in Fig. 1. Abbreviations in McCrimmon's Factor IV are the same as those of Table 1.

these species. We suspect the latter because of the large range of vegetation size available for nesting and the apparent lack of selectivity for vegetation size in other colonies by the species studied.

The order of species along the nest stability factor (factor II) in our study and factor IV in McCrimmon's study correspond. The only species out of place is the Little Blue Heron in Lower Middle Marsh (Fig. 3) but the factor score is not significantly different from the adjacent Snowy Egret. The differences in the magnitude of factor scores between the 2 studies on these factors are probably the result of different variables measured and measuring techniques. Nevertheless, the pattern is very striking and it is our interpretation that the basis for the similarity of the stability factor in our study and McCrimmon's is a species-specific preference for a stable nest-site. It is noteworthy that the courtship display of the male of all the species studied here is centered on the nest-site. Jenni (1969:249) noted that the male ". . . performs his displays on a sturdy site offering considerable support, and the nest was usually built in the same place." Most of the behavior of the mated pair also occurs on the display and nest-site (Jenni 1969, Burger 1978). It remains to be shown that the patterns in nest-site stability found in our study and McCrimmon's are consistent for other colony sites or for more than 1 year within colonies.

TABLE 9

MEAN NEST HEIGHT (M) FOR 6 SPECIES OF WADING BIRDS ($\bar{x} \pm$ SD [N])

	Colony					
	Swash Bay		Middle Marsh			
Species	SSW	NNE	Middle	Lower Middle	Clark's Island	Spectacle Island
Snowy Egret	0.14 ± 0.05 (51)	0.12 ± 0.06 (103)	1.11 ± 0.38 (11)	1.1 ± 0.53 (30)	2.2 ± 0.49 (34)	2.2 ± 0.94 (47)
Louisiana Heron	0.14 ± 0.06 (18)	0.12 ± 0.05 (23)	1.0 ± 0.4 (8)	0.81 ± 0.28 (55)		
Little Blue Heron				1.5 ± 0.22 (17)		
Black-crowned Night Heron			1.3 ± 0.35 (8)		2.6 ± 0.93 (30)	2.6 ± 0.91 (43)
Great Egret			1.7 ± 0.46 (53)	1.7 ± 0.74 (28)		
Glossy Ibis		0.11 ± 0.05 (8)		1.2 ± 0.63 (9)	2.4 ± 0.34 (21)	2.9 ± 0.34 (6)
Mean vegetation height[a]	0.42 ± 0.08 (71)	0.36 ± 0.11 (134)	2.12 ± 0.63 (80)	2.07 ± 0.71 (140)	4.70 ± 1.49 (85)	4.74 ± 1.47 (95)

[a] Of plants with nests.

Summarizing, our analysis points to the stability of the nest-site as a key character for choice of a site. The courtship and mating behavior of herons and egrets within their territories may be the mechanism by which the stability of the nest-site is assessed and either accepted or rejected for a more (or less) stable site.

Social factors and nest-site selection.—Jenni (1969) noted that vertical stratification occurred in the heronry he studied, but the stratification was more or less pronounced or absent depending on the year. New sites were selected each year by most species because the previous year's nests had fallen apart during the nonbreeding season. Burger (1978) has suggested that vertical stratification occurs as a means of reducing competition for nest-sites, especially in vegetationally homogeneous colonies. However, in the Swash Bay colonies, where the vegetation was homogeneous, essentially no vertical stratification occurred, probably because of the low height (1 m). The most diverse colony sites (MM, LMM) in terms of both vegetation and bird species showed increased stratification in vertical nest position (Table 9). McCrimmon (1978) also found a similar pattern for the Phillip's Island Colony. If nest-sites are selected on the basis of their stability, vertical stratification may or may not be a result, depending on a species preference and vegetation in the colony. If the stability of sites is correlated with their vertical position, then stratification would be a consequence of selecting stable sites. However, if nest-site stability and vertical position are poorly correlated, which may occur in colonies like the ones Jenni (1969) studied, then vertical stratification is not likely to be consistent from colony to colony, or even for different years in the same colony.

One aspect with which we have not dealt is the effect that social interactions may have on nest-site selection. Burger (1978) has suggested that large species dominate the smaller ones and force smaller species to nest lower in the vegetation than they otherwise would. This, in effect, produces vertical stratification of species in a colony according to body size. Body size here refers to body length with the neck extended (a measure of interaction distance), not body weight (Burger 1978). However, our data do not show the predicted pattern in every colony. The Glossy Ibis nested higher than the longer-bodied Snowy Egret in the 2 Massachusetts colonies (Table 9). Snowy Egrets nested at the same height as the longer Louisiana Heron in the Middle Marsh colonies. The longest species, the Great Egret, nested the highest of all species in the Middle Marsh colonies, but they were only 70 cm higher on the average, which is well within the estimated interaction distance (2 m) for the Great Egret. These inequities could be explained by postulating that vegetation factors prevent the effects of social interactions from being fully realized. As our data on vegetation used as nest support suggest (Table 8), nearly all of the birds were nesting in the most rigid plants while other areas of the colony or other plant types were not used. This resulted in the consistent pattern of clumping of nests we found (Table 5), since the rigid plants tended also to be clumped. The Swash Bay colonies were "homogeneous" in the sense that *Iva* was the only shrub present, but the pattern of nesting was still clumped because only certain parts of the vegetation could support nests, namely the lower parts close to the center of the shrub. As pointed out earlier, the nests in the NNE colony were actually highly uniform in dispersion (if the unvegetated center of the colony is excluded from the area) (see Table 5), a pattern which matched the older and more uniformly spaced *Iva* compared to the SSW colony. These results suggest that the structure of the vegetation strongly influenced nest dispersion and probably also the position of the nest-site. Perhaps social interactions modify the pattern only when: (1) a colony is fully occupied, i.e., has no more vegetation for nesting and (2) vegetation allows a wide range of nest placement, i.e., acceptable sites occur at all levels within the vegetation. The Swash Bay colonies met the first condition, in that every bush was used and that inter-nest distances were 0.4–1.0 m, but not the second, since no vertical stratification occurred. Lower Middle Marsh colony met both conditions and vertical stratification was pronounced. Horizontal separation was also greater than the Swash Bay colonies ($\bar{x}$ = 1.6 m). Although extensive areas within the Middle Marsh colony were not used for nesting, nest-sites were stratified. Again this seems to be due to the vegetation since the 3 main species of waders did not use the same species of plant for nesting and, therefore, tended to be horizontally segregated. Thus, the vertical stratification was still manifested even though the vegetation height was not different for the plant species used and the horizontal segregation precluded social interactions involving nest height.

Neither of the Massachusetts colonies was fully occupied and vertical stratification was minimal (Table 9). The various species tended to nest in spatially distinct parts of the colony in different species of plants (Table 8). Inter-nest distance tended to be high (Table 6). The vegetation in these colonies was the highest and most varied in height of all colonies studied.

Thus, the dispersion pattern of nests is probably more strongly influenced by the availability of suitable vegetation in the colony than by social interactions. Birds appear to nest in any available vegetation that will support a nest. Where only a limited diversity of nest support species are present, nests are placed according to stability requirements. This may result in stratification if a large enough vertical range of suitable sites exist and/or social interactions are intense. Nests may not be vertically or horizontally stratified despite social interaction, even in fully occupied colonies, if the vegetation does not permit it.

However, that does not mean that social factors play no role in the colonial nesting habit of wading birds. Social attraction brings individuals together to nest and brings a variety of species together in multi-species colonies. Krebs (1974) has argued that the colony may serve as an information center to increase feeding rates of individuals and Custer and Osborn (1978) present indirect evidence that supports this hypothesis. Within the colonies we studied social factors had little consistent (measurable) effect on where nests were placed. The vegetation and the preferences of species for particular nest-site characteristics, most notably their stability, was seemingly critical to the selection of nest-sites.

SUMMARY

Nests of 5 species of wading birds were identified and marked during the breeding season at 6 locations from Massachusetts to North Carolina. At the end of the breeding season 12 characteristics of nest-site location were measured. Nest locations were mapped to examine dispersion and nearest neighbor relationships. Multivariate analyses were used to describe and compare sites and species.

We found that variations in nest-sites between colonies were greater than between species; colonies differed mainly in the variety and size of vegetation; birds preferred to nest in vegetation that offered relatively stable nest-sites; and the dispersion of nests in the colonies was related to vegetative patterns. The interaction of these factors with the number of bird species and the abundance of birds in the colony seemed to determine whether nest-sites were stratified, segregated or randomly distributed.

ACKNOWLEDGMENTS

We thank J. W. Bill Akers, M. A. Byrd, J. O. Fussell, III, B. A. Harrington, J. J. Hatch and T. F. Wieboldt for marking the nests and later relocating them for us. M. A. Beaver, E. A. Custer, P. H. Hochman and J. O. Fussell, III, assisted in the fieldwork.

We thank D. A. McCrimmon, Jr., for helpful discussions throughout the course of this study. D. L. Drzal typed the manuscript. This research was supported by the Biological Indicators Program, Office of Biological Services, U.S. Fish and Wildlife Service.

LITERATURE CITED

Bent, A. C. 1926. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. 135.

Burger, J. 1978. The patterns and mechanism of nesting in mixed-species heronries. Pp. 45–58 *in* Wading birds, Res. Rep. No. 7, (A. Sprunt, IV, J. C. Ogden and S. Winkler, eds.). New York, New York.

——— and L. M. Miller. 1977. Colony and nest site selection in White-faced and Glossy Ibis. Auk 94:664–676.

Clark, P. J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445–453.

Cooley, W. W. and P. R. Lohnes. 1971. Multivariate data analysis. Wiley, New York, New York.

CUSTER, T. W. AND R. G. OSBORN. 1977. Wading birds as biological indicators: 1975 colony survey. U.S. Fish and Wildl. Serv., Spec. Sci. Rep. Wildl. No. 206.

——— AND ———. 1978. Feeding habitat use by colonially-breeding herons, egrets and ibises in North Carolina. Auk 95:733–743.

DUSI, J. L.. 1966. The identification and characteristics of nests, eggs and nestlings of some herons, ibises and anhingas. Alabama Birdlife 14:2–8.

———AND R. T. DUSI. 1968. Ecological factors contributing to nesting failure in a heron colony. Wilson Bull. 80:458–466.

EYLES, D. 1938. A nesting study of the Tybee Island heronry. Oriole 3:1–4.

GERSBACHER, E. O. 1939. The heronries at Reelfoot Lake. J. Tennessee Acad. Sci. 14:162–180.

JENNI, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alchua County, Florida. Ecol. Monogr. 39:245–270.

KREBS, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour 51:99–134.

LOWE-MCCONNELL, R. H. 1967. Biology of the immigrant Cattle Egret, *Ardeola ibis*, in Guyana, South America. Ibis 109:168–179.

MAXWELL, G. R., II AND H. W. KALE, II. 1977. Breeding biology of five species of herons in coastal Florida. Auk 94:689–700.

MCCRIMMON, D. A., JR. 1978. Nest-site characteristics among five species of herons on the North Carolina coast. Auk 95:267–280.

MEANLEY, B. 1955. A nesting study of the Little Blue Heron in eastern Arkansas. Wilson Bull. 67:84–99.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER AND D. H. BENT. 1970. Statistical package for the social sciences. 2nd ed. McGraw-Hill, New York, New York.

OSBORN, R. G. AND T. W. CUSTER. 1978. Herons and their allies: atlas of Atlantic coast colonies, 1975 and 1976. Biological Serv. Prog., U.S. Fish. Wildl. Serv. FWS/OBS-77/08.

PATTEN, G. 1952. Inside a heronry. The Bokmakierie 4:8–9.

RALPH, C. J. AND C. L. RALPH. 1958. Notes on the nesting of egrets near San Rafael, California. Condor 60:70–71.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

DEPT. ZOOLOGY, MICHIGAN STATE UNIV., EAST LANSING, MICHIGAN 48824 (DLB); U.S. FISH AND WILDLIFE SERVICE, PATUXENT WILDLIFE RESEARCH CENTER, LAUREL, MARYLAND 20811 (RGO, TWC). (PRESENT ADDRESS RGO: OFFICE OF BIOLOGICAL SERVICES, NATIONAL WESTERN ENERGY AND LAND USE TEAM, FORT COLLINS, COLORADO 80521.) ACCEPTED 25 JAN. 1979.

Wilson Bull., 92(2), 1980, pp. 221–228

THE INFLUENCE OF AGE ON THE BREEDING BIOLOGY OF RING-BILLED GULLS

Gerard T. Haymes and Hans Blokpoel

The influence of age on breeding parameters has been studied for many bird species. In larids, breeding parameters that have been examined include: (1) date of laying (e.g., in the Black-legged Kittiwakes [*Rissa tridactyla*], Coulson and White 1958); (2) clutch-size (e.g., in Arctic Terns [*Sterna paradisaea*], Coulson and Horobin 1976) and (3) breeding success (e.g., in Herring Gulls [*Larus argentatus*], Chabrzyk and Coulson 1976). In Ring-billed Gulls (*Larus delawarensis*), Ryder (1975) showed a general relationship between plumage, as a gross measure of age, and some reproductive parameters.

This paper examines the influence of age on: (1) the date of clutch initiation, (2) nest location, (3) clutch-size, and (4) hatching success of Ring-billed Gulls. It also examines the influence of age on each of the last 3 parameters for early nesters and for late nesters, separately.

STUDY AREA

This study took place in 1977 on the Eastern Headland (Leslie Spit) of the Toronto Outer Harbour, near Toronto, Ontario, Canada. Leslie Spit is a man-made peninsula of clean fill and dredged spoil extending about 5 km into Lake Ontario. The area, and its rapid colonization by larids were described by Blokpoel and Fetterolf (1978). In 1977 there were about 20,000 pairs of Ring-billed Gulls nesting in 4 sub-colonies separated by narrow inlets. The 2 largest of these sub-colonies were used in this study. No banding has been conducted on the Eastern Headland, but many banded birds that had been banded elsewhere were present.

METHODS AND MATERIALS

Through systematic searches of the 2 sub-colonies, nests of banded birds were located and marked with numbered stakes. The band numbers were obtained by trapping birds on the nest with walk-in traps similar to those described by Weaver and Kadlec (1970) (N = 134) or by reading them with binoculars (N = 30).

Of the 164 banded birds found nesting in the 2 sub-colonies, 151 had been banded as chicks and their exact ages could be determined. For the 13 birds that had been banded during a year other than their hatching year, only minimum ages could be determined. Of those birds 10 could be included in the oldest age category that we used in this study (≥7-years-old). The remaining 3 birds were not used.

All eggs in each staked nest were numbered and nests were examined every second or third day, weather permitting, until hatching. For nests that already contained eggs when we first located them, dates of clutch initiation were determined from hatching dates using an incubation period of 27 days. We plotted nest locations on maps from which distance between nests and the center of the colony were then calculated.

Data for some of the nests were incomplete due to a number of minor problems, such as

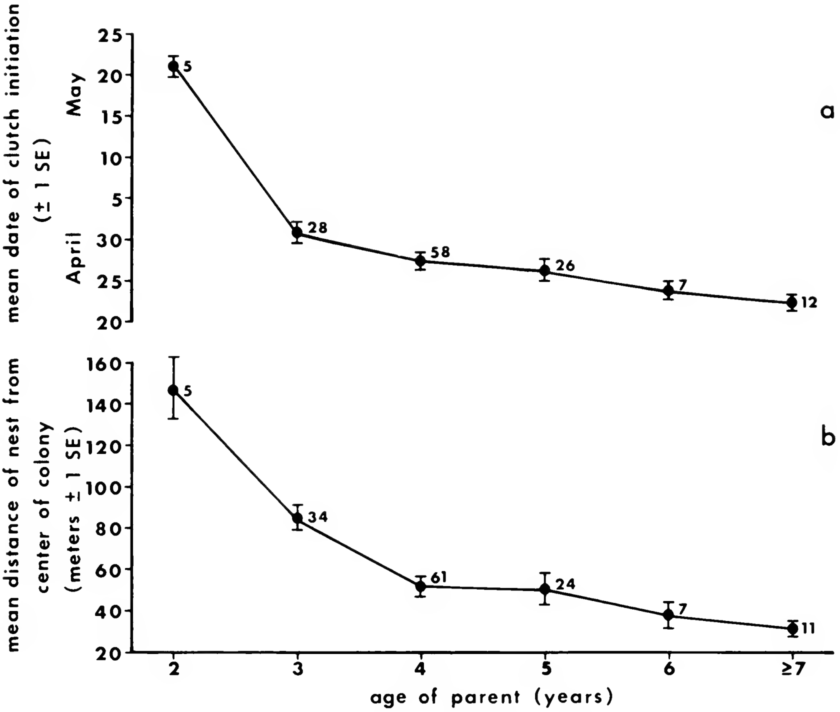


FIG. 1. (a) The mean date of clutch initiation and (b) the mean distance of nests from the center of the colony for Ring-billed Gulls of known age at the Eastern Headland, 1977. The numbers on the figures refer to the number of nests.

fading of the numbers on the stakes. As a result sample sizes vary slightly throughout the analyses. As the results for the 2 sub-colonies were not significantly different in any respect, data for the 2 then were pooled to increase sample sizes.

RESULTS

In 1977 egg-laying on Leslie Spit began before 15 April (estimated at 10 April) and continued into July. The date when the first egg was laid in a nest (i.e., date of clutch initiation) by a banded bird was 17 April.

The mean date of clutch initiation for each of 6 age categories of Ring-billed Gulls is shown in Fig. 1a. The mean date of clutch initiation was consistently earlier as age increased. There was a significant correlation between age and date of clutch initiation ($r_s = 0.479, P < 0.001$) (Spearman rank correlation coefficient).

Coulson (1968) showed that kittiwakes, nesting near the center of the

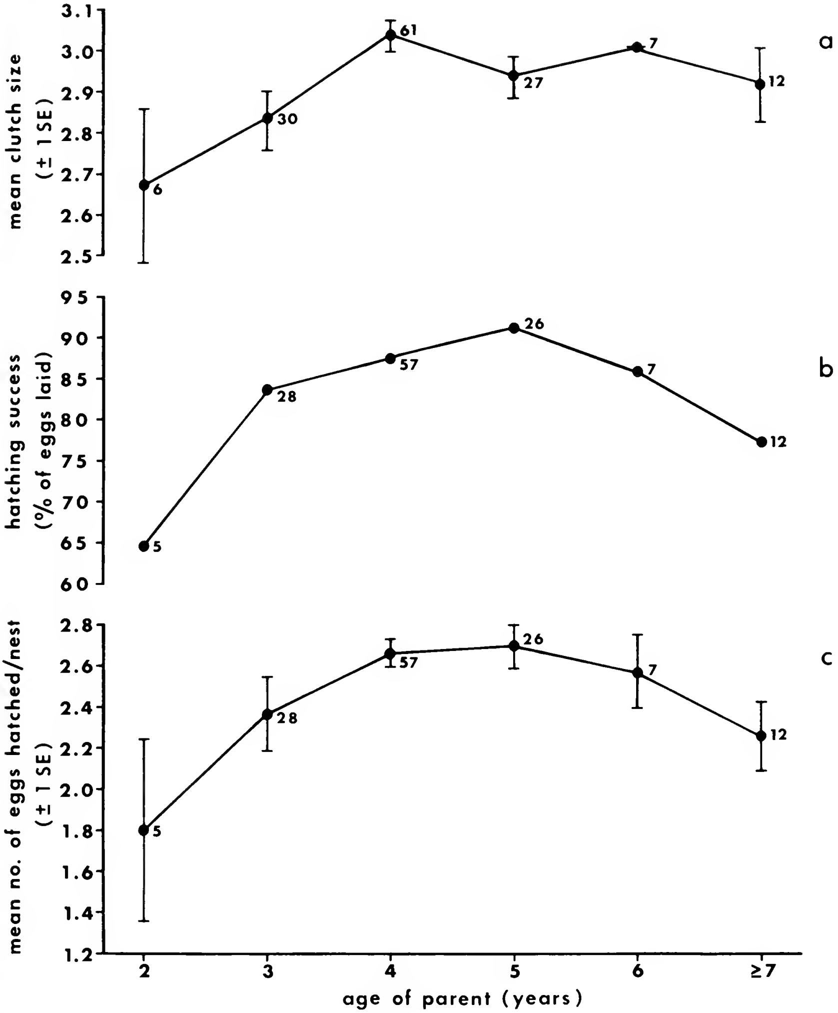


FIG. 2. (a) Mean clutch-size, (b) hatching success and (c) the mean number of eggs hatched per nest for Ring-billed Gulls of known age at the Eastern Headland, 1977. The numbers on the figures refer to the number of nests.

colony, laid eggs earlier in the season than gulls on the periphery. Consequently, we estimated the center of the colony as the geometric center of the clutches that were initiated by banded birds on or before 21 April (N = 14 and N = 11 in the 2 sub-colonies). The mean distance between nests and the center of the colony decreased as parental age increased

TABLE 1

NEST LOCATION, MEAN CLUTCH-SIZE AND HATCHING SUCCESS FOR YOUNG AND OLD RING-BILLED GULLS NESTING EARLY AND LATE IN THE SEASON, AT THE EASTERN HEADLAND, 1977

	Early[a]		Late[a]	
	≤3 years	≥4 years	≤3 years	≥4 years
Number of nests	9	76	23	13
Percent central (≤50 m of center)	11.1%[b]	72.4%[b,c]	13.0%	15.4%[c]
Mean clutch-size (±1 SE)	2.88 ± 0.10	2.95 ± 0.03	2.78 ± 0.09[d]	3.00 ± 0.00[d]
Hatching success	96.2%[e]	88.4%	73.4%[e]	84.6%

[a] See text.
[b] $P < 0.001$ (Fisher test).
[c] $P < 0.001$ (Fisher test).
[d] $P < 0.1$ (Fisher test).
[e] $P < 0.01$ (Fisher test).

(Fig. 1b). The Spearman rank correlation coefficient between age and distance from the center of the colony was significant ($r_s = 0.524$, $P < 0.001$).

The clutch-size of Ring-billed Gulls of known age at Leslie Spit ranged from 2–5 eggs. The mean clutch-size increased with parental age up to age 4 and then levelled off, or slightly declined (Fig. 2a). From ages 2–4, inclusive, there was a significant correlation coefficient ($r_s = 0.309$, $P < 0.005$).

The hatching success (the number of hatched eggs, expressed as the percentage of the total number of eggs laid) increased with parental age from 64.3% for 2-year-old birds to 90.9% for 5-year-old birds and then decreased to 77.1% for ≥7-year-old birds (Fig. 2b). The increase in hatching success with parental age from ages 2–5 was significant ($P < 0.02$, linear trend for proportions, Snedecor and Cochran 1967). The difference in hatching success between 5-year-old birds and ≥7-year-old birds was not statistically significant (NS, 2 × 2 χ^2-test with Yates correction for continuity, Siegel 1956).

The number of eggs hatched per nest showed a pattern similar to that of hatching success for the 6 age categories (Fig. 2c). There was a significant correlation between this measure of reproductive success and age from the 2-year-old through the 5-year-old categories ($r_s = 0.216$, $P < 0.025$). The decline in the number of eggs hatched per nest from ages 5–≥7 was significant ($r_s = -0.333$, $P < 0.05$).

Table 1 indicates the influence of parental age (≤3-years-old, ≥4-years-old) on nest location, clutch-size and hatching success during 2 different time periods. Clutch initiation dates were partitioned into an early period (on or before 1 May, the date when 75% of all banded birds had initiated clutches) and a late period (after 1 May). Only those nests for which information on all 4 parameters was available were used in this analysis.

In the early period the proportion of old (≥4-year-old) birds nesting centrally (within 50 m, the median distance of all banded birds, of the center of the colony) was significantly higher than that of young birds nesting near the center. In the late period that difference disappeared.

The mean clutch-size of young birds was less than that of old birds in both time periods, but the difference was not statistically significant in either case. The hatching success was similar for old and young birds in the early time period. However, the hatching success of young birds was significantly reduced in the late period, whereas that of old birds did not change significantly.

DISCUSSION

The walk-in traps caused no apparent damage to the incubating birds or their eggs. Captured Ring-billed Gulls returned to incubate their eggs a few minutes after being released.

The high proportion of young birds in our sample is probably not indicative of the actual age distribution within the colony. Although annual banding of Ring-billed Gulls on the Great Lakes has continued since the 1950's, the large banding programs conducted in 1972 and 1973 on the lower Great Lakes partially explain the large number of banded 4- and 5-year-old birds in 1977. In addition, Ludwig (1967) reported that band loss on Ring-billed Gulls becomes common after 5 years wear. Loss of bands, as well as annual adult mortality, explain the absence of banded birds more than 11 years old and the small proportion of banded birds over 6 years old. The oldest band read during this study was worn by the bird for 11 years. Several bands showed extensive wear, but only 2 bands on trapped birds were unreadable.

In this study we knew the age of only 1 bird per nest. A close correlation between the age of the male and that of the female in breeding pairs has been shown for the kittiwake (Coulson 1966) and the Arctic Tern (Coulson and Horobin 1976) and a weaker correlation was found for the Red-billed Gull, *Larus novaehollandiae*, (Mills 1973). We assumed that Ring-billed Gulls tend to have mates of about the same age. That assumption appears to be justified by the strong correlations we found between the age of 1 parent and several breeding parameters.

At Leslie Spit in 1977, Ring-billed Gulls consistently nested earlier in the season and closer to the center of the colony as age increased. These results are consistent with those of Ryder (1975) who found that pairs of Ring-billed Gulls containing 1 or 2 birds with immature plumage laid eggs late in the season and close to the periphery of the colony.

In studies of the influence of age on the breeding success of other larids, clutch-size and hatching success were found to increase with age (Coulson and White 1958, Chabrzyk and Coulson 1976). Our data showed that mean clutch-size of Ring-billed Gulls increases with parental age up to age 4 and then levels off. Hatching success and the number of eggs hatched per nest increased with parental age up to age 5. However, our data demonstrated a decline in hatching success and in the number of eggs hatched per nest in older (≥6-year-old) birds. To the best of our knowledge, a decline in reproductive success in old birds has not been reported for other larids. The data of Coulson and Horobin (1976) suggested a decline in clutch-size and egg volume in old (≥8-year-old) Arctic Terns, but no corresponding decline in breeding success.

The influence of age on the breeding parameters of gulls in an early and late laying period were addressed in this study. Young birds were found to nest away from the center of the colony regardless of the time of clutch initiation. This observed behavior may indicate an inability of young birds to establish territories among older birds and/or a difference in the time of first arrival on the colony. Old birds while nesting centrally early in the season, nest farther from the center late in the season, probably due to a lack of central nest-sites at that time.

Coulson and White (1961) found that young kittiwakes laid smaller clutches than did older birds and that birds of all ages laid smaller clutches late in the season. In our study the mean clutch-size of young Ring-billed Gulls was slightly below that of old birds, but only the mean clutch-size of young Ring-billed Gulls declined slightly in the late period.

The hatching success of early-nesting, young Ring-billed Gulls was as high as that of early-nesting old birds. Hatching success of young birds decreased significantly in the late period, whereas that of older birds did not change substantially. The reduction in hatching success in late-nesting young birds suggests that they were perhaps less able to cope with the problems of laying late than were older, more experienced breeders. Such problems may have included low density of breeding pairs, lack of synchrony (Parsons 1975, 1976), and increased human pressure (hikers, boaters, etc.) as the season progressed.

SUMMARY

The influence of parental age on the breeding biology of Ring-billed Gulls was studied on the Eastern Headland of the Toronto Outer Harbour in 1977. Ring-billed Gulls nested consistently earlier in the season and closer to the center of the colony as age increased. Mean

clutch-size increased with parental age up to age 4 and then levelled off. Hatching success and the number of eggs hatched per nest increased with parental age up to age 5. The data suggest a decline in hatching success and the number of eggs hatched per nest for birds that are more than 5 years old.

Young (2- and 3-year-old) Ring-billed Gulls tended to nest away from the center of the colony regardless of the date of clutch initiation. The mean clutch-size of young birds was slightly below that of old (≥4-year-old) Ring-billed Gulls both early and late in the season. Early in the season the hatching success of young birds was similar to that of old birds. Hatching success of young birds, but not of old birds, declined substantially in the late period.

ACKNOWLEDGMENTS

The Toronto Harbour Commission kindly allowed us to work on the Eastern Headland and supplied the field accommodation. We thank the following persons and institution for permission to use their banding data: A. Bunker, A. R. Clark, C. H. Richards and W. E. Southern, and the Long Point Bird Observatory whose banders included M. S. W. Bradstreet, H. Krug, R. Rogers, R. B. Sutherland, R. R. Tasker and D. V. Weseloh. K. Newell of the Population and Survey Division, Canadian Wildlife Service supplied the banding data. R. J. Prins assisted in the field. P. Angehrn drew the figures. H. Beznaczuk and G. E. J. Smith assisted with the statistical analysis. S. G. Curtis, J. E. Bryant and R. D. Morris commented on the manuscript.

LITERATURE CITED

BLOKPOEL, H. AND P. M. FETTEROLF. 1978. Colonization by gulls and terns of the Eastern Headland, Toronto Outer Harbour. Bird-Banding 49:59–65.

CHABRZYK, G. AND J. C. COULSON. 1976. Survival and recruitment in the Herring Gull, *Larus argentatus*. J. Anim. Ecol. 45:187–203.

COULSON, J. C. 1966. The influence of the pair bond and age on the breeding biology of the Kittiwake Gull, *Rissa tridactyla*. J. Anim. Ecol. 35:269–279.

———. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217:478–479.

——— AND J. HOROBIN. 1976. Influence of age on breeding biology and survival of Arctic Tern, *Sterna paradisaea*. J. Zool. (London) 178:247–260.

——— AND E. WHITE. 1958. The effect of age on the breeding biology of the Kittiwake, *Rissa tridactyla*. Ibis 100:40–51.

——— AND ———. 1961. An analysis of the factors influencing the clutch size of the Kittiwake. Proc. Zool. Soc. Lond. 136:207–217.

LUDWIG, J. P. 1967. Band loss—its effect on banding data and apparent survivorship in the Ring-billed Gull population of the Great Lakes. Bird-Banding 38:309–323.

MILLS, J. A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull, *Larus novaehollandia scopulinus*. J. Anim. Ecol. 42:147–162.

PARSONS, J. 1975. Seasonal variation in the breeding success of the Herring Gull: an experimental approach to prefledging success. J. Anim. Ecol. 44:553–573.

———. 1976. Nesting density and breeding success in the Herring Gull, *Larus argentatus*. Ibis 118:537–546.

RYDER, J. P. 1975. Egg-laying, egg size and success in relation to immature-mature plumage of Ring-billed Gulls. Wilson Bull. 87:534–542.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York, New York.

SNEDECOR, G. AND W. G. COCHRAN. 1967. Statistical methods. Iowa State Univ. Press, Ames, Iowa.

WEAVER, D. K. AND J. A. KADLEC. 1970. A method for trapping breeding adult gulls. Bird-Banding 41:28–31.

ONTARIO HYDRO, BIOLOGICAL RESEARCH SECTION, RC-15, 800 KIPLING AVE., TORONTO, ONTARIO M8Z 5S4, CANADA AND CANADIAN WILDLIFE SERVICE, ONTARIO REGION, 2721 HIGHWAY 31, OTTAWA, ONTARIO K1G 3Z7, CANADA. ACCEPTED 12 JAN. 1979.

Wilson Bull., 92(2), 1980, pp. 229–244

NICHE RELATIONSHIPS BETWEEN TURQUOISE-BROWED AND BLUE-CROWNED MOTMOTS IN THE YUCATÁN PENINSULA, MEXICO

JORGE E. OREJUELA

As part of an overall comparison of the ecology and behavior of the Turquoise-browed (*Eumomota superciliosa*) and Blue-crowned (*Momotus momota*) motmots in the Yucatán Peninsula (Orejuela 1975, 1977), I investigated niche relationships between the species. In that region the Turquoise-browed Motmot generally occupies the drier sites with lower vegetation in the periphery, whereas the Blue-crowned Motmot occupies the wetter and higher forests of the central core (Ridgway 1914, Paynter 1955, Klaas 1968, Orejuela 1977). Where the habitats merge or interdigitate there is overlap of the distributions. In recent years there has been a dramatic reduction in the high forest that is the preferred habitat of *M. momota* (Pennington and Sarukhan 1968), presumably allowing the expansion of *E. superciliosa* and increasing the areas of sympatry. This situation permitted study of niche-parameters in areas of both joint and exclusive occurrence of the respective species.

Various aspects of behavior and ecology of the 2 motmots have been dealt with elsewhere (Orejuela 1977). Among these, it is pertinent here to mention that, whereas *E. superciliosa* nests colonially in large, steep banks, *M. momota* nests solitarily in small, concealed banks.

In this study I examined use, by each species, of 3 different categories of resources: space, food, and time, on the assumption that interactions between species and important differences in niches would likely involve use of 1 or more of these (Pianka 1969, Schoener 1974).

STUDY AREAS AND METHODS

Habitat occurrence.—One aspect of spatial relationships is habitat occupation. To study characteristics of habitats, I examined vegetation in 2 areas in southern Campeche, 1 in the vicinity of Escárcega (18°37′N, 90°44′W) occupied preferentially by *E. superciliosa*, and the other in the Mayan ruins of Chicanná near Xpujil (18°30′N, 89°26′W) where *M. momota* occurs alone.

I selected 6 plots for vegetation sampling in each area, to encompass the variety of forest types in areas adjacent to the motmot nesting banks. In sampling the vegetation from 27 June to 2 July 1974, I generally followed the method of James and Shugart (1970), but used square quadrats, 10 m × 10 m. Variables measured were: (1) percent canopy cover = the proportion of an area covered by leaves viewed from below; in each quadrat, 20 vertical sightings were taken along 2 transects; at each sighting, I estimated the percent of the vegetation visible through a 30-cm tube held 0.5 m overhead; (2) canopy height = the height of the tallest trees within the quadrat; (3) density = the number of individual trees by species within the quadrat; (4) basal area = area covered by tree trunks within the quadrat, based on diameter-breast-height measurements of all trees greater than 2 cm dbh; and (5) number of shrubs and vines, counted on 2 perpendicular strips 2 m × 10 m within the quadrat.

Use of habitats.—To study habitat-related behavior, I observed birds in areas adjacent to the nesting banks. The frequency of performance of the behavioral activities in 4 different structural levels of the vegetation was estimated.

Interspecific behavioral interactions.—I made observations in 3 jointly occupied sites near Escárcega, 1 west and 2 east of town. The site west of town was characterized by a small patch of forest with trees averaging 15 m high in the area adjacent to a nesting bank. A larger patch of suitable habitat was located about 500 m away. The 2 patches of suitable habitat were connected by a strip of secondary forest about 6–10 m high. This corridor was the preferred foraging habitat of several *E. superciliosa*, while *M. momota* foraged mostly in the habitat adjacent to the nesting bank.

Diets.—A quantitative analysis of diets was done by stomach analysis. Twenty-seven *E. superciliosa* and 13 *M. momota* were collected in the rainy season in 1973. One hundred *E. superciliosa* and 32 *M. momota* were collected at approximately weekly intervals from late February to the end of July 1974.

Stomachs were preserved in 10% neutral buffered formalin; contents were flushed into Petri dishes and significant parts, such as heads, wings and legs were separated for indentification, counting and volume determinations. Estimates of volume of food items were obtained from comparisons of length or width measurements of significant fragments with measurements of these characters in a standard reference collection of insects of known volumes. Volumes of reference items were determined by the amount of water displaced in a graduated cylinder or in a 2-ml syringe. Data were converted to percentages of total numbers and total volume for better comparison. Identification of food items was carried to the family level.

SPATIAL RELATIONSHIPS

Table 1 shows major differences between those habitats where *E. superciliosa* and *M. momota*, respectively, were found at high densities. Low, open canopy and dense understory (many shrubs and vines) accompanied the high densities of *E. superciliosa*. These forests lost 60–80% of the leaves during the dry season. Conversely, high, dense canopy and open understory favored high densities of *M. momota*. Only 20–40% leaf drop occurred in the dry season in these forests.

The tree species diversity calculated from density values with the information theoretical measure (Shannon 1949) was slightly higher in habitats favored by *E. superciliosa* (H = 1.44) than in those favored by *M. momota* (H = 1.36). Most of the difference was accountable to greater tree species richness (51 species in habitats favored by *E. superciliosa*, and 40 species in habitats of *M. momota*). The overlap (Horn 1966) of tree species was 0.13. There were 21 species in common between habitats of high density of *E. superciliosa* and habitats of high density of *M. momota*.

Three of the plots selected for vegetation sampling, near Escárcega, were used exclusively by *E. superciliosa*, while the other 3 were used by both *E. superciliosa* and *M. momota*. There were considerable differences

TABLE 1

CHARACTERISTICS OF HABITATS WHERE *E. SUPERCILIOSA* AND *M. MOMOTA* OCCURRED AT HIGH DENSITIES

Variable	*M. momota*		*E. superciliosa*
Canopy cover ($\bar{x}$ [range]) (%)	73 (62–88)		58 (35–79)
Canopy height (m) ($\bar{x}$ [range])	21 (16–25)		14 (8–22)
Number of shrubs and vines ($\bar{x}$ [range])	66 (39–91)		80 (30–133)
Leaf drop (%)	20–40		60–80
Number of tree species	40		51
Tree species diversity[1]			
% numbers	1.36		1.44
% basal area	1.10		1.16
Tree species overlap[2]			
% numbers		0.23	
% basal area		0.13	
Most important tree species[3]			
Manilkara zapota	35	*Lysiloma bahamensis*	34
Unknown A	20	*Blephardium mexicanum*	19
Gliricidia sepium	18	*Dyospyrus spectabilis*	18
Unknown B	15	unknown C	12
Drypetes latirifolia	11	*Bursera simaruba*	9
Brosimum alicastrum	9	*Vitex gaumeri*	9
Talisia olivaeformis	8	*Cecropia peltata*	7
Bursera simaruba	8	*Cochlospermum vitifolium*	5
Ehretia tunifolia	5	*Metopium brownei*	4

[1] Based on Shannon's (1949) information theoretical measure.
[2] Based on Horn's (1966) overlap index.
[3] Importance value = relative density + relative basal area.

between these sets of habitats (Table 2). *E. superciliosa* habitats showed a significantly lower canopy cover ($t = 5.63$, df = 118, $P < 0.05$), lower canopy height ($t = 6.78$, df = 12, $P < 0.05$), and higher number of shrubs and vines ($t = 5.27$, df = 4, $P < 0.05$), than habitats where both species occurred. Canopy height in jointly occupied habitats was intermediate between exclusive habitats of *E. superciliosa* and *M. momota*. Of 51 different tree species in the 2 sets of habitats, 10 were present in both types of habitats. The tree species overlap (Horn 1966), calculated from species densities, was 0.33.

E. superciliosa appeared more flexible in habitat requirements than *M.*

TABLE 2

HABITAT CHARACTERISTICS OF AREAS OCCUPIED EXCLUSIVELY BY *E. SUPERCILIOSA* AND AREAS OCCUPIED BY BOTH *E. SUPERCILIOSA* AND *M. MOMOTA* IN THE VICINITY OF ESCÁRCEGA, CAMPECHE

Variable	*E. superciliosa/ M. momota*		*E. superciliosa*
Percent canopy cover ($\bar{x}$ [range])	75 (72–79)		42 (35–81)
Canopy height (m) ($\bar{x}$ [range])	17 (10–22)		11 (8–13)
Number of shrubs and vines ($\bar{x}$ [range])	45 (30–58)		114 (99–133)
Tree species diversity[1]			
% numbers	1.22		1.25
% basal area	1.03		1.04
Tree species overlap[2]			
% numbers		0.33	
% basal area		0.50	
Most important tree species[3]			
Lysiloma bahamensis	36	*Blephardium mexicanum*	34
Dyospyrus spectabilis	35	*Lysiloma bahamensis*	33
Unknown C	20	*Cecropia peltata*	14
Vitex gaumeri	17	*Bursera simaruba*	10
Metopium brownei	7	*Cochlospermum vitifolium*	9
Chrysophila argentea	7		

[1] Based on Shannon's (1949) information theoretical measure.
[2] Based on Horn's (1966) overlap index.
[3] Importance value = relative density + relative basal area.

momota. The former species was able to occupy low, partly deciduous forests with many shrubs and vines, as well as medium-stature, partly deciduous forests with few shrubs and vines. *M. momota* only occupied forests with few shrubs and vines, and preferred forests of medium-to-high height.

Use of habitats.—Table 3 shows differences in 3 main types of behavioral use of habitats. It appeared that *E. superciliosa* performed calling, preening and foraging at approximately the same level in the habitat; all were most frequent at tree level 1. *E. superciliosa* foraged considerably in forest-edge situations and a great portion of the food was obtained on the wing. *M. momota*, on the other hand, generally foraged in levels of the

TABLE 3

FREQUENCY OF BEHAVIORAL ACTIVITIES OF *E. SUPERCILIOSA* AND *M. MOMOTA* ACCORDING TO HABITAT STRUCTURE

	Ground		Shrub (1–5 m)		Tree level 1 (5–15 m)		Tree level 2 (15–25 m)	
Level	*E.s.*	*M.m.*	*E.s.*	*M.m.*	*E.s.*	*M.m.*	*E.s.*	*M.m.*
Behavior								
Feeding	xx[1]	xxx	xx	xx	xxx	x	—	x
Calling	—	—	xx	—	xxx	xx	x	xxx
Preening	—	—	xx	x	xxx	xx	x	xxx

[1] One, 2 and 3 x's represent rare, common and frequent performance, respectively.

vegetation different from levels where it preened and called. Foraging was common at tree levels 1 and 2. *M. momota* foraged mostly inside the forest.

Interspecific behavioral interactions.—At the nesting bank west of town, I witnessed many cases of interspecific hostility. *M. momota* repeatedly displaced and sometimes chased *E. superciliosa* whenever individuals of either of 2 pairs of this species approached the nest bank where the former had a nest. By this means, the *M. momota* eventually obtained exclusive rights to a bank 6 m wide.

The nesting banks in the sites east of Escárcega were rather large (15 m wide) and well-concealed. Adjacent to the nesting banks were large, semicircular open areas (50–75 m radius) bordered by forests 10–15 m high. Opposite the nesting banks there were large patches of tall forest (15–25 m). The lower forests were generally used by *E. superciliosa* and the taller forests by *M. momota*, although crossovers frequently took place. I observed very little interspecific aggression at these sites. Neither species seemed to react aggressively to the presence of the other, even when 1 species gave its species-specific call in the vicinity of a member of the other species.

The situation described in the sites east of town resembled what Cody (1974) labeled partial interspecific territoriality. It appeared that whenever there were sufficient suitable habitat patches and large, concealed nesting banks, the socially dominant *M. momota* reduced its aggression toward *E. superciliosa*. However, when the patches were too small or too far apart from each other or from the nesting banks, and/or the nesting banks were small and fairly open, interspecific aggression occurred. *M. momota*, in such situations, also displayed aggression toward Great Kiskadee (*Pitangus sulphuratus*), Social (*Myiozetetes similis*) and Boat-billed (*Megarhynchus pitangua*) flycatchers.

TROPHIC RELATIONSHIPS

When closely related species of birds overlap in distribution, competition for food is usually reduced by differences in prey size (Hespenheide 1966, Ashmole 1968, Ohlendorff 1974), different kinds of prey (Lack 1945, Holmes and Pitelka 1968, Baker and Baker 1973), and/or differences in foraging behavior (MacArthur 1958, Orians and Horn 1969, Snow and Snow 1971, Morse 1973).

Although abundance of prey populations was not measured, both motmot species were found to be principally opportunistic insectivores. Insects accounted for 93.7% by volume of the diet of *E. superciliosa* and 84.2% of *M. momota*; gastropods, arachnids, chilopods and plant reproductive parts were also consumed.

An overall comparison of the diets of *E. superciliosa* and *M. momota* revealed several major differences (Table 4). The contribution of hymenopterans and lepidopterans to the diet of *E. superciliosa* was considerable (26.1% of the total diet), whereas in *M. momota* these 2 taxa comprised only 4.2% of the total consumption. The percentages of coleopterans were 39.5% for *E. superciliosa* and 51.9% for *M. momota. E. superciliosa* consumed a substantially higher proportion of actively flying insects and a lower proportion of ground arthropods than *M. momota.* As an index of the breadth of the food niche I used the Shannon (1949) information theoretical measure. Prey diversity by volume was higher for *E. superciliosa* (H = 1.3) than for *M. momota* (H = 1.0). The richness factor of the diversity measure was higher for *E. superciliosa* (53 families) than for *M. momota* (37 families). Certain families might have been under represented because of the smaller sample size of *M. momota.*

The degree of specialization was calculated from the formula R = 1 − H/Hmax (Horn 1968). In this formula, H is Shannon's diversity measure and Hmax equals log of N (N = the number of categories). *M. momota* showed a greater degree of specialization (R = 0.39) than *E. superciliosa* (R = 0.27), when volume data were used. Overlap measurements based on families of prey taxa indicated an interspecific food overlap of 70%, based on Horn (1966).

There were marked seasonal changes in diets (Table 5, Fig. 1). Mean prey volume of *E. superciliosa* during the dry season was 0.3 ml. During the wet season, *E. superciliosa* took significantly larger prey ($\bar{x}$ = 0.4 ml) ($t = 3.17$, df = 316, $P < 0.05$). Particularly significant was the contribution of prey of volumes 0.5–1.0 ml. *M. momota* also consumed significantly larger prey in the wet season (0.6–1.2 ml; $t = 4.0$, df = 79, $P < 0.05$). There was a decrease in the diversity of prey taken during the wet season in both species.

TABLE 4

OVERALL COMPARISON OF THE DIET OF *E. SUPERCILIOSA* AND *M. MOMOTA*: NUMBER AND VOLUME OF FOOD ITEMS IN EACH FOOD CATEGORY

	Momotus momota			*Eumomota superciliosa*		
Taxonomic group	No.	% no.	% vol.	No.	% no.	% vol.
Gastropoda	15	9.5	0.9	12	2.0	0.6
Chilopoda	4	2.5	0.8	2	0.3	0.3
Diplopoda	4	2.5	3.8	—	—	—
Scorpionida	2	1.3	0.4	—	—	—
Araneida	7	4.4	1.6	4	0.7	1.2
Amaurobiidae	—	—	—	2	0.3	0.2
Dysteridae	1	0.6	0.1	—	—	—
Thomicidae	—	—	—	1	0.2	0.1
Lycosidae	5	3.2	1.1	—	—	—
?	1	0.6	0.4	1	0.2	0.9
Collembola	—	—	—	1	0.2	0.1
Odonata	—	—	—	2	0.4	0.2
Aeshnidae	—	—	—	1	0.2	0.1
?	—	—	—	1	0.2	0.1
Orthoptera	36	22.8	15.4	38	6.4	15.0
Acrididae	8	5.1	2.7	30	5.1	9.9
Tettigoniidae	8	5.1	8.7	1	0.2	0.5
Gryllidae	15	9.5	2.5	5	0.8	4.2
Mantidae	1	0.6	0.7	—	—	—
Phasmatidae	1	0.6	0.3	—	—	—
Blattidae	2	1.3	0.3	—	—	—
?	1	0.6	0.2	2	0.3	0.4
Mallophaga	—	—	—	2	0.3	0.1
Hemiptera	7	4.3	2.1	49	8.4	3.1
Gelastocoridae	—	—	—	1	0.2	0.1
Corizidae	1	0.6	0.6	—	—	—
Reduviidae	1	0.6	0.2	1	0.2	0.1
Largidae	—	—	—	1	0.2	0.1
Pyrrhocoridae	—	—	—	13	2.2	1.1
Coreidae	1	0.6	0.4	9	1.5	0.7
Pentatomidae	4	2.5	0.9	23	3.9	0.9
?	—	—	—	1	0.2	0.1
Homoptera						
Cicadidae	9	5.7	10.0	26	4.4	9.7
Coleoptera	57	36.0	51.8	241	40.3	39.7
Cicindelidae	—	—	—	5	0.8	0.4
Carabidae	8	5.1	4.7	8	1.3	1.9
Leiodidae	—	—	—	2	0.3	0.3

TABLE 4
CONTINUED

Taxonomic group	*Momotus momota*				*Eumomota superciliosa*		
	No.	% no.	% vol.		No.	% no.	% vol.
Silphidae	—	—	—		2	0.3	0.1
Cantharidae	1	0.6	0.4		2	0.3	0.1
Cleridae	—	—	—		2	0.3	0.1
Buprestidae	1	0.6	0.2		19	3.2	5.4
Nitidulidae	—	—	—		1	0.2	0.1
Tenebrionidae	1	0.6	0.7		5	0.8	0.7
Passalidae	—	—	—		5	0.8	2.4
Scarabaeidae	38	24.1	44.4		98	16.5	21.4
Trogidae	—	—	—		1	0.2	0.1
Cerambycidae	1	0.6	0.3		22	3.7	2.6
Chrysomelidae	—	—	—		8	1.3	0.6
Curculionidae	3	1.9	0.6		52	8.8	2.8
?	4	2.5	0.5		9	1.5	0.7
Lepidoptera	10	6.3	3.7		35	6.0	9.2
Papilionidae	3	1.9	1.1		14	2.4	2.7
Pieridae	—	—	—		—	—	—
Liparidae	3	1.9	1.1		—	—	—
Sphingidae	—	—	—		4	0.7	2.1
?	4	2.5	1.5		17	2.9	4.4
Diptera							
Asilidae	—	—	—		2	0.3	0.1
Hymenoptera	6	3.7	0.5		176	29.6	15.2
Braconidae	—	—	—		2	0.3	0.1
Chalcididae	—	—	—		1	0.2	0.1
Chrysididae	—	—	—		1	0.2	0.1
Mutillidae	—	—	—		12	2.0	2.7
Scoliidae	1	0.6	0.2		—	—	—
Formicidae	3	1.9	0.1		19	3.2	0.6
Vespidae	—	—	—		10	1.7	1.0
Sphecidae	—	—	—		2	0.3	0.1
Apidae	1	0.6	0.1		128	21.5	10.4
?	1	0.6	0.1		1	0.2	0.1
Reptilia	1	0.6	0.1		3	0.5	0.9
Monocotyledonea			0.1				—
Dicotyledonea			8.5				3.4
Total no. items	158				593		
Food diversity (no.)[1]		1.3				1.3	
Food overlap (no.)[2]				0.7			
Food diversity (vol.)[3]			1.0				1.3
Food overlap (vol.)[4]				0.7			

[1] Based on Shannon's (1949) information theoretical measure, and using number data.
[2] Based on Horn's (1966) overlap index, and using number data.
[3] Based on Shannon's (1949) information theoretical measure, and using volume data.
[4] Based on Horn's (1966) overlap index, and using volume data.

TABLE 5
COMPARISON OF SIZES OF PREY TAKEN BY *E. SUPERCILIOSA* AND *M. MOMOTA* IN THE YUCATÁN PENINSULA

Species	Size class of prey (cm)						
	≤0.24	0.25–0.50	0.51–0.75	0.76–1.00	1.01–1.50	1.51–2.00	>2.00
			Dry season				
E. superciliosa	75.2[1]	8.7	6.6	5.6	3.8	—	—
M. momota	33.3	32.0	2.7	10.7	18.7	2.7	—
			Wet season				
E. superciliosa	35.8	17.3	34.7	9.8	2.3	—	—
M. momota	19.3	25.0	11.4	5.7	18.2	12.5	8.0
			Overall				
E. superciliosa	53.6	13.4	22.0	7.9	3.0	—	—
M. momota	25.8	28.2	7.4	8.0	18.4	8.0	4.3

[1] Percent of number of items.

In the dry season there was smaller contribution of coleopterans to the diet of both motmots. During the dry season, the small contribution of coleopterans in *E. superciliosa* was compensated for by large proportions of orthopterans, hymenopterans (*Apis* spp.) and homopterans. The reduction in coleopterans in *M. momota* was compensated for by increased orthopterans and homopterans (mainly cicadas). In the wet season, large coleopterans (Scarabaeidae and Passalidae) and lepidopteran larvae were consumed by *E. superciliosa*. *M. momota* also increased intake of coleopterans (Scarabaeidae, Tenebrionidae), lepidopteran larvae and fleshy fruits. Greater detail on dietary composition is given by Orejuela (1975).

In the change from dry to wet season, there were reductions in orthopterans, homopterans and hemipterans in the diet of *M. momota*, and in hymenopterans in the diet of *E. superciliosa*. Large numbers of coleopterans were taken by both species in the wet season. The most significant differences in diet preference were observed during the dry season. At this time, both species broadened the spectrum of prey consumed.

Trophic morphology and behavior.—The interplay between morphology and behavior of a species imposes certain constraints on the kind and size of prey taken. Table 6 indicates differences in morphology and behavior between *E. superciliosa* and *M. momota*. These differences in trophic adaptations underlie dietary differences discussed above.

Body size differences were correlated with prey size. *E. superciliosa* consumed significantly smaller prey ($\bar{x}$ = 0.4 ml) than *M. momota* ($\bar{x}$ = 0.9

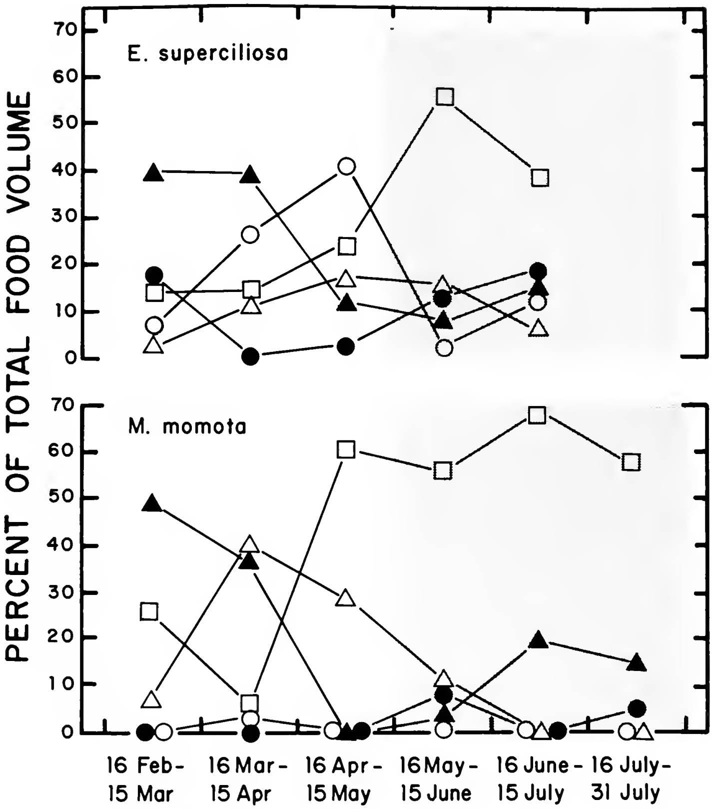


FIG. 1. Changes through time in the proportion of the most important food items in the diets of *E. superciliosa* and *M. momota*. Squares = Coleoptera, open circles = Hymenoptera, solid circles = Lepidoptera, open triangles = Hemiptera-Homoptera and solid triangles = Orthoptera. Stippled area indicates wet season.

ml) ($t = 5.51$, df = 345, $P < 0.05$). Differences in bill shape were also correlated with prey differences. Ashmole (1968) stated that long, light bills are particularly useful to species which capture active flying insects. The bill of *E. superciliosa* is long and light; it is also flat, wide and finely serrated. The diet of *E. superciliosa* showed a substantial amount of actively flying insects such as hymenopterans. The short, deep, narrow and deeply serrated bill of *M. momota* seems particularly suited for handling large insects, crushing mollusks and crushing seeds.

Differences in bill shapes have probably resulted from intense selection during the dry season when food was most likely to have been limiting. During the rainy season, both motmot species used the most abundant

TABLE 6

MORPHOLOGICAL AND BEHAVIORAL COMPONENTS OF THE FEEDING ADAPTATIONS OF *E. SUPERCILIOSA* AND *M. MOMOTA*

Components	*E. superciliosa*	*M. momota*
Morphological		
Body weight (g)	63.9 (N = 150)	110.4 (N = 45)
Bill shape[1]		
length (mm)	32.2	29.3
depth (mm)	10.0	11.8
width (mm)	11.5	9.4
serrations (no.)	45.7	10.9
depth/length	0.3	0.4
Central rectrix		
length (mm)	199	227
barbless section	long	short
Behavioral		
Sociality	colonial: group forager	territorial: solitary forager (pairs)
Flight pattern	short flights: flaps and glides: many flycatchings: maneuverable	long, straight flights: only flaps: few flycatchings: direct flight
Foraging tactic	sit-and-wait	widely foraging

[1] Measurements taken at nostril level.

and energy-rich prey (large coleopterans) irrespective of the divergent specializations of their bills.

"Sit-and-wait" and "widely foraging" (Pianka 1966) were the 2 important tactics used by motmots in capturing prey. *E. superciliosa* preferred the sit-and-wait tactic. The predator waited on a perch until a moving prey came close. A fast flycatching sally or short pursuit with a quick bill-snapping secured the prey. This foraging pattern undoubtedly furnished many small items to the diet. Its advantage lies in the economy of pursuit time and the small handling cost (Schoener 1971). *M. momota* favored a more widely foraging tactic. By means of rapid and direct flight, several patches were exploited in brief periods. The cost of this method lies in the search for suitable prey (Schoener 1971). For *M. momota* the energy return per large prey item presumably balances the high cost of searching and handling prey. This tactic was probably costly during the dry season when insect abundance was low, but very rewarding in the wet season.

TEMPORAL RELATIONSHIPS

The time of activity of motmots varied both daily and seasonally. During the dry season, both species confined their activities to the cooler times of the day: early morning and late afternoon. During the rainy season, temperatures were milder and more food was available; both motmots extended their activity periods to nearly all times of the day, although there was a tendency for greater activity during the morning.

Energetic consideration probably influenced the time of activity. *E. superciliosa* excavated their nest burrows in March, prior to the hottest months (April and May). In March, excavating activities were often performed during hot hours, but generally most work took place later in the afternoon. Skutch (1964) mentioned that "*M. momota* excavated during mid-day hours, in the rainy season when the climate was milder." The incubating parents spent the hottest hours inside the nest-tunnel, where the temperature was about 10°C cooler than ambient temperature. During the hottest hours, *E. superciliosa* sought cover under brushy areas, and *M. momota* sought shade under the tree canopy.

Activity periods were estimated from systematic observations. *M. momota* started its activity period before daylight and it was still actively foraging in the evening. It called until approximately 19:15. At this time, *E. superciliosa* was already roosting. The apparently small temporal separation of activities may have been an important factor in the differential use of resources between the motmot species. During the non-overlap period, *M. momota* may have had exclusive "rights" to many cicadas, millipedes and spiders, which constitute a significant portion of its diet.

DISCUSSION

Changes in resource use.—*E. superciliosa* and *M. momota* differed in their response to the seasonal changes by using different numbers of prey categories. A "food generalist" is a species using several prey categories with considerable frequency, whereas a "food specialist" is one using fewer prey categories (Morse 1971). There is strong selection for generalized diets in areas with considerable environmental fluctuations because of the unpredictability of resources (Orians 1972). Resource predictability varies both seasonally and between habitats. In Yucatán, resource uncertainty was highest during the dry season and in low partly deciduous forest types. Diets were more generalized in both species in the dry than in the wet season and in *E. superciliosa*, the inhabitant of the drier sites, than in *M. momota*. The greater relative food specialization of *M. momota* during the wet season might be due in part to its slightly greater body size. It is easier for a larger species to meet its energy demands during the favorable season by selecting fewer, but large items (Schoener 1971).

Variability of resources and the social system.—Gregarious and solitary existence are the 2 extremes of the range of social systems. The degree of sociality is influenced by seasonal fluctuations in food abundance, environmental predictability and availability of nesting sites (Crook 1965, Horn 1968, Brown and Orians 1970).

Brereton's (1970) study of parrots showed a tendency of solitary species to inhabit uniform, moist environments, while in arid regions there was a preponderance of gregarious species. There was a similar relationship between social system and environment in the 2 motmots: *M. momota*, the solitary species, lives in the more uniform, more moist environment, and the gregarious *E. superciliosa* inhabits the more unpredictable and drier habitats (Orejuela 1977).

The gregarious habit of *E. superciliosa* is enhanced by the selection of large, steep, and often high banks for nesting. Their nest-holes are naturally protected against most predators and the alarm signals of colony members may serve as an additional protection. Kruuk (1964) suggested that higher synchronization of breeding activities within a colony may decrease exposure time to predators. This may be the case with *E. superciliosa*. The general concealment of nests of *M. momota* may be the strategy by which solitary birds evade predators.

Interaction of niche parameters.—The totality of resources of an area may be partitioned in several ways. MacArthur and Levins (1964) suggested 2 general methods of niche specificity: (1) spatial separation through behavioral interaction; and (2) differences in resources because of structural specializations. The 2 motmots differed in both methods of niche specificity, and differences in use of space and food operated together to decrease the ecological overlap between the species. An idea of the overall interspecific niche overlap between *E. superciliosa* and *M. momota* was obtained by multiplying the mean interspecific niche overlap values for the 3 niche dimensions considered. Percent overlap values from 4 independent habitat measures (tree species diversity, canopy cover, canopy height and number of shrubs and vines) gave a mean spatial interspecific overlap value of 0.57. Percent overlap values from 6 measurements of trophic parameters (including numbers and sizes of prey during wet vs dry seasons as well as taxonomic composition of prey) gave a mean overlap value of 0.62. Temporal interspecific overlap was 0.95. Multiplication of the mean overlap values for the 3 dimensions gave a value of 0.33. There may be other independent dimensions that would tend to reduce interspecific overlap or increase the effective ecological distance between the competitors.

Because of differences in population sizes and in niche breadths between *E. superciliosa* and *M. momota*, the overlap affects them differently. Pianka (1969) suggested that interspecific competition should be more deleterious for the species with the smaller population size or with the narrower niche. Of the 2 species of motmots, *M. momota* had a smaller population size and narrower niche breadth in important dimensions (range of habitat types and diversity of diet) and thus might be expected to be at a disadvantage, even though it exhibits behavioral dominance over *E. superciliosa.*

Effect of man.—In the Yucatán Peninsula, extensive deforestation programs are being enacted, and the removal of already reduced tall forest (20-30 m) is an accelerating process, especially in the southern half of the peninsula. Agricultural and ranching zones are being carved out of the forest and a complete system of roads is under construction. The roads connecting the periphery with the newly opened central core of the peninsula provide avenues of invasion for opportunistic, colonizer species. Thus, the rapidly increasing demands for tolerance of habitat modification may first reduce, then even reverse, the competitive superiority of *M. momota* exhibited in interspecific hostile interactions. It is possible that *E. superciliosa* may restrict *M. momota* to a narrower range of habitats where they are together. If habitat modification goes even further, *E. superciliosa* may replace *M. momota* locally. A combination of factors may be involved in the habitat restriction and/or replacement: increased numbers of *E. superciliosa* because of increased availability of nesting banks, and the proliferation of low partly deciduous forest types; reduction of patches of medium-to-high partly deciduous forest in areas of overlap; increased predation on *M. momota* because of exposure of nesting areas; and exploitation competition by *E. superciliosa.* The last factor may operate similarly to the situation described by Stocker (1972) for voles (*Microtus* spp.). The subordinate species is present in much greater densities than the dominant species, and it may exploit the resources to the detriment of the dominant species, even if the dominant occasionally excludes subordinates.

SUMMARY

The motmots, *Momotus momota* and *Eumomota superciliosa*, were studied for possible competitive relationships in southern Campeche, Mexico, during parts of 1973 and 1974. Geographical and ecological distributions, nesting habits, food composition and feeding behavior were examined in each species.

The preferred habitats of *M. momota* were characterized by medium to high partly deciduous forest whereas *E. superciliosa* occupied fairly open forests of low partly deciduous aspect. The species displayed differences in the occupation of nesting habitats. *M. momota* nested solitarily in small nesting banks, while *E. superciliosa* formed nesting colonies in large steep banks. There were several cases of interspecific aggression at the nesting banks. At 1 site *M. momota* excluded *E. superciliosa*, but in another place both species nested in

the same bank. The diets of the motmots differed in kinds of prey, amounts of the same prey type, prey size, foraging behavior and, to a lesser extent, in time of foraging. *M. momota* foraged mostly on the ground where it generally obtained fewer but larger prey. *E. superciliosa* preferred small actively flying insects during the dry season and larger prey in the rainy season.

The accelerated habitat modification in the Yucatán Peninsula may affect *M. momota* more adversely than *E. superciliosa*, because of the former's greater habitat specificity, greater food specialization and smaller population density. *E. superciliosa* may even profit from man's activities; it can nest in exposed road banks and its preferred habitats are low, secondary forests which are proliferating rapidly.

ACKNOWLEDGMENTS

I extend special thanks to Dr. Ralph J. Raitt for providing advice and encouragement throughout the study. In addition, I wish to thank Señor Raul Narváez of Zoh Laguna, Señor Oscar Cedeño of Escárcega and Señor Felipe Osorio of Chicanná. I am grateful to my wife Kristin for her help with the fieldwork.

Financial assistance was provided by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and by the Society of the Sigma Xi through a Grant-in-Aid of Research.

LITERATURE CITED

ASHMOLE, N. P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). Syst. Zool. 17:292–304.

BAKER, M. C. AND A. E. BAKER. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecol. Monogr. 43:193–212.

BRERETON, J. LE G. 1970. A self-regulatory, density independent continuum in Australian parrots. M.S. paper given at Br. Ecol. Soc. Int. Symp. The scientific management of animal communities for conservation (E. Duffy and A. S. Watt, eds.). Univ. East Anglia, Blackwell Sci. Publ., Oxford and Edinburgh, United Kingdom.

BROWN, J. L. AND G. H. ORIANS. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239–262.

CODY, M. L. 1974. Competition and the structure of bird communities. Monogr. Pop. Biol. Princeton Univ. Press, Princeton, New Jersey.

CROOK, J. H. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. London 14:181–218.

HESPENHEIDE, H. A. 1966. The selection of seed size by finches. Wilson Bull. 78:191–197.

HOLMES, R. T. AND F. A. PITELKA. 1968. Food overlap among coexisting sandpipers on northern Alaska tundra. Syst. Zool. 17:305–318.

HORN, H. S. 1966. Measurement of overlap in comparative ecological studies. Am. Nat. 100:419–424.

———. 1968. The significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). Ecology 49:682–694.

JAMES, F. C. AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

KLAAS, E. E. 1968. Summer birds from the Yucatan Peninsula, Mexico. Mus. Nat. Hist. Univ. Kansas Publ. 17(14):579–612.

KRUUK, H. 1964. Predators and anti-predatory behaviour of the Black-headed Gull (*Larus ridibundus*). Behaviour, Suppl. 11.

LACK, D. 1945. The ecology of closely related species with special reference to the cormorant (*Phalacrocorax carbo*) and the shag (*Phalacrocorax aristotelis*). J. Anim. Ecol. 14:12–16.

MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

——— AND R. LEVINS. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proc. Natl. Acad. Sci. 51:1207–1210.

MORSE, D. H. 1971. The insectivorous bird as an adaptive strategy. Ann. Rev. Ecol. Syst. 2:177–200.

———. 1973. The foraging of small populations of Yellow Warblers and American Redstarts. Ecology 54:346–355.

OHLENDORFF, H. M. 1974. Competitive relationships among kingbirds (*Tyrannus*) in Trans-Pecos Texas. Wilson Bull. 86:357–373.

OREJUELA, J. E. 1975. Comparative ecology and behavior of Turquoise-browed and Blue-crowned motmots in the Yucatan Peninsula. Unpubl. Ph.D. thesis, New Mexico State Univ., Las Cruces, New Mexico.

———. 1977. Comparative biology of Turquoise-browed and Blue-crowned motmots in the Yucatan Peninsula, Mexico. Living Bird 16:193–208.

ORIANS, G. H. 1972. Ecoethological aspects of reproduction (discussion). Pp. 27–39 *in* Symposium on breeding behavior and reproductive physiology of birds (D. S. Farner, ed.). Denver, Colorado.

——— AND H. S. HORN. 1969. Overlap in foods of four species of blackbirds in the potholes of central Washington. Ecology 50:930–938.

PAYNTER, R. A., JR. 1955. The ornithogeography of the Yucatan Peninsula. Peabody Mus. Nat. Hist. Bull. 9.

PENNINGTON, I. D. AND J. SARUKHAN. 1968. Manual para la identificación de campo de los principales árboles tropicales de México. Inst. Nal. Inves. For. Mexico, D.F.

PIANKA, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. Ecology 47:1055–1059.

———. 1969. Sympatry in desert lizards (*Ctenotus*) in Western Australia. Ecology 50:1012–1030.

RIDGWAY, R. 1914. The birds of North and Middle America: a descriptive catalogue of the higher groups. U.S. Natl. Mus. Bull. 50.

SCHOENER, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369–404.

———. 1974. Resource partitioning in ecological communities. Science 185:27–39.

SHANNON, C. E. 1949. The mathematical theory of communication. Pp. 3–91 *in* The mathematical theory of communication (C. E. Shannon and W. Weaver, eds.). Univ. Illinois Press, Urbana, Illinois.

SKUTCH, A. F. 1964. The life history of the Blue-diademed Motmot (*Momotus momota*). Ibis 106:321–332.

SNOW, B. K. AND D. W. SNOW. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. Auk 88:291–322.

STOCKER, R. E. 1972. Competitive relations between sympatric populations of voles (*Mi-Crotus montanus* and *M. pennsylvanicus*). J. Anim. Ecol. 41:311–329.

DEPT. BIOLOGY, NEW MEXICO STATE UNIV., LAS CRUCES, NEW MEXICO 88003. ACCEPTED 12 JAN. 1979.

Wilson Bull., 92(2), 1980, pp. 245–246

GENERAL NOTES

Courtship feeding in some emberizine finches.—Courtship feeding is well known in cardueline finches (Lack, Auk 57:169–178, 1940; Newton, Finches, Collins, London, England, 1972), however, several authors have noted its apparent absence in the Emberizinae (Andrew, Ibis 103:315–348, 1961; Lemon, Can. J. Zool. 46:141–151, 1968). These authors were referring specifically to the buntings (*Emberiza* spp.) and New World sparrows (*Zonotrichia* spp., *Melospiza* spp.). We describe herein courtship feeding in several species of emberizine finches hoping that others will look for this behavior in this group so that we may more properly evaluate the distribution and significance of this behavior in finch taxa.

On 12 July 1978, we saw 4 instances of courtship feeding in the White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) at Tioga Pass, Mono Co., California. The first observation followed the appearance of a pair returning from a feeding bout. Together they perched on a small lodgepole pine (*Pinus murrayana*), within 15 cm of their nest, which contained 3 eggs in their tenth day of incubation. The female crouched and gaped while vibrating her wings. The male, with insects hanging from his bill, leaned over and placed some in the female's mouth. Upon returning to the nest, the female quickly settled down and turned her eggs. The male followed her, perched on the rim of the nest, reached over her right side and fed her a second time. He continued placing food in her mouth a third and fourth time, reaching over her and almost standing on her back. The male, chipping loudly, subsequently left the nest-site and flew to an adjacent willow (*Salix* sp.). We had also seen this male courtship feeding on 10 July during the incubation of the same clutch.

On 12 March 1976, at the Anza Borrego State Park, San Diego Co., California, a Black-throated Sparrow (*Amphispiza bilineata*) (the female?) making sharp chip notes flew onto a small rock. A second individual (the male?) flew toward the first and fed it with 1 thrusting motion. The female made swallowing movements, then both flew off. In contrast to the White-crowned Sparrow, no displays were seen before, or after courtship feeding.

Phillips (p. 909 *in* Bent, U.S. Natl. Mus. Bull. 237, O. L. Austin, ed., 1968) reported on 2 observations of "billing," or possibly courtship feeding in Rufous-winged Sparrows (*Aimophila carpalis*) in Arizona. Parmelee (pp. 1652–1677 *in* Bent 1968) reported that male Snow Buntings (*Plectrophenax nivalis*) frequently feed the female during egg-laying and incubation. Fairfield (pp. 1635–1652 *in* Bent 1968) observed a male Chestnut-collared Longspur (*Calcarius ornatus*) approach an incubating female with a bill full of insects, but apparently was frightened off by the close proximity of the blind. This was never observed again during many hours of watching, suggesting that the behavior was anomalous. Barlow (Kansas Ornithol. Soc. Bull. 11:2, 1960) reported "symbolic" courtship feeding in the Lark Sparrow (*Chondestes grammacus*) preceding copulation. Baptista (unpubl.) noted the absence of courtship feeding in Yellow-faced Grassquits (*Tiaris olivacea*), but regularly observed this behavior in the Melodius Grassquit (*T. canora*) (Baptista, J. F. Orn. 119:91–101, 1978). In the last species, courtship feeding may be preceded by song and display in the male and wing quivering in the female. Skutch (Pac. Coast Avif. 31:1–448, 1954; cited *in* Johnston, Kansas Ornithol. Soc. Bull. 13:25–32, 1962) noted that males of the Variable Seedeater (*Sporophila aurita*) and Buff-throated Saltator (*Saltator maximus*) fed the female at the nest. Maria Elena Pereyra (pers. comm.), Moore Laboratory of Zoology, noted that captive Black-crested Finches (*Lophospingus pusillus*) from Argentina regularly courtship feed. Lack (Occ. Pap. Calif. Acad. Sci. 21:1–158, 1945) and Orr (Condor 47:177–201, 1945) reported courtship feeding throughout courtship and incubation in several genera of Galapagos finches (*Geospiza*, *Certhidea*, *Platyspiza*, and *Camarhynchus*). Lack (1945) noted 1 instance of a pair of Vegetarian Tree-finches (*Platyspiza crassirostris*) passing food back and forth several times. Baptista (unpubl.) made several similar observations of *T. canora*.

Andrew (1961) reported this behavior as definitely absent in 3 species of *Emberiza*, *Melospiza melodia* and *Z. leucophrys*. Blanchard (Univ. Calif. Publ. Zool. 46:1–177) studied White-crowned Sparrows in great detail and did not report courtship feeding. The behavior described herein must be rare in this species. Miller and Miller (Caldasia 47:105, 1968) noted that males of the congeneric Rufous-collared Sparrow (*Z. capensis*) do not bring food to the female at the nest or elsewhere.

Courtship feeding may be more widespread among emberizines than previously thought. If confined to the nest-site, this behavior may be easily overlooked. The behavior may be rare in species from temperate regions but common in tropical forms; investigators should look for it.—EILEEN ZERBA AND LUIS F. BAPTISTA, *Moore Lab. Zoology, Occidental Coll., Los Angeles, California 90041.* *Accepted 15 Mar. 1979.*

Wilson Bull., 92(2), 1980, pp. 246–248

Cleptoparasitism by Ring-billed Gulls of wintering waterfowl.—Cleptoparasitism, or interspecific robbing of food, has been reported in several gull species, and was recently reviewed by Payne and Howe (Wilson Bull. 88:349–351, 1976). They reported Ring-billed (*Larus delawarensis*) and Bonaparte's gulls (*L. philadelphia*) stealing earthworms from Dunlin (*Calidris alpina*) and Black-bellied plovers (*Pluvialis squatarola*). Bent (U.S. Natl. Mus. Bull. 113, 1921) reported Ring-billed Gulls apparently trying to steal food from Red-breasted Mergansers (*Mergus serrator*). Kallander (Bird Study 24:186–194, 1977) reported piracy by Black-headed Gulls (*L. ridibundus*) on Lapwings (*Vanellus vanellus*), and Fuchs (Ibis 119:183–190, 1977) studied cleptoparasitism by Black-headed Gulls of Sandwich Terns (*Sterna sandvicensis*). The purpose of this note is to report observations of cleptoparasitism by Ring-billed Gulls of wintering waterfowl in the Texas Panhandle.

Interactions between Ring-billed Gulls and wintering waterfowl were observed at Buffalo Springs Lake (91 ha), 6.5 km east of Lubbock, Lubbock Co., Texas. Twenty-four hours of observation were conducted between 09:00 and 13:00 CST from 28 January to 4 March 1978. Observations were made by driving the lake perimeter and watching gulls and waterfowl with 8 × 50 binoculars.

Species and numbers of ducks on the lake varied considerably from day to day, with low numbers on days of high human activity (i.e., boating and fishing on the warmer, sunny days); 92% of the observations of cleptoparasitism were made on stormy, overcast days.

Pied-billed Grebes (*Podilymbus podiceps*), Western Grebes (*Aechomophorus occidentalis*), American Coot (*Fulvia americana*), Ring-billed Gulls and some ducks fed on small fish that were apparently abundant and easily caught. Seven species of anatinine ducks were present, with Pintail (*Anas acuta*), Mallard (*A. platyrhynchos*) and Green-winged Teal (*A. crecca*) in greatest abundance. Aythyinine ducks included Redhead (*Aythya americana*), Canvasback (*A. vaslisineria*), Lesser Scaup (*A. affinis*), Common Goldeneye (*Bucephala clangula*) and Bufflehead (*B. albeola*).

Fish stealing behavior of Ring-billed Gulls was of 2 types: the "air drop" and the "surface drop." The "air drop" started when a gull, flying over ducks, suddenly plummeted downward with partially folded wings toward a duck. At the last moment the gull extended its wings and settled on the water as the duck dived. The "surface drop" was observed approximately 90% of the time and began when a gull, sitting on the water near a duck, flew along the surface toward the duck. The gull then swooped downward as if to land on the duck's back. Gulls never actually contacted a duck as the duck always dived at the last moment. This is

TABLE 1
VICTIMS OF RING-BILLED GULL FISH STEALING

Species	Gull "drops"			Successful steals		
	male	sex?	female	male	sex?	female
Common Goldeneye	14		20	2		0
Common Merganser	1		12	0		0
Bufflehead	10		0	2		0
Lesser Scaup	6		4	1		1
Canvasback	0		4	0		1
Mallard	1		0	0		0
American Coot		3			3	
Total	32	3	40	5	3	2

similar to the food stealing behavior described by Bent (1921) for Ring-billed Gulls, and Sage (Br. Birds 48:117, 1955) for Black-headed Gulls. The steal was successful if the gull immediately picked up a small fish from where the duck had been sitting on the water.

Often 3–5 gulls sat near a diving duck and appeared to watch the duck closely. Gulls never sat among the anatinine ducks unless an aythyinine duck was present. When a gull flew toward a solitary duck, the duck waited until the gull was about to touch it before diving. This occurred even though it seemed apparent that the gull was flying toward the lone duck.

Of the recorded drops (Table 1), 55 of 75 occurred in a series of 2 or more. The gull dropped toward a duck, sat looking around until the duck surfaced, and then flew over and dropped toward it again; 6 consecutive drops by a gull on a female Common Goldeneye was the longest recorded series.

All but 4 incidents of cleptoparasitic behavior were upon diving ducks. The other victims were American Coots and a Mallard. The 3 American Coots victimized were feeding close to the shoreline when a gull flew over and landed nearby. One of the coots immediately dropped its fish, which was then eaten by the gull. On the other 2 occasions, coots flew with a gull in pursuit, dropping their fish while in flight as the gull approached. The gull landed and retrieved the fish. Gulls were not observed sitting near the coots for extended periods of time.

A male Mallard was observed picking up and dropping a small fish in the water. A gull flying 50 m from the Mallard flew toward the duck and performed an "air drop." The Mallard took flight with the fish in its bill as another gull joined in pursuit. An aggressive interaction took place between the 2 gulls and continued for 6 sec as the Mallard landed approximately 100 m away, still in possession of the fish.

The observed success rate of fish stealing by the gulls was 13.3% (Table 1). However, determination of success was difficult due to the speed with which gulls ate a stolen fish, and the generally intense activity at the site of the attack. Sixty percent of the thefts occurred in successive drops with gull aggression terminating upon the release of the fish by the victim.

Ring-billed Gulls commonly secured fish by skimming the water, or by landing to make the catch. At other times the same gulls "air dropped" or sat near ducks and engaged in fish stealing. Feeding gulls also fought among themselves for fish. One gull was observed to chase another for 30 sec in an attempt to steal a fish. No successful intraspecific fish stealing was observed, however.

Although 10 of the approximately 40 Ring-billed Gulls present during the observation period were in immature plumage, only 1 immature appeared to be "air dropping" onto ducks. As this immature gull flew 0.5 m above 1 male and 2 female Common Mergansers (*M. merganser*), the ducks dived, although the gull did not land.—JIM W. GRACE, *Dept. Range and Wildlife Management, Texas Tech Univ., Lubbock 79409.* *Accepted 20 Feb. 1979.*

Wilson Bull., 92(2), 1980, p. 248

Commensal foraging of Scissor-tailed Flycatchers with Rio Grande Turkeys.—During a 15-month study of Rio Grande Turkeys (*Meleagris gallopavo intermedia*) in southern Texas, Scissor-tailed Flycatchers (*Muscivora forficata*) were observed foraging in association with Turkeys on 4 separate occasions in April 1977 and in August in 1976 and 1977. All observations were made on the Welder Wildlife Foundation or Rooke Ranch in San Patricio and Refugio counties near Corpus Christi, Texas. Turkeys were common residents; scissor-tails were common spring and fall migrants and uncommon summer nesters.

Male and female scissor-tails foraged with flocks of 2, 8, 14 and 16 male and female Turkeys. Typically, scissor-tails foraged from low, exposed vegetation adjacent to feeding and/or walking Turkeys, whose movements repeatedly flushed grasshoppers and other insects. Foraging associations lasted 3–8 min and consisted of 1 or more passes over the moving Turkeys; no scissor-tail forays occurred over stationary Turkeys. The following is an example of 1 incident.

On 13 August 1977, at 18:55 CDT 8 adult male Turkeys, in single-file, actively fed in recently bulldozed mesquite-bristlegrass (*Prosopis glandulosa* and *Setaria* spp.). An adult male scissor-tail landed 1 m above the ground on a brush pile that was 2 m from the feeding Turkeys. After 15 sec, it flew over the Turkeys, caught a grasshopper that was flushed by the Turkeys, and returned to its perch. It then flew ahead of the Turkeys and perched at 2 m in a mesquite tree that was 5 m from the feeding Turkeys. As the middle of the Turkey flock passed the tree, the scissor-tail flew over the Turkeys and caught an unknown insect in the air. The scissor-tail then flew 20 m ahead of the Turkeys, landed briefly, flew back to the end of the line, and made 3 quick passes less than 0.5 m over the Turkeys' heads. On the third pass it caught a grasshopper. The Turkeys and scissor-tail were then frightened away by the observer's activities.

Feeding associations are reported among ducks, wading birds and other waterbirds (Siegfried, Ibis 113:236–238, 1971; Anderson, Wilson Bull. 86:462–463, 1974; Kushlan, Auk 95:677–681, 1978). In addition, North (Ibis 86:171, 1944) described a behavior similar to the scissor-tail/Turkey association in which he observed Carmine Bee-eaters (*Merops nubicus*) foraging from the backs of bustards (*Choriotis* spp.) as they walked through the grass flushing insects. W. C. Glazener and C. R. Watts (pers. comm.) have also observed foraging associations between scissor-tails and Turkeys on the Welder Refuge. However, my observations represent a commensal foraging association not previously described in the literature.

Financial support was provided by the Rob and Bessie Welder Wildlife Foundation. I am grateful to S. L. Beasom and L. D. Foreman for their editorial comments and to F. Rooke, Jr. and the Welder Refuge for providing study areas. Special thanks to W. C. Glazener for discussion of Turkey and scissor-tail behavior.—BRUCE W. BAKER, *Dept. Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, Texas 77843.* (Present address: *Bur. Land Management, P.O. Box 1869, Rock Springs, Wyoming 82901.)* *Accepted 10 Mar. 1979.*

Wilson Bull., 92(2), 1980, p. 249

Red-bellied Woodpecker predation on nestling American Redstarts.—On 3 June 1977, I was observing a nest of American Redstarts (*Setophaga ruticilla*) at the Patuxent Wildlife Research Center, Laurel, Maryland. The nest was shaded and supported by a tangle of grapevines hanging 7.6 m above the ground in an 18 m tree. The adult birds had been feeding 3 two-day-old young in the nest.

At 14:45, while both adults were absent, I watched a female Red-bellied Woodpecker (*Melanerpes carolinus*) fly to the nest, remove 1 nestling and depart with it. The parents returned just before the woodpecker returned. The woodpecker again carried off a nestling, seemingly unaffected by the scolding and mobbing of the adult redstarts. A few minutes later the woodpecker carried off the remaining nestling. Returning a fourth time, the woodpecker sat atop the nest tree for several minutes still being mobbed by the redstarts. When it left the male redstart followed. The female remained near the nest chipping loudly and moving around the nest. Several times she hopped into the nest and scratched with her feet. The male returned to the empty nest carrying food, ate it himself, and began chipping with the female. The whole episode took 20 min. I do not know whether the woodpecker was feeding its young.

Bent (U.S. Natl. Mus. Bull. 174, 1939) reported the Red-bellied Woodpecker to be omnivorous, eating many kinds of insects, seeds, berries and fruits. He did not mention predation on young birds. Conner (Auk 91:836, 1974) noted predation by a red-belly on Carolina Chickadee (*Parus carolinensis*) nestlings. The closely related Red-headed Woodpecker (*M. erythrocephalus*) is known to prey upon eggs and young of various hole-nesting species, including the Common Flicker (*Colaptes auratus*), Purple Martin (*Progne subis*), Eastern Bluebird (*Sialia sialis*) and Tufted Titmouse (*P. bicolor*) (Bent 1939). This is the first report of a woodpecker removing young from the nest of an open-nesting bird, and the second report of predation by the Red-bellied Woodpecker on young birds.—Doris J. Watt, *Dept. Zoology, Univ. Oklahoma, Norman, Oklahoma 73019. Accepted 1 Mar. 1979.*

Wilson Bull., 92(2), 1980, pp. 249–250

Nest predation by the speckled king snake.—Nest predation has been regarded as the greatest cause of nest mortality in open-nesting passerines (Lack, The Natural Regulation of Animal Numbers, Oxford Press, London, England, 1954). Some species have incurred as much as a 76% loss of nests due to predation (Best, Auk 95:9–22, 1978). It is often difficult to imagine how the more heavily depredated species manage to survive each year; with such a high degree of nest predation occurring annually, it seems that the actual act would be observed often. This is not the case. Pettingill (Living Bird 15:33–41, 1976) cited only 12 incidents that he and/or his students had seen during the preceding 35 years.

In early August 1973, a Dickcissel (*Spiza americana*) nest with four 6- to 7-day-old young was found in a lightly grazed prairie near Manhattan, Riley Co., Kansas. The nest was about 15 cm from the ground in an indigo plant (*Baptisia* sp.). A blind was placed within 30 cm of the nest in midmorning and was left vacant until 15:30 to allow the female attending the young to become accustomed to its presence. At that time, the blind was entered with a "go-away." After a tripod-mounted camera was positioned to record feeding behavior, the "go-away" left 1 of us (SF) in the blind. Within minutes the parent was attending the nestlings, seemingly undisturbed by photography.

After 1 h, a speckled king snake (*Lampropeltis getulus holbrooki*) approached the nest. Placing its head in the nest, it seemingly detected the nestlings. This pose lasted 1–2 sec. Then, as in a strike, the snake quickly threw its body over the nest preventing escape of the young. The female Dickcissel, now on a shrub at some distance gave several alarm notes. The snake took 1 young from the nest by encoiling and strangling it about the neck and upper body, holding the nestling about 15 cm from the nest while doing so. At the same time the snake swallowed another nestling by pulling it from the nest by its head and then ingesting it head foremost. These activities were photographed without apparent notice by the snake. When the photographer temporarily left the blind for a better view, the snake left the nest. At this point it had completely swallowed the 1 young bird and asphyxiated the other. The 2 remaining young immediately left the nest and the adult female (the adult male was absent during the entire episode) showed intense distraction behavior. She flew near the snake and within 60 cm of the photographer, chirping and falling with both wings down and spread. The snake departed, regurgitating the 1 nestling and leaving the strangled young hanging in the foliage. The female's distraction behavior then subsided and she appeared to lead the surviving young from the nest-site.

On 19 July 1978, a Red-winged Blackbird (*Agelaius phoenecius*) nest was found (by CF) on the Konza Prairie Natural Research Area, Geary Co., Kansas. The nest, 70 cm from the ground in a dense growth of *Apocynum sibiricum*, held 4 nestlings (1- to 3-days-old) and 1 egg (later found to be infertile). The nest was still intact on our next visit on the morning of 21 July. Later, at 13:47 of the same day, Facemire saw a speckled king snake at the nest. The snake, about 90 cm long, had one-third of its body supported by the nest, but not covering the nestlings to prevent escape as with the Dickcissel. As nestlings this young could not leave the nest, apparently the snake was not stimulated to pin them down with several body coils. The snake nudged and prodded each young bird with its head, and then began ingesting the smallest nestling head first. The snake returned to the ground before completely swallowing this nestling (which took 3–5 min). (Best [Auk 91:168–169, 1974] noted the same behavior in the blue racer [*Coluber constrictor*].) The snake then left the area. The nest was inspected immediately (by CF) and only 1 chick was missing. The next largest nestling had apparently been "tasted" as the natal down of the head and neck were wet with saliva.

The nest was visited again at 17:50 on 22 July. The eyes of the largest young had opened during the intervening 28 h, but there were no other changes. Next visited at 09:54 on 24 July, the nest was found empty, but otherwise undisturbed and presumably was depredated in our absence.

Pettingill (1976) and Best (1974) both reported nest predation by snakes of the genus *Lampropeltis*, but in addition to this being, as far as we know, the first record of direct observation of a predator at either a Dickcissel or a Red-winged Blackbird nest, it is seemingly the first record of nest predation by the speckled king snake.—CHARLES F. FACEMIRE, *Dept. Fishery and Wildlife Sciences, New Mexico State Univ., Las Cruces, New Mexico 88003* AND STEPHEN D. FRETWELL, *Div. Biology, Kansas State Univ., Manhattan, Kansas 66506.* (Present address CF: *Dept. Ecology, Ethology and Evolution, 515 Morrill Hall, Univ. Illinois at Urbana-Champaign, Urbana, Illinois 61801.*) *Accepted 29 Mar. 1979.*

Wilson Bull., 92(2), 1980, pp. 250–251

Screech Owl eats fish and salamander in winter.—On 17 February 1978, Rising picked up a freshly dead gray female Screech Owl (*Otus asio*) from along the Pennsylvania Turnpike, at Neffs, Lehigh Co., Pennsylvania. The owl (Royal Ontario Museum No. 130,693) had in its stomach the precaudal portion of a two-lined salamander (*Eurycea bislineata*) (identified by Schueler, and deposited in the Natl. Mus. Nat. Sci., Ottawa, Canada) as well as vertebrae and other parts of a 5–6 cm fish. The snout-vent length of the salamander was ca. 45 mm. Bent (U.S. Natl. Mus. Bull. 170, 1938) lists "salamanders" (no specific details) as among the foods taken by Screech Owls, although from his reports these constitute, at most, a minor and occasional portion of their diet. In a 30-year study of Screech Owl natural history in northern Ohio, VanCamp and Henny (N. Am. Fauna No. 71, 1975) did not find evidence of feeding on salamanders, though they did find that Screech Owls occasionally ate fish. At the time this owl was killed substantial snow cover extended as far south as southern Maryland and Delaware and had persisted for several weeks.

It had been thought until recently that northern *E. bislineata* hibernated in winter, but Ashton and Ashton (J. Herpt. 12:295–298, 1978) recently found that in southwestern Ohio salamanders remained active in streams until stream temperatures dropped below 7°C, when they moved into subterranean winter retreats where the water was above that temperature. The salamander taken by this owl must have been active at the time of its capture. The juxtaposition of it with fish remains in the owl's stomach suggests that it was in open water (Screech Owls are thought to capture aquatic prey at times, VanCamp and Henny 1975), perhaps near a spring or in a cave.—J. D. RISING, *Dept. Zoology, Univ. Toronto, Toronto, Ontario M5S 1A1 and Dept. Ornithology, Royal Ontario Museum, Toronto, Ontario M5S 2C6 Canada* AND F. W. SCHUELER, *Dept. Zoology, Univ. Toronto, Toronto, Ontario M5S 1A1 Canada.* *Accepted 27 Apr. 1979.*

Wilson Bull., 92(2), 1980, pp. 251–252

Marsh Hawks feeding on waterfowl.—We observed 3 instances of Marsh Hawks (*Circus cyaneus hudsonicus*) feeding on waterfowl, 1 in Manitoba in 1972 and 2 at Horicon National Wildlife Refuge, Wisconsin, in 1977. Marsh Hawks were abundant in both areas.

At 09:55 on 25 April 1972, at Marshy Point, Manitoba, Blohm flushed a female or immature Marsh Hawk from the remains of a freshly killed Pintail (*Anas acuta*) hen. The carcass was in a grassy area about 10 m from water. Feathers were strewn about, back muscles had been removed and the breast muscle was partially consumed. The visceral cavity was opened, and portions of the proventriculus had been eaten. Well-developed ovarian follicles indicated that the hen was in good pre-laying condition.

At Horicon, Livezey flushed a Marsh Hawk, either a female or an immature, from the carcass of a Blue-winged Teal (*A. discors*) hen at approximately 11:00 on 13 June 1977. The teal was located in a dense, unmowed alfalfa field where several species of ducks (Blue-winged Teal, Gadwall [*A. strepera*] and Pintail) nested during the season. The breast, viscera and parts of the neck had been removed. The remains consisted of the feet, sternum, head and wings.

Again, at Horicon on 12 October 1977, at 14:45, Van Dyke flushed a female or immature Marsh Hawk from the remains of a crippled Mallard (*A. platyrhynchos*) drake on a mudflat bordering open water and an extensive stand of softstem bulrush (*Scirpus validus*). This duck was an experimental bird in a study of crippling loss at Horicon, and its wing was known to have been broken, rendering the bird flightless. The carcass was decapitated, with the head and neck lying beside the trunk. The heart, esophagus, trachea, most of the liver and small portions of the lungs, neck and breast muscle were eaten. The warmth of the visceral remains, lack of dried blood and moistness of the lungs, eyes and nictitating membranes indicated a very recent death. The duck did not appear to be emaciated at the time of death.

Previous food studies have indicated that Marsh Hawks primarily prey on small rodents (McAtee, U.S.D.A. Circ. No. 370:26–28, 1935; Errington and Breckenridge, Am. Midl. Nat. 7:831–848, 1936; Bent, U.S. Natl. Mus. Bull. 167:85–87, 1937; Randall, Wilson Bull. 52:165–172, 1940; Hecht, Wilson Bull. 63:167–176, 1951; Weller et al., Wilson Bull. 67:189–193, 1955), although the diet has been known to include larger prey and carrion (Errington and Breckenridge 1936; Cruickshank, Auk 56:474–475, 1939; Randall 1940). Evidence from food studies also indicated that waterfowl eaten by Marsh Hawks were ducklings (Errington and Breckenridge 1936, Bent 1937, Hecht 1951) or crippled adults (Errington and Breckenridge 1936).

Bent (1937) described a Marsh Hawk that pirated a duck (species not included) from a Peregrine Falcon (*Falco peregrinus*). However, other workers have observed Marsh Hawks attack and, in some cases, kill adult or nearly-grown waterfowl. Griffiths et al. (Br. Birds 47:25, 1954) saw a female or immature Hen Harrier (*Circus c. cyaneus*) attack, pick up and then drop a European Wigeon (*A. penelope*) along the coast of Hampshire, England; and Paulson (pers. comm.) watched a female Marsh Hawk stoop repeatedly at an adult Blue-winged Teal in Wisconsin. The teal avoided injury by diving underwater at each approach of the hawk. Hammond (Auk 65:297–298, 1948) saw a Marsh Hawk, identified as a probable adult female, attack and kill an immature American Wigeon (*A. americana*) in North Dakota. This duck was fully feathered and thought to be capable of flight. Finally, Beske (pers. comm.) took an adult Blue-winged Teal with a trained female Marsh Hawk in Wisconsin. We feel that our observations support the notion that Marsh Hawks are capable of preying on adult waterfowl, although these instances appear to be rare.

We wish to thank Frances Hamerstrom, Robert A. McCabe and Stanley A. Temple for helpful comments on this manuscript.—ROBERT J. BLOHM, FRED VAN DYKE AND BRADLEY C. LIVEZEY, *Dept. Wildlife Ecology, 226 Russell Labs, Madison, Wisconsin 53706.* (Present address RJB: *Office of Migratory Bird Management, U.S. Fish and Wildlife Service, Laurel, Maryland 20811.*) *Accepted 20 Jan. 1979.*

Wilson Bull., 92(2), 1980, pp. 252–253

Detrimental effects of cecal defecation in winter roosting Willow Ptarmigan.—Willow Ptarmigan (*Lagopus lagopus*) roost in snow holes, presumably for protection from cold and predators. The following account illustrates that snow roosting can have detrimental effects that may lead to predation on Willow Ptarmigan.

On 31 January 1976, on Karlsøy Island, Troms Co., Norway (70°00′N, 19°55′E) 1 of our pointing dogs retrieved a live Willow Ptarmigan. The bird appeared to be in good health, except that the tips of 3 outer primaries of 1 wing were frozen together by a clot of frozen cecal excrement. The bird had been flushed while feeding, and being unable to fly was captured by the dog. On 27 December 1976, on an adjacent island, a second Willow Ptarmigan, with the tips of several primaries of 1 wing similarly frozen together, was captured by the dog. Both birds were autopsied and were apparently in good condition.

Both ptarmigan seemed to have contaminated their wing tips with cecal excrement while in snow roosts. Ptarmigan shift position slightly while roosting, as evidenced by the distribution of woody droppings and slightly enlarged roost chambers. If shifting occurred shortly after cecal defecation wing tips could conceivably become contaminated and eventually freeze.

Willow Ptarmigan apparently feed only during daylight hours and may spend more than 16 h in snow roosts during midwinter nights. Inclement weather may further prolong roosting times (Irving, Condor 69:69–71, 1967). Woody droppings are commonly found in evacuated snow roosts. The question of whether or not ptarmigan normally excrete cecal contents in snow roosts was raised. In the winter of 1977, 60 recently evacuated snow roosts were examined. Each contained woody droppings. Only 3 contained cecal excrement, which in each case lay uppermost on the pile of woody droppings, presumably having been excreted last. Quite frequently cecal excrement was found lying within several meters of recently evacuated snow roosts. Krafft (Viltet, Jegerforb. Viltunders. 51–59, 1952) found cecal droppings in only 2 of 55 Willow Ptarmigan snow roosts examined, and in 2 instances, cecal droppings were found in the exit tracks within 5 m of the opening. Thus, pasty cecal droppings, as opposed to woody droppings, are seldom excreted in snow roosts.

The frequency and timing of emptying of the cecum in wild Willow Ptarmigan and the closely related Rock Ptarmigan (*L. mutus*) are poorly documented. A majority of birds shot during April in central Alaska appeared to have emptied their ceca in the early morning. Some ceca showed evidence of being emptied, possibly for a second time, during the late afternoon (Gasaway, Comp. Biochem. Physiol. 53A:115–121, 1976).

Our observations suggest that cecal excretion among wild Willow Ptarmigan during the short days of subarctic midwinter normally occurs just after snow roosts are abandoned. The length of time spent in the roost may be 1 factor influencing the timing of cecal excretion. Occasionally, Willow Ptarmigan excrete cecal droppings in snow roosts, presumably when experiencing extreme conditions of short days and winter storms. This can result in frozen wing tips and may increase susceptibility to predation.

We wish to thank Dr. Hans Grav and Prof. Johan B. Steen for their review of the manuscript.—HOWARD PARKER AND INGOLF HANSSEN, *Inst. Medical Biology, Div. Wildlife Biology, Box 977, 9001 Tromsø, Norway.* *Accepted 19 Jan. 1979.*

Wilson Bull., 92(2), 1980, pp. 253–258

Observations on the life history of Willets on Long Island, New York.—Prior to 1966, Willets (*Catoptrophorus semipalmatus*) nested along the Atlantic coast north to New Jersey with an isolated population in Nova Scotia. In June 1966, 3 nests with eggs were found in salt marshes at Jones Beach State Park and at Tobay Beach, both in Nassau County on the western portion of the south shore of Long Island. These were the first known New York State nesting records (Davis, Wilson Bull. 80:330, 1968). The following year, the species had spread about 12 km eastward to Oak Beach, Suffolk Co., and by 1968 67 km further to Tiana Beach at Shinnecock Bay. The species is still increasing and spreading on Long Island; it is presumed that this population spread northward from the New Jersey coast. I began studying Willets at Shinnecock Bay in 1969.

General accounts of Willet behavior and nesting biology were given by Forbush (Birds of Massachusetts and Other New England States, Pt. 1. Mass. Dept. Agric., Boston, Mass., 1928), Bent (U.S. Natl. Mus. Bull. 146, Pt. 2, Washington, D.C., 1929) and Palmer (*in* Shorebirds of North America, G. D. Stout, ed., Viking Press, New York, 1967). The previously most intensive research on nesting Willets was reported by Tomkins (Wilson Bull. 44:46–47, 1932; 67:291–296, 1955; 77:151–167, 1965). The purpose of this paper is to report results obtained in a 10-year study of nesting Willets on Long Island.

Methods.—Willet nests were located by watching adults and searching the salt marshes. Adults were trapped on their nests with wire trip-step traps or occasionally captured with scoop nets. The average time needed to trap 23 adults on nests was 2 h and 25 min. I captured 20 adult males, 20 adult females and 1 bird of unknown sex, which included 23 new birds, 17 returns and 1 repeat. Four males and 6 females were caught with a scoop net and the rest by traps. One can usually approach to within 1.5–2 m before the incubating bird flies from the nest, provided that the non-incubating bird is not close enough to give the alarm. In such a case, the incubating bird usually left long before I could get near the nest.

Adults, eggs and newly-hatched young were weighed and measured. Older young could never be found. The location of each nest was recorded and distances between nests were measured. Attempts were made to obtain previous data on incubation period and methods of sexing adults. Data on earlier Willet returns and recoveries were obtained from the Bird-Banding Office.

Nesting area.—In 1968, 1969 and 1970, only 1 pair nested at Tiana. There were 3 nests in 1971 and 1972, 5 nests in 1974 and 7 in 1975. The nesting area was 3 km long and of varying width. Willets nest in salt marshes just barely above the high tide mark, but some nests are washed out by unusually high tides that may occur once a month. Nests are well concealed in short grass, about 20 cm high. Tomkins (1965) reported that Willet nests are normally at least 61 m apart, although he once found 2 nests within a paced distance of 13 m. At Tiana, 1 pair nested within 13 m of another nest and still another pair 28 m from an adjacent pair. All other nests were at least 60 m apart.

It is very difficult to find Willet nests before the 4 eggs are laid and the birds have started incubation. Out of 31 nests that I have found, 25 already contained 4 eggs and one, 5 eggs. Only 5 nests were found before the clutch was complete.

Banding.—The Bird-Banding Office reported that 1017 Willets were banded in North America from 1930–1972 with 19 returns and recoveries for the same period. Among returns were 5 young banded in western Canada, of which 2 were recovered in the same region, 1 in Missouri, 1 in Mexico and 1 in Costa Rica. An adult from the same area was also recovered in Mexico. A young banded in Georgia was recovered in French Guiana and an adult from Alabama in Guyana. Five adults banded in California were retaken there, mostly near the place of banding and in the same, or the following year.

From 1969–1978, I succeeded in banding 23 adults and 31 young and obtained 17 returns, all at Shinnecock Bay. Two of the returning birds were banded as young and the rest as adults. The young, both males, were recaptured as nesting adults 2 and 3 years after banding on nests 204 m and 365 m from their hatching spot. These are the only known cases showing that Willets return to nest near their place of hatching. It would appear from records of the Bird-Banding Office that no other bander has attempted to trap adults on their nests.

The 15 adults that returned were taken on nests from 30–112 m from a previous nest, usually the one of the preceding year. These 15 returns included 10 separate birds. Eight were retaken only once. One male, first banded on the nest in 1969, was retaken 5 times, the latest in 1977. A female banded in 1976 was retrapped in 1977 and 1978. Two of these birds apparently established age records for the species. The male banded in 1969 was at least 9 years old in 1977 (Fig. 1) and a male banded in 1971 was at least 4 years old in 1974.

Adults.—A primary purpose of this study was to determine if adult Willets could be sexed. After a few years experience with Piping Plovers (*Charadrius melodus*), I was able to sex nearly all adults by plumage and call notes. Likewise, over 16 years I was able to sex all but 2 of 89 trapped American Oystercatchers (*Haematopus palliatus*).

Little guidance on sexual differences was found in the literature. Bent (1929) stated that the sexes are alike. Forbush (1928) reported that the female is larger than the male, and Palmer (1967) called the sexes similar. Measurements of specimens in the National Museum of Natural History showed no sexual differences (Watson, pers. comm.). Tomkins (1965) collected 12 breeding birds (6 males and 6 females) and found females to average slightly larger than males. These specimens were located in the research collection of the University of Georgia. From the specimen data the 6 males averaged 219 g and the 6 females 283 g. It would seem that no one has previously weighed and measured mated pairs trapped on their nests.

FIG. 1. Oldest known Willet, a 9-year-old male retrapped on 27 May 1977.

Data from adult Long Island Willets caught on their nests are given in Table 1. At 11 nests where I caught both birds, the average wing length of males was 183.9 mm and of females 194.4 mm. Average tail length of males was 67.8 mm and of females 71.5 mm. Average bill length of males was 53.9 mm and of females 56.6 mm. Average weight of males was 211.1 g and of females 241.3 g.

Females exceeded males in wing length in all cases and in tail length in 10 cases. The other pair had tails of equal length. In bill length, the female was greater in 7 cases, equal in 2 and less in 2, but these 2 were the same pair caught in successive years. Females exceeded males in weight in 10 pairs. In the other pair, the male weighed slightly more than the female. All female weights were taken after egg-laying was complete.

No overlap in wing length occurred within mated pairs, although a small amount of overlap occurred within the population (Table 1). Slight overlap was found in tail and bill length, but only the heaviest male slightly exceeded the lightest female in weight. Thus, it appears that most specimens, and nearly all mated pairs, can be sexed by size and weight.

As is obvious from the capture data, both sexes shared in incubation, but brood patches were not found on either sex. As shown in Table 1, 2 pairs remained mated for 2 years.

Eggs.—All complete clutches contained 4 eggs, except 1, which contained 5. Tomkins (1965) mentioned 2 sets of 5 taken by an earlier collector. Measurements of 66 eggs varied from 36.5–40.0 mm by 49.5–57.0 mm and averaged 38.0 × 53.5 mm. Weights of the same 66 eggs taken at various stages of incubation ranged from 31.5–44.4 g and averaged 38.5 g.

Weights of eggs in 9 clutches, whose date of hatching was known, were plotted as a function of days before hatching. The regression line of best fit drawn by eye suggested an average weight loss of about 0.2 g per day during incubation. This would give a weight loss of about 5 g during the incubation period and would account for about half of the variation in weight found. The remainder can be accounted for by variation in size of the eggs. Tomkins

TABLE 1
MEASUREMENTS AND WEIGHTS OF ADULT WILLETS CAPTURED ON THEIR NESTS

	Male					Female				
Year	Band	Wing (mm)	Tail (mm)	Bill (mm)	Weight (g)	Band	Wing (mm)	Tail (mm)	Bill (mm)	Weight (g)
					Mated pairs					
1971	1063-73835	183	66	52	206.2	983-01457	191	72	55	229.2
1972	1063-73835	185	67	53	215.6	983-01457	194	72	56	261.3
1975	1063-73835	185	68	53	213.0	1233-18872	193	72	57	236.3
1974	983-01456	180	69	50	203.0	1233-18868	197	72	57	223.2
1975	983-02824	181	65	56	213.0	1233-18870	195	69	56	246.2
1973	1003-69169	187	70	52	210.7	1003-69167	196	70	58	263.3
1974	1233-18856	190	69	57	211.8	1233-18855	196	75	55	249.0
1975	1233-18856	185	69	57	211.6	1233-18855	197	74	55	240.7
1975	1233-18865	179	69	54	211.6	1233-18887	192	73	59	240.6
1975	1233-18871	183	68	52	207.2	1233-18873	190	69	58	247.6
1974	1233-18867	185	66	57	218.2	1233-18866	197	68	57	217.2
	$\bar{x}$ (11)	183.9	67.8	53.9	211.1	$\bar{x}$ (11)	194.4	71.5	56.6	241.3
				Birds whose mates were not caught						
1969	1063-73835	186	66	51	199.0					
1970	1063-73835	189	68	53	206.4					
1977	1063-73835	181	67	53	202.5					
1971	983-01456	177	69	51	202.1					
1975						1233-18868	198	74	56	221.0
1972	1003-69408	174	66	54	204.2					
1973						1003-69168	190	73	55	226.5
1974	1233-10865	181	66	53	208.3					
1976						1013-34768	191	69	56	244.8
1977						1013-34768	188	67	54	231.8
1977						733-94555	191	71	58	236.5
1977						1013-34268	194	71	58	257.7
1978	1013-35012	186	63	53	200.9					
1978	1013-35029	182	68	54	203.6					
1978						733-94555	188	73	57	244.1
	$\bar{x}$ (8)	182.0	66.6	52.8	203.4	$\bar{x}$ (7)	191.4	71.1	56.3	237.5
	$\bar{x}$ (19)	183.1	67.3	53.4	207.8	$\bar{x}$ (18)	193.2	71.3	56.5	239.8

(1965) weighed 1 clutch frequently throughout a 29-day incubation period and found an average loss of 4.5 g.

Weights of 12 complete clutches of 4 eggs each were compared to the weight of the female after laying. Clutch weight ranged from 57.8–73.6% of the female weight and averaged 64.9%. The range in these values is attributed to the stage of incubation at which the eggs were weighed and to the condition of the female when captured. Tomkins (1965) found a similar value, 65%, for a single clutch.

FIG. 2. Willet egg and newly-hatched young.

Incubation period.—The incubation period of the Willet was given as 21–23 days by Sprunt and Chamberlain (South Carolina Bird Life, Univ. S. C. Press, Columbia, S. C., 1949) and 22 days by Palmer (1967). Bent (1929) gave no information. Tomkins (1932) reported the period as 24–25 days based on only 1 clutch. Subsequent observations (Tomkins 1965) gave 22–29 days, but the longest period was apparently due to frequent weighing of the eggs, which kept the adults off the nest for longer than normal periods. I have an incubation period of 27 days for 1 clutch and 32 days for another, but the latter is certainly longer than normal, as the birds were kept off the nest for too long periods. Thus, the incubation period seems to range from 21–29 days, or less.

Hatching dates obtained for 9 clutches range from 9–19 June. Assuming an average 24-day incubation period, most clutches were apparently completed between 16 and 26 May.

Young.—The eyes of newly-hatched young (Fig. 2) are very dark brown, almost black, similar to those of adults. The young remain in the nest only a few hours, leaving after all are dry. Weights of 25 newly-hatched young from 7 nests varied from 23.6–30.6 g and averaged 28.0 g. For 3 nests in which all the eggs and young were weighed, the young averaged 70.9% of the egg weights. Tomkins (1965) gave 22.5 g as the weight of a single chick.

Willet young are difficult to find from the time of leaving the nest throughout the growing period. I have never been able to find young after the day of hatching. Possibly, the adults carry them away from the nest area. Wayne (Birds of South Carolina, Contrib. 1, Charleston Museum, Charleston, S. C., 1910) reported an observation in which he watched an adult carry the 4 young, 1 at a time, at least 440 yd. If I had not trapped both adults and the young had just hatched, I usually tied the young to a stake and placed the trap over them in order to capture the adult. In one instance, I placed the trap over a brood of young, but neglected to tie them down. I went back in 1 h and the young were 23 m from the nest. I have never been able to find young at a greater distance than this from the nest, nor any young more than 1 day old, consequently, no weights or measurements during the growing stage have been obtained. This is in sharp contrast to young Piping Plovers which I could find almost anytime, up until flight (32 days). Young oystercatchers could also be found readily until flight stage (41 days).

Acknowledgments.—This paper was very kindly updated (1978 data) and revised by Gilbert S. Raynor on behalf of the late LeRoy Wilcox. All inquiries or reprint requests should be directed to him as follows: MR. GILBERT S. RAYNOR, SCHULTZ ROAD, MANORVILLE, LONG ISLAND, NEW YORK 11949.—LEROY WILCOX (deceased), *Oceanic Duck Farm, Speonk, Long Island, New York 11972.**Accepted 15 Mar. 1979.*

Wilson Bull., 92(2), 1980, pp. 258–260

Unusual egg deposition in Mourning Doves.—The Mourning Dove (*Zenaida macroura*) is a determinate layer with a genetically controlled clutch-size of 2. Hanson and Kossack (Ill. Dept. Conserv. Tech. Bull. 2, 1963) mentioned no larger clutches in their extensive work, yet Harrison (A Field Guide to Birds' Nests, Houghton Mifflin Co., Boston, 1975) records clutch-size as "2, occasionally 3, rarely 4." Other workers have at times recorded >2-egg clutches, and both Quay (Mourning Dove Studies in North Carolina, Game Div., N.C. Wildl. Res. Comm., 1951) and Moore and Pearson (The Mourning Dove in Alabama, Ala. Coop. Wildl. Res. Unit, 1941) questioned the origin of the additional eggs in the cases they observed, i.e., whether they were produced by 1 or more females. Nice (Auk 39:457–474, 1922) found 3 nests that contained more than the normal clutch, and cited 8 previous reports of 4-egg clutches and 40 of 3-egg clutches.

In a study of nesting ecology and nest-site selection in Mourning Doves on Purdue Wildlife Area (PWA), Tippecanoe Co., Indiana, I examined 106 nests in 1975 and 228 in 1976, most in plots of deciduous shrubs or pine (*Pinus sylvestris*, *P. resinosa* and *P. strobus*). I found several >2-egg clutches and some other instances of abnormal egg deposition in doves that should help explain the origins of extra eggs.

Early March 1976 was exceptionally warm with daytime temperatures often above 15°C and night temperatures about 5°C; several nestings were initiated during this period. Colder weather returned in mid-March with highs just above freezing and lows to −8°C, followed by moderating temperatures in late March with lows only occasionally falling below 0°C. During this period, several intact or freshly broken (not punctured) eggs were found beneath pines many meters from the nearest nest. Although not previously described for Mourning Doves, these layings were apparently adventitious, perhaps resulting from warm weather initiation of follicular development and intervening cold weather having a depressing effect on nest-building and associated behavior. Nesting by doves is delayed in exceptionally cold springs (Hanson and Kossack 1963).

As elsewhere, doves frequently used old nests of other birds on PWA, usually adding some nesting material (McClure, Iowa Agric. Exper. Stat. Res. Bull. 310:355–415, 1943; Hanson and Kossack 1963). In 3 instances, however, single eggs were deposited in nests of other species without addition of nesting material. One of these, an old American Robin (*Turdus migratorius*) nest, was unoccupied when the egg was laid about 29 April 1975. However, the other 2 nests were active at the time of laying. On 17 April 1976, a dove was flushed from a Common Grackle (*Quiscalus quiscula*) nest containing 1 fresh dove egg. The nest was under construction and the egg rested on wet mud and organic matter. The egg was gone the next day and on 24 April the nest contained 3 grackle eggs. On 9 May 1975, a female Cardinal (*Cardinalis cardinalis*) was flushed from a nest containing 1 Mourning Dove egg and 3 Cardinal eggs, all fresh. No additional eggs were deposited, and the nest was taken by a predator on 13 May. This nest was in a small eastern white pine only 66 cm above ground, much lower than other dove nests found in conifers. Holcomb (Wilson Bull. 79:450–451, 1967) and Nice (1922) also reported dove eggs in nests of other species. Nice's (1922) observations differed from my cases and those of Holcomb (1967) in that the dove was incubating and a pair of dove eggs was present.

I found 4 nests in 1976 that contained 3 eggs (1.8%), a somewhat higher rate than the 0.5% found in other studies (Moore and Pearson 1941, Quay 1951). In the first nest, which was 1.5 m high in a eastern white pine, the adult dove was incubating 2 fresh eggs on 10 April. On 14 April, a third egg appeared in the nest and by 26 April the nest contained 1 egg and 2 two-day-old chicks. The third egg hatched on 28 April but the very small young had disappeared by 2 May. The second nest, about 6 m high in a blue spruce (*Picea pungens*), had obviously been abandoned when found on 12 April. Two eggs had been incubated approximately 6 days but the third was translucent. A third nest, found on 15 June, about 2.5 m high in autumn olive (*Elaeagnus umbellata*), contained 2 eggs incubated about 4 days; an adult was present. On 16 June, this nest was unattended but contained a third translucent egg. The nest still contained 3 eggs on 18 June and was obviously abandoned. The fourth nest was 2 m high in an autumn olive and contained 2 eggs on 15 July. Another egg was added shortly before or after the first 2 hatched, between 23–28 July. The third egg never hatched and had disappeared from the nest by the time the young fledged on 10 August.

Both in these occurrences and in the literature of 3-egg nests, the usual sequence of events has the third egg deposited substantially later than the first 2 (Nice 1922, Moore and Pearson 1941). I believe that all 3-egg nests result from the addition of an egg by a second bird rather than a dove laying a 3-egg clutch. Whitman (The Behavior of Pigeons, Vol. III, Carnegie Inst., Washington, D.C., 1919) and Klinghammer (pers. comm.) found no cases where captive doves laid >2-egg clutches. I think the phenomena of adventitious laying, egg deposition in nests of other species, and apparent 3-egg clutches are all an expression of the same physiological-behavioral complex, with the first 2 helping define the latter.

Egg-laying occurs shortly after nest completion in the Mourning Dove (Moore and Pearson 1941) and there are times that, because of weather circumstances or nest destruction, no nest exists to receive an egg. Faced with this situation, a dove may simply drop the egg; or it may deposit it in the nearest available nest, occasionally that of another species. This latter response is undoubtedly enhanced by frequent use of old nests of conspecifics and other species by doves in normal nesting activities. Egg deposition in dove and non-dove nests in most likely in unattended, abandoned, or old nests, although Swank (Ecology 36:495–505, 1955) found that once incubation has begun, defense by doves of territory near the nest is practically eliminated. It is doubtful that females depositing superfluous eggs ever attempt to incubate these eggs, for lack of prior behavioral interaction between male and female at this "new" site would probably make site fidelity and incubation coordination unlikely.

Since occasionally 3 eggs are laid sufficiently close to allow fledging of 3 young (Nice 1922), nest depositing behavior may have some selective advantage over simply dropping the egg. Balanced against this potential of rarely producing 3 fledgings is the potential disrupting effect of a third (or fourth) egg in the nest. Two of my 4 three-egg clutches were abandoned, confirmed by repeated visits and extended observations. In general, nest abandonment was rare (2.7% for both years combined). I do not know whether the additional egg caused abandonment or whether the nest was abandoned prior to deposition of the third egg. Holcomb (Wilson Bull. 80:105, 1968) found addition of icterid (*Molothrus* and *Agelaius*) eggs to 6 Mourning Dove nests caused no abandonment.

Four-egg nests are apparently even less common than 3-egg nests, although a few have been recorded (Nice 1922, Moore and Pearson 1941). All accounts, including mine, indicate that this is a different phenomenon than that involved in previously discussed observations. On 29 March 1975, I flushed a bird from a nest containing 2 opaque eggs that was 2.25 m high in a red pine. By 15 April an adult evidently had been killed at the nest, but the nest and 2 eggs remained intact. On 26 April a bird was flushed from the same nest which then contained 4 eggs; the 2 newest were about 6 days incubated. All eggs were subsequently taken by a predator. This is undoubtedly the sequence in similar situations where 2 of the 4 eggs were addled or a dove was incubating 2 of its own eggs in addition to those of another species in that species' nest (Nice 1922). Although neither has been reported from wild doves, other possible reasons for 4-egg nests include polygyny or female homosexuality. In none of the reported incidences was irregular incubation behavior evident as would probably be the case in either of these instances (Nice 1922).

I am indebted to Mary E. Clawson and Mark E. Obringer for assistance in nest searches. Erich Klinghammer and Charles M. Kirkpatrick made helpful comments on the manuscript for which I am appreciative. This is Journal Paper No. 6986 from Purdue Agricultural Experiment Station.—Harmon P. Weeks, Jr., *Dept. Forestry and Natural Resources, Purdue Univ., West Lafayette, Indiana 47907.* *Accepted 1 Mar. 1979.*

Wilson Bull., 92(2), 1980, pp. 260–261

Female Sharp-tailed Grouse copulates with Greater Prairie Chicken in Minnesota.—Sharp-tailed Grouse (*Pedioecetes phasianellus*) × Greater Prairie Chicken (*Typanuchus cupido pinnatus*) hybrids have been recorded in practically all areas where the 2 species are sympatric (Ammann, The Prairie Grouse of Michigan, Mich. Dept. Conserv., Lansing, Michigan, 1957). We could find no published account of a copulation between the species, although there are at least 5 records in Wisconsin from 1947 through 1960 (Hamerstrom, pers. comm.) of a female sharptail copulating with a prairie chicken. Such a mating was also observed on a lek in Minnesota in 1977 and is reported here.

Observations from blinds were made at leks associated with the 575-ha Pembina Trail Preserve, 24 km southeast of Crookston. The primary lek ("Pembina") under observation had 18, 15 and 19 regular male prairie chickens in 1975, 1976 and 1977, respectively. A sharptail lek, 4.8 km from the Pembina lek, had 10, 11 and 7 males in 1975, 1976 and 1977, respectively. In 1977, a new sharptail lek with 3 males was established 400 m from the Pembina lek.

In the spring of 1975 we observed on the Pembina lek: 1 visit by a displaying hybrid male, several irregular visits by a displaying sharptail male, and a hybrid female copulating with a prairie chicken. In the spring of 1976 a sharptail male defended an exterior territory. In the spring of 1977 a hybrid male defended an exterior territory.

On 20 April 1977, TJK was in a blind on the Pembina lek. From 05:00–06:00 18 male and 4–6 female prairie chickens were present. Three copulations were observed. At 06:25 a prairie chicken and sharptail female walked onto the lek from the direction of the new sharptail lek. Both females came within 15 m of the blind, which allowed good comparative observations. The sharptail was noticeably lighter, had no pinnae, but did have distinct V-barring on the breast and the tail was pointed with white margins. At 06:50 the sharptail female walked directly to a centrally located prairie chicken male, crouched in a receptive posture and the male immediately mounted and copulated. There was little preliminary display close to the female prior to mounting. After the male dismounted, the female shook her feathers and by 07:00 had left the lek.

On the same morning WDS watched from a vehicle the new sharptail dancing ground and at 05:20 recorded 3 sharptail males actively displaying and 1 inactive bird, whose behavior was typical of a female. The birds were flushed at approximately 05:35 and at least 1 flew in the direction of the nearby Pembina lek. It is possible that the sharptail female which copulated at 06:50 on the Pembina lek was flushed from this sharptail lek.

We suggest that the establishment of the sharptail lek in 1977 near the Pembina lek increased the likelihood of a receptive sharptail female encountering a receptive prairie chicken male. No sharptail females were observed on the Pembina lek during the 1975 or 1976 field seasons. Lumsden (pers. comm.), who has had extensive experience observing mixed leks of prairie chickens and sharptails, makes the following comment regarding this documentation. "It is likely that the sharptail female observed was pure, however, some hybrids can only be certainly identified in the hand. The history of observations of hybrids from previous years suggests that there could be some F_2 or F_3 which might be difficult to identify."

Appreciation is expressed to Dr. Fred Hamerstrom, who reviewed the paper and made unpublished data available. Dr. Lewis Oring and Mr. Harry Lumsden also reviewed the paper and made helpful comments.—W. DANIEL SVEDARSKY AND THOMAS J. KALAHAR, *Northwest Agricultural Experiment Station, Univ. Minnesota, Crookston, Minnesota 56716.* *Accepted 7 May 1979.*

Wilson Bull., 92(2), 1980, pp. 261–263

Cavity nesting of the Akepa on the island of Hawaii.—Four races of the Akepa (*Loxops coccineus*) occur on different Hawaiian islands: *L. c. coccineus* on Hawaii, *L. c. ochracea* on Maui, *L. c. rufus* on Oahu and *L. c. caeruleirostris* on Kauai. The Oahu race has been considered extinct (Berger, Hawaiian Birdlife, Univ. Press of Hawaii, Honolulu, Hawaii, 1972), but a bird recently sighted on that island (Ralph and Pyle, Am. Birds 31:376–377, 1977) may reconfirm its existence. The Kauai race is still fairly common. Although the U.S. Fish and Wildlife Service (Federal Register, Pt. IV, 1976:47180–47198) lists the Maui and Hawaii races as endangered, we found the latter race relatively common between 1400 and 1900 m elev. in the Kau forest.

We found the first nest and eggs of the Akepa on the island of Hawaii on 12 May 1976, when a female flew from a cavity in an ohia tree (*Metrosideros collina*) 90 m east of the Kahuku Ranch cabin at 1884 m elev., near the upper edge of the Kau Forest Reserve. The tree was about 14 m tall and 79 cm in diameter at breast height; the opening of the nest cavity was 12.7 cm high, 5.1 cm at its widest and 83.8 cm above the ground. The nest contained 3 dull white eggs with brown spots circling the larger end. The 1 egg measured was 12.5 × 16.3 mm. The forest within 200 m of the nest-site was both closed canopy ohia, with a fern (*Dryopteris* sp.) understory, and open canopy ohia with a pukiawe (*Styphelia tameiameiae*) understory. During preparation for a U.S. Fish and Wildlife Service bird survey of the Kau forest, we found the Akepa to be most numerous in this ecotone.

About 4 h after we discovered the nest, the adult female returned to incubate the eggs. An adult male Akepa was foraging about 35 m from the nest tree, and 30–40 adults were seen or heard near Kahuku Ranch cabin.

Nine days later, when we checked the nest, the female Akepa was incubating. We observed agonistic behavior between 2 male Akepa in an adjacent tree. An immature Akepa

TABLE 1

MATERIALS USED IN CONSTRUCTION OF HAWAIIAN AKEPA (*L. C. COCCINEUS*) NESTS

Nest lining	Abundance
Higher vascular plants:	
Metrosideros collina (misc. pieces of bark)	+[1]
Misc. pieces of roots	+
Uncinia uncinata, *Carex* sp. (?) and *Gahnia* sp. (?) (sedge leaves)	*[2]
Astelia sp. (leaf parts)	+
Ferns and fern allies:	
Asplenium spp. (rhizomes), *Grammitis hookeri* (rhizomes) and Hymenophyllaceae (rhizomes)	*
Xiphopteris saffordii (fronds)	—[3]
Grammitis hookeri (fronds)	—
Dryopteris paleacea (fern scales)	+
Bryophytes:	
Rhizogonium spiniforme	—
Thuidium crenulatum	*
Bryophytes	+

Nest body	Abundance
Higher vascular plants:	
Metrosideros (1 leaf)	+
Metrosideros (bark)	+
Metrosideros (?) (1 twig—1 mm diameter, 2 cm long)	—
Microlaena stipoides (leaves)	—
Astelia (leaf)	—
Uncinia uncinata (pieces of leaves)	—
Machaerina angustifolia (shredded leaves)	+
Ferns:	
Asplenium spp. (rhizomes), *Grammitis hookeri* (rhizomes) and Hymenophyllaceae (rhizomes)	*
Grammitis hookeri (fronds)	—
Hymenophyllum (?)	—
Xiphopteris saffordi (fronds)	+
Dryopteris paleacea (?) (fern scales)	—
Bryophytes:	
Rhizogonium spiniforme	+
Dicranum speirophyllum	+
Bazzania cordistipula	—
Thuidium crenulatum	*
Bryophytes (pieces of 6 other species ?)	+

[1] Species present only as traces.
[2] Dominant components used in construction.
[3] Species in low numbers.

followed another adult male into a tree nearby, begging and fluttering its wings. At 07:48 the female Akepa left the nest and flew to an adjacent ohia tree, where courtship feeding by the male took place.

On 28 May the nest contained 2 young and 1 unhatched egg. The nestlings had pinkish skin and very fine medium grey down on the back of the head, back and wings; the gape was reddish-pink and the corners of the mouth were light yellow; the feet were yellow. We estimated that they were 2–3 days old, which indicated an incubation period of at least 2 weeks.

On 28 May we installed a remote sensor and camera to record activity at the nest. There was some difficulty with the system, but from dawn to dark on 7 June 1976, the female visited the nest 35 times and the male 33 times, to feed the young and remove fecal sacs.

On 6 June the 2 young weighed 9.5 and 10.0 g. Two days later the nest still contained 2 nestlings and 1 egg. By 11 June the nestlings were fully feathered and ready to fledge, and on 14 June they were gone, apparently having fledged. The nest measured 10 cm in outside diameter, 8 cm inside diameter and 3 cm deep. It has been deposited with the National Museum (USNM No. 47307). The body of the nest was constructed primarily of fern rhizomes (probably *Asplenium* spp., *Grammitis hookeri* and various Hymenophyllaceae) and bryophytes (primarily *Thuidium crenulatum*). Additionally, a few fronds from *G. hookeri* were used, as well as shredded leaves of several unidentified sedge and grass species. The lining was composed primarily of grass and sedge (*Uncinia uncinata*) leaves which were for the most part shredded, with smaller amounts of bryophyte (*T. crenulatum*) and some fern rhizomes. A complete list of plants is given in Table 1.

Before discovery of the Akepa nest on Hawaii, only 2 of Hawaii's 37 extant endemic passerine taxa were known to nest in tree cavities: the Kauai Oo (*Moho braccatus*; Sincock, unpubl.) and the Hawaiian Creeper (*Loxops maculatus mana*; Scott, unpubl.). We found several inactive nests in tree cavities in the Kau forest that were apparently those of drepanidids. Since discovery of the Akepa nest, C. van Riper and J. M. Scott (Condor 81:65–71, 1979) have found several tree cavity nests of the Hawaiian Thrush (*Phaeornis o. obscurus*). On 22 March 1978, M. Collins, U.S. Forest Service, found the second known nest of the Hawaii Akepa (Collins, pers. comm.); it was 8 m up an ohia tree, in a cavity. On 11 May 1978, P. Pyle found the third known nest, 6 m up the limb of a fallen Koa (*Acacia koa*), also in a cavity. This nest contained 1 egg.

It remains to be determined whether cavity nesting is characteristic of the Akepa on Hawaii. Cavity nesting in trees suggests artificial nesting structures might be used. We are presently testing several types of artificial nesting structures in Hawaii.

Acknowledgments—We appreciate reviews of earlier drafts of this manuscript by A. J. Berger, A. Stana Federighi, C. J. Ralph and C. van Riper, III. Permission to include the observations of Mark Collins and Peter Pyle on the second and third known Akepa nest on the island of Hawaii is gratefully acknowledged. We wish to thank Jim Jacobi for identifying the plant material used in the nest.—John L. Sincock, *Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, P.O. Box 197, Koloa, Hawaii 96756* and J. Michael Scott, *Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, Mauna Loa Field Station, P.O. Box 44, Hawaii National Park, Hawaii 96718.* *Accepted 5 Jan. 1979.*

Wilson Bull., 92(2), 1980, pp. 263–264

Longevity of Hawaiian honeycreepers in captivity.—I know of no published records on the longevity of Hawaiian honeycreepers (Drepanididae). I began to raise members of this family in captivity during January 1968. Since that time C. Robert Eddinger, my former student, and I have kept 5 species in large (1.2 × 1.8 × 2.4 m) cages in our offices at the University of Hawaii: Kauai Amakihi (*Loxops virens stejnegeri*), Hawaii Amakihi (*L. v. virens*), Anianiau (*L. parva*), Kauai Creeper (*L. maculata bairdi*), Nihoa Finch (*Psittirostra cantans ultima* [=*Telespyza ultima* of Banks and Laybourne, Condor 79:343–348, 1977]), and Apapane (*Himatione sanguinea*). All except the Nihoa Finches and 1 Apapane were hand-raised from the nestling stage.

We had little difficulty maintaining most of the species; the general diet used was discussed by Eddinger (Avic. Mag. 77:113–114, 1971) and by Berger (Hawaiian Birdlife, Univ. Press of Hawaii, Honolulu, Hawaii, 1972). The most critical period for hand-raised birds is during the first months of cage life; those that survive this period often live for many years.

Loxops virens stejnegeri.—Eddinger began to hand-raise 4 nestlings on 17 May 1969. One bird died on 1 November 1970 (age 18 months); 2 other birds died on 3 and 5 August 1971, at an age of 26½ months; the fourth bird lived until 8 May 1978 to an age of 9 years.

Loxops v. virens.—I obtained 2 nestlings on 22 January and 2 others on 31 January 1968. One, with a badly deformed leg, learned to stand on 1 leg. However, this bird was never able to fly, and it suvived only 3.5 months. The other birds lived for periods of 43, 49 and 56 months.

Loxops parva.—Eddinger obtained 8 nestling Anianiau between 17 May and 23 June 1969. Six of these birds died at ages between 5.5 and 13 months (a veterinarian diagnosed the cause of death as either enteritis or visceral gout). The other 2 birds reached ages of 27 and 42 months, respectively.

Eddinger also took 3 nestling Anianiau on 23 June 1970. One bird died on 4 January 1974, at an age of 4.5 months; a second bird, on 1 August 1977, age 85.5 months. The third bird died on 15 Jan. 1980, age 114.75 months.

Loxops maculata bairdi.—Eddinger found the first nest of the Kauai Creeper with young on 26 April 1970. He collected the nest and 2 nestlings on 20 May. One of these birds died 13 days later, but the second bird lived until 4 July 1972, reaching an age of approximately 26.5 months.

Psittirostra cantans ultima.—John Sincock of the U.S. Fish and Wildlife Service mist-netted 14 Nihoa Finches for me in West Palm Canyon of Nihoa Island on 9 June 1969. These were delivered to me in Honolulu by Eugene Kridler on 11 June. All but 3 of the birds were in immature plumage at that time. My early experiences with these birds are described in Hawaiian Birdlife. Four birds died between 20 June and 15 December 1969. On 9 June 1970, I loaned Jack Throp, Director of the Honolulu Zoo, 2 male Nihoa Finches to place with his 3 remaining female Laysan Finches (*Psittirostra c. cantans*; see Throp, Elepaio 31:31–34, 1970). The 2 Nihoa Finches died on 19 July 1974 (age 61 months) and 17 March 1976 (age 81 months). The remaining 8 birds reached the following ages (in months): 18.5, 25, 25, 71.5, 72, 72.4, 94 and 112.

Himatione sanguinea.—This species proved to be more difficult to maintain in captivity. Eddinger hand-raised 6 nestlings; the longest living ones died at the ages of 16.5 and 19.5 months. However, a bird in adult plumage that was brought to me from the island of Hawaii is still alive 6 years later.—ANDREW J. BERGER, *Dept. Zoology, Univ. Hawaii, Honolulu, Hawaii 96822. Accepted 1 Apr. 1979.*

Wilson Bull., 92(2), 1980, pp. 264–265

Interspecific nesting of Clay-colored and Field sparrows.—Few records of interspecific breeding between Clay-colored Sparrows (*Spizella pallida*) and congeneric species are known. A hybrid Clay-colored Sparrow × Brewer's Sparrow (*Spizella breweri*) was reported by Cockrum (Wilson Bull. 64:149, 1952) and Storer (Wilson Bull. 66:143–144, 1954) identified a hybrid Clay-colored Sparrow × Chipping Sparrow (*Spizella passerina*) collected by A. D. Tinker in Michigan, where several species of *Spizella* are regular breeders.

Between 1960 and 1975, mixed nesting pairs comprising Clay-colored Sparrows and either Field Sparrows (*Spizella pusilla*), or Chipping Sparrows, have been recorded 3 times in New York State, where the Clay-colored Sparrow has only recently begun to breed (Bull, The Birds of New York State, Doubleday, Garden City, New York, 1974). Two of the reports involve a nesting of a Chipping Sparrow and a Clay-colored Sparrow pair near Ithaca, Tompkins Co., in June 1960 (McIlroy, Kingbird 11:7–10, 1961) and a Clay-colored Sparrow mated to a Field Sparrow in June 1974 near Millbrook, Dutchess Co. (Finch and Smart, Kingbird 24:211, 1974; Bull, Supplement to Birds of New York State, Wilkin's/Printers, Cortland, New York, 1976).

The third instance mentioned above occurred in 1972 and involved a pair of Field Sparrows and a male Clay-colored Sparrow nesting at the edge of a 9.3-ha Scotch pine (*Pinus sylvestris*) plantation just southeast of Foster Lake, 4 km WSW of Alfred, Allegany Co. I was conducting a breeding bird census there for the fourth consecutive year (for a detailed description of the area see Brooks, Audubon Field Notes 23:743–744, 1969). There was 1 territorial male Clay-colored Sparrow in this plantation in the summers of 1970 and 1971 and there were 2 territorial males there in 1972. At the same time this area had 26 territorial male Chipping Sparrows in 1970, 15 in 1971 and 23 in 1972. There were 6 Field Sparrows in 1970, 7 in 1971 and 9 in 1972. A pair of Clay-colored Sparrows had nested successfully in 1971, and an unsuccessful nesting had occurred in June 1972.

The nest of the mixed trio, discovered by Dr. Harold Axtell on 5 July at 14:00 EDT, was 15 cm up in a clump of goldenrod (*Solidago* sp.) amidst young choke cherry (*Prunus virginiana*), about 1 m from a row of Scotch pine and spruce (*Picea* sp.). By 15:00 the first egg had hatched. On 6 July 3 eggs had hatched, while 1 (infertile) egg remained. The nest was studied for up to 3 h daily from 5 July until 15 July from a partly hidden vantage point nearby. On 15 July, 3 newly-fledged young were being fed by adults of both species in a nearby choke cherry. At this time we could discern no field marks suggesting that the young were anything but Field Sparrows.

The nesting clearly involved 2 adult Field Sparrows and a male Clay-colored Sparrow. The 2 birds doing most of the incubating, brooding and feeding of the young were 1 Field Sparrow (judged to be the female) and the male Clay-colored Sparrow. No evidence of agonistic behavior among the adult birds was ever seen. The male Clay-colored Sparrow, of apparent normal plumage, sang both the typical territorial song of a Clay-colored Sparrow and also a deep, buzzy—but seemingly otherwise typical—territorial song of a Chipping Sparrow. I was unable to capture any of the young for study of possible hybrid characteristics. No Clay-colored Sparrows have been found in this plantation in subsequent years of censusing. I wish to thank Harold Axtell, Lou Burton, Clarence Klingensmith and Gordon Ogden for their observations and assistance.—Elizabeth W. Brooks, *1435 Waterwells Road, Alfred Station, New York 14803. Accepted 15 June 1979.*

Wilson Bull., 92(2), 1980, pp. 265–266

Cory's Shearwater off the South Carolina coast.—On 28 July 1973, my ornithology class and I observed 2 Cory's Shearwaters (*Puffinus diomedea*) on the Atlantic Ocean about 15 km east of Charleston, South Carolina. I collected 1 of the birds, which proved to be a female of the Mediterranean race (*P. d. diomedea*). It had an exposed culmen of 50 mm, a bill depth of 16 mm and a wing length (chord) of 343 mm with about 3 mm of the tip missing.

The white in the underwing extended from 50 mm distally from the shoulder until it became dark for the distal 100 mm. The bird was prepared as a study skin (Charleston Mus. No. CB 2) and sent to George E. Watson who confirmed the subspecific identification (Watson, pers. comm.; 16 August 1973).

The bird showed molt well underway, although the extent of molt in the primaries and tail was too ill-defined to describe. The extensive molt, and the fact that the bird was far from its breeding grounds, led Watson to conclude that this was a young, prebreeding female, of indeterminate age because the age of first breeding is unknown in this species. Usually breeding adults in the Mediterranean would be feeding small young in late July and would begin to molt in early fall (Watson, pers. comm.; 16 August 1973, 20 April 1976).

The Mediterrean race has been reported from only 2 North American locations: 5 specimens in 3 different years off Long Island, New York, and 4 birds off the Florida Keys (Murphy, Auk 39:58–60, 1922; Murphy, Serial Atlas of the Marine Environment: Distribution of North Atlantic Birds, Am. Geogr. Soc. 1967; Bull, Birds of New York, Doubleday, Garden City, New York, 1974:60). The present record suggests that this species may be more widely distributed in the western Atlantic than previous records indicate. A systematic examination of collections from North American waters should be made to delineate the distribution of this subspecies.

That the specimen was an immature bird supports the hypothesis that birds summering in the western Atlantic are prebreeders (Bourne, p. 157 *in* Handbook of N. A. Birds, Vol. 1, Palmer, ed., Yale Univ. Press, New Haven, Connecticut, 1962). Recent observations of Cory's Shearwaters during June–July off South Carolina (P. Laurie, pers. comm.) indicate that the species is more common in this area than was earlier thought (Sprunt and Chamberlain, South Carolina Bird Life, Univ. South Carolina Press, Columbia, South Carolina, 1970:63).

I wish to thank George E. Watson for his identification and comments on the note, and E. Burnham Chamberlain for providing information from The Charleston Museum. The boat trip was funded by the Department of Biology at The Citadel. This note was prepared while I held a grant from the Charleston Cultural, Scientific and Educational Foundation.—DENNIS M. FORSYTHE, *Dept. Zoology, Univ. Aberdeen, Scotland.* (Present address: *Dept. Biology, The Citadel, Charleston, South Carolina 29409.*) *Accepted 2 Apr. 1979.*

Wilson Bull., 92(2), 1980, pp. 266–268

The use of measurements in sexing Common Murres from Newfoundland.—The Common Murre (*Uria aalge*) is a widely distributed species that shows substantial geographic variation based on coloration (Salomonsen, The Atlantic Alcidae, Göteborgs Kungl. Vetenskaps=och Vitterhets=Samhälles Handlingar, Sjätte Foljden, Ser. B., Band 3, No. 5, 1944) and measurements (Tuck, The Murres, Can. Wildl. Serv. Monogr. No. 1, 1961; Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. and B. W. Tucker, Handbook of British Birds, Vol. V, H. F. and A. Witherby, London, England, 1965). The subspecies occurring in Newfoundland is *U. aalge aalge* (see Tuck 1961). When studying the breeding biology of any species, the ability of investigators to distinguish between adult males and females obviously gives a more complete picture of the roles played by each sex. When a breeding biology and behavioral study of Common Murres was started in 1977 in Newfoundland, efforts were made (using data collected during an earlier study of the helminth parasites of auks conducted there [Threlfall, Can. J. Zool. 49:461–466, 1971]) to determine whether or not the murres could be sexed using only meristic characters. Birkhead (Breeding Ecology and Survival of Guillemots (*Uria aalge*), Ph.D. thesis, Oxford Univ., Oxford, England, 1976) was

TABLE 1

MEAN WEIGHTS AND MEASUREMENTS OF 238 COMMON MURRES FROM NEWFOUNDLAND

				Culmen (mm)			
		Weight (g)	Wing (mm)	Length	Depth	Tarsus (mm)	Tail (mm)
Male	Mean ± SD	1006 ± 80	200.9 ± 5.4	44.3 ± 2.2	14.3 ± 1.0	40.1 ± 3.2	48.6 ± 3.9
(N = 121)	Range	775–1202	180.0–213.0	40.0–49.0	11.5–16.5	34.0–49.0	40.0–59.5
Female	Mean ± SD	979 ± 76	202.3 ± 5.1	42.4 ± 2.0	14.1 ± 0.9	39.2 ± 2.9	49.7 ± 4.4
(N = 117)	Range	815–1187	188.0–217.0	36.0–46.0	11.5–16.0	29.5–50.0	34.0–66.0

able to sex some birds after observing copulation and noted that males had larger beaks than females.

Common Murres were shot, or obtained from gill-nets in which they became trapped and drowned. The birds were weighed and measured (wing, culmen [length and depth], tarsus, tail) using the methods outlined in Witherby et al. (1965), and sexed while being examined for endoparasites. A total of 238 birds (121 males, 117 females), were taken in the Witless Bay Sea Bird Sanctuary (228 birds) and on Funk Island (10 birds), Newfoundland from May–July of 1966–1968. Data were analyzed using an IBM370/158 computer and an SPSS package, to obtain basic statistical values (Table 1). A Stepwise Discriminate Function Analysis (BMD 07M; Automatic Computation No. 2, Dixon, W. J., ed., Univ. Calif. Publ., 1970) was also performed. Only those specimens for which all values were available were used in the latter analysis (109 males, 105 females). It proved impossible to sex this species on the basis of measurements with any degree of certainty. When the measurements of 109 known males were analyzed the results indicated that 74 birds were males and 35 were females. In the case of 105 known females, 74 were identified as females and 31 as males.

No differences in the plumage of the 2 sexes were noted, a fact that has been pointed out by others. However, behavioral actions and patterns may be of use in sexing the species, when much more is known about them.

The measurements of *U. a. aalge* obtained during the present study expand the known size range for the subspecies, e.g., male wing length range = 180.0–213.0 mm (contra 195–210 mm [Witherby et al. 1965]); female wing length range = 188.0–217.0 mm (195–207 mm [Witherby et al. 1965]).—WILLIAM THRELFALL AND SHANE P. MAHONEY, *Dept. Biology, Memorial Univ., St. John's, Newfoundland A1B 3X9, Canada.*

Wilson Bull., 92(2), 1980, pp. 269–271

ORNITHOLOGICAL LITERATURE

CIEN AVES DE EL SALVADOR. By Walter A. Thurber. Ministerio de Educacion, Direccion de Publicaciones, San Salvador, El Salvador, 1978:XXXV + 200 pp., 170 + color photographs, several range maps. Price not given.—This book (mostly in Spanish) includes full page color photographs of 100 species of birds occurring in El Salvador. Some species have additional smaller photographs depicting different plumages, nests or young. A short paragraph (with an English translation) describes some of the natural history of each bird. Resident species dominate, but a number of North American migrants (with accompanying range maps) are included.

Walter Thurber, an American who has lived in El Salvador since 1966, has banded and photographed birds and studied their behavior for 10 years. In this book he returns some of his acquired knowledge to that country in a form that will be of interest to a wide range of its people. Short chapters on avian biology, bird study and bird protection should do much toward habitat preservation and bird conservation. A history of ornithological studies and a bibliography are included.

The book was printed in El Salvador and is of high quality. Some photographs may not meet exacting standards and there are a few noncritical typographical errors, but I am most favorably impressed by Thurber's efforts and those of the Ministerio de Educacion, which published it. Anyone concerned with Central American birds will find this work of interest. The hardcover edition can be obtained from the Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14853 for $16 plus $1 postage.—STEPHEN M. RUSSELL.

BIRDS OF PENNSYLVANIA: WHEN AND WHERE TO FIND THEM. 3rd. ed. (rev.). By Merrill Wood, illus. by Dorothy L. Bordner, 1979. 146 pp., 201 line drawings, paper cover. Order from Pennsylvania State Univ., Box 6000, University Park, Penn. 16802. $2.00.—A pocket-size guide to distribution (by counties), status and breeding of Pennsylvania birds.—R.J.R.

OWLS: THEIR NATURAL & UNNATURAL HISTORY. By John Sparks and Tony Soper. Taplinger Publ. Co., New York, 1979 (1970):206 pp., color frontispiece, 16 black-and-white plates, many drawings. $8.50.

SWANS OF THE WORLD. By Sylvia Bruce Wilmore. Taplinger Publ. Co., New York, 1979 (1974):229 pp., 8 black-and-white plates, many maps and line drawings. $8.50.—Both of these books are unrevised paperback reissues of books originally published in hard cover. Sparks and Soper was reviewed in The Wilson Bulletin 1972 [84]:360 and Wilmore was reviewed in 1975 [87]:434–435. As a note on inflation, Wilmore's book costs almost as much as the original edition, while Sparks and Soper's book costs considerably more.—R.J.R.

THE APPENDICULAR MYOLOGY AND PHYLOGENETIC RELATIONSHIPS OF THE PLOCEIDAE AND ESTRILDIDAE (AVES: PASSERIFORMES). By Gregory Dean Bentz. Bulletin of Carnegie Museum of Natural History, No. 15, 1979:25 pp., 2 tables, 5 figures. $2.00.—The phylogenetic relationships of the Ploceidae and Estrildidae are analyzed mainly on the structure of the forelimb and hindlimb muscles. Monophyly of the assemblage is hypothesized on the basis of common possession of a conical bill adapted to granivory, on biochemical affinities and in pterylographic similarities previously reported. The present study provided no myological synapomorphies to cluster the entire group in support of this hypothesis. Myological characters provide synapmorphies for all but the first branching point of a cladogram, and autapomorphies for most taxa. The Passerinae are the most primitive group myologically, and presumably the sister group of the remainder of the assemblage. The Estrildidae are more highly derived than are the Ploceidae. The Viduinae are included among the Estrildidae rather than the Ploceidae. Problems of classification are reviewed and a classification reflecting current understanding is presented.—(From the author's abstract).

WILDFOWL OF THE WORLD. By Eric Soothill and Peter Whitehead. Blandford Press, Poole, Dorset; Dist. in U.S. by Sterling Publishing Co., Inc., New York, 1978:297 pp., 128 color photos. $14.95.

DUCKS, GEESE, AND SWANS OF THE WORLD. By Paul A. Johnsgard. University of Nebraska Press, Lincoln, Nebraska, 1978:404 pp., approx. 280 line drawings and maps, 59 color photos. $35.00.

WATERFOWL: DUCKS, GEESE, AND SWANS OF THE WORLD. By Frank S. Todd. Sea World Press, San Diego, California, 1979:399 pp., 788 color photos. $44.95.

Each of these books attempts to survey the Anatidae of the world through a combination of text and illustrations. Though their purposes are similar, the various authors have approached their tasks from different points of view. Soothill and Whitehead's book is the smallest—a brief introduction to the waterfowl is followed by an annotated list of important wetlands arranged alphabetically by country. Most of the book is devoted to a series of species accounts arranged conveniently with the text and a color photo on facing pages. The text concisely summarizes the appearance, distribution and habits of the species, and an outline map shows its distribution. The color photographs, many being of captive birds, are adequate for their purpose. There are a few errors, e.g., the photos of the Australian and Northern Shovelers (*Anas rhynchotis* and *A. clypeata*) on pp. 189 and 191 are transposed. The book is marred by incompleteness. One wonders why the authors, having considered nearly all species of waterfowl, failed to finish the job and include, e.g., the handsome and highly specialized Torrent Duck (*Merganetta armata*).

Johnsgard's similarly organized book is far more comprehensive. The text of the species accounts is longer and more detailed than in the other books, containing information on vernacular names, measurements and weights, field marks, relationships, and suggested readings, as well as the usual natural history and distributional information. The many line drawings are uninspired, and the 59 color photographs are inferior to those in the other 2 books. Some are grainy or printed with too much or not enough contrast. A large number are reprinted from Johnsgard's earlier book, Waterfowl (1968), and a comparison shows many differences in color balance in the 2 books, raising a question about the accuracy of the colors shown. Johnsgard provides the most references to the research literature, citing over 300 other works, compared to about 113 for Todd and only about 34 by Soothill and Whitehead. This list is especially useful because the references are cited in the text.

The book by Todd is the largest and most opulent of the 3 reviewed here. Like the others, it contains a combination of written and illustrative material reviewing the waterfowl of the world, and like the others, the bulk of the text is arranged as a series of species accounts following a standard taxonomic sequence. The writing is more informal in tone and organization, and there is a wealth of information on the usual topics, but with a greater emphasis on aesthetic and conservational aspects of waterfowl study. Unique features include a table summarizing information on distribution, weights, reproduction and status, as well as a brief discussion of waterfowl photography. It is in the illustrations that this book far exceeds the others reviewed here, or any other for that matter. More than 780 color photographs illustrate virtually all living forms of waterfowl. The quality of these photographs lies not only in their technical excellence and superior reproduction, but in the variety of postures, behaviors and structural specializations illustrated. Beyond this, the photographs, most of them taken in nature rather than in captivity, often evoke an almost poetic appreciation for the relationship of the species and its habitat. This book is clearly a labor of love.

Here, then, are 3 additions to the endless waterfowl literature. Todd's book is by far the best in its illustrations, and if I could but only 1, this would be it. Johnsgard's book is the best general reference to the waterfowl of the world in a single volume, but visually inferior. The work by Soothill and Whitehead is, by most standards, an attractive and relatively inexpensive volume, but compared to the others has the least to recommend it.—ROBERT J. RAIKOW

PHYLOGENETIC ANALYSIS AND PALEONTOLOGY. By Joel Cracraft & Niles Eldredge (eds.). Columbia University Press, New York, 1979:233 pp., 35 line drawings. $9.00 (paper), $22.50 (cloth).—The 8 papers in this book are derived from a symposium convened at the North American Paleontological Convention II, held at Lawrence, Kansas, in 1977. Various opinions and arguments are presented by Cracraft, Eldredge, P. D. Gingerich, E. S. Gaffney, S. S. Bretsky, A. J. Boucot, and E. O. Wiley on such matters as the methods and purposes of phylogenetic inference and classification, the use of fossils in hypothesizing ancestor-descendent relationships, and the gradualist versus punctuated-equilibrium models of evolution. Although there are few matters relating specifically to birds, the questions debated are central to all areas of systematic biology, including ornithology.—R.J.R.

INDIANA BIRDS AND THEIR HAUNTS: A CHECKLIST AND FINDING GUIDE. By Charles E. Keller, Shirley A. Keller and Timothy C. Keller. Indiana University Press, Bloomington and London, 1979:214 pp., 14 maps. $6.95 (paper), $12.50 (cloth).—This book is divided into 2 parts. Part 1, "The Haunts," describes 63 birding areas in sections treating the north, central and southern parts of the state. For each there is a description of the area, information on how to reach it, a list of birds to be seen at various seasons and the location of nearby accommodations. For many areas there is also a list of references to papers dealing with birds of the region. Part II of the book, "The Birds," is an annotated checklist of Indiana birds with information on distribution, abundance and former and current status. Altogether, this is an uncommonly thorough regional guide.—R.J.R.

GUIDE TO THE NATIONAL WILDLIFE REFUGES. By Laura Riley and William Riley. Anchor Press/Doubleday, Garden City, New York, 1979:653 pp., 181 maps, 27 color photos. $14.95.—The nearly 400 National Wildlife Refuges in the United States are not as well-known to many ornithologists as the better publicized state and national parks, but offer a great variety of opportunities to study and observe birds and other wildlife. This book provides brief summaries of useful information for potential visitors to the refuges in all 50 states. For each refuge there is a discussion of the habitat, flora and fauna, and information on how to reach the refuge, hours and seasons that it is open, best times to visit, nearby accommodations, weather conditions, appropriate clothing, points of interest nearby, and the refuge's address and telephone number for further information.—R.J.R.

Wilson Bull., 92(2), 1980, pp. 272–273

ORNITHOLOGICAL NEWS

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student membership awards in the Wilson Ornithological Society are available because of funds generously donated in the memory of Aaron M. Bagg, a former president of the Society. Application forms for the awards to be granted in 1981 may be obtained from John L. Zimmerman, Division of Biology, Kansas State University, Manhattan, Kansas 66506. The deadline for applying is 1 November 1980. A Bagg Student Membership Award provides a 1-year membership in the Wilson Ornithological Society for successful nominees.

REQUEST FOR ASSISTANCE

C.W.S. shorebird colour-marking.—In 1980, the Canadian Wildlife Service will be continuing a large-scale shorebird banding and colour-marking project in James Bay. Since 1974, over 45,700 shorebirds of 27 species have been captured and much information on migration and dispersal routes is being obtained. Observers are asked to look out for and report any colour-dyed or colour-banded shorebirds that they may see. Reports should include details of species, age (if possible), place, date, time, colour-marks and a note of the number of that species present. For colour-dyed birds please record the colour and area of the bird that was dyed. For colour-bands and standard metal leg bands, please record which leg the bands were on, whether they were above or below the 'knee,' the colours involved, and the relative position of the bands if more than one was on a leg (e.g., lower right leg, blue over metal, etc.). All reports will be acknowledged and should be sent to *Dr. R.I.G. Morrison, Canadian Wildlife Service, 1725 Woodward Drive, Ottawa, Ontario K1G 3Z7 Canada.*

International shorebird surveys, 1980–81.—The International Shorebird Survey scheme is organised by the Canadian Wildlife Service and Manomet Bird Observatory to obtain information on shorebird migration and distribution for conservational and research purposes. The scheme was started in 1974 and is providing a continental picture of shorebird distribution through surveys carried out by volunteers in eastern Canada and the U.S.A., the Caribbean Islands and Central and South America. In 1980, we plan to continue and extend the scheme in as many areas as possible. Any observer who may be able to participate in regular survey counts of shorebirds during spring, autumn and winter periods is asked to contact one of the undersigned. Occasional counts from observers visiting shorebird areas on an irregular basis would also be most welcome.

For areas in Canada: Dr. R.I.G. Morrison, Canadian Wildlife Service, 1725 Woodward Drive, Ottawa, Ontario K1G 3Z7 Canada.

For areas in the U.S.A., Caribbean Islands, Central and South America: Brian A. Harrington, Manomet Bird Observatory, Manomet, Massachusetts 02345.

New York State breeding bird survey.—The Federation of New York State Bird Clubs is initiating, in 1980, a five-year distribution survey of the breeding birds of New York State. The objectives and methods will be similar to those of survey projects in Britain and Ireland, and in Maryland, Massachusetts and Vermont in this country. The project is a joint endeavor of the Federation with the New York State Department of Environmental Conservation, the Cornell University Laboratory of Ornithology, the National

Audubon Society and the New York State Museum. Participation by interested birders of the state is invited. For information on participation write to: Dr. Gordon M. Meade, Federation Atlas Project Chairman, 27 Mill Valley Road, Pittsford, New York 14534.

NOW AVAILABLE

The Proceedings of the Illinois Non-game Wildlife Symposium are now available at no charge. Write: Natural Heritage Section, Illinois Dept. of Conservation, 600 N. Grand Ave., West, Springfield, Illinois 62706.

NEW LIFE MEMBER

Randy Hill, a Life Member of WOS, is a Humboldt State University wildlife management graduate. He is especially interested in habitat requirements and habitat utilization of non-game birds and raptors, and has worked specifically on Peregrine Falcon (*Falco peregrinus*) distribution and nesting in northwest California. Mr. Hill and his wife Elaine, also a wildlife management graduate, enjoy photography, hiking, sports and travel (to Australia and Hawaii last year) and "of course, birdwatching."

NEW LIFE MEMBER

Gilbert S. Grant, a WOS Life Member, is a recent doctoral graduate of the University of California completing his thesis "Avian incubation: egg temperatures, nest humidity and behavioral thermoregulation in a hot environment." Dr. Grant's post-doc was through the University of Hawaii on the incubation physiology of albatrosses and petrels. Dr. Grant has a number of publications to his credit, ranging from distributional notes to behavior and breeding biology studies. His primary interest outside of ornithology is nature photography.

Wilson Bull., 92(2), 1980, pp. 274–287

PROCEEDINGS OF THE SIXTY-FIRST ANNUAL MEETING

Curtis S. Adkisson, Secretary

The Sixty-first Annual meeting of The Wilson Ornithological Society, and the third jointly with The Cooper Ornithological Society, was held Wednesday, 19 March to Sunday, 23 March 1980, at the La Quinta Royale Motor Inn, Corpus Christi, Texas. The hosts for the meeting were Corpus Christi State University and the Coastal Bend Audubon Society. Dr. Brian R. Chapman chaired the local arrangements committee. Three hundred fifty-eight persons attended the meeting.

The meeting opened with an informal social Wednesday night at the motel. On Thursday morning the societies were welcomed by Dr. B. Allen Sugg, President of Corpus Christi State University. Presidents George A. Hall and Dennis Power responded for the Wilson and Cooper Ornithological societies, respectively. After the first business meeting, the paper sessions began.

The annual banquet was held in the Sala Grande of the motel on Saturday night. Albert Heiene, Director of the Corpus Christi Museum, gave an excellent banquet address, featuring the humorous side of his work, and that of his colleagues, in science education of the public.

At the banquet, First Vice-President A. S. Gaunt announced the following awards:

Edwards Prizes (for best papers appearing in The Wilson Bulletin in 1979)

1) First Edwards Prize to Ellen R. Ketterson, "Aggressive behavior in wintering Dark-eyed Juncos: determinants of dominance and their possible relation to geographic variation in sex ratio" (Wilson Bull. 91:371–383).
2) Second Edwards Prize to Charles R. Brown, "Territoriality in the Purple Martin" (Wilson Bull. 91:583–591).

Margaret Morse Nice Award

Nancy L. Newfield, "Hummingbirds wintering in the New Orleans area"

Louis Agassiz Fuertes Grant

Gregory S. Butcher, "Coloration in Orioles, the genus *Icterus*"

Paul A. Stewart Awards

Bruce B. Edinger, "Investigations of behavioral isolating mechanisms in two morphs of the Northern Oriole (*Icterus galbula*) in a zone of sympatry"

Diane E. Riska, "Breeding biology and communication behavior of the Brown Noddy, *Anous stolidus* (Aves: Laridae), Dry Tortugas, Florida"

Gregory A. Perkins, "Status of Giant Canada Geese (*Branta canadensis maxima*) nesting in northwest Illinois"

Scott R. Winterstein, "Ecology and sociobiology of the Black-throated Magpie-jay"

Alexander Wilson Prize (for best student paper at this meeting)

M. W. Collopy and K. Collopy, "Growth energetics of Golden Eagles"

Field trips included opportunities to observe a lek of Attwater's Prairie Chicken, to visit the Aransas National Wildlife Refuge, at which Whooping Cranes were the objects of major interest as well as the Welder Wildlife Foundation.

FIRST BUSINESS MEETING

The first business meeting, held on 20 March 1980, was presided over by President George A. Hall, who announced the posting of the list of new members. He also appointed the Alexander Wilson Prize Committee, consisting of M. S. Ficken, J. V. Remsen, Jr., R. Szaro and C. Weise.

Treasurer Robert D. Burns presented the Treasurer's Report.

REPORT OF THE TREASURER

8 JUNE 1979 TO 31 DECEMBER 1979

GENERAL FUNDS

Cash balance received from E. Hoover, 8 June 1979			$ 3,500.00

RECEIPTS

Membership Dues			
1979	$ 6,464.50		
1980	14,290.00		
Total Dues		$20,574.50	
Sustaining for 1979	$ 200.00		
Sustaining for 1980	200.00		
Total Sustaining		$ 400.00	
Subscriptions to *The Wilson Bulletin*			
For 1979	$ 2,894.00		
For 1980	4,804.00		
Total Subscriptions		$ 7,698.00	
Back issues of *The Wilson Bulletin*		1,558.30	
Interest and Dividends		5,570.78	
Royalties		305.04	
Contributions from Authors and Others		2,468.79	
Contributions from Life Members and Patrons		2,172.44	
Total Receipts, 8 June 1979 to 31 December 1979			$ 44,076.85

DISBURSEMENTS

The Wilson Bulletin (Printing and Engraving)	$30,632.05	
Secretary's Expense	22.22	
Treasurer's Expense	418.28	
Ornithological Societies of North America	2,993.07	
Total Disbursements		$ 34,065.62

GENERAL CASH FUND

Checking Account, 31 December 1979	$14,893.99	
Savings Account, 31 December 1979	278.59	
Total Cash on Hand		$ 15,172.58

VAN TYNE MEMORIAL LIBRARY FUND

RECEIPTS		
Sales of Duplicates and Books	$ 1,623.47	
DISBURSEMENTS		
Purchase of Books	380.08	
Balance of Library Funds		$ 1,283.39

LOUIS AGASSIZ FUERTES RESEARCH FUND

RECEIPTS	$ –0–	
DISBURSEMENTS		
Patricia A. Gowaty	200.00	

MARGARET MORSE NICE FUND

RECEIPTS	$ –0–	
DISBURSEMENTS		
Craig Perdue	100.00	

ERNEST P. EDWARDS PRIZE

RECEIPTS		
E. P. Edwards	$ 350.00	
DISBURSEMENTS		
Glen Woolfenden	225.00	
David Ainley	125.00	

PAUL A. STEWART AWARDS

RECEIPTS	$ 800.00	
DISBURSEMENTS		
Robert Cohen	200.00	
Christopher Herlugson	200.00	
Susan Hannon	200.00	
Bruce Pugesek	200.00	

AARON BAGG STUDENT MEMBERSHIP AWARD FUND

RECEIPTS		
Anonymous	$ 200.00	
DISBURSEMENTS		
17 Student Awards	170.00	
Balance in Bagg Fund		$ 30.00

ENDOWMENT FUNDS

Balance received from E. Hoover	$ 8,000.00	
Life Membership Payments	5,674.50	
Total Receipts		$ 13,674.50

Amount sent to Investment Trustees	$13,290.00	
Balance in Endowment Savings Account 31 December 1979		$ 384.50
Investments Held as of 31 December 1979		
Cash Equivalents	$ 4,332.73	
U.S. Govt. & Govt. Guaranteed Bonds	25,875.30	
International Bank	7,672.50	
Canadian Provincial Bonds	3,343.75	
Corporate Bonds	21,652.50	
Convertible Corporate Bonds	2,950.00	
Convertible Preferred Stocks	6,750.00	
Common Stocks	59,851.50	
Total Investments		$132,428.28
Total General Endowment Fund		$132,812.78

GEORGE M. SUTTON COLOR PLATE FUND

Investments Held as of 31 December 1979		
Cash Equivalents	$ 1,000.00	
International Bank Bonds	852.50	
Canadian Provincial Bonds	3,875.00	
Corporate Bonds	8,718.75	
Common Stocks	12,675.00	
Total Sutton Investments		$ 27,121.25
Total Combined Wilson Ornithological Society Endowment Funds		$159,934.03

SECOND BUSINESS MEETING

The second business meeting was convened by President George A. Hall on Saturday, 22 March 1980. The proposed new members were elected unanimously.

The Secretary reported on the actions of the Council at its Thursday night meeting. A major item was the announcement of the Society's need for a dues increase. Dues for 1981 will be: students, $14.00; regular, $16.00; sustaining and family, $25.00. The cost of life membership will continue to be $250.00. The Secretary also reported that Jon C. Barlow was re-elected as Editor of *The Wilson Bulletin.*

Reports presented at this meeting or to Council are summarized below.

AUDITING COMMITTEE REPORT—1979

We, the undersigned, have examined the Treasurer's records, bank statements, cancelled checks and other financial records dated 8 June through 31 December 1979. The financial status of The Wilson Ornithological Society is that as stated as of 31 December 1979 and as amended 20 March 1980. Our examination indicates that all income and disbursements have been properly credited and debited from the proper accounts as authorized.

William A. Klamm, *Member*
Clait E. Braun, *Member*

MEMBERSHIP COMMITTEE REPORT—1979

During the last year the Society gained 339 new members of which 86 were students, 32 were reinstated past members and six involved life membership payments. With the dropping of about 40 members from the roles due to their withdrawal or non-payment of dues, the total gain in membership is about 300.

Robert C. Whitmore, *Chairman*

STUDENT MEMBERSHIP COMMITTEE REPORT—1979

Aaron Bagg student membership awards were advertized in the *Bulletin*, and requests for nominees were sent to 192 Society members. The committee made awards to 23 students. Eighteen students were nominated for Society membership, and these were invited to join. There is no doubt that Society members play the major role in recruiting new student members and if more would take a few minutes to suggest student nominees each year we would reach more people and dramatically increase student membership.

John L. Zimmerman, *Chairman*
Charles F. Leck
Roland R. Roth
Stephen M. Russell

EDITOR'S REPORT—1979

This was a very busy year. Rate of submission of new manuscripts increased over 1978. We published 92 manuscripts in 1979, of which 75 had been accepted during Jerry Jackson's editorship. With the increased submission rate and the necessity of reducing the size of the *Bulletin*, the rate of acceptance has decreased somewhat. In 1979 the time between receipt and publication of manuscripts was 18–24 months, due partly to the backlog of manuscripts. It is apparent that an increasing number of articles are being subsidized through page charges, and this can help us maintain the size of the journal.

In the past year, Trudy Rising left *The Wilson Bulletin* staff to take a new editorial job. I am grateful for her assistance during the first year of operation. In September 1979, Margaret May assumed the position of Assistant Editor. In addition I have had the able help of four student editorial assistants.

All in all I have enjoyed editing *The Wilson Bulletin*, and look forward to the opportunities of the next year.

Jon C. Barlow, *Editor*

LIBRARY COMMITTEE REPORT—1979

During the past year the Van Tyne Memorial Library, with the constant efforts of Janet Hinshaw, has continued its steady growth. Major efforts and acquisitions are in the following areas. We are building up our collection of translations from foreign journals. Sales of duplicates brought about $700.00, greatly helping with the funding of the library. Some 35 new books, records and journals were purchased. The library continues to receive 149 journals and newsletters through 115 exchanges, and received 45 complimentary subscriptions and gifts: 195 titles were received, including 1 subscription. During the year, 2000 items were donated by members: 61 books, 1328 reprints, 138 reports and pamphlets, 467 periodical issues, 3 translations and 3 theses.

Donations were made by 27 members. Of these, A. J. Berger supplied 1177 items, including nearly all of the above books and reports. Other donors were W. Belton, K. Bildstein, J. Blick, C. E. Braun, C. R. Brown, G. A. Clark, S. Goodman, J. Hinshaw, H. Horton, C. Kagarise, L. H. Kelso, H. F. Mayfield, M. J. Mengel (for Univ. Kansas Mus. Nat. Hist.), P. Myers, R. B. Payne, C. Ross, R. W. Schreiber, D. Siegel-Causey, A. Simon, R. W. Storer, J. G. Strauch, Jr., J. Tate, Jr., G. J. Wallace, S. R. Wilbur, T. Will and L. R. Wolfe.

Once more we thank all of the membership, and encourage their even greater support and use of The Wilson Ornithological Society's fine library.

William A. Lunk, *Chairman*

REPORT OF THE JOINT RESOLUTIONS COMMITTEE

The following resolutions were read and passed at the second business meeting:

WHEREAS in recognition of the need for the United States Fish and Wildlife Service, State Conservation Agencies and the Canadian Wildlife Service to prepare long-range recovery and management plans for endangered and threatened wildlife and for other species of ecological or economic importance, and,

WHEREAS in recognition of the importance of acquiring the best biological input for the initial plans and for subsequent scientific reviews,

THEREFORE BE IT RESOLVED that The Wilson and Cooper Ornithological societies jointly commend the responsible agencies for their initiative in consulting both government and outside specialists on these species, and,

FURTHERMORE, encourage these agencies to extend this policy to all such related plans during both their inception and subsequent reviews.

WHEREAS, The Cooper and Wilson Ornithological societies at their third joint meeting held at Corpus Christi, Texas, 19–23 March 1980, visited nearby Aransas National Wildlife Refuge, and,

WHEREAS, the members of these societies were treated to excellent views of Whooping Cranes, and endangered species wintering at Aransas NWR, as well as thousands of other waterbirds, and,

WHEREAS, many of these birds, including the Whooping Cranes, cross international boundaries and therefore require international recognition and protection, and,

WHEREAS, the international and national significance of Aransas NWR can more fully be recognized by the United States accession to the RAMSAR Convention on Wetlands of International Importance,

THEREFORE, BE IT RESOLVED that the Cooper and Wilson Ornithological societies express their appreciation to the State of Texas on its role in protecting its migratory wildlife and these societies further recommend that the State of Texas urge the United States Government to accede to the RAMSAR Convention and to list Aransas National Wildlife Refuge as the first United States wetland to be recognized as of international importance under that convention.

WHEREAS, in recognition of the need to preserve and protect the environmental, economic and aesthetic values of our nation's coastal areas, the President of the United States has declared 1980 to be the Year of the Coast, and,

WHEREAS, there is a national effort underway to create a coordinated public information campaign about the values of and threats to coastal zones and resources,

IT IS HEREBY RESOLVED by the Cooper and Wilson Ornithological societies, jointly to support the Year of the Coast campaign during 1980 and encourage our members to participate in local information and education programs.

WHEREAS, nongame fish and wildlife populations have many values important to society, including ecological, aesthetic, social, economic, educational, scientific, recreational and others, and,
WHEREAS, these resources and their associated values can be maintained and perpetuated only through well designed research and management programs, and,
WHEREAS, current research and management programs for nongame fish and wildlife are severely constrained by voids in the fundamental information and by inadequate levels of funding to strengthen essential programs, and,
WHEREAS, bills (H. R. 3292 and S. 2181) seeking to establish a joint federal-state Fish and Wildlife Conservation Act, and strengthen nongame fish and wildlife programs, have passed the House and will shortly be presented to the full Senate,
THEREFORE, BE IT RESOLVED that the Cooper and Wilson Ornithological societies jointly hereby urge the Senate to pass S. 2181 and furthermore urge the Conference Committee to resolve the differences between the two bills to the greatest benefit to nongame wildlife and return a bill to Congress, to adopt such a revised bill immediately and to insure implementation of the federal-state nongame Fish and Wildlife Conservation Act, and further resolve to urge the President to sign it into law.
BE IT FURTHER RESOLVED, that we encourage the U.S. Congress in its next session to take action to fund such a Conservation Act on a sound, sustained basis by assigning to it revenues from a tax on appropriately related items.

WHEREAS, the State of Alaska contains unique and fragile ecosystems which are as yet largely unaltered by mankind and which are of scientific, educational, economic and recreational value to the United States, and,
WHEREAS, the United States Senate has postponed its debate on the Alaska Lands bills (S. 9) and Tsongas Amendment 626 until after 5 July 1980 with the possible result that no bill will be passed this session to protect these national lands in Alaska, and,
WHEREAS, in consequence, Secretary of the Interior, Cecil D. Andrus on 12 February 1980, withdrew 40 million acres of land under the authority of the Federal Land Policy and Management Act to be managed as wildlife refuges by the Fish and Wildlife Service or as natural resource areas by the Bureau of Land Management, and,
WHEREAS twelve million more acres may be subsequently withdrawn if Congress does not itself protect these national lands,
THEREFORE, BE IT RESOLVED that the Wilson and Cooper Ornithological societies jointly commend and support Secretary Andrus on his actions, and,
FURTHERMORE, encourage the Senate to support speedily the passage of the Tsongas substitute bill, Amendment 626, which most nearly matches that passed by the House of Representatives (H. R. 39) which appropriately protects the Alaskan lands.

WHEREAS, the Wilson and Cooper Ornithological societies held their third joint meeting on 19–23 March 1980, at Corpus Christi, Texas, at the invitation of Corpus Christi State University and the Coastal Bend Audubon Society and were treated to convenient and comfortable housing and meeting rooms, and,
WHEREAS, important and interesting scientific papers on a variety of subjects were presented to satisfy the full spectrum of participants and precise timing enabled concurrent sessions to operate successsfully, and,
WHEREAS, there was in addition a full range of accessory activities including conveniently placed poster papers, entertaining and instructive movies and prospects of a delicious and entertaining banquet, and,

WHEREAS, the field trips before and after the meeting were well organized so as to enable us to enjoy the richness of bird life in this region,
IT IS THEREFORE RESOLVED that we, the members of the Wilson and Cooper Ornithological societies jointly express our grateful appreciation to our hosts, Corpus Christi State University and the Coastal Bend Audubon Society, and especially to Brian Chapman, Jerome Jackson and field trip organizer, Ray Little, and the members of their committees, whose planning, organization, hospitality and perseverance have made this meeting an especially enjoyable experience.

NOMINATING COMMITTEE REPORT—1979

As the final item of business the Nominating Committee, chaired by Clait Braun, submitted the following slate of officers for 1980–81: President, George A. Hall; First Vice-President, Abbot S. Gaunt; Second Vice-President, Jerome A. Jackson; Secretary, Curtis A. Adkisson; Treasurer, Robert D. Burns; Elected Member of Council (term expires in 1983) Mary H. Clench. There being no further nominations, it was moved, seconded and passed that the Secretary be instructed to cast a unanimous ballot for the slate.

PAPERS SESSION

R. D. Ohmart, J. Rice and B. W. Anderson, Arizona State Univ., *Species turnover rates in contiguous riparian habitats.*

J. P. Myers, Museum of Vertebrate Zoology, Univ. Calif., *Turning off territorial behavior: Merlins and Sanderlings in the winter.*

R. Greenberg, Museum of Vertebrate Zoology, Univ. Calif., *Comparative exploitation systems of two tropical wintering* Dendroica.

S. M. Smith, Mt. Holyoke College, *Demand behavior: a reinterpretation of courtship feeding.*

J. A. Mosher and K. Titus, Univ. Maryland, *Nest-site habitat partitioning by woodland breeding raptors.*

G. T. McQuate, 24 Canterbury Drive, Athens, Ohio, *Habitat selection in the Yellow-breasted Chat in southwestern Virginia.*

J. Cracraft, Univ. Illinois, *The impact of alternative methods of phylogenetic reasoning on the analysis of avian relationships: the Ciconiiformes revisited.*

W. E. Lanyon, American Museum of Natural History, *The generic status of the Flammulated Flycatcher of Mexico.*

J. D. Rising, Univ. Toronto, *Savannah Sparrows (*Passerculus sandwichensis*) and Bergmann's rule.*

L. F. Baptista and M. L. Morton, Occidental College, *Song dialects and mate selection in montane White-crowned Sparrows.*

R. B. Payne, Univ. Michigan, *Song sharing and its ecological consequences in Indigo Buntings.*

J. C. Barlow, Royal Ontario Museum, *Variation in song in the West Indian* Vireo "griseus" *superspecies complex.*

M. F. Passmore, Rob and Bessie Welder Wildlife Foundation, *Reproduction in juvenile Ground Doves.*

R. E. MacMillen, Univ. California, *Nonconformance of standard metabolism to body mass in Hawaiian Honeycreepers.*

D. P. Hector, Oklahoma State Univ., *Hunting behavior of the Aplomado Falcon (*Falco femoralis*) in eastern Mexico.*

P. D. Drye, III and R. D. Brown, Univ. North Carolina, *Prey selection in wild, free-ranging American Kestrels.*

R. D. Crawford, Univ. North Dakota, *Hatching asynchrony in rails.*

J. B. Brannon, Univ. Texas, *Behavior and ecology of a breeding Harris' Hawk population in Texas.*

R. N. Conner, J. G. Dickson and B. A. Locke, Southern For. Expt. Stat., Texas, and Stephen F. Austin State Univ., *Herbicide killed trees may be potential cavity sites for woodpeckers.*

T. E. Olson, Colorado State Univ., *Agricultural land use changes and Mourning Dove production in northeastern Colorado.*

E. J. Temeles, Louisiana State Univ., *Sexual size dimorphism in the New World Falconiformes.*

W. B. McGillivray, Univ. Kansas, *Co-variation of environment and phenotype: phenetic affinities of the Dickcissel.*

S. Robinson, Dartmouth College, *Ecological and social interactions of two species of* Vireo.

J. A. Gradwohl and R. Greenberg, Univ. Calif., *Formation, composition and movement of mixed species forest flocks in lowland Panama.*

J. E. Skaley, Cornell Univ., *Habitat analysis of common passerine species using aerial photography.*

B. W. Miller and B. Bohmke, San Antonio Zoo, *Nest construction and nesting behavior of the Giant Pitta (*Pitta caerulea*).*

L. A. Ryel, Michigan Dept. Natural Resources, *Population change in Kirtland's Warbler.*

K. J. Cook, Western State College, *An hypothesis of Flammulated Owl ecology.*

B. A. Locke, Stephen F. Austin State Univ., Nacogdoches, *Estimating Red-cockaded Woodpecker populations in east Texas.*

G. L. Miller, M. A. Byrd and R. A. Beck, Mississippi State Univ. and College of William and Mary, *The population, habitat, behavioral and foraging ecology of the Red-cockaded Woodpecker (*Picoides borealis*) in southern Virginia.*

E. J. Finck and J. K. Wilson, Kansas State Univ., *Comparison of Common Nighthawk (*Chordeiles minor*) nesting on annually burned and unburned tallgrass prairie.*

J. L. Zimmerman, Kansas State Univ., *Clutch-size in Dickcissels.*

B. E. Petersen, Wildlife Research Center, Colorado, *Lek attendance patterns of female Sage Grouse.*

S. R. Emmons, 1918 Southdown Ct., Fort Collins, Colorado, *Lek attendance of male Sage Grouse.*

P. D. Boersma, Univ. Washington, *Incubation and burrow temperatures of Fork-tailed Storm-petrels.*

D. A. McCrimmon, Jr., Cornell Lab. of Ornithology, *The status of populations of the Great Blue Heron in upstate New York.*

J. C. Kricher, Wheaton College, *Analysis of the range expansion of the Tufted Titmouse (*Parus bicolor*) in Massachusetts and its effect on the Black-capped Chickadee (*Parus atricapillus*).*

A. Cruz and D. W. Johnston, Univ. Colorado and Univ. Florida, *Ecology and behavior of the West Indian Red-bellied Woodpecker.*

H. H. Hadow, Coe College, *Behavioral events surrounding fledging of a Hairy Woodpecker.*

J. P. Myers and F. A. Pitelka, Univ. California, *Seasonal abundance and habitat use patterns of shorebirds at two sites in northern Alaska.*

G. L. Hunt, Jr., Univ. California, *Distribution and abundance of marine birds in the southeastern Bering Sea.*

D. James, M. J. Lockerd and C. R. Preston, Univ. Arkansas, *Ozark avian community patterns.*

D. M. Power, Santa Barbara Museum of Natural History, *Evolution in some California islands birds.*

T. L. Bucher, Univ. California, *Energy metabolism and breathing patterns in parrots.*

M. C. Moore, Univ. Washington, *The physiology of territorial behavior in White-crowned Sparrows: the role of male-female interactions.*

L. R. Jones, Utah State Univ., *The effect of photoperiod and temperature on testicular growth in captive Black-billed Magpies.*

R. B. Stiehl, Univ. Wisconsin–Green Bay, *Brood chronology of the Common Raven.*

G. A. Bartholomew, Univ. California, *A comparison of the energetics of hummingbirds and sphinx moths.*

F. Hamerstrom, Plainfield, Wisconsin, *Effect of voles on mating systems of Harriers.*

B. C. Thompson, Texas A & M Univ., *Attributes of Cliff Swallow colonies on natural substrates in north-central Washington.*

W. H. Baltosser, New Mexico State Univ., *Ecological relationships among nesting hummingbirds.*

F. S. Shipley and S. D. Fretwell, Kansas State Univ., *The evolution of clutch-size variability in Red-winged Blackbirds.*

C. S. Robbins and D. D. Boone, Migratory Bird and Habitat Research Lab., Maryland, *Effect of forest fragmentation on breeding bird populations in the Middle Atlantic states.*

J. V. Remsen, Jr., Louisiana State Univ., *Contribution of flooded forest and water-edge habitats to bird species richness in Amazonia.*

Carl E. Bock and T. L. Root, Univ. Colorado, *Winter biogeography of North American landbirds.*

C. J. Ralph, Inst. of Pacific Islands Forestry, *An analysis of the processes of colonization and extinction in a modern avifauna.*

S. Fretwell, Kansas State Univ., *Seasonal regulation and patterns of community structure.*

B. A. Harrington and S. Groves, Manomet Bird Observatory and Univ. British Columbia, *Autumn molt and migration of Black-bellied Plovers in eastern North America.*

F. L. Carpenter, Univ. California, *Territory and migration in Rufous Hummingbirds.*

J. H. Rappole, Univ. Georgia, *Timing of migration and route selection in North American songbirds.*

D. K. Jansen, Univ. Wisconsin–Stevens Point, *Spring migration route of Greater Sandhill Cranes from Florida to northwest Wisconsin.*

R. K. Anderson, Univ. Wisconsin–Stevens Point, *Separation and reunion of a mated pair of Greater Sandhill Cranes.*

W. B. Quay, Univ. Texas Medical Branch, *Comparative studies on the avian endolymphatic sac, a neglected organ with evidence of sensory function.*

V. M. Mendenhall, Patuxent Wildlife Research Center, Maryland, *Energy reserves in hatchling Barn Owls (*Tyto alba*).*

F. J. Cuthbert, Univ. Minnesota, *The relationship between reproductive success and colony site use in Caspian Terns.*

R. C. Laybourne, U.S. Fish and Wildlife Service, *Microscopic examination of the down of birds.*

K. G. Cunningham, Univ. California, *Bioenergetics of the Loggerhead Shrike: relation between lifestyle and metabolism.*

L. K. Southern and W. E. Southern, ENCAP, Inc. and Northern Illinois Univ., *Occurrence and significance of nest-site tenacity in Ring-billed Gulls.*

S. R. Winterstein, New Mexico State Univ., *Growth and development of nestling Beechey Jays.*

M. W. Collopy and K. Collopy, Univ. Michigan, *Growth energetics of Golden Eagles.*

P. A. Gowaty, Clemson Univ., *Sex ratio adjustment of Eastern Bluebirds (*Sialia sialis*) in South Carolina.*

E. Zerba, Occidental College, *Incubation temperatures in montane White-crowned Sparrows.*

D. H. White, C. A. Mitchell, C. J. Stafford and M. Garner, Patuxent Wildlife Research Center, Texas, Maryland and Texas, *Black Skimmer declines in Texas may be DDE-related.*

C. E. Grue, Patuxent Wildlife Research Center, Maryland, *Effect of an organophosphate pesticide on parental care in wild female Starlings.*

M. K. Rylander, Texas Tech. Univ., *The ecological significance of tarsometatarsal length in sandpipers.*

K. E. Church, Univ. Wisconsin–Green Bay, *Demographic characteristics of a Gray partridge (*Perdix perdix *L.) population in east-central Wisconsin.*

D. Schamel and D. Tracy, Univ. Alaska, *Ecological implications of nest-site tenacity in phalaropes—an hypothesis.*

N. L. Ford, St. John's Univ., Minnesota, *Do "floaters" exist?*

R. A. Ryder, Colorado State Univ., *Status of the Boreal Owl in Colorado 1896–1979.*

C. van Riper, III, CPSU/UC Davis, *Avifauna of the Kohala Mountain region, Hawaii.*

E. A. Hibbard, Rte. 1, St. Cloud, Minnesota, *Bird mortality associated with power plant and transmission line structures in Minnesota.*

K. L. Bildstein, Winthrop College, *The function of avian mobbing: Northern Harriers and passerines.*

S. M. Russell and S. P. Martindale, Univ. Arizona, *Do Cassin's Sparrows have dual breeding ranges?*

T. G. Marr, New Mexico State Univ., *Nestling feeding ecology of Cactus Wrens (*Campylorhynchus brunneicapillus*) in southern New Mexico.*

M. H. Balph and D. F. Balph, Utah State Univ., *A test of status signaling in Pine Siskins.*

R. L. Paterson, Jr., VPI & SU, Virginia, *Possible unrecognized spring migration routes of Wilson's Phalarope.*

T. C. Maxwell, Angelo State Univ., *Avifaunal change since the late 19th century in west-central Texas.*

T. and A. Manolis, Univ. Colorado, *A simple technique for weighing birds at feeders without capture.*

R. F. Martin, Univ. Texas, *Reproductive correlates of environmental variation and niche expansion in the Cave Swallow.*

R. R. Roth, J. T. Paul, Jr. and P. S. Martin, Univ. Delaware, *Predicting diversity from a diversity of indices.*

J. W. Hardy, Univ. Florida, *Voices of New World nightbirds, owls, goatsuckers and their allies.*

D. J. Watt, M. E. Douglas and G. D. Schnell, Univ. Oklahoma, *Hypothesis testing in behavioral studies: use of quantitative matrix comparisons.*

J. K. Meents, Hazleton Environmental Sciences, *Effects of winter navigation on waterfowl, waterbird and raptor populations of the St. Lawrence River.*

D. L. Mueller, D. F. Balph and M. H. Balph, Utah State Univ., *Experiments on the response of captive raptors to areas of differing prey availability.*

C. F. Leck, Rutgers Univ., *The annual population cycle of Mockingbirds in suburban New Jersey.*

P. E. Woods and C. Bens, Miami Univ., *Stereotyped aggressive display in the White-breasted Nuthatch.*

D. F. DeSante, Point Reyes Bird Observatory, *The abundance and year-to-year variability of migrant landbirds on southeast Farallon Island.*

ATTENDANCE

ALABAMA: *Birmingham*, Thomas and Gina Imhof, Joseph Imhof, Harriet Wright.

ALASKA: *Fairbanks*, Daniel D. Gibson, Brina Kessel.

ARKANSAS: *Fayetteville*, Joan Ballam, Charles Grisham, Norma Hoffrichter, Douglas James, Debra Mohr, Mercedes Mondecar, Charles Preston, Robin Rhinehart, Charlie Wooten.

ARIZONA: *Cave Creek*, Eleanor Radke; *Portal*, Chris Barkam; *Sonoita*, Jane Church; *Tempe*, Jane Durham, Robert D. Ohmart, Robert C. Szaro; *Tuscon*, Donald Lamm, Ruth Ogden, Stephen M. Russell.

CALIFORNIA: *Berkeley*, Russell Greenberg, J. P. Myers; *Bodega Bay*, Kimberly Smith; *Davis*, Charles van Riper, III; *Hayward*, Howard and Bessie Cogswell; *Irvine*, Keith Conningham, George L. Hunt, Jr., R. E. MacMillan, Stephen D. Thompson; *Laguna Beach*, F. Lynn Carpenter; *Long Beach*, Charles T. Collins; *Los Angeles*, Luis F. Baptista, George A. and Elizabeth Bartholomew, Jean Brody, Sigurd and Elise Bruhn, Nicholas E. and Elsie C. Collias, Barbara B. DeWolfe, Thomas R. Howell, Catherine Jacobs, Martine Jozan, Lloyd and Julie Kiff, Martin L. Morton, Maria E. Pereyra, Ralph Schreiber, Jennifer Meux White, Telford H. Work, Eileen Zerba: *Point Reyes*, Dave DeSante; *Riverside*, William Laudenslayer; *Sacramento*, John R. Gustafson; *San Diego*, Joseph R. Jehl, Jr.; *San Francisco*, Laurence Binford, Stephen M. Long; *San Jose*, Richard and Francis Mewaldt; *San Luis Obispo*, Fern R. and S. L. Tainter: *Santa Barbara*, Dennis M. Power; *Tarzana*, Theresa L. Bucher.

COLORADO: *Boulder*, Chip Blake, Carl E. Bock, Cynthia Carey, Alexander Cruz, Bill Ervin; *Denver*, Charlie and Lisa Chase; *Eldorado Springs*, Terry Root; *Fort Collins*, Clait Braun, Steve Emmons, Brett Petersen, Ronald A. and Audrey Ryder, Gustav A. Swanson; *Gunnison*, Kevin Cook; *Wellington*, Dan Butler.

DELAWARE: *Newark*, John T. Paul, Jr., Roland R. Roth.

FLORIDA: *Coral Gables*, Peter G. Merritt, Edwin O. Willis; *Gainesville*, John W. Hardy; *Miami*, Caby Sasila; *Vero Beach*, Betty and Edwin Lovell.

GEORGIA: *Athens*, John and Bonnie Rappole; *Statesboro*, Bill P. Lovejoy.

HAWAII: *Honolulu*, C. John Ralph.

ILLINOIS: *Chicago*, Joel Cracraft; *DeKalb*, William and Linda Southern; *Northbrook*, Julie K. Meents; *Rockford*, Marion Doyle, Vernon M. Kleen, Marjorie S. Lewis, Milton and Norine Mohlburg.

INDIANA: *Hanover*, J. Dan and Juanita R. Webster; *Terre Haute*, James and Amy Mason.

IOWA: *Cedar Rapids*, Harlo H. Hadow, Robert and Jean Vane; *Davenport*, Peter C. Petersen.

KANSAS: *Admire*, Ed and Jean Schulenberg; *Baldwin City*, Calvin Cink, Roger L. Boyd; *Lawrence*, W. Bruce and Sandra McGillivray; *Manhattan*, Elmer J. Finch, Stephen and Adair Fretwell, Frank S. Shipley, Howard C. Townsend. John L. Zimmerman.

LOUISIANA: *Baton Rouge*, J. V. Remsen.

MARYLAND: *Annapolis*, Chris Grue; *Frostburg*, Jim Mosher: *Laurel*, Chandler S. Robbins; *Owings Mills*, Jean Worthly, Bill Worthly; *Patuxent*, Vivian Mendenhall.

MASSACHUSETTS: *Manomet*, Kathleen S. Anderson, Brian A. Harrington, Natalie T. Houghton, Linda E. Leddy; *Norton*, John C. Kricher; *South Hadley*, Susan M. Smith.

MICHIGAN: *Ann Arbor*, Michael W. Collopy, Robert Payne, Robert W. and Louise Storer, Laura Sweany; *Jackson*, Robert A. Whiting; *Kalamazoo*, Raymond Adams, David Powell, John Stiner; *Lansing*, Lawrence Ryel; *Pleasant Lake*, Hubert Zernickow.

MINNESOTA: *Collegeville*, Norman L. Ford; *Marshall*, Henry C. and Gertrude Kyllingstad; *Minneapolis*, Francie Cuthbert, Bruce Fall; *St. Cloud*, Edmund and Virginia Hibbard.

MISSISSIPPI: *Gulfport*, Judith A. Toups; *Mississippi State*, Jerry Jackson, Matt Matthews, Randy Schultz, Jeff Stewart.

MISSOURI: *Columbia*, Keith E. Evans, Cathy Lefever.

MONTANA: *Polson*, Marcella Bishop.

NEBRASKA: *Omaha*, William A. De Graw, Bill Gidley, John Parker, Roger Sharpe, Lynn Vacanti.

NEW HAMPSHIRE: *Lebanon*, Peter Stettenheim; *Kingston*, William T. Tucker.

NEW MEXICO: *Albuquerque*, Jim Neal; *Artesia*, Miriam Axelrod; *Las Cruces*, William H. Baltosser, Barbara L. Kimbell, Thomas G. Marr, Ralph J. Raitt, Scott R. Winterstein.

NEW JERSEY: *Glassboro*, David Raimist; *Kendall Park*, Charles Leck; *Mount Holly*, Katherine G. Davis; *Princeton*, Scott K. Robinson.

NEW YORK: *Albany*, Kenneth P. Able; *Buffalo*, Arthur Clark; *Ithaca*, Helen Lapham, Donald A. McCrimmon, Jr., James C. Skaley; *Jamaica*, Frederick Shaeffer; *Millbrook*, Donald E. Kroodsma; *Monticello*, Thomas and Mickie Mutchler; *New York*, Susan R. Drennan, Wesley E. and Vernia H. Lanyon, Richard Plunkett; *Phoenix*, Roy S. and Cathie B. Slack; *Port Jervis*, Dorothy Hughes.

NORTH CAROLINA: *Cullowhee*, Michael Tove; *Chapel Hill*, Helmut C. and Nancy Mueller.

NORTH DAKOTA: *Grand Forks*, Richard D. Crawford.

OHIO: *Ada*, Nelson J. and Janet Moore; *Athens*, Grant McQuate; *Cincinnati*, Cathy Bens; *Columbus*, Abbot S. and Sandra L. L. Gaunt, Lucy M. Siekierski; *Gambier*, Robert Burns, Robert Olney; *Hudson*, Neil Henderson; *Lakewood*, William A. and Nancy Klamm; *Oxford*, John Smallwood, Paul E. Woods; *Toledo*, Eliot J. Tramer; *Waterville*, Harold F. and Virginia Mayfield; *Wooster*, Michael Kern.

OKLAHOMA: *Bartlesville*, Emma H. and John Messerly; *Norman*, Doris J. Watt; *Stillwater*, William R. Eddleman, Dean Hector.

OREGON: *Lake Oswego*, John Crowell, Jr.

PENNSYLVANIA: *Chester Springs*, Phillips B. and Berrell Street; *Pittsburgh*, Kenneth C. Parkes; *Slippery Rock*, Genevieve M. Tvrdik.

SOUTH CAROLINA: *Chester*, Mrs. W. C. Stone, Sr.; *Clemson*, Patricia A. Gowaty; *Rock Hill*, Keith L. Bildstein.

TENNESSEE: *Knoxville*, Marcia Davis, Beth Lacy; *Maryville*, Ralph J. Zaenglein; *Norris*, Linda J. Turner.

TEXAS: *Alice*, Richard O. Albert, Margaret A. Land; *Arlington*, Robert Neill; *Austin*, Jack Brannon, Charles and Dorothy Hartshorn, Edgar B. Kincaid, Robert F. Martin, Paul Mason, Rose Ann Rowlett; *Austwell*, Steve Labuda; *College Station*, Keith Arnold, R. Douglas Slack, Bruce C. Thompson; *Corpus Christi*, Laura Artmann, Susan Barnard, Steven Barnes, William F. Bowles, Jr., Brian R. Chapman, Monica Clint, James Davis, Mary Ellen Duick, Susan Finnegan, Robert Garza, John Glover, Tom Grantland, John Gregory, Steve Kelley, Ted Jones, Diane Lechuga, Roy Lehman, June Leibfarth, Ray McCracken, James McFarlen, Jesse Miller, Roxanne Montandon, Madeline Morgan, Ruth O'Brien, Janey D. Peabody, Leslie Peart, Chris Pease, David Potter, Barbara Shaw, Susanne Thomas, Joe Trevino, Joy L. Watson, Conway Yount, Warren Zehner;

Dallas, Warren Pulich, Steve R. Runnels; *Edinburg*, Pauline James, Edna Rodriguez; *Galveston*, Allan J. Mueller, W. B. Quay; *Houston*, Barry Hinderstein, Carol Meyer, Linda Walsh; *Huntsville*, Kelley Bryan, Ralph Moldenhauer; *Kerrville*, John E. Galley; *Kingsville*, Allan H. Chaney, Richard Schmidt, Mrs. Douglas Wilds; *Lake Jackson*, Vick Wade; *Lubbock*, Eric G. Bolen; *McAllen*, John Arvin; *McKinney*, Ken Steijman; *Nacogdoches*, Richard N. Conner, Brian Locke; *Port Aransas*, Julie Kinney, Warren Pulich, Jr.; *Portland*, Bob Hill, Ray Little; *Rockport*, Doris McGuire; *San Angelo*, Terry Maxwell; *San Antonio*, Mary Anna Bishop, Bruce W. and Carolyn Miller, Russell Smith; *Sinton*, Gene W. Blacklock, Marcia M. H. Wilson; *Victoria*, Kirke King, Christine Mitchell, Donald H. White.

UTAH: *Logan*, David F. and Martha H. Balph, Lee Jones.

VIRGINIA: *Blacksburg*, Curtis Adkisson, Kathleen Groschupf, Robert L. Patterson, Jr.; *McLean*, Warren B. King; *Manassas*, Roxie Laybourne; *Williamsburg*, Ruth A. Beck, Mitchell A. Byrd.

WASHINGTON: *Greenbank*, Jean W. Cohn; *Seattle*, Michael Moore.

WASHINGTON, D.C.: Richard C. Banks, Judith L. Hand, George Jonkel, George E. Watson.

WEST VIRGINIA: *Morgantown*, George A. Hall.

WISCONSIN: *Green Bay*, Kevin E. Church, Richard B. Stiehl; *Milwaukee*, Millicent Ficken, Robert Vane, Charles Wiese; *Plainfield*, Frederick and Francis Hamerstrom; *Stevens Point*, Raymond Anderson.

BRITISH COLUMBIA: *Burnaby*, Niko Verbeek.

MANITOBA: *Winnipeg*, Spencer G. Sealy.

NEW BRUNSWICK: *Sackville*, A. J. Erskine.

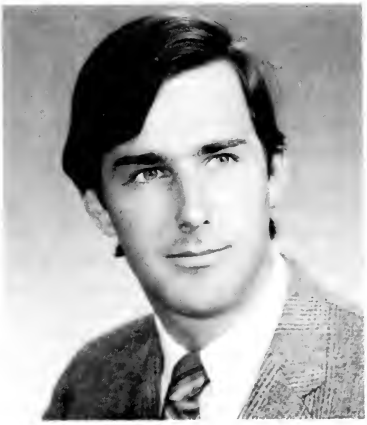
ONTARIO: *Toronto*, Jon C. Barlow, J. B. Falls, Margaret May, James Rising.

QUEBEC: *Westmount*, George and Mary Montgomery.

NUEVO LEON: *San Nicholas De Los Garza*, Allan R. Phillips.

ADDRESS NOT PROVIDED: Carol Friedman, Carol Oleson, Ethan Temeles.

NEW LIFE MEMBER



Mr. Bruce Beehler, a Life Member of the society, is currently a graduate student in population biology at Princeton University. His primary research interest at the moment is in comparative socioecology of birds of paradise, although Mr. Beehler is also interested in structuring of bird communities along altitudinal gradients and biogeography and speciation in Papuan birds. He has published two small books, one on Adirondack birds, the other on birds of northeastern New Guinea. Several short papers have also appeared on distribution and ecology of New Guinea birds. Besides his ornithological interests Mr. Beehler is an active back-packer, cyclist and mountain climber.

NEW LIFE MEMBER

Michael R. Joyce, a Life Member of the society, is the Senior Wildlife Biologist for Woodward-Clyde Consultants, Anchorage, Alaska. His main professional interest is the study of the response of avian communities to natural or man-induced changes in their habitats. Mr. Joyce particularly enjoys projects involving wetland avifauna, passerines associated with forest and woodland habitats and raptors. He has prepared reports in this area for government, industry and development commissions. For relaxation Mr. Joyce enjoys skiing, hiking, fishing and photography shared with friends and family.

This issue of *The Wilson Bulletin* was published on 18 July 1980.

THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "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 (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss 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.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Dr. Robert C. Whitmore, Division of Forestry, West Virginia University, Morgantown, West Virginia 26506.

CONTENTS

GENERAL NOTES

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 92, NO. 3 SEPTEMBER 1980 PAGES 289–424

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

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.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and esewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

Adult male Goldie's Bird of Paradise *(Paradisaea decora).*
Photograph by W. S. Peckover.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 92, NO. 3 SEPTEMBER 1980 PAGES 289–424

Wilson Bull., 92(3), 1980, pp. 289–301

GOLDIE'S BIRD OF PARADISE: DISPLAY, NATURAL HISTORY AND TRADITIONAL RELATIONSHIPS OF PEOPLE TO THE BIRD

MARY LECROY, ALFRED KULUPI AND W. S. PECKOVER

Goldie's Bird of Paradise (*Paradisaea decora*) occurs only on Normanby and Fergusson islands in the D'Entrecasteaux Archipelago, Papua New Guinea. Its display and habits have not been previously reported. Because of its restricted range, it is high on the list of 33 species of birds of paradise in Papua New Guinea about which the Wildlife Division desires information to aid in the formulation of conservation policies. Our visit to Fergusson Island to study *P. decora* was a result of the close ties between the Wildlife Division and members of the Papua New Guinea Bird Society.

The D'Entrecasteaux Archipelago is close to the southeastern tip of New Guinea, and is less than 18 miles from nearest New Guinea mainland. *P. decora* has not been found on Goodenough or Dobu, other islands in the group. That it is not on Goodenough is an unexplained distributional anomaly, as that island is within sight of Fergusson and suitable forest is present. Dobu is a relatively small, low island, heavily populated and with little remaining undisturbed forest. The absence of *P. decora* is not surprising as it is a species of the mid-mountain forests.

Both Fergusson and Normanby have large human populations in some areas; the lower ridges are, or have been, gardened to the top. Where there are fewer people, ridges have forested tops and *P. decora* is plentiful. So long as sufficient forest remains, these birds should remain unthreatened.

METHODS

We observed *P. decora* from 8–11 November 1978, for a total of 18 h. Our base was Nade, on the southwest coast of Fergusson Island. Residents of Nade who were familiar with the

FIG. 1. Tree fruit most frequently taken by *P. decora*, *Medusanthera laxiflora* (Icacinaceae).

displays of *P. decora* led us to their display arena on a ridge northwest of Nade. The very steep trail led upward through active and fallow garden areas until virtually undisturbed lowland forest was reached at about 750 ft (250 m). Two adult males, the first *P. decora* seen, were feeding on the ground in an area free of undergrowth at 1100 ft (360 m). One display tree was beside the trail at 1200 ft (400 m).

The weather during our stay was unusually good for the season. The days were generally sunny, with some periods of overcast skies. We had rain only once, during the night of 6–7 November; whereas, the Whitney South Sea Expedition encountered heavy rains on Fergusson in November 1928 (Hannibal Hamlin, unpubl.).

STUDY AREA

The display arena consisted of 4 main trees, with another used occasionally. They were spaced in a rectangle approximately 100 × 50 yards (92 × 46 m) on a steep, south-facing slope just below the crest of a ridge, at 1200 ft (400 m) elev., in mature lowland forest with a fairly even but open canopy about 90–100 ft (30–33 m) high. The display trees were of at least 3 species but were similar to each other in that they had tall, straight trunks and a rather shallow crown that was not densely leaved. The displays were performed on mid-canopy limbs 60–70 ft (20–23 m) from the ground. Some brief display occurred in the outer branches, but the main displays took place on limbs near the center of the tree. The main display limbs were quite open and the observer could look up and see the displaying bird against the sky.

We estimate that 8–10 plumed males displayed in this arena, usually 2 to a tree. On occasions when 3 or 4 plumed males were displaying in the same tree, the additional birds

FIG. 2. *Plerandra stahliana* (Araliaceae), said to be a food tree of *P. decora*.

had apparently moved in from other arena trees. No more than 2 females and 6 unplumed males were seen at a time.

RESULTS

Foraging and comfort activities.—Only plumed males were observed feeding and, usually, only when they left the display tree to feed nearby. Fruit of *Medusanthera laxiflora* (Icacinaceae), a black seed covered by pink flesh on 1 side only (Fig. 1), was apparently a preferred food item. It grew in clusters on a slender understory tree ca. 30 ft (10 m) tall. Nade men told us that this tree grows only in the forest. In fact, these trees commonly grow beneath the display trees and are perhaps disseminated by the birds themselves. Once a bird fed on red fruits growing in clusters on another understory tree.

Another tree, *Plerandra stahliana* (Araliaceae) (Fig. 2), had no ripe fruits during our visit, but local residents indicated that it was also a food source for *P. decora*. This tree is said to grow on the coast as well as in the forest. A grub, approximately 2 in (50 mm) long, was also said to be eaten by *P. decora* and to live in decayed wood.

As noted above, *P. decora* visits the ground to feed. We saw 2 plumed males foraging in forest litter at 1100 ft (366 m) and another male feeding on the ground beneath a display tree. Once an unplumed male quietly foraged for several minutes around a decayed tree trunk near a display tree and elicited no response from the adult male present in the display tree. Ground foraging has not been reported for other species of *Paradisaea* as far as we have been able to ascertain. That this is usual in *P. decora* is indicated by the fact that local residents were well aware of this habit and expected to see the species at the particular spot where we first encountered it.

Twice *P. decora* visited knot holes on trees, which were apparently filled with water. Once a male flew from a display tree to such a knot hole and drank, then returned to the display tree. On another occasion, a female bathed in a knot hole. When she flew, water drops could be seen falling from her feathers. Both of these knot holes were about 30 ft (10 m) from the ground.

Plumed males preened frequently between bouts of display, paying special attention to the flank plumes.

Leaf plucking.—Plumed males regularly plucked leaves near or over a main display limb, and as a consequence the display limbs appeared more open than the remainder of the crown of the display tree. A male would take a leaf by the petiole, break it off with a twist of his head and drop it. Six bouts of leaf plucking, each with only 1 male present, were observed in 2 different display trees. Five bouts occurred when there was no display activity in the arena and the birds had been quiet for some time. Once a male plucked leaves during a brief display. Usually a male reached up and broke off single leaves over his head, but 4 times it was observed that one flew up and caught a small limb in his bill, pulling it down to his original perch. He then either bit off a branch with several leaves (once) or held the branch under his foot and plucked individual leaves (3 times). In 1 bout a bird plucked and dropped 17 leaves in quick succession.

Calls.—We noted a varied assortment of loud, unmusical calls given by *P. decora*, both during display and sporadically during non-display periods. A first attempt at describing these calls and their contexts is given below.

Wok-wok.—this call, usually given by the male when no female is present, is often answered by non-displaying males in other trees. It appears to be mainly a contact call between males, and is undoubtedly homologous to the crow-like calls reported for other species of *Paradisaea*.

Whick-whick.—this call has 2 forms. The low-intensity, softer version, heard in the same circumstances as *wok-wok*, also appears to be a contact call between males. The high intensity *whick-whick* is very loud, liquid and ringing, and the bird jerks his head back sharply as he calls. This call occurred in 2 contexts, the usual one being when a female was present in the display tree, but it was also twice given just before the male dived rapidly out of the display tree and out of sight down the side of the ridge. No other bird was seen on either occasion.

"Growling."—this is a low call given by a single male at the beginning of a display bout with a female present. In fact, "growling" seemed to indicate presence of a female, often before she was seen by us.

Duetting.—duetting is done by 2 males displaying together, often in the presence of a female. This begins as a loud ringing metallic *waak* given alternately by the males. As the duet continues the ringing notes become increasingly rapid until a continuous metallic rattling is given by both birds and is best described as "gargling." Duetting is the characteristic call at an active arena and can be heard ringing through the forest for quite some distance. Duetting only involved 2 males. Duetting birds stand 4–10 ft (1.5–3.5 m) apart, usually facing each other, and give the duetting call almost always with plumes raised. One, or both birds, may run up and down the limb while duetting.

Display postures.—Plumed males.—Display occurred either on a horizontal or sloping, nearly vertical, limb. On horizontal limbs, the male stood across the limb with his head slightly below horizontal. The wings were open and were moved up and down with a rowing motion; they were always below the level of the back. The flank plumes were raised in 2 stages—the shorter plumes were raised until their shafts were vertical, then the longer ones were brought up until their shafts were also vertical. The plumes cascaded back and down; at no time did they fall forward over the bird's head. (In repose these 2 groups of flank plumes are obvious—the tail shows between them.) The central tail wires are also raised during display.

When the male is displaying on a steeply sloping limb, his body is parallel to the limb. In such cases he may move either up or down the limb, but the head, wing and plume positions are as above, except that the rowing movement of the wings may go below the level of the limb although never above the level of the back.

Displaying males were never observed to hang upside down from a limb. The only time the head was much below the level of the body was when the male was moving down a sloping limb.

Unplumed males.—The unplumed males were very active in the display tree, hopping about the female, or females. Except for the absence of plume erection, their display postures were indistinguishable from those of plumed males. These unplumed males could be told from females by their larger size (wing averaging 177 mm in unplumed males and 159 mm in females; see Table 1 for additional measurements) as well as by behavior.

Females.—The females were very quiet in the display tree and remained

TABLE 1
MEASUREMENTS OF *PARADISAEA DECORA*[a]

	Wing range ($\bar{x}$ ± SD)	Tail range ($\bar{x}$ ± SD)	Exposed bill range ($\bar{x}$ ± SD)	Tarsus range ($\bar{x}$ ± SD)	Weight[b]
Plumed males	176–182 (180 ± 2.0) N = 9	134–144 (139 ± 2.9) N = 8	33.5–35.0 (33.9 ± 0.49) N = 8	42.0–46.0 (43.7 ± 1.17) N = 9	237
Unplumed males	174–182 (177 ± 2.5) N = 9	136–145 (140 ± 3.4) N = 9	33.0–34.5 (33.5 ± 0.59) N = 8	42.0–44.5 (43.3 ± 0.75) N = 9	—
Females	156–165 (159 ± 4.0) N = 4	124–130 (128 ± 3.0) N = 4	32.0–34.0 (32.9 ± 1.03) N = 4	38.0–39.0 (38.5 ± 0.57) N = 4	—

[a] Measurements in mm of museum skins.
[b] Weight in g of male photographed.

motionless for long periods. When soliciting copulation, they opened their wings slightly and quivered them rapidly. No sound was heard.

Display.—The longest and most complete bout of display we observed was on 11 November. When we arrived at 06:10 display was already in progress, and it continued for an hour. This display bout is described in detail below and then other, less complete, bouts are compared with it.

At 06:10 three plumed males were present and 2 were duetting. The third male disappeared soon after our arrival. There were up to 6 unplumed birds present, 2 of which were identified as females on the basis of smaller size and quiet behavior. The unplumed males hopped actively about.

One female sat on the horizontal display limb between the duetting males, and the other was on a limb nearby. The display and duetting by the 2 males increased in intensity. A few times these males chased away the unplumed males, but they mostly ignored them.

At the peak of the dual display and duetting, 1 male stopped performing and moved away from the main display area, sitting quietly throughout the remainder of the display. The display was continued by the remaining plumed male, whose movements had become very slow and the display almost static; there was no audible vocalization. The unplumed males had moved in until they were all around the female, and 2 or 3 of them started making rowing movements with their wings. The plumed males made no attempt to drive them away. The female stood quietly near the displaying plumed male.

At this point the female left the main display area several times, but returned almost immediately. Sometimes the plumed male went with her. Throughout this period the male's plumes remained in display position.

While standing near the displaying male, the female began soliciting by quivering her wings, held slightly out from the body. The male continued his slow and rhythmic display. Several times in the 5 min that the female solicited, 1 displaying unplumed male moved in and copulated with the female and once 2 unplumed males in succession copulated with her. These copulations were brief, lasting only a few seconds, and there was no preliminary neck rubbing, although once the unplumed male did put his wings down around the body of the female (see below). The female did not leave or stop soliciting after these copulations, but remained near the displaying plumed male.

After about 30 min of display, the plumed male began hopping stiffly up and down near the soliciting female (from below we could see that his feet left the limb and came back to the same place). He edged over to the female, put his neck and breast on her back and rubbed back and forth. Then he mounted her, brought his wings down around her body and they copulated. While still mounted he rubbed his neck and breast on her back again, and then they copulated again. In all, the copulatory sequence lasted for approximately 30 sec.

After the plumed male had copulated with the female, all of the birds remained in the tree and the entire sequence of events was repeated, starting with duetting and joint displays by the 2 plumed males. We had no way of knowing whether or not the male that now displayed alone was the one that had displayed alone during the previous display bout. The unplumed males were around as before, were chased away on several occasions during the duetting and joint displays by the 2 plumed males, but were tolerated during the period of intense display by the single adult male. Once again they copulated briefly several times with the soliciting female. The displaying plumed male copulated with the female as before, dismounted and moved immediately to the second female and copulated with her—this copulation lasting only a few seconds. The first female moved away about 10 ft (3.5 m), after the male dismounted, and began preening. After the second copulation all birds left the tree. It was then 07:15.

On 1 other occasion we observed copulation in the presence of unplumed males (8 November, 13:45). In this case there were 4 unplumed males, 1 female and 4 plumed males in the tree. The sequence of events was as described above except that 4 plumed males were displaying together and there was much chasing of unplumed males. When a single plumed male began his display, the other 3 sat quietly in the tree, and the unplumed males did not interfere or attempt to copulate with the female. The displaying male mounted and copulation lasted about 25 sec.

Six other times 2–5 unplumed males were observed in display trees, both with and without females present. Usually, the 1–4 plumed males displaying together chased the unplumed birds when they appeared. Only once did a plumed male interrupt a static display to chase an unplumed male.

We observed 1 display sequence that ended in copulation, when no unplumed birds were present in the tree. This was on 8 November, 12:00–12:20. When the single female appeared in the tree there were 2 plumed males present. She was greeted by low growling by at least 1 male. For the most part the second male sat quietly in the same tree, but twice approached and displayed briefly near the female. The main display perch in this tree was a sharply sloping limb. The female sat on a horizontal limb branching from it. The male hopped slowly up and down the sloping limb, zigzagging his body back and forth as he did so, so that he alternately presented back, front and side views to the female. The female watched him continuously, sometimes facing him, sometimes peering sideways at him with head cocked. This female appeared quite wary and frequently flew to the outer branches, where the male followed her and displayed. They always quickly came back together to the main display perch. Movements by the male around the female were always slow and deliberate. Several times he gave high intensity *whick-whick* calls in front of the female, but generally no calls accompanied the display. After 15 min of display by the male the female began soliciting and the male gradually moved closer to her, hopped up and down on the branch next to her (we did not see neck and breast rubbing on this occasion) and mounted her with his wings down around her body. Copulation lasted about 15 sec. Then both birds flew from the tree in opposite directions.

On 9 and 10 November displays were sporadic and bouts were of short duration. There seemed to be fewer plumed males in the vicinity of the arena. Females were seen only 4 times and they remained in display trees only briefly. Each time their arrival occasioned growling by the male(s).

Twice unplumed males were seen in a display tree. Both times they were chased away, but the display was terminated. No female was seen on either occasion.

In contrast, on these 2 days there were frequent short bouts of display that usually consisted of duetting if there were 2 plumed males in the tree and loud calling, *whick-whick* and *wok-wok*, if there was only 1 male per tree. Display postures were sometimes assumed.

DISCUSSION

The following brief discussion refers only to our observations of *P. decora*. A comparison of *P. decora* with other species of *Paradisaea* and a discussion of the development of polygyny and evolution within the genus *Paradisaea* will be published at a later date.

P. decora displays in an "exploded arena," i.e., one in which individual courts are sufficiently widely separated for the owners to require vocal rather than visual contact (Gilliard 1969:53). In our study the arena comprized 4 main trees with a fifth used occasionally. Two to 4 plumed males displayed in each tree. It seems likely from our observations that there are usually 2 plumed males per tree, with a third and fourth male sometimes coming to the tree, probably from adjacent trees. These additional males were sometimes, but not always, present when unplumed males as well as females were in the display tree. These third and fourth males did not perform the duetting display and usually disappeared soon after it began.

It is noteworthy that 1 of the 2 males duetting when a female is present moves aside and sits quietly just at the point when the duet reaches peak intensity. The remaining male continues to display, usually silently, in a slow and rhythmic manner, uninterrupted by the second male. This suggests that there is a dominant male in any 1 tree, perhaps insuring that mating is not interrupted.

The frequent calling between trees by males and the duetting of pairs of males in trees when no female is nearby seem to us to be a possible means for setting up and maintaining a male-male hierarchy within the arena group. Gilliard (1969:53) has suggested that the loud calls of birds displaying in exploded arenas enable the birds to remain in auditory contact. We would go a step further and suggest that it also serves to establish and maintain a male-male hierarchy among the 8–10 birds within the arena observed. This would explain why there are so many reports of long periods of male display among arena birds when there are apparently no females present.

Once this hierarchy is set up, any individual male has a "territory" within the arena—a tree in which he is either dominant or not, depending on his interactions with the other male in the same tree. A female coming into the arena may then select a tree (not necessarily a male, but more appropriately stated, a locality within the arena complex that is attractive to her for some reason). In so doing she then triggers display by the males in that tree. If there are 3 or 4 males present, 1 or 2 males soon quietly leave, and a pair of duetting males remains. We saw no indication that the female chooses one or the other male—and we looked for it. Rather it seems to us that the relationship between these 2 males (and probably among all of the males in the arena) had already been determined, perhaps by duetting when no female was present. This would explain why 1 male stops displaying and sits quietly among the foliage while the other continues a static display and eventually mates with the female. To us this implies that choice of the male by the female is not necessary to explain polygynous mating systems in arena birds, as has usually been postulated, but that they may be understood in terms of male-male dominance hierarchies alone. That females permitted copulation by unplumed males and that a plumed male copulated in succession with the 2 females present lend support to the idea that mating is controlled by a male-male dominance hierarchy. Competition among males for dominance can explain the evolution of ornate display plumes and large size, having evolved in response to agonistic encounters and used secondarily in courtship. It is unnecessary to invoke choice of the most "attractive" male by the female, as is currently done in the literature.

That plumed males tolerated the presence of unplumed males in the display tree and permitted repeated copulations by them with the female to whom the male was displaying we find extremely difficult to explain. In the arena of *P. decora* that we observed there was at least 1 band of unplumed males that moved around through the arena trees. In a tree where only males were present or in one with a female and with 2 or more plumed males displaying together, the unplumed males are chased away. Here we believe that the unplumed males are chased because the displays are those concerned with setting up or maintaining the male-male dominance hierarchy (LeCroy, unpubl.). When a single male is displaying to a female with the slow, rhythmic movements that are characteristic of the display shortly before copulation, such bands of unplumed males are not only not driven away, but are actually allowed to copulate with the female, and neither male interferes. One might assume that the unplumed males are inept or infertile and that therefore such copulations rarely result in a fertile egg. This may well be the case, especially since the copulations we saw were of short duration. However, an unplumed male Raggiana Bird of Paradise (*P. raggiana*) is known to have sired young in captivity (Delacour 1964:232), and this cannot be ruled out in *P. decora*. One may imagine that an unplumed male on the court of a dominant plumed male is in a stressful situation in which ineffective copulations of short duration are the rule. In the captive situation mentioned above no plumed male was present and actual copulation was not observed.

If fertile eggs do in fact result in the wild from copulations with unplumed males, such behavior might be tolerated, in an evolutionary sense.

Kin selection can be invoked as an explanation if the unplumed males were closely related to the dominant males in an arena, as they might very well be if the dominant males in these long-lived birds do most of the mating. But evidence of relatedness in bird of paradise display groups will not be soon forthcoming, so we are left with a behavioral enigma which on the face of it appears maladaptive in neo-Darwinian terms.

On the other hand, the ability of unplumed males to sire young might ensure the survival of populations in the event of shortages of plumed males. This could well explain how it was possible for the heavy cropping of plumed males of some species of *Paradisaea* in the nineteenth and early twentieth centuries to continue unabated for nearly 50 years (Gilliard 1969:32).

We also don't know the age at which display plumes are acquired by males in the wild or how hormonal levels mediate plumage changes or behavioral parameters. It is entirely possible that the various plumage stages seen in museum skins do not represent yearly molts. Individuals may differ greatly in the age at which they acquire fully adult plumage, and lack of a position in the male hierarchy could conceivably inhibit plume growth.

TRADITIONAL RELATIONSHIPS OF THE PEOPLE TO THE BIRD

Like other ethnic groups of Papua New Guinea, the people of Nade, Morima and other nearby villages on Fergusson Island have myths and folklore about the colorful bird of paradise of their area. The people of Nade told us that, historically, these birds were very important and there was a great deal of interaction between birds and people. Old traditions relating to Goldie's Bird of Paradise are said to be dying out, but the bird is still greatly respected and is an important spiritual token to 1 group of villages. The plumes are apparently no longer sought for human adornment.

The people talked much about a beautiful dance they perform on very special occasions—an interpretive imitation of the birds displaying. It has special magic and because of this, performers must observe some rigid social taboos that include not eating certain foods for more than 1 week before the day of the dance; other taboos were not revealed to us. The performers are required to submerge themselves in a cold water stream for a long period while preparing their minds for the dance. Just before the dance, a magic chant is offered to the originator of the dance—this bird of paradise.

The dance itself is performed by 2 men dressed in grass skirts with *P. decora* plumes on the rump and cassowary (*Casuarius* sp.) feathers, from the mainland, stuck in armbands and carried. They mimic the sound of the birds as they dance. The women and other decorated men stand around the dancers. The women wear no plumes, carrying leaves instead.

There is apparently a widespread belief in Papua New Guinea that the birds of paradise with tail wires are able to use them to secure grubs. People on Fergusson told us that *P. decora* could probe with the tail wires into a hole in rotten wood and cause a grub to come to the surface where it could be captured. We were told a similar story in the Kratke Mountains in the Eastern Highlands.

Color plays an important part in the identification of birds by the villager. On Fergusson the dull, unplumed males and similarly garbed females are called *Wagolina*, which interpreted literally means "dull." The fully plumed males are given a different name—*Siae*.

Traditional hunting methods.—Before the National Government declared birds of paradise protected in 1966, Fergusson Islanders occasionally hunted *P. decora* for its plumes. One popular hunting method used a snare leg trap called a "dell." The hunter made a loop at the end of a long vine and took it to a display tree or a fruiting food tree. At the selected site on a fruiting tree, the hunter would drop most of the fruit, leaving only a few attached to the branch. The loop was then placed where the bird was expected to perch. The hunter made a hiding place below, taking the end of the string into his blind. If a bird did not soon arrive, he would mimic its cries to lure it. As soon as the bird stepped into the loop the hunter gave the string a sudden pull, catching the bird by the legs and pulling it down to where he was hidden.

Another method of capture involved making a fine net of pandanus fibers and setting it across a gully used by the birds. After choosing a suitable location, the hunter would cut down some of the trees to make an easier flight path. The net was then set between 2 trees and ca. 20 ft (6.5 m) above the ground. The hunter hid nearby; as soon as a bird flew into the net, he would climb one of the trees, lower the net, capture the bird and re-set the net.

Traditionally, the people believe that there is an almighty ruler of all creation. Each living thing, flora or fauna, has a human and spiritual component, the harmony of relationships being determined by the spiritual components of the totality of living things. If the spiritual component is upset, then disorder results and confusion and disharmony in the human world is the inevitable consequence.

It is believed that hunting success depends on observing certain norms of behavior. No man whose wife is pregnant may accompany a hunting party. Men who are going on a hunt may not sleep with their wives the night before. Failure to observe these restrictions would bring bad luck to the expedition. Perhaps some member of the party would get hurt or the hunt would be unsuccessful.

The people were quick to quote examples of such misfortunes where the taboos had not been observed. As a matter of fact, we were told that the reason no bird went into our nets (set up to secure birds for photography), was that the wife of a man who accompanied us was pregnant. The bird in the frontispiece was lured in by a local resident, caught (probably by the first hunting method mentioned above) and brought to us. After being photographed, weighed and measured, it was banded and released.

SUMMARY

Our observations of display at an arena of *P. decora* on Fergusson Island, Papua New Guinea, are described. Four trees comprized the arena and 8–10 plumed males were in attendance. Displays included male-male displays, female-male displays and displays by unplumed males. Copulations of plumed and unplumed males with females were observed. We stress the importance of setting up male-male hierarchies and postulate that plumes have evolved mainly in response to male-male pressures; display of plumes to a female may be secondary. The female does not seem to select a male but may be drawn to a particular limb within the arena, mating with whichever male is displaying. This is supported by the fact that soliciting females allowed unplumed males to copulate with them. That plumed males permit this would indicate that either these matings virtually never produce offspring in the wild or some form of kin selection is involved.

We have also given a brief description of the traditional role of *P. decora* in the Fergusson Island culture.

ACKNOWLEDGMENTS

The Wildlife Division of the Department of Lands and Environment is the organization charged with advising the Government of Papua New Guinea, through the Minister for Environment and Conservation, on action necessary to insure long term conservation of wildlife species. The idea of our joint study was formulated in talks with the former head of the Division, Mr. Fred Parker. We are grateful to him and to the Division for their interest and support.

To Nade residents Mr. Zebulon and Mrs. Ainesa Esekaia we express our sincere thanks for their many kindnesses and to Mr. Aiseya Todinale we are grateful for his expert knowledge of *P. decora*, which he shared with us and which made this study possible.

We would also like to thank Dr. Jared Diamond, Ms Helen Hays, Dr. Wesley Lanyon, Dr. Kenneth Parkes, and Dr. Francois Vuilleumier for reading the manuscript and for their very helpful comments and discussions; and Mr. John S. Womersley for identifying the food plants for us.

LITERATURE CITED

DELACOUR, JEAN. 1963. Notes on Austral and southern Pacific birds. IX. New Guinea. Avicult. Mag., 69:231–234.

GILLIARD, E. THOMAS. 1969. Birds of paradise and bower birds. Nat. Hist. Press, New York, New York.

DEPT. ORNITHOLOGY, AMERICAN MUSEUM OF NATURAL HISTORY, CENTRAL PARK W. AT 79TH ST., NEW YORK, NEW YORK 10024 (ML); WILDLIFE DIV. P.O. BOX 2585, KONEDOBU, PAPUA NEW GUINEA (AK) AND 14 BALANDA ST., JINDALEE, Q'LAND 4074, AUSTRALIA (WSP). ACCEPTED 13 APR. 1979.

Wilson Bull., 92(3), 1980, pp. 302–311

VOCAL AND TERRITORIAL BEHAVIOR IN THE WHITE-EYED VIREO

Richard A. Bradley

The vocal repertoire and displays of the White-eyed Vireo (*Vireo griseus*) are poorly documented. This paper presents results of a study to elucidate the role of song in the behavior of this species.

Work was done on a population of *V. g. griseus* in Gainesville, Alachua Co., Florida. The White-eyed Vireo in northern Florida is a bird of scrubby second growth, forest edge and early successional marsh-thicket-edge habitats. In the Gainesville area such habitat is plentiful, but it is irregularly distributed in small patches. Much of the suitable habitat lies along the course of Hogtown Creek and cleared right-of-ways under power transmission lines.

The patchy habitat provides a variety of territorial situations. Some males defend lone territories surrounded by unsuitable areas. Others have many neighbors. One such cluster of territories included 11 territorial males in an area of about 14 ha, with a mean territory size of 1.3 ha. In crowded areas agonistic encounters were relatively frequent.

I color-banded a part of the above local population to study the singing behavior of territorial males as well as their offspring. Territoriality and the associated agonistic behavior were studied; little courtship behavior was observed. During the spring and summer of 1977 and 1978 a total of 66 individuals was captured, measured, color-banded and released. These individuals were observed and tape recorded on subsequent visits.

METHODS

Nylon mist nets were used to capture vireos attracted to tape playback of conspecific song. On occasion a mounted White-eyed Vireo model was placed near the speaker. The taped songs were played back on a Uher CR 134 cassette recorder, using a composite tape of White-eyed Vireo songs recorded from various males in the southeastern U.S. Each study bird was banded with a U.S. Fish and Wildlife Service aluminum band as well as 3 colored plastic bands arranged in a unique combination. The sex of each adult was determined by the presence of an enlarged cloacal protuberance (males) or a functional brood patch (females). Young birds could not be sexed other than by observing their behavior. Birds during their first year of life are referred to as "hatching-year" birds.

Tape recordings of the vocalizations of marked birds were made using a Nagra III open reel recorder and a Sennheiser 805 unidirectional microphone at a tape speed of 19 cm/sec. Audiospectrographic analyses were made using the Kay Elemetrics 7029A Sona-Graph. All of the tapes made during this study have been deposited in the Bioacoustics Archive of the Florida State Museum, Gainesville, Florida. Some motion pictures were taken with a GAF ST602 super 8mm movie camera and analyzed using a Bell and Howell 1623Z stop-action projector.

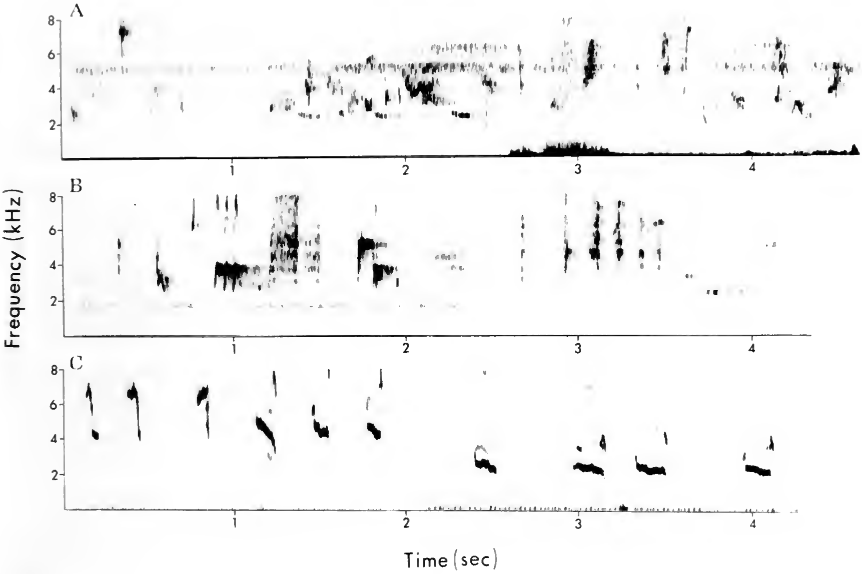


FIG. 1. Wide-band audiospectrograms of White-eyed Vireo vocalizations: A. the subsong of a hatching-year male; B. rambling song of an adult male in the presence of an adult female; C. distress squeals of an adult male vireo in the hand.

RESULTS

Subsong and rehearsed song.—Subsong in this species is characterized by soft warbling and poorly defined notes. The song is more loosely organized than adult song and is more or less continuous (Fig. 1A). Some of the notes have a harsh chatter-like quality typical of the other adult vocalizations ("chatter" vocalization, "rambling song").

Within 2 weeks subsong is replaced by rehearsed song. This is an intermediate stage between the unorganized warbling subsong and typical discrete adult song (sensu Lanyon 1960). Males sing rehearsed song for a period of several weeks during which this song gradually evolves into discrete song.

Male White-eyed Vireos begin to sing at an early age. The earliest date that I observed subsong was 1 June. The singing male was positively identified as a hatching-year bird (dark iris and juvenal plumage). The earliest egg date I have for this region is 10 April (N = 6 clutches). With an incubation period of 15 days (Bent 1950) and a nestling period of 11 days (estimate) this bird probably fledged no earlier than 6 May. Many

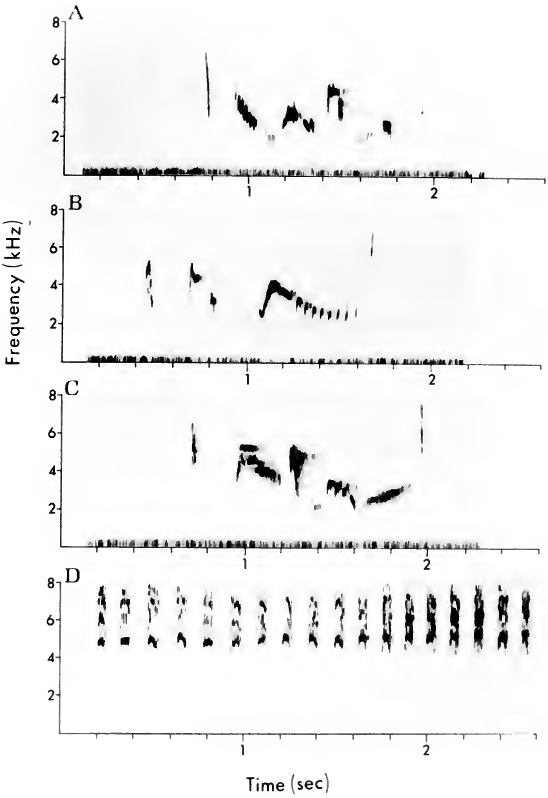


FIG. 2. Wide-band audiospectrograms of White-eyed Vireo vocalizations: A, B, and C. 3 examples of adult male discrete song recorded from 1 individual's repertoire; D. agonistic chatter vocalization.

birds fledged by early May. I thus estimate that some young males begin subsong within 2 weeks of fledging.

Hatching-year White-eyed Vireos often follow their fathers around the home territory. These birds are occasionally fed by the adult male. Sometimes the hatching-year birds cooperate in the defense of the home territory. For example, playback experiments elicit the same agonistic behavior from young birds as they do from adults. Some young birds (presumably males) sing rehearsed song simultaneously with their fathers' discrete song. Others use only the chatter vocalization and are assumed to be hatching-year females. Young birds may also display using head-forward postures, displacement preening and supplanting attacks (described later in text).

Late in the summer young males sang more or less typical "discrete song" with shorter than normal inter-song intervals. These first-year birds also sing the rambling song. In fact, they seem to use it more frequently than adults males. Birds of the year continue to sing after dispersal from the home territory and may establish and defend a vacant or abandoned territory. By the end of August the song of young males is typical of discrete song. Few, if any, adult males are still singing at this time.

Discrete song.—The discrete song is given only by males. It is composed of several loud whistled notes combined with sharp tick notes and short buzzes. The song often begins with a high pitched or strongly inflected note, includes a series of rapidly uttered complex notes and concludes with another sharp or inflected note. The song is short ($\bar{x}$ = 1.02 sec, N = 213 song patterns) and relatively loud. It has often been described as having an explosive character (Fig. 2A–C).

Discrete song is delivered at a rate of 10–20 times per min depending upon the activity state of the singing male. Song can be heard throughout the day, but I observed a decided peak in the 2 h following sunrise. During the 1977 season, I first heard song in late February. Song persisted well past the nesting period, with sporadic adult song until at least 3 July.

The repertoire of each male contains a number of different song patterns or motifs. Each of these is a reproducible song of fixed structure (Fig. 2). The mean repertoire size recorded from 41 color-banded males was 5.2 patterns. Two males had repertories of 13 motifs. I believe that most males sing at least 10 patterns and the low average reflects insufficient sampling. Different motifs used by 1 male are rarely very similar. Individual song figures or notes, however, occur repeatedly in a particular male's repertoire. A male usually sings only 1 or 2 motifs during a particular song bout. A song bout is 1 continuous series of song motifs uttered at a regular rate, usually for 5–10 min. Song bouts are separated by longer pauses from 5 min to several hours. One male sang 99 repetitions of 1 motif before pausing. Less than 5 min later the same male sang 41 renditions of this motif before changing patterns. Males increase the variety in their song performance when responding to an intruding male or playback of a conspecific's song. Recordings from 8 color-banded males were analyzed before and after playback. These males averaged 1.8 motifs in 5-min song bouts recorded before playback and 5.5 motifs in 5-min bouts immediately following playback.

Discrete song is used primarily in territorial defense. Adult territorial males spend much of each day during the breeding season patrolling the territory while singing. An intruding male is often located by song, and song itself plays an important role in the agonistic sequence. During counter-singing bouts, territorial males do not attempt to "match" motifs, as sometimes happens in other species that sing complex repertoires (Hinde 1958, pers. obs.).

Rambling song.—This song is longer than typical song and may last 5–10 sec or more. The structural character of rambling song is also distinctive. Rambling songs are composed of some typical song notes, some notes suggestive of the aggressive chatter as well as other harsh staccato notes (Fig. 1B). The rambling song is usually delivered at a lower amplitude than discrete song. It is interesting to note that hatching-year males utter this song as often, or more often, than discrete song during their transition from rehearsed to discrete song. Rambling song is used in an epigamic context. When this song was heard from a male not engaged in territorial defense, it was frequently followed by approach of the female and copulation. After copulation the male ceases rambling song. After a pause of 1–5 min the male begins to sing discrete song and patrol his territory.

An analogous song type has been described for the Red-eyed Vireo (*V. olivaceous*). In this species the male makes a fanned-tail display while singing a warbling, continuous version of the song (Lawrence 1953). This Red-eyed Vireo display was observed during courtship and preceded copulation. The Bell's Vireo (*V. bellii*) also sings a run-on song during courtship (Nolan 1960, Barlow 1962). Nolan (1962) describes a continuous "faint squeaky song" in the courtship of Red-eyed and Yellow-green (*V. o. flavoviridis*) vireos.

Chatter vocalization.—The chatter vocalization is a rapid series of harsh noisy rasp sounds composed of wide frequency band pulses in an irregular rhythmic pattern (Fig. 2D). The call may be more or less continuous, but is often given in short intense bursts, lasting 3–5 sec. Similar notes are incorporated into subsong of juveniles and rambling song of adult males.

This vocalization is uttered in agonistic contexts, especially in territorial encounters between males. The most frequent response to taped playback of discrete song with simultaneous presentation of a model includes this call. The male ceases singing, assumes an alert sleeked posture, then utters the scolding chatter. The male stands horizontally, erects the crest feathers slightly and chatters. During the utterance the feathers of the throat bulge out (Fig. 3E). This chatter display may be analogous to the head-forward display that is accompanied by the *myaah* call in Red-eyed Vireos (Barlow and Rice 1977).

The chatter is also given in response to "pishing" sounds made by a person or when mobbing a potential predator, and by the female in response to a distress squeal of her mate. The chatter is the most common call of adult female White-eyed Vireos. Females often given this call while the male is engaged in a counter-singing bout with a neighbor, and occasionally in response to taped playback of the discrete song.

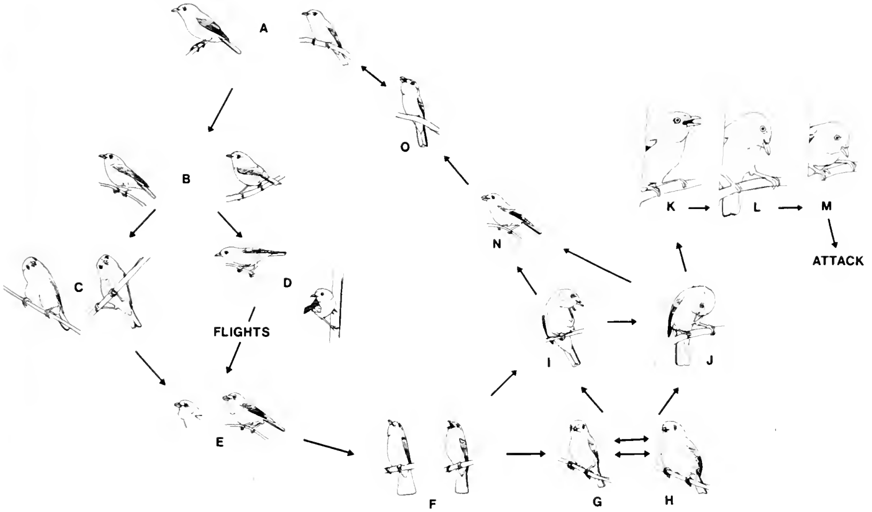


FIG. 3. An ethogram of the territorial response of a male White-eyed Vireo drawn from stop-frame motion picture analysis: A. relaxed posture; B. alert posture; C. sidelooking; D. flight intention movements; E. chatter vocalization; F. high-intensity song; G, H. the sleek-fluff display; I. displacement preening; J. redirected attack; K, L and M. a sequence from nervous song through attack; N. chatter vocalization; O. discrete song.

Distress squeal.—Captured White-eyed Vireos occasionally utter a sharp dissonant and repetitive squeal (Fig. 1C). This call is surprisingly loud and has a penetrating quality. It may serve to startle a would-be predator, or summon the assistance of a mate.

Alert posture.—When a territorial male hears the song of a conspecific within his territory he assumes an alert posture. This behavior also appears in response to the aggressive chatter call or the distress squeal. In the alert posture the body feathers are adpressed to the body (Fig. 3B,D).

Flight intention and supplanting attack.—I have given the name flight intention movements to various postures associated with high anxiety (Fig. 3D). These postures resemble the alert pose, but include exaggerated neck movements in the intended direction of flight and are often accompanied by wing flicks. Flight intention may act as a threat behavior. Flight intention movements, including wing and tail flicking, have also been observed in Bell's Vireo (Barlow 1962). Barlow states that flight intention indicates an internal conflict between the tendencies to flee, attack or court another vireo. Short flights over the head of the intruder often follow the flight intention pose. The bouts of flight are sometimes accompanied by the chatter call. If these flight threats and chatter fail to dislodge an intruder a supplanting attack will occur. As with Red-eyed Vireos (Barlow and Rice 1977) supplanting attacks occur between males at poorly defined territorial boundaries.

Sidelooking.—One behavior that has not been mentioned by other authors is sidelooking. This involves a tilting of the head towards the intruder-stimulus (Fig. 3C). It may represent actual monofocal staring or perhaps listening. The behavior is exaggerated and is not always directed at the stimulus. It is possible that this is merely intense search behavior.

Sleek-fluff display.—When a male White-eyed Vireo is confronted with a persistent intruder or model he will frequently present a sleek-fluff display. I have given this name to alternate sleeking then fluffing of the body feathers in a deliberate manner at intervals of about 1 sec (Fig. 3G–H). This action is effective in producing a flash of pale plumage which can be seen even through fairly dense vegetation. The sleek-fluff display does not appear similar to the ruffled-spread body feather action exhibited by other vireo species during the "swaying display" described by Nolan (1962) and others. It may, however, be related to the ruffled feather tail-fanning of agonistic encounters of Bell's Vireo (Barlow 1962).

Displacement preening.—When an intruder does not leave in response to the chatter calls or overhead flights, displacement preening activities may occur. This behavior resembles typical preening but includes vigorous pecking at the feet or perch. Displacement preening is often accompanied by nervous sidelooking. The pecking redirected attack behavior probably results from a conflict of motivation.

Grappling.—When supplanting attacks fail to chase an intruding vireo from the territory an actual contact fight may occur. The birds fly toward each other, interlock feet and beat each other with their wings. They also peck at their opponent as they tumble to the ground. The term "grappling" was applied by Barlow and Rice (1977) to this attack behavior.

Integrated territorial response.—The response of a resident White-eyed Vireo to an intruder is predictable. There is a sequence of different actions dependent upon the nature of the intruder-stimulus. The responses range in intensity from initial interest to final attack (Fig. 3).

Initial interest response is given by a male that hears the song of the species in his territory. The male will assume the alert posture and cease song. He then flies to the general area of the intruder, remaining fairly high in the canopy. If the intruder remains in the area the male will exhibit signs of increased excitement and utter the chatter vocalization (Fig. 3E).

In the second phase of response, the male may resume singing or continue chattering while searching actively. The song is a high-intensity song, uttered from a stiff erect posture (Fig. 3F). The search activity includes exaggerated sidelooking (Fig. 3C), flight intention (Fig. 3D), short flights over the intruder, or a supplanting attack. The intruder usually departs, but if it remains the resident male may display exaggerated preening activity (Fig. 3I) and pecking at his own feet or a nearby twig (Fig. 3J). The sleek-fluff action may also occur (Fig. 3G–H). Barlow (1962) describes an incident in which a White-eyed Vireo used "maximal tail-fanning" prior to attack. Although I have noticed that the tail is partly spread, then closed, in rapid succession during high-intensity song (Fig. 3F) I have not witnessed other tail-fanning.

If none of the above actions succeed in displacing the intruder the male may fly at his opponent and attack, with bill and feet. Grappling lasts only seconds and is accompanied by vigorous agonistic chatter from both individuals. The defeated bird then flies off silently, and the victor will preen or commence discrete song at a moderate intensity (rate about 1 song/5 sec).

The response of a resident female is not nearly so intense as that of her mate. She may approach and search actively, often uttering the agonistic chatter. I have not observed displacement preening, pecking, sleek-fluff, discrete song or rambling song from a female.

When a tape recorder is the intruder-stimulus the male vireo will respond in the typical manner. The search activity is very intense but no attack occurs. Even the presence of a mounted vireo fails to elicit an attack, although close approach does occur.

DISCUSSION

It is instructive to compare the behavioral repertoire of the White-eyed Vireo observed in this study to that described for other species of the genus. The chatter vocalization serves as the principal agonistic and localization call in this species and is analogous to the *myaah* call of the Red-eyed Vireo, the *ehhh* call of the Philadelphia Vireo (*V. philadelphicus*) (Barlow and Rice 1977) and the *chee* call in Bell's Vireo (Barlow 1962). The rambling song probably serves primarily in courtship of White-eyed Vireos and is similar to the run-on warbling song of Red-eyed and Yellow-green vireos (Nolan 1962) and the congested song of Bell's Vireo (Barlow 1962). Behaviors, including an alert posture, head forward threat, displacement preening, supplanting attack and grappling are shared with other vireos. Barlow (1962) describes tail-fanning for the White-eyed Vireo. I have not observed it during this study. Barlow and Rice (1977) describe an agonistic "bubble" song in Philadelphia Vireos not observed in Red-eyed or Bell's vireos. I did not hear any "bubble" song during the current study.

I have described 2 displays that have not been mentioned by other authors. The first is an exaggerated sidelooking which appears during intense search behavior. The second I named the sleek-fluff display. The sleek-fluff display may be analogous to the ruffled tail-fanned posture of other species (Barlow 1962). Both of these displays are associated with agonistic encounters between males; they share spread body plumage, presumably to make the displaying individual appear larger or more formidable. In the sleek-fluff display the tail is often partly spread, though not as widely as in the Red-eyed Vireo's tail-fanned posture.

The development of song behavior has not been described for any species of vireonid. I have presented some evidence that song learning occurs relatively early in the White-eyed Vireo. Preliminary analysis of the songs of 3 hatching-year White-eyed Vireos indicates that most of the motifs in their repertories are identical copies of their fathers' motifs (9 of 12 motifs). The other motifs are shared with immediate territorial neighbors. Adkisson and Conner (1978) describe the incorporation of calls from a variety of other species into the songs of White-eyed Vireos.

SUMMARY

This paper presents initial results of work on a population of White-eyed Vireos in Gainesville, Florida. The study involved color-banding a large part of the local population to study song in territorial males and their offspring. During the spring and summer of 1977 and 1978 over 60 territorial males were captured, measured, color-banded and released. These individuals were observed and tape recorded on subsequent visits.

Discrete song is the typical species-specific song. Each male sings 5–15 different song types with a mean length of 1.02 sec. Rambling song is a long, loosely structured song that includes many harsh notes. Rambling song was observed in epigamic contexts and has related counterparts in repertories of other *Vireo* species. The chatter vocalization is a series of short harsh sound bursts uttered during agonistic encounters between males, or by a female in response to an intruding male's song.

I have described 2 displays that have not been mentioned by other authors, sidelooking and sleek-fluff. Exaggerated sidelooking appears during intense search behavior. The sleek-fluff display may be analogous to the ruffled tail-fanned posture of other species.

Several displays common to other vireos were observed including, alert posture, head-forward threat, displacement preening, supplanting attacks and grappling. Song learning is apparently very rapid. Young birds sing fully developed songs by the end of their first summer.

ACKNOWLEDGMENTS

I would like to thank Dr. J. W. Hardy for his encouragement and support during the course of this study. I would also like to thank Robert Repenning and Joan Whittier for assistance in the field. I am grateful to the following people who read 1 or more drafts of the manuscript and made many useful suggestions: Oliver Austin, Luis Baptista, Donald Borror, Dick Franz, Bill Hardy, Robert Lemon, Robert Payne, Rhoda Rybak and Tom Webber. I would also like to thank Curtis Adkisson, Jon Barlow and an anonymous reviewer for editing the final version of this paper.

LITERATURE CITED

ADKISSON, C. S. AND R. N. CONNER. 1978. Interspecific vocal imitation in White-eyed Vireos. Auk 95:602–606.

BARLOW, J. C. 1962. Natural history of the Bell Vireo *Vireo bellii* Audubon. Univ. Kansas Publ., Mus. Nat. Hist. 12(5):241–296.

——— AND J. C. RICE. 1977. Aspects of the comparative behavior of Red-eyed and Philadelphia vireos. Can. J. Zool. 55:528–542.

BENT, A. C. 1950. Life histories of North American wagtails, shrikes, vireos and their allies. U.S. Natl. Mus. Bull. 197.

HINDE, R. A. 1958. Alternative motor patterns in chaffinch song. Anim. Behav. 6:211–218.

LANYON, W. E. 1960. The ontogeny of vocalizations in birds. Pp. 321–346 *in* Animal sounds and communication, (W. E. Lanyon and W. N. Tavolga, eds.). Publ. No. 7 A.I.B.S. Washington, D.C.

LAWRENCE, L. DE K. 1953. Nesting life and behavior of the Red-eyed Vireo. Can. Field-Nat. 67:47–87.

NOLAN, V., JR. 1960. Breeding behavior of the Bell Vireo in southern Indiana. Condor 62:225–244.

———. 1962. The swaying display of the red-eyed and other vireos. Condor 64:273–276.

FLORIDA STATE MUSEUM, UNIV. FLORIDA, GAINESVILLE, FLORIDA 32611. (PRESENT ADDRESS: DEPT. BIOLOGY, UNIV. NEW MEXICO, ALBUQUERQUE, NEW MEXICO 87131.) ACCEPTED 31 JULY 1979.

COLOR PLATE

The color plate Frontispiece of Goldie's Bird of Paradise (*Paradisaea decora*) has been made possible by an endowment established by Dr. George M. Sutton.

Wilson Bull., 92(3), 1980, pp. 312–329

DISPLAY BEHAVIOR OF OVENBIRDS (*SEIURUS AUROCAPILLUS*) I. NON-SONG VOCALIZATIONS

M. Ross Lein

Although detailed investigations of single displays have furnished insights into their proximate causation and adaptive roles in regulating social behavior (Smith 1977, Sebeok 1977), they contribute relatively little to our understanding of the evolution of animal communication at a somewhat higher level. Smith (1969a) and Moynihan (1970) pioneered consideration of the evolutionary pressures shaping the total display repertoire of a species. However, such studies are hampered by a paucity of information about the size and composition of repertoires of most animals, since detailed inventories are time-consuming and are frequently by-passed by workers studying single displays or small portions of a repertoire. Generalizations are therefore based on a few species whose display behavior is known in sufficient detail, and their validity depends on how well additional studies conform to the patterns found.

During investigations of behavior of wood warblers (Parulidae) I obtained information on the display repertoires of various species. In this paper I describe the non-song vocalizations of breeding Ovenbirds (*Seiurus aurocapillus*) and suggest some of the functional aspects of vocal communication and the evolutionary pressures that possibly have shaped its display repertoire. The songs of males and visual displays will be dealt with in subsequent papers.

The Ovenbird is an excellent subject for behavioral investigation. It is widely distributed and abundant throughout the wooded regions of North America, occupying open woodlands, generally with little underbrush but with an abundance of fallen leaves, logs and rocks (Bent 1953, Griscom and Sprunt 1957). This warbler's vocal nature during the breeding season, its open habitat and its largely terrestrial lifestyle facilitate observation. Although Ovenbirds are drably (and possibly cryptically) colored, they are easily followed on the forest floor. The sexes are monomorphic, but may be distinguished reliably through the use of behavioral characters.

Hann's (1937) extensive life history study of the Ovenbird included observations on behavior. However, descriptions of non-song vocalizations in the literature are limited and little recording and audiospectrographic analysis of such displays have been undertaken. Since wood warblers are numerous in both the tropical and temperate regions of the Americas, the Ovenbird invites behavioral comparisons leading to the elucidation of the evolution of its displays. Also, as a monomorphic species in a family whose temperate zone representatives are predominantly sexually-dimorphic in plumage (Hamilton 1961), its behavior may provide insights into the interaction between the visual and vocal components of the display repertoire.

METHODS

Fieldwork was conducted in the breeding season from 1970–1972 at 2 locations in New England. The main study area was the Pickman Area, Concord Field Station of the Museum of Comparative Zoology of Harvard University, Bedford, Middlesex Co., Massachusetts. The second area was a farm in South Lyndeboro, Hillsboro Co., New Hampshire. The habitat in both locations consisted of open second-growth mixed forest with a sparse understory, regenerated on fields abandoned 50–75 years ago. This forest is dominated by large white pines (*Pinus strobus*) 25–30 m in height. The main deciduous trees are maples (*Acer rubrum* and *A. saccharum*) and oaks (*Quercus* spp.), with some gray and paper birches (*Betula populifolia* and *B. papyrifera*) and other hardwood species.

I made detailed observations on 5 pairs of Ovenbirds in 1970, 3 pairs in 1971 and 7 pairs in 1972. Other pairs were observed more casually. During 1971 and 1972 nine males were individually color-banded; I identified unbanded males by their location and distinctive songs. I followed a known individual or pair for extended periods, making a verbal record of behavior with a cassette recorder. The sex of unbanded birds could usually be determined from distinctive vocalizations or other behaviors (Hann 1937, this study). High-fidelity recordings of vocalizations for audiospectrographic analysis were made whenever possible with a Nagra IIIB tape recorder and a Norelco D-119ES cardioid dynamic microphone. The continuous observation periods were typically at least 30 min long, often lasting up to several hours, enabling me to determine the status of birds in the breeding cycle and to obtain a representative sample of their behavior. I was usually able to work within 15–30 m of the birds. They were visibly disturbed by my presence only when I moved too close to them or to a nest, or during the nestling and fledgling periods. Such disturbance was obvious from their behavior and I have allowed for it in interpretation of the results. Most observations were made during the period of maximum activity (between dawn and 11:00 EDT), but comparative observations were made at all times of the day.

During the continuous observations I noted locations of birds on their territories relative to mates, neighbors and nests—features of critical importance in interpretation of displays. Territorial boundaries were determined by noting song perches and locations of territorial disputes. I transcribed the observation tapes and tabulated all occurrences of each identifiable display, along with pertinent contextual details. Sonograms were made with a Kay Elemetrics 6061B audiospectrograph using the wide-band filter and high-shape setting over a frequency range of 160–16,000 Hz and were used to identify each vocalization. Because of the impossibility of eliminating background noise, I have used tracings of selected records for illustration, rather than the actual sonagrams.

In interpreting the functional significance of Ovenbird vocalizations, I follow the method of Smith (1965, 1977) in determining and classifying the messages encoded by displays. Readers unfamiliar with this terminology should consult these works.

I recorded 7 types of vocalizations (excluding song) from male Ovenbirds, and 6 from females. Since there is only 1 possible homology between the calls of the sexes, I describe them separately. The term recorded means that the vocalization was tape-recorded and identified from sonagrams. The entire sample of recorded vocalizations from birds of known sex and status has been included in the analysis.

RESULTS

Male vocalizations.—Seven vocalizations were distinguishable, in addition to "song" and "flight song."

(1) *Soft sip* (Fig. 1A–D).—*Soft sip* is a high-pitched call, virtually inaudible at distances of more than 15–30 m, or when there is wind or background noise. It is an extremely brief note, and may grade into *chep* by the addition of a stronger descending arm (see below).

I recorded *soft sip* on 20 occasions, but heard it frequently. Ten occasions involved a male interacting with his mate; 7 times the male was moving toward the female or was chasing her. Once a male gave a long series of *soft sips* following a copulation.

In 8 recorded cases "flight songs" were prefixed by a series of *soft sips*, and presumably identical vocalizations were heard prefixing other "flight songs." Hann (1937) noted a "few sharp chips" at the beginning of "flight songs."

I recorded *soft sip* only once during male-male encounters, given by a male flying toward a territorial boundary where his opponent was singing. Vocalizations believed to be *soft sip* were often heard during other encounters, but the rapid movements of males prevented recording such low volume sounds.

Soft sip was recorded in 2 other circumstances. Although I believe it was given by males on all occasions, none of these cases involved banded birds. Long sequences of *soft sip* were given twice, presumably by the same bird, in response to a screaming Broad-winged Hawk (*Buteo platypterus*) perched nearby. I recorded *soft sip* from birds scolding me at nests on 3 occasions. Known females never used this vocalization.

Weeden and Falls (1959) described a "sharp high-pitched note" given by males in response to other Ovenbirds or to human disturbance. This may be *soft sip*. Nice (1931) also noted a high-pitched *tchip* used by scolding males and commented that it graded into a lower-pitched *tchuck*, which probably is the same as *chep* (see below).

The common feature of all uses of *soft sip* seems to be a conflict between tendencies to fly and to engage in some other activity. This conflict may be the result of low light intensity (in association with "flight song," which is given primarily at dusk [Eaton 1957]), simultaneous attack and escape tendencies (during territorial encounters), or simultaneous tendencies to flee and to remain in place (in response to "predators" and mates). The display may thus indicate a state of indecision with regard to several behavioral alternatives, 1 or more of which may involve locomotion.

(2) *Chep* (Fig. 1H–L).—Some examples of this call show a slight ascending arm (Fig. 1K) or 1 or more rapid frequency modulations of the descending arm (Fig. 1L). All variations of the call may be used by the

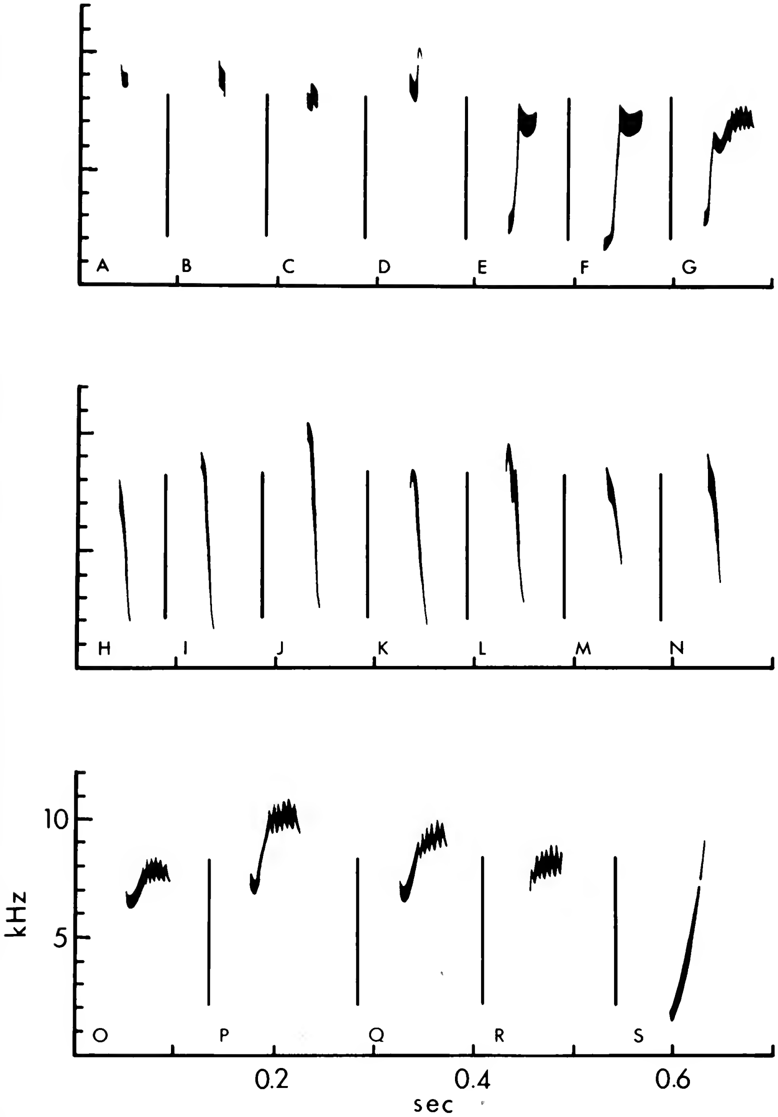


FIG. 1. Vocal displays of male Ovenbirds. A–D: *soft sip* vocalization. E–G: *Pink* vocalization. The example in G appears intermediate between *pink* and *seep*. H–L: *chep* vocaliztion. Different examples show the range of variation observed in this study. M–N: Intermediates between *soft sip* and *chep* vocaliztions. O–R: *seep* vocalization. The extreme variant in R was rarely recorded. S: *whip* vocalization.

same bird, or by different birds, in the situations described below. *Chep* is much louder than *soft sip* and may be heard at greater distances. *Soft sip* grades into *chep* through intermediates with short descending arms (Fig. 1M, N) that are higher-pitched and may be described as *chip* rather than *chep*. They are rarely used and thus are not described as a separate display.

Chep was recorded in 3 different circumstances. It was most common during territorial encounters and was given prior to, or during male-male chases; in several instances it seemed to be given in direct response to song of an opponent. It was used frequently during male-female interactions as well. Males gave it while perched near their mates or moving with them, and it was recorded on 4 occasions during chases of females by males. Its use in this situation resembles that of *soft sip*, but *soft sip* was given when the birds were in closer proximity. *Chep* was also used in response to my presence near a nest or fledged young; it was recorded 9 times and heard more frequently.

Various workers have described calls that are probably equivalent to *chep*. Weeden and Falls (1959) report a low-pitched *chuck* used at the end of male-male encounters. Stanwood (1911), Nice (1931) and Hann (1937) describe the calls of scolding males as "*cheh–cheh–cheh*," "*tchuck*" and "*chirp*," respectively.

Its frequent use during chasing indicates that *chep* may represent a message concerning the tendency to behave aggressively. The differences between the uses of *chep* and *soft sip* suggest that *chep* indicates a higher probability of aggressive behavior than that shown by *soft sip*. Otherwise, the messages of the 2 calls seem quite similar.

(3) *Pink* (Fig. 1E,F).—This is a sharp, explosive-sounding vocalization which ends with a characteristic "flag" produced by a short period of rapid frequency modulation.

Pink was recorded on 15 occasions during both male-male and male-female interactions. It was heard more frequently, but its similarity to *whink* (see below) prevents positive identification without the aid of sonagrams. Of the 5 recordings made during male-male encounters, 4 were prior to, or during chases. It was twice observed to occur in apparent response to a song by a nearby male. Once a male uttered *pink* as he moved toward an intruding male.

Pink was more common during male-female interactions. I recorded it in 9 such cases and heard it much more often. On 4 occasions the male was simply near the female; no interaction occurred. Twice, however, it was given by males chasing their mates. On 4 other occasions males gave *pink* as they approached their mates; twice the male was flying to copulate with his mate.

Pink was associated with both overt aggressive and sexual activity. It may be uttered just before a male flies to chase another male, or during hesitant flight as a male flies in to copulate with his mate, strongly suggesting that it indicates indecision regarding locomotion and in addition, provides a general message concerning the tendency to interact with the recipient. The cause of indecision appears to depend on the precise circumstances surrounding production of the display. The message may specify, as well, a conflict between escape tendencies and some alternate class of behavior (sexual or aggressive).

(4) *Seep* (Fig. 1O–R).—This is a brief vocalization characterized by its "jagged" terminal portion. Some variation is present in the different examples. In several cases the initial portion of the note was much reduced (Fig. 1R). One male gave several notes which appear to be intermediate between *seep* and *pink* (Fig. 1G), but no other intermediates were recorded.

Seep was recorded on 25 occasions; 20 of these involved male-female interactions. I recorded *seep* during 3 male-male encounters; on each occasion females were present and interacted with the males prior to, or during the encounters. The male giving *seep* in these latter cases had invaded another territory, apparently in response to on-going courtship activities of the residents. Once a male gave *seep* in the absence of a female during a break between bouts of male-female interaction. The only other recording of *seep* in the absence of a female was obtained when I inadvertently flushed a male who gave the call as he flew away.

This display is used primarily in male-female communication. In 14 of 20 such cases it was associated with movement toward the female; the remaining cases involved its use in close proximity to the female. It was often used in conjunction with *ple-bleep* and incomplete songs (see below). Several times it may have been given in response to female *high tsip* or *tsip series* (see below).

Seep is clearly connected with male-female interactions and the message probably specifies that the communicator will engage in a pair bond-limited subset of activities. It might appear that the display is indicative of a strong sexual tendency, but the call was never recorded in connection with copulation attempts. Therefore, the message probably does not specify sexual behavior, but may designate the likelihood of "association" behavior. *Seep* was often associated with flight and may thus also signal probable locomotion.

(5) *Whink* (Fig. 2A–C).—This call has a buzzy or nasal-sounding quality that is produced by repeated large frequency modulations occurring during the note. Some examples (Fig. 2B,C) vary slightly from the typical form (Fig. 2A). One recording (Fig. 2C) has an initial portion resembling that of

pink. Perhaps there is a relationship between these 2 calls although true intergradation was not recorded. *Whink* is usually given as a series of calls at a rate of about 5 vocalizations per sec.

Whink was used only by males, and in the absence of conspecifics only as a part of the introductory segment of "flight song" (Lein 1973). It was often associated with *ple-bleep* and "song" during both male-male and male-female interactions, but was equally frequent as an isolated display. I heard it more frequently during male-female interactions, but these, in turn, were more numerous than encounters between males.

Six of 9 recordings made during male-male encounters were obtained while active chasing or fighting was occurring. *Whink* was frequently heard during other kinds of chases. It also was recorded during male-female chases, twice involving apparently aggressive contact by the male with his mate. *Whink* was used in the introduction of "flight songs" given by males as they copulated with their mates on 2 occasions. *Whink* resembles *ple-bleep* in motivation and message and is discussed with the latter call.

(6) *Ple-bleep* (Fig. 2D–F).—This is a 2-note vocalization. The notes differ slightly in form; they resemble *whink* but are lower in frequency and different in sound.

Ple-bleep is individually distinctive. Fig. 2D–F shows typical calls of 3 males. No indication of significant intra-individual variation was seen; all examples for each male match that illustrated. Incomplete *ple-bleeps*, consisting of only the first note, were recorded rarely.

Ple-bleep is a regular part of the introduction of "flight song," along with *whink*. It was very common during male-male encounters; of 15 recordings made in such circumstances, 10 were during active chasing or fighting. On several occasions it was definitely the bird initiating a chase that gave the display. *Ple-bleep* was equally common during male-female interactions, and was heard during male-female chases. It was given more commonly by males very near to, or following their mates. It was also recorded during apparent copulation attempts, often along with incomplete "flight song."

Whink and *ple-bleep* were both recorded during intense male-male and male-female interactions. Their occurrence together in these situations and in "flight song," suggests that their motivation and messages are very similar. Were it not for their use in "flight song" and during successful copulations, it would be easy to conclude that these displays indicate an aggressive motivation and an attack message. Both *whink* and *ple-bleep* seemingly reflect ambivalence regarding locomotion. This indecision is especially apparent when the call is used during "flight song" and when the male approaches the female in an obviously hesitant manner. The

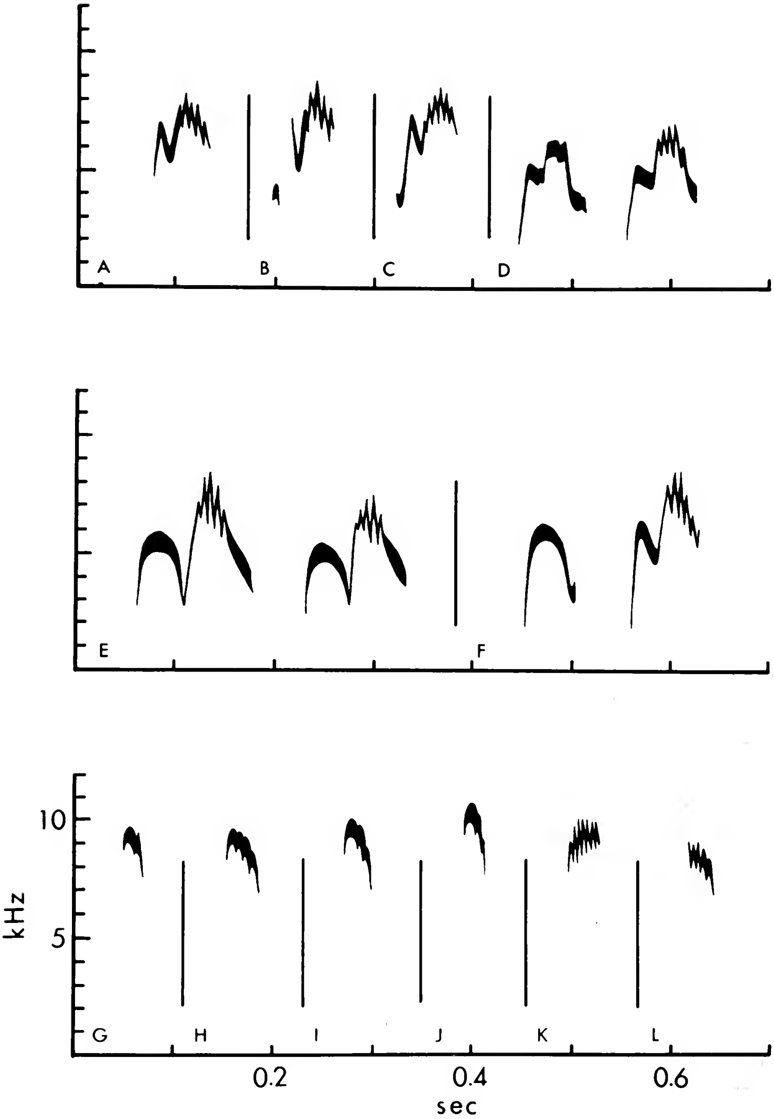


FIG. 2. Vocal displays of Ovenbirds. A–C: *whink* vocalization of males. D–F: *ple-bleep* vocalization of males. The 3 examples show the stereotyped differences that characterize the displays of individual males. G–J: Typical *high tsip* vocalization of females. K–L: *high tsip* variants with high frequency modulation rates.

displays would thus seem to encode messages of locomotory and indecisive behavior, both at high probability and intensity. The reason for the indecision should be available to the recipient from contextual information. There would also appear to be a message relating to a high probability of interaction involving contact.

Whink is given by itself more often than is *ple-bleep*. The latter display is usually preceded by several *whink* calls. This suggests the 2 displays encode different probability or intensity statements about the degree of locomotory indecisiveness, with *ple-bleep* perhaps specifying a higher probability of flight. The fact that the *ple-bleep* displays of different males are stereotyped in their detailed form implies that individual identification may be an important function of these calls.

(7) *Whip* (Fig. 1S).—*Whip* is a very low volume call which was recorded only once, although it may have been heard on several other occasions. The recorded calls were from a male moving and giving *soft sip* very near his mate. He gave *whip* twice after being chased by his mate. On another occasion a call that was probably identical was heard during a male-male chase. The number of observations is too few to determine the motivation or significance of this display.

Female vocalizations.—Six female vocalizations were distinguished.

(1) *High tsip* (Fig. 2G–J).—*High tsip* typically contains 3 or 4 frequency modulations producing a "saw-tooth" pattern on a sonagram. Infrequently I recorded notes with a more rapid modulation rate and an increase in frequency during their utterance (Fig. 2K). These notes were used in the same circumstances as the typical form and intergraded with it (Fig. 2L). *High tsip* also grades into *chep*; this transition is discussed with the latter display.

High tsip is the most common display of female Ovenbirds during male-female interactions. During the pre-incubation stages of the breeding cycle female Ovenbirds can be located with ease because of their persistent use of this vocalization. *High tsip* occurs most frequently as a response to the mate's songs when the birds are 15 m or more apart. It is also given irregularly as the pair moves together across the forest floor, sometimes in response to the mate's approach or in response to other male vocalizations such as *seep* or *whink*.

High tsip cannot be connected with any particular set of situations or motivational tendencies. It may encode a message specifying the female's readiness to associate with the male since it is used almost exclusively during the courtship period, or during other male-female interactions. There does not appear to be a more specific behavioral message encoded in the signal. One of the most important functions of this display may be the identification of the displaying bird as a female. The calls vary within individuals and are so similar among different birds that it is doubtful if individual identity is encoded.

(2) *Tsip series* (Fig. 4A,B).—This vocalization consists of a series of *high tsip* notes and is classified as a separate display because of its stereotyped form and distinguishable usage. It typically consits of 6–10 *high tsip* notes, but as many as 25 repetitions were recorded. A number of irregularly spaced *high tsips* usually follow it. The notes occur at intervals of about 0.1 sec at the start of the series; the rate of delivery and frequency of the notes decreases (Fig. 4B), giving the display a characteristic fading-out effect. Many examples of *tsip series* are preceded by a single *chep*.

Tsip series was used in situations similar to those of *high tsip* but with some noteworthy distinctions. All records of *tsip series* were obtained from females moving in close association with mates or responding to the actions of mates. As with *high tsip*, *tsip series* was used most conspicuously as a response to the mate's song. However, females used *tsip series* rather than *high tsip* when the male sang very near to them (within 15 m). It was also given frequently in response to a flight by the male toward the female, or in cases where the male was very near (within 3 m). Females also gave *tsip series* as they took off on short flights near a male.

The similarity of uses of this display and *high tsip* suggests that they encode similar messages. *Tsip series* encodes a message specifying association. The frequent conjunction of *tsip series* and flight, situations in which flight might be expected (as when a male suddenly flies toward the female), suggests an additional message of locomotory behavior. By vocalizing as she moves, or when her mate sings, a female can keep the male aware of her location and movements, thus maintaining contact. In addition, the display identifies the communicator as a female and may serve as a form of appeasement display that inhibits male aggression. Alternatively, it may allow the avoidance of misdirected attack from an aggressive male who suddenly encounters another Ovenbird and who may not immediately identify the conspecific as a female.

(3) *Chep* (Fig. 3A–K).—The female *chep* vocalization resembles that of males, but is distinguishable on sonagrams by the presence of a strong harmonic, which is usually reduced or absent in the male vocalization (see Fig. 1H). *High tsip* grades into *chep* by an increase in the descending terminal arm of the *high tsip* and a loss of the initial modulation (Fig. 3D–F). These notes are intermediate in pitch and the series may be represented by the verbal descriptions *tsip*, *chip* and *chep*. Intermediates are uncommon and are not described as a separate display.

Another variant of *chep* (Fig. 3G–K) begins at a lower frequency than the typical *chep* and shows a strong harmonic structure. Some examples (Fig. 3I, J) show an ascending arm, giving the note a chevron shape. These

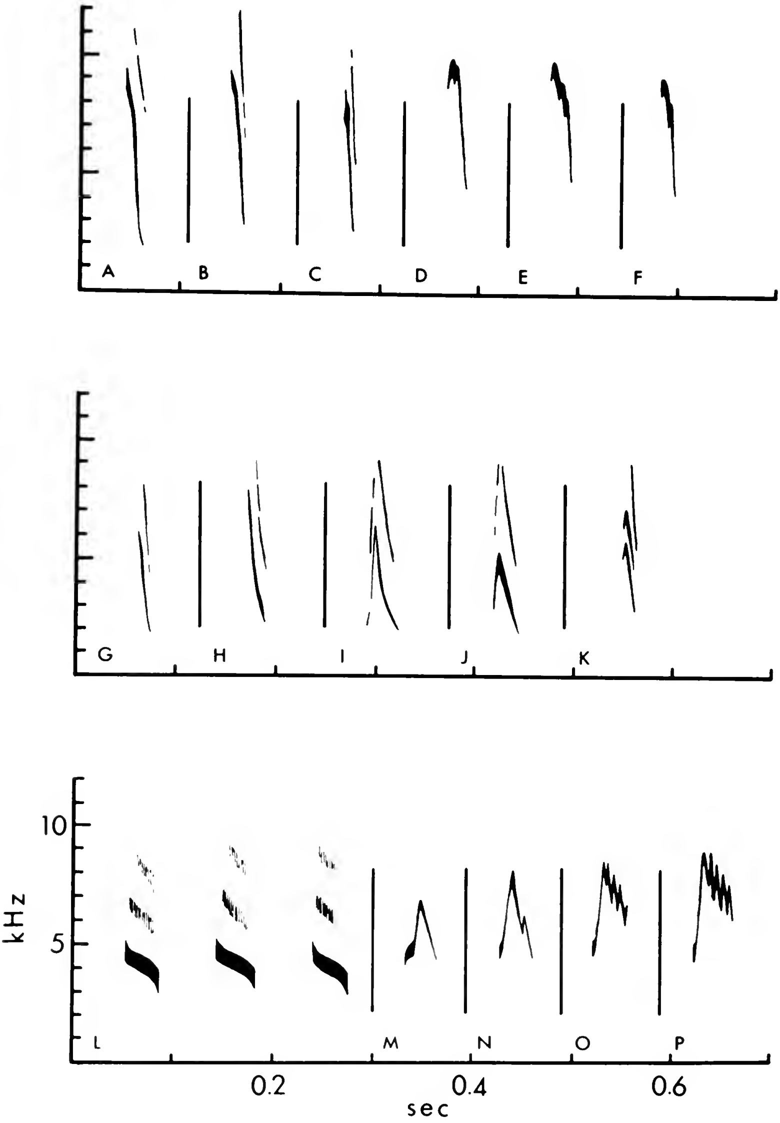


FIG. 3. Vocal displays of female Ovenbirds. A–C: *chep* vocalization. D–F: intermediates between *chep* and *high tsip* vocalizations. G–K: low frequency *chep* variants. L: "whimper" vocalization. Only 3 notes from a long series are illustrated. M–P: *seet* vocalization.

variants sound harsher than typical *chep* and may be described as *chup* or *chuck*. Full intergradation is demonstrated in the recordings of these variants. Hann (1937) commented that the *chirp* of female Ovenbirds when scolding was lower-pitched than that of males.

Females gave *chep* while moving with mates; transitions from *high tsip* to *chep* also occurred in this situation. Females used *chep* in response to a mate's song; *tsip series* given in similar circumstances was frequently prefixed by a single *chep*. *Chep* was given by females several times when they supplanted or chased their mates. In the only known female-female encounter during this study, vigorous chasing was accompanied by repeated *chep* vocalizations.

The other common use of *chep* was as part of the alarm reaction of female Ovenbirds to my approach to nests or fledglings. In these cases *chep* was given very vigorously and was continued until I moved away. This is the only situation in which the low frequency variants were recorded, although both types of *chep* were uttered by the same females on the same occasions.

Chep appears to encode messages relating to the relative probabilities of escape or attack behavior or, possibly, a more general message regarding the probability of locomotion without specifying the nature of the locomotory act.

(4) *Chitter* (Fig. 4C,D).—This display is a series of similar notes distinguishable from *tsip series* by the more rapid rate of delivery of the notes, and by the steady, rather than declining, rate of delivery. These 2 features produce a totally different sound impression, that of a continuous twitter rather than a series of distinct notes. The rarity with which this display was recorded leads to some ambiguity in its description. I recorded 2 distinct types of notes with the above patterning. Some examples (Fig. 4C) had *chip* notes with a long descending arm and little modulation of the fundamental frequency. Others (Fig. 4D) had highly modulated notes resembling *high tsip* notes in form but of a lower frequency. Once a bird switched from *chip* to *tsip* in the middle of a *chitter*. For this reason, plus the fact that the limited sample allows no separation by usage, the 2 types have been combined here.

On 5 occasions *chitter* was recorded from females giving a precopulatory display. At least twice it was followed by an apparently complete copulation. Females interacting with mates gave similar calls on other occasions, but ground vegetation prevented observation of the birds' postures or possible copulation attempts. Hann (1937) described the "mating call" of female Ovenbirds as a "series of chirps given in close succession." This description may include both *chitter* and *tsip series*.

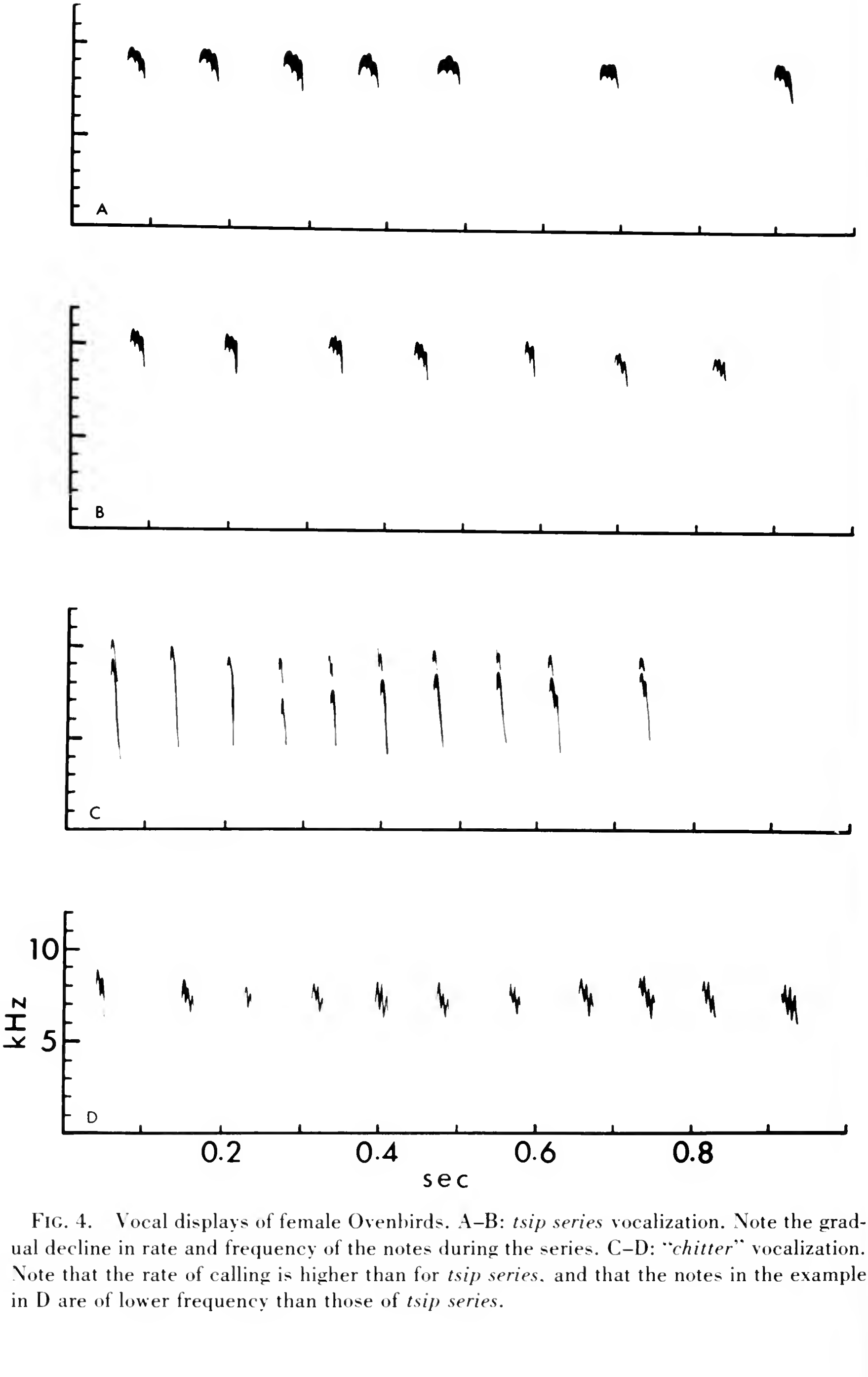


FIG. 4. Vocal displays of female Ovenbirds. A–B: *tsip series* vocalization. Note the gradual decline in rate and frequency of the notes during the series. C–D: "*chitter*" vocalization. Note that the rate of calling is higher than for *tsip series*, and that the notes in the example in D are of lower frequency than those of *tsip series*.

Chitter seems to be associated with a strong tendency on the part of the female to engage in sexual behavior. The message may be as specific as this would imply, but the use of this vocalization with the precopulatory display suggests a message concerning inhibited locomotor tendencies as well.

(5) "Whimper" (Fig. 3L).—This is a very soft vocalization, audible only within 5–10 m. The individual notes consist of a fundamental plus at least 2 weaker harmonics, and are repeated in long series lasting up to several seconds. "Whimper" was heard only once. A female gave it repeatedly during a strong distraction display as I banded the young in her nest. The significance of this vocalization is uncertain.

(6) *Seet* (Fig. 3M–P).—*Seets* are chevron-shaped notes that vary in the amount of modulation of the descending arm. The highly modulated notes have the highest peak frequency. Those notes lacking modulation (Fig. 3M) may be described as *chip*. All the notes illustrated were recorded in a single series lasting less than 2.0 sec, given by a female during an intense distraction display.

DISCUSSION

The Ovenbird is a remarkably vocal species, with regard to both the variety and frequency of vocal displays. I have described 13 different vocalizations in the present paper. Two distinct types of songs can also be recognized (Hann 1937, Lein 1973), giving a total of at least 15 vocal displays used by breeding birds. There are also several vocalizations used by nestlings and fledglings in begging or alarm situations (Nice 1931, Hann 1937). Various postures and other visual displays are also used (Hann 1937, Freeman 1950, Lein 1973), suggesting a total display repertoire as large as that of many social vertebrates (Smith 1969a, Moynihan 1970). It is clear that vocal communication is a major component of behavioral interaction among Ovenbirds. It thus warrants careful attention in any consideration of the evolutionary forces shaping the behavior of the species.

Table 1 summarizes the non-song vocalizations of adult Ovenbirds and the situations in which they are used, as determined by this investigation. Three points are worthy of special attention. First, there is almost no overlap between the vocal repertoires of the sexes. Only *chep* may be homologous in the 2 sexes and even it shows what appear to be sex-specific differences.

I suggest that this non-overlap of repertoires assists in sex recognition in a species which is monomorphic in appearance. Hamilton (1961) has argued that sexual dimorphism in plumage in migratory, temperate-zone parulids is an adaptation insuring unambiguous sex recognition, resulting

TABLE 1

SUMMARY OF THE VOCALIZATIONS OF BREEDING OVENBIRDS AND THE SITUATIONS IN WHICH THEY ARE USED

		Situation					
Vocalization	Sex	Male-female association	Copulation	Male-female chases	Male-female interactions	Alarm reactions	"Flight song"
Soft sip	M	++[a]	+	++	+	+	+
Chep	M	+		++	++	++	
Pink	M	++	+	+	+		
Seep	M	+++			+	+(?)	
Whink	M	++	+	+	++		+
Ple-bleep	M	++	+	+	++		+
Whip	M	+					
High tsip	F	+++					
Tsip series	F	++		+			
Chep	F	+		+		++	
Chitter	F	++	+				
"Whimper"	F					+	
Seet	F					+	

[a] The number of plus (+) symbols indicates the relative frequency of uses for that vocalization only, and do not refer to comparisons between vocalizations.

in a simplified and shorter courtship in species which face a breeding season of restricted duration. I believe that Ovenbird vocalization represents an alternate solution to this problem. Ovenbirds provide information regarding the sex of an individual through sexually-dimorphic vocalizations rather than through distinctive male and female plumages. My comparative investigations of other warblers support this suggestion. The Chestnut-sided Warbler (*Dendroica pennsylvanica*), a sexually-dimorphic species, has at least 6 vocalizations used in male-female interactions, of which 3 are identical in both sexes (Lein 1973). This compares with 1 shared vocal display out of 11 recorded in such encounters in the Ovenbird (Table 1). A similar explanation has been proposed for sexually-dimorphic vocalizations in the monomorphic Black-capped Chickadee (*Parus atricapillus*) (Ficken et al. 1978).

This reliance on vocal labels of sex identity may be related to the terrestrial habits of the Ovenbird. Sexual dimorphism in wood warblers generally involves a rather brightly-colored or conspicuous male plumage. If the olive-brown coloration of Ovenbirds indeed serves as camouflage, such an evolutionary option might be precluded. Vocalizations, unlike plumage patterns, can be turned off or on at will. However, this means that sexually-monomorphic birds may have to vocalize more frequently in order to provide relatively continuous information on their sexual identity, especially during close encounters. This suggestion is supported by my observation that female Ovenbirds are much more vocal during the pre-incubation period than are females of the sexually-dimorphic warblers I have studied (Lein 1973).

Table 1 also demonstrates the second point, that most vocalizations are used in a variety of situations. As intensive studies of complete display repertoires accumulate it is becoming evident that this is a general phenomenon (Smith 1977) and that the concept of each display possessing a single, precise meaning (e.g., "threat" display) is unlikely to be true in most cases. It appears that evolutionary pressures related to the misinterpretation of extremely similar displays and problems associated with very rare displays may restrict the total size of display repertoires (Smith 1969a, Moynihan 1970). Therefore, selection may favor displays that encode rather general messages which can be interpreted in various ways, depending on the recipient and on contextual information (Smith 1977:189). My findings on Ovenbirds are clearly in accord with this suggestion. Most displays were recorded in such a variety of situations that it is difficult to extract features that are common to all their usages. The messages that I suggest are thus very broad, the most common being one relating to the probability of locomotion. This message seems to be particularly common in the repertoires of other species as well (Smith 1969b).

The results of the generalized messages encoded by Ovenbird displays is that the effectiveness of communication must depend very heavily on contextual information available to recipients. Although detailed information on the responses of different classes of recipients to the same display is not available for the Ovenbird (or for most other species), the fact that identical vocalizations are given by male Ovenbirds in situations as different as territorial fights and copulation attempts suggests that contextual information must be critical for efficient communication. Important contextual variables are likely to include spatial features such as the location of the interaction in relation to territory boundaries, nests or mates, and temporal features such as immediately preceding events or the history of interactions between the individuals. Detailed studies of response of different recipients to the same display is a critical next step in increasing our understanding of the communication process.

The third point is the large proportion of vocal displays that are used in male-female interactions. Eleven of 13 vocalizations are used in such situations, a higher proportion than in other warblers I have studied (Lein 1973). This suggests that the pre-incubation period, which is when most male-female interactions occur, may involve rather difficult behavioral adjustments between the members of the pair and that, therefore, a major portion of the space in the limited total repertoire has been "allotted" by natural selection to this important behavioral task. This idea is supported by the high proportion of their time that the members of Ovenbird pairs spend in association and interaction during this phase of the breeding cycle (83.4% of 452 min of observation on birds whose exact breeding status was known) in comparison to the dimorphic Chestnut-sided Warbler (16.4% of 373 min).

SUMMARY

During a 3-year study of the behavior of Ovenbirds in New England, 13 non-song vocalizations were recorded from breeding adults. Most of these vocal displays are used in a broad range of situations, suggesting that they encode very general messages and that specificity in communication depends largely on the nature of the recipient and on contextual information. Most of the vocalizations are restricted to a single sex, possibly to assist in sex recognition in a species that is monomorphic in appearance. The use of 11 of the 13 vocalizations in male-female interactions suggests that pair-formation and courtship in this species involve complex behavioral adjustments.

ACKNOWLEDGMENTS

I thank Professor Ernst Mayr, my graduate supervisor, for his support and encouragement in all phases of this study. I am also grateful to Professor and Mrs. Mayr for permitting my invasion of their summer retreat during 3 field seasons. W. John Smith provided valuable guidance regarding techniques and theoretical approaches, and improved the manuscript with his critical comments, as did Thomas E. Dickinson. Facilities and equipment were made available by the Museum of Comparative Zoology, Harvard University. Financial support was provided by Harvard University, the Carl A. and Katharine F. Richmond Fund, and National Science Foundation Grants GB7346 and GB19922 to Harvard University (R. C. Rollins, Principal Investigator).

LITERATURE CITED

BENT, A. C. 1953. Life histories of North American wood warblers. U.S. Natl. Mus. Bull. 203.

EATON, S. W. 1957. A life history study of *Seiurus noveboracensis*. St. Bonaventure Univ., Sci. Stud. 19:7–36.

FICKEN, M. S., R. W. FICKEN AND S. R. WITKIN. 1978. Vocal repertoire of the Black-capped Chickadee. Auk 95:34–48.

FREEMAN, F. J. 1950. Display of Ovenbirds, *Seiurus aurocapillus*. Auk 67:521.

GRISCOM, L. AND A. SPRUNT, JR. (eds.). 1957. The warblers of America. Devin-Adair Co., New York, New York.

HAMILTON, T. H. 1961. On the functions and causes of sexual dimorphism of North American species of warblers and orioles. Am. Nat. 95:121–123.

HANN, H. W. 1937. Life history of the Oven-bird in southern Michigan. Wilson Bull. 49:145–237.

LEIN, M. R. 1973. The biological significance of some communication patterns of wood warblers (Parulidae). Ph.D. thesis, Harvard Univ., Cambridge, Massachusetts.

MOYNIHAN, M. 1970. Control, suppression, decay, disappearance and replacement of displays. J. Theoret. Biol. 29:85–112.

NICE, M. M. 1931. A study of two nests of the Ovenbird. Auk 48:215–228.

SEBEOK, T. A. (ed.). 1977. How animals communicate. Indiana Univ. Press, Bloomington, Indiana.

SMITH, W. J. 1965. Message, meaning, and context in ethology. Am. Nat. 99:405–409.

———. 1969a. Messages of vertebrate communication. Science 165:145–150.

———. 1969b. Displays and messages in intraspecific communication. Semiotica 1:357–369.

———. 1977. The behavior of communicating. Harvard Univ. Press, Cambridge, Massachusetts.

STANWOOD, C. J. 1911. Time of incubation of the Ovenbird. J. Maine Ornithol. Soc. 13:18–20.

WEEDEN, J. S. AND J. B. FALLS. 1959. Differential responses of male Ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76:343–351.

DEPT. BIOLOGY, UNIV. CALGARY, CALGARY, ALBERTA T2N 1N4 CANADA. ACCEPTED 1 FEB. 1979.

LOUIS AGASSIZ FUERTES, MARGARET MORSE NICE AND PAUL A. STEWART AWARDS

The Wilson Ornithological Society announces the availability of three awards for 1981. Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists, particularly for the development of research interests among amateur ornithologists and students. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic institutions. Each proposal is considered primarily on the basis of possible contribution to ornithological knowledge. Although grantees are not required to publish their studies in *The Wilson Bulletin*, it is hoped that they will submit their manuscripts to the editor of *The Wilson Bulletin* for consideration.

Most statements applicable to the Fuertes Awards also apply to the Nice Award. However, the Nice Award is limited to applicants not associated with a college or university. It is intended to encourage the independent researcher without access to funds generally available at colleges. High school students are eligible.

The Paul A. Stewart Awards will be awarded to support investigations pertaining to economic ornithology and studies of bird movements based on banding and analyses of recoveries and returns. Stewart Awards will be equally available to students, amateurs and professionals.

One Nice, 1–2 Fuertes and several Stewart Awards will be granted. Amount given for each award is $200.00. Interested persons may write to Carl D. Marti, *Dept. Zoology, Weber State College, Ogden, Utah 84408.* Completed applications must be received by 1 March 1981. Final decisions will be made by the Council of The Wilson Ornithological Society at the annual meeting of the Society, June 1981.

Wilson Bull., 92(3), 1980, pp. 330–340

FEEDING OF SECONDARY NESTLINGS BY POLYGYNOUS MALE BOBOLINKS IN OREGON

James F. Wittenberger

The manner by which individuals allocate their reproductive efforts to maximize fitness has recently attracted much attention in studies of animal behavior (Trivers 1972, Pianka and Parker 1975, Dawkins 1976, Stearns 1976, Wittenberger 1979). One important aspect of reproductive effort in birds is parental care of nestlings. The parental behavior of monogamous birds involves optimizing brood size, maximizing food delivery rates and enhancing protection from adverse weather, brood parasitism, or predation. In polygynous species males also have opportunities for distributing parental care among several concurrent sets of offspring, perhaps optimizing the distribution of their care among broods.

Bobolinks (*Dolichonyx oryzivorus*) are single-brooded polygynous birds that breed in a broad range of grassland habitats. In Wisconsin polygynous males feed their primary nestlings (i.e., those of their first mates) almost exclusively (Martin 1971, 1974). Only rarely do they deliver food items to secondary nestlings (i.e., those of their second mates). I report here that polygynous male Bobolinks in Oregon regularly provision both primary and secondary nestlings, and I examine some of the conditions associated with this behavior.

Polygynous males should theoretically deliver each load of food to the brood in which it will produce the largest incremental gain in male fitness. Since older nestlings have higher reproductive value, males should deliver most food items to primary nestlings, unless other factors have overriding importance (Willson 1966). One potentially overriding factor is the relative nutritional condition of primary and secondary broods. If primary nestlings are relatively satiated with food while secondary nestlings are undernourished, males might gain more by delivering the food to their secondary nestlings. Factors affecting the nutritional condition of primary and secondary nestlings would then be important in determining how polygynous males distribute food among their broods. Such factors may include brood size, weather conditions and food availability, all of which will be evaluated here.

STUDY AREA AND POPULATION

My study comprised 27.3 ha of mesic meadow 2 km NW of P-Ranch Patrol Station on Malheur National Wildlife Refuge, 100 km S of Burns, Oregon. The study site was situated in the area occupied by the earliest males and females to arrive on the refuge each spring (1973–1976), and it supported the highest breeding densities of both males and females on the refuge (Wittenberger 1976, 1978).

The habitat consisted of grassy meadows intermixed with conspicuous patches of sedge (*Carex* spp.) that grow in poorly drained places. Predominant forb species were dandelion (*Taraxacum officinale*), cinquefoil (*Potentilla glomerata*), yarrow (*Achillea millefolium*), thistle (*Cirsium arvense*), dock (*Rumex crispus*) in the wetter areas, cow parsnip (*Heracleum lanatum*), red clover (*Trifolium pratense*) and vetch (*Vicia americana*).

The study area was irrigated with a consistent water supply from March or April until late June each year, resulting in flooding of peripheral areas adjacent to where Bobolinks bred. It was also grazed by cattle in autumn and winter, though not while Bobolinks were present, and mowed for hay in late summer.

The Bobolink population at Malheur Refuge is an isolated one consisting of from 90–150 adults of each sex, depending on the year. From 20–27 males bred each year on my study area, of which 6–17 were polygynous. Only 2 males ever attracted 3 mates, both in 1975. Breeding is highly synchronous. Females selected mates from about 20 May to 10 June, and nests contained nestlings from about 11 June to 7 July. Additional details of Bobolink breeding biology on the refuge are presented elsewhere (Wittenberger 1978).

METHODS

Individual males and females were identified by both colored plastic leg bands and by unique plumage characteristics. All males and about half of all females discussed here were banded. In 1973 males were also marked on their scapulars with green or red Esterbrook Flo-Master ink to facilitate individual recognition from a distance.

Territories were mapped by flushing territorial males and recording at least 20 points where they landed (see Wiens 1969). Pair bonds were ascertained from prolonged association of a female with a particular male and, when possible, by the occurrence of copulations. Polygynous pairings were verified by simultaneous observation of all mates on a territory and by locating nests.

Nests were found by watching females return to them at dusk, by watching females carrying nest materials and by accidentally flushing females from them. Nest contents were monitored daily at mid-day. Nestlings in each nest were weighed collectively with a triple-beam balance to the nearest 0.1 g. Nestlings were assumed to have died of exposure when found dead with rain-soaked bodies and full stomachs. They were assumed to have starved when found with empty stomachs or when they disappeared singly during mild weather (known predators took entire broods). Predation was inferred from losses of entire broods and from signs of disturbance around the nest.

Observations of parental behavior were made with binoculars from blinds mounted on 2 stationary 2-m tall towers, from a small portable blind and from the top of a step-ladder placed 75–125 m from the nearest nest under observation. Food items fed to nestlings were identified with 10× binoculars from a blind placed about 5 m from the nest.

Food abundance was sampled in 1975 and 1976 with a 38-cm diameter sweep net. In both years 2 samples of 50 sweeps were taken daily on each of 14 contiguous territories in the area where most polygynous matings occurred (1 sample was taken at random on each half of each territory). Caterpillar biomass was calculated by regression analysis after measuring specimen lengths, drying specimens of each length until no further weight reductions could be obtained and weighing specimens to the nearest 0.1 mg (see Wittenberger 1976).

RESULTS

Male feeding of secondary nestlings.—All polygynous males fed secondary nestlings in 1973, 1974 and 1975, but only 1 of 5 did in 1976. They began feeding secondary nestlings when their primary nestlings reached

TABLE 1
AGE OF PRIMARY AND SECONDARY YOUNG OF POLYGYNOUS MALES AT THE TIME THEY BEGAN FEEDING SECONDARY NESTLINGS[1]

Year	No. of polygynous males	No. of males that fed secondary young	Age of primary young (range)	Age of secondary young (range)
1973	4	4	10[2]	4–6
1974	4	4	7[2]	1–4
1975	5	5	12–13	7–10
1976	5	1	15	8

[1] Data include all territories on which both nests were found; in 1975 and 1976 many polygnous males were not included because either their primary or their secondary nest was destroyed by flooding, or predators at an early stage.

[2] Age of primary nestlings was the same for every male.

a specific age that differed each year (Table 1). No relationship between age of secondary nestlings and the beginning of male assistance at secondary nests was evident.

Polygynous males continued to feed nestlings and fledglings from their primary nests after beginning to feed secondary nestlings. I did not examine this behavior closely in 1973, but 1 indication that males continued feeding primary fledglings that year was the discovery of a 13-day-old banded fledgling in 1 male's secondary nest. That fledgling had been reared in the male's primary nest about 23 m away. In 1974 and 1975 every male continued feeding primary fledglings while feeding secondary nestlings. In 1975 I determined that 4 of 5 males were feeding only 1 primary fledgling at the time they began feeding their secondary nestlings. I did not ascertain how many were being fed by the remaining male. The primary fledglings fed by each male were not being fed by the corresponding primary female. Bobolinks divide their broods a few days after fledging, with each parent exclusively feeding about half the brood (Martin 1971, pers. obs.).

Nutritional condition of nestlings.—One indication of a nestling's nutritional condition is its weight at a standard age. The mean weight of 10-day-old primary nestlings just prior to forced fledging was similar in 1973 and 1974, but was significantly lower ($P < 0.05$) in 1975 and 1976 (Table 2). The fledging weights of all nestlings belonging to both monogamous and polygynous males were used for this analysis because they did not differ significantly as a function of male mated status. The data for 1975 were analyzed separately for early and late nests because young that hatched more than 5 days before a storm of 13–25 June ended, fledged at significantly lower weights. The primary nestlings of all polygynous males studied that year were hatched in early nests.

TABLE 2
MEAN NESTLING WEIGHTS ± SD (G) JUST PRIOR TO FLEDGING ON DAY 10 POST-HATCHING[1]

Year	Primary nests[2]	Secondary nests[2]
1973	23.5 ± 2.3 (5)[a]	24.2 ± 1.9 (4)[a]
1974	24.0 ± 1.5 (17)[a]	22.8 ± 2.2 (3)
1975 (early)[3]	20.0 ± 1.4 (6)[b]	—
1975 (late)[3]	23.3 ± 0.8 (7)[a]	19.4 ± 2.1 (4)[b]
1976	20.7 ± 2.2 (9)[b]	22.2 ± 0.1 (2)

[1] Significant differences between years are indicated by superscripts for each status of nests, with a > b (Student's *t*-test, $P < 0.05$). Number of nests is given in parentheses.

[2] Standard deviation indicates variability between broods, not nestlings.

[3] Early nests hatched more than 5 days before a rainstorm of 13–25 June ended; late nests hatched fewer than 5 days before a rainstorm of 13–25 June ended.

Males delivered as much food as females to older secondary nestlings in 1973 and 1974, and this probably accounts for the high fledging weights of secondary nestlings in those years. The low fledging weights of secondary nestlings in 1975 reflect the lateness that males began feeding them. In 1976 brood reductions caused smaller brood sizes in secondary nests, and this probably allowed secondary females to deliver as much food per nestling as the male and female combined could deliver to primary nests.

A second indication of a nestling's nutritional condition is the strength of its gaping response. Both primary and secondary nestlings nearly always displayed very strong gaping respones in 1975 and 1976, but they rarely did so in 1973 or 1974. In the former 2 years nestlings always extended their necks to the fullest extent possible and gaped vigorously whenever I visited the nest (except in the late nests in 1975). In 1973 and 1974

TABLE 3
NESTLING MORTALITY RATES FOR POLYGNOUS AND MONOGAMOUS MALE BOBOLINKS

	Primary nests of polygynous males			Secondary nests of polygynous males			Nests of monogamous males		
		% mortality			% mortality			% mortality	
Year	No. nestlings (and nests)	All causes	Starved	No. nestlings (and nests)	All causes	Starved	No. nestlings (and nests)	All causes	Starved
1973	25 (5)	0.0	0.0	26 (5)	7.7	7.7	67 (14)	9.0	0.0
1974	39 (8)	2.6	0.0	23 (5)	34.8	8.7	66 (12)	10.6	3.0
1975	59 (11)	50.8	1.7	61 (13)	55.7	29.5	47 (9)	65.7	2.1
1976	60 (11)	45.0	5.0	49 (12)	73.3	32.7	23 (4)	56.5	39.2

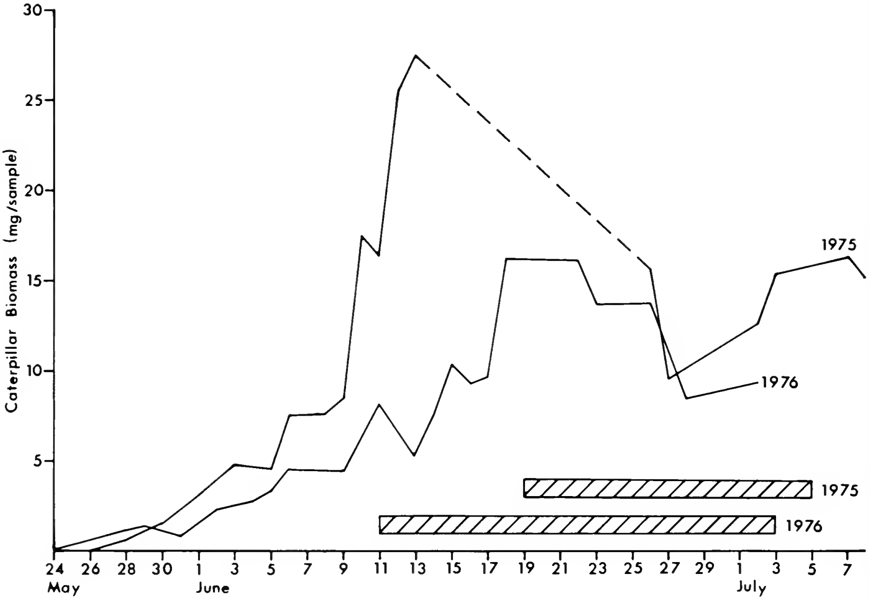


FIG. 1. Relative abundance of caterpillars on the study area during 1975 and 1976. Diagonally-hatched bars indicate the period when primary nests contained young each year. The dashed line from 13–25 June 1975 spans a period of continuous rainstorms when samples could not be taken.

nestlings never extended their necks fully, and they exhibited little or no gaping response when I visited the nest.

Few primary nestlings of polygynous males starved in any year of the study, but significantly more nestlings of nearby monogamous males starved in 1976 than in 1973–1975 (Table 3). The territories of monogamous males were often adjacent to those of polygynous males, but many were in wetter areas, 100–400 m from the mesic meadows occupied by polygynous males (Wittenberger 1976). Starvation rates were markedly higher among secondary nestlings in 1975 and 1976 than in 1973 or 1974, possibly because males provided them with less food in the former 2 years.

Food availability.—The preferred food items fed to nestling Bobolinks are lepidopteran and sawfly (Tentridididae [Hymenoptera]) caterpillars (Wiens 1969, Martin 1971, Wittenberger 1978). The diet of nestlings on my study area consisted of 65.6% caterpillars in 1974 (N = 2318), 59.0% in 1975 (N = 2064) and 54.2% in 1976 (N = 2818). I did not record the types of food items delivered to nestlings in 1973. The proportion of caterpillars in the nestling diet was significantly different every year (χ^2 =

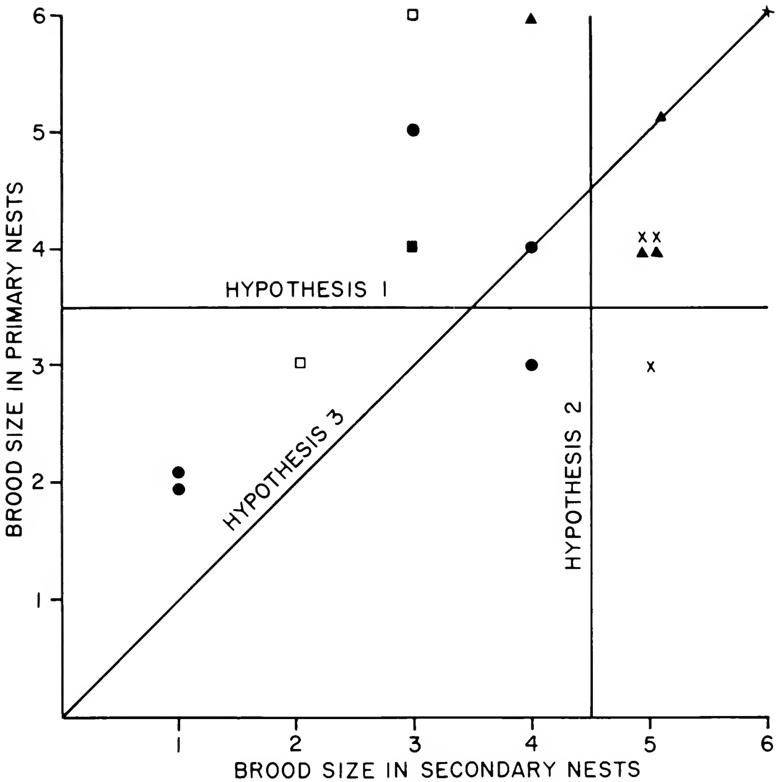


FIG. 2. A test of 3 hypotheses relating brood size to the propensity for males to feed secondary nestlings (see text). An hypothesis is supported if all points fall to the right or below the line representing it. X = 1973, ▲ = 1974, ● = 1975, ■ = 1976. □ = instances when males did not feed their secondary nestlings at all. In cases where males began feeding secondary nestlings after their primary nestlings had fledged, brood size for the primary nest was assumed equal to the number of young that had successfully fledged because fledgling mortality could not be monitored.

68.9, df = 2, $P < 0.001$), suggesting that caterpillars were less available relative to alternative food resources in the latter 2 years.

Caterpillar densities were sampled with a sweep net only in 1975 and 1976. A quadrat sampling method used in 1974 proved unsatisfactory, and caterpillars were not sampled in 1973.

In 1975 caterpillar densities increased exponentially, until shortly before nestlings hatched, and then declined markedly during the continuous heavy rains and cold weather of 13–25 June (Fig. 1). Caterpillar densities increased again after the storm ended, but they never reached the level

TABLE 4

RATE THAT POLYGYNOUS MALES FED THEIR SECONDARY NESTLINGS AS A FUNCTION OF BROOD SIZE IN THEIR PRIMARY NESTS[1]

Brood size in primary nest	No. males	H of observation	Mean brood size in secondary nest	Mean age of secondary broods	Trips/h to secondary nest[2]
4	3	16	4.96	6.7	5.49
5	2	22	5.00	2.5	1.92
6	2	20	4.50	6.0	0.40

[1] Data based on first 2 days that males fed seondary nestlings (only data from 1973 and 1974 were used).

[2] Trips/h differ significantly at $P < 0.001$ between all sizes of primary broods (Student's *t*-test).

prior to the storm. In 1976 caterpillar densities were even lower than in 1975, despite fair weather throughout June and July.

Brood size in primary and secondary nests.—The impact of male food deliveries on nestling survival should be a function of brood size. Females should be better able to feed small broods without male assistance, other factors being equal, so small broods in the primary nest or large broods in the secondary nest should increase the propensity for polygynous males to feed secondary nestlings.

I examined 3 hypotheses relating brood size to the occurrence of male feeding of secondary nestlings: (1) males begin feeding secondary nestlings when brood size in the primary nest drops below a specific level; (2) males begin feeding secondary nestlings when brood size in the secondary nest exceeds a certain level and (3) males begin feeding secondary nestlings when brood size in the secondary nest exceeds that in the primary nest. I chose as my threshold levels a brood size of 4 primary nestlings for hypothesis 1 and a brood size of 4 secondary nestlings for hypothesis 2, but any other level can be evaluated with the same data.

I tested the 3 hypotheses by plotting the brood size present in each male's primary nest at the time he began feeding secondary nestlings against brood size in the same male's secondary nest at that time (Fig. 2). The results do not fit any of the 3 hypotheses, regardless of which specific brood size or combination of brood sizes is postulated as the threshold stimulus.

Although brood sizes in a male's primary and secondary nests evidently do not determine whether a male will feed secondary nestlings, they may affect the amount of effort he invests in each brood. Data taken during the first 2 days of male assistance at secondary nests indicate that the amount of care allocated to secondary nestlings is inversely related to brood size in the corresponding primary nest (Table 4). Sample sizes were

TABLE 5
MORTALITY OF NESTLINGS CAUSED BY PREDATION AND FLOODING CONVERTED TO A DAILY RATE

	1973	1974	1975	1976
Primary nests				
Number of nestlings	92	97	106	83
Predation	0	4	5	16
Adverse weather	2	3	53	12
Total due to environmental hazards	2	7	58	28
No. of nestling-days	794	947	685	649
Risk of mortality/day	0.003	0.007	0.085	0.043
Secondary nests				
Number of nestlings	26	23	61	49
Predation	0	0	0	17
Adverse weather	0	7	16	3
Total due to environmental hazards	0	7	16	20
No. of nestling-days	243	178	398	290
Risk of mortality/day	0.000	0.039	0.040	0.069

not sufficient to control for nestling age or other factors and the data are based on relatively few males, but these variables are unlikely to explain the large differences observed. The data for males with primary broods of 5 young were based on younger secondary nestlings, but males fed 7–8 day old primary nestlings only 30% faster than 2–3 day old primary nestlings (N = 248 nest-h of observations), suggesting that age alone is not responsible for the observed difference.

Relative reproductive value of primary and secondary nestlings.—The reproductive value of secondary nestlings decreases relative to that of primary nestlings when hatching interval between primary and secondary nests increases or when nestling mortality caused by predation or flooding increases. The mean interval between hatching of primary and secondary nestlings of polygynous males was 6.0 days in 1973 (N = 5, range = 4–9), 4.4 days in 1974 (N = 5, range = 3–6), 3.8 days in 1975 (N = 10, range = 2–5) and 7.2 days in 1976 (N = 5, range = 3–9). The interval averaged significantly longer in 1973 and 1976 than in 1975 (Student's *t*-test, $P < 0.05$).

Mortality of secondary nestlings caused by predation and flooding was low in 1973, intermediate in 1974 and 1975 and high in 1976 (Table 5). Mortality risk per nestling-day was calculated by dividing the number of nestling-days monitored each year into total mortality. The risk per day was higher for secondary than for primary nestlings in 1974 and 1976, lower in 1975 when many primary nestlings hatched during heavy rainstorms and similar in 1973. Much of the predation in 1976 was by a single pair of Sandhill Cranes (*Grus canadensis*) that fed regularly on the study area that year. (In the previous 3 years cranes were absent from my study area.)

An index of relative reproductive value of secondary nestlings was calculated as R × I, where R = mortality risk/day and I = mean hatching interval between primary and secondary nests. The index represents the cumulative probability that the secondary nest will fail due to predation or flooding before it reaches the stage already reached by the primary nest. The higher the index value, the lower is the relative reproductive value of secondary nestlings that year. The index values are 0.00 for 1973, 0.17 for 1974, 0.15 for 1975 and 0.50 for 1976.

DISCUSSION

The results show that males adjust the distribution of their parental allocations according to prevailing conditions. Polygynous males began feeding secondary nestlings when their primary nestlings reached a specific, but different, age each year, suggesting that the nutritional condition of primary nestlings is important in determining how polygynous males distribute their parental investments. Additional evidence supports the same conclusion. Primary nestlings fledged at significantly heavier weights and exhibited noticeably weaker gaping responses in the 2 years (1973, 1974) when polygynous males began feeding secondary nestlings earliest, and nestling starvation was highest in the year (1976) when most polygynous males did not feed secondary nestlings at all.

The behavior of polygynous males just prior to feeding secondary nestlings shows that males could be responding directly to the condition of primary nestlings. Before delivering food at their secondary nests, polygynous males almost invariably landed first near their primary nests and cocked their heads downward, apparently listening for the high-pitched squeaks given by hungry nestlings. Then they usually flew to their secondary nests and fed the nestlings there, although sometimes they dropped down and fed their primary nestlings instead. Occasionally males showed similar behavior before going off to forage, first perching near the primary nest and then perching near the secondary nest, cocking their heads each time. Upon returning with food, they usually repeated the sequence before finally feeding their secondary nestlings. In 1 extreme instance a male flew back and forth between his primary and secondary nest 4 times, landing and cocking his head each time, before finally feeding his secondary nestlings.

The annual variations in nestling condition may have resulted from annual variations in food availability and weather conditions. The poor condition of primary nestlings in 1975 was associated with cold rainy weather during mid-June, which reduced caterpillar abundance and probably also increased the maintenance energy requirements of nestlings. In 1976 caterpillars were even less abundant than 1975, and again nestlings were undernourished (despite fair weather).

Brood size per se in the primary and secondary nest does not act as a proximate stimulus for evoking the onset of male parental care at secondary nests, but brood size in the primary nest does appear important in determining how much food males deliver to secondary nestlings. Patterson, Erckmann and Orians (in press) found that polygynous male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) shift their parental care to secondary nests following experimental reduction of primary broods, but this response appears to differ from that of male Bobolinks. Only 1 of 7 male Bobolinks on my study area abandoned his primary nest entirely following natural brood reductions, and none did so in Martin's (1971) study area. That male abandoned his 7-day-old primary nestlings after 4 of 6 had died. His secondary nest contained six 5-day-old nestlings when he began feeding them exclusively. None of his primary nestlings fledged, but 5 of his secondary nestlings did.

The relative reproductive value of secondary nestlings may affect whether males deliver food at secondary nests, since it was lowest in the 1 year when males failed to feed secondary nestlings. However, the earliness that males began feeding secondary nestlings in the other nests was not correlated with their relative reproductive value. Secondary nestlings had the highest reproductive value in 1973, but polygynous males began feeding them later than in 1974. They had similar reproductive value in 1974 and 1975, but polygynous males began feeding them substantially later in 1975 than in 1974. Also, in order to adjust their parental allocations to the relative reproductive value of secondary nestlings, males would have to detect annual changes in the likelihood that their nests will be destroyed by predators or adverse weather. Since both predation pressure and weather conditions are often unpredictable, there may not be any cues that males could use to detect such changes.

SUMMARY

Polygynous male Bobolinks in Oregon helped feed secondary nestlings (i.e., those of their second mates) in 3 of 4 years studied. This behavior differed from that of male Bobolinks in Wisconsin, which rarely feed secondary nestlings (Martin 1971, 1974). In Oregon, males began feeding secondary nestlings when their primary nestlings reached a specific age that varied between years, regardless of brood size in either of their nests. However, the number of trips made by males to their secondary nests was correlated with brood size in their primary nests. Males began feeding secondary nestlings later, or not at all, in years when

primary nestlings were in poorer nutritional condition. Their poorer condition in those years was associated with reduced food availability. The relative reproductive value of secondary nestlings was lower in the 1 year when polygynous males did not feed them, but it was not correlated with the earliness that males began feeding them in the other 3 years.

ACKNOWLEDGMENTS

I am grateful to W. H. Buskirk, I. L. Heisler, M. K. Lukens and R. Acevedo for their assistance in the field. W. J. Hamilton, III, provided encouragement and advice throughout the study. G. H. Orians, W. A. Searcy, S. Rohwer, L. B. Best and R. Pulliam offered many helpful comments on the manuscript. I thank J. P. Mazzoni, E. L. McLaury and their staff at Malheur National Wildlife Refuge for their cooperation and assistance. This research was partially funded by the Zoology Department of the University of California at Davis, and the results were written-up while I was supported by NSF grant BNS 76-09651.

LITERATURE CITED

DAWKINS, R. 1976. The selfish gene. Oxford Univ. Press, New York, New York.

MARTIN, S. G. 1971. Polygyny in the Bobolink: habitat quality and the adaptive complex. Ph.D. thesis, Oregon State Univ., Corvallis, Oregon.

———. 1974. Adaptations for polygynous breeding in the Bobolink, *Dolichonyx oryzivorus*. Am. Zool. 14:109–119.

PATTERSON, C. B., W. J. ERCKMANN AND G. W. ORIANS. 1980. An experimental study of parental investment and polygyny in blackbirds. Am. Nat. In press.

PIANKA, E. R. AND W. S. PARKER. 1975. Age-specific reproductive tactics. Am. Nat. 109:453–464.

STEARNS, S. C. 1976. Life-history tactics: a review of ideas. Quart. Rev. Biol. 51:3–47.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 *in* Sexual selection and the descent of man, 1871–1971, (B. Campbell, ed.). Aldine, Chicago, Illinois.

WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8:1–93.

WILLSON, M. F. 1966. The breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr. 36:51–77.

WITTENBERGER, J. F. 1976. Habitat selection and the evolution of polygyny in Bobolinks (*Dolichonyx oryzivorus*). Ph.D. thesis, Univ. California, Davis, California.

———. 1978. The breeding biology of an isolated Bobolink population in Oregon. Condor 80:355–371.

———. 1979. A model for delayed reproduction in iteroparous animals. Am. Nat. 114:439–446.

ZOOLOGY DEPT. NJ-15, UNIV. WASHINGTON, SEATTLE, WASHINGTON 98195.
ACCEPTED 1 MAR. 1979.

Wilson Bull., 92(3), 1980, pp. 341–351

FORAGING ECOLOGY OF PTARMIGAN AT MEADE RIVER, ALASKA

Joseph B. Williams, Dave Best and Colleen Warford

Alaskan Willow Ptarmigan (*Lagopus lagopus*) are herbivorous birds that migrate southward in autumn through mountain passes in the Brooks Range and move northward in late winter to their principal nesting grounds on the arctic slope (Irving et al. 1967). The winter diet of this species consists principally of willow (*Salix* spp.) buds and twigs (West and Meng 1966, Weeden 1969). However, dietary patterns of ptarmigan on their major nesting grounds (tundra north of the Brooks Range) are poorly known. Therefore, this study was initiated to answer the following: (1) How do food preferences of Willow Ptarmigan vary through the summer? (2) How does habitat type influence the grazing of Willow Ptarmigan? (3) What impact does the Willow Ptarmigan have on willows?

STUDY AREA AND METHODS

Our study site was situated along the Meade River near the village of Atkasook, Alaska (70°27′N, 157°55′W). Batzli and Brown (1976) presented a description of the vegetation and soils of the area.

To ascertain the amount of time ptarmigan devote to various activities we constructed a daily activity budget (Orians 1961) by recording the behavior of birds at a signal emitted every 10 sec from an electronic metronome (Wiens et al. 1970). We categorized behavior as follows: (1) stand or crouch, (2) walk, (3) feed, (4) attack and (5) other—all other activities observed such as preening, vocalizing and flying. We timed birds during all periods of the day. To avoid bias, we followed individual birds only 5 min.

To determine diets we collected ptarmigan from tundra adjacent to our study area and stored the contents of their crops in FAA (10% formalin, 5% glacial acetic acid, 50% ethyl alcohol and 35% water). Additionally, some Eskimos gave us crops from birds they had killed. We sorted crop contents into categories, dried all material at 105°C for 24 h, then weighed each subsample. Comparison with a reference collection of plant parts allowed identification of most dietary items. Dry weights from each category from the same month were pooled for analysis. Results are expressed as percent of total dry weight for each month.

To elucidate dietary preferences in different habitat types, we erected 2 × 2-m enclosures in several habitat types (upland tundra—high center polygons, upland tundra—low center polygons, moist lake margin, streamside shrub, dry bank edge) and observed foraging by captive ptarmigan. After depriving the birds of food for 3 h, we placed them in the enclosure, allowed them to habituate to their new surroundings for 15 min and then observed (from a blind) the number of pecks on each plant species for 30 min. After approximately 1 week of captivity, birds grew accustomed to their cages and freely foraged on vegetation within them. Plant availability was determined by a stratified random sampling regime using the point frame method (Kershaw 1974). For each enclosure, we established 6 transects from a random numbers table and identified the vascular plant species closest to each point at 10 cm intervals. In 1976 two trials on each habitat type were completed using juvenile birds (ca. 250 g). In 1977 we ran 6 trials on each habitat type using an adult female (ca. 500 g).

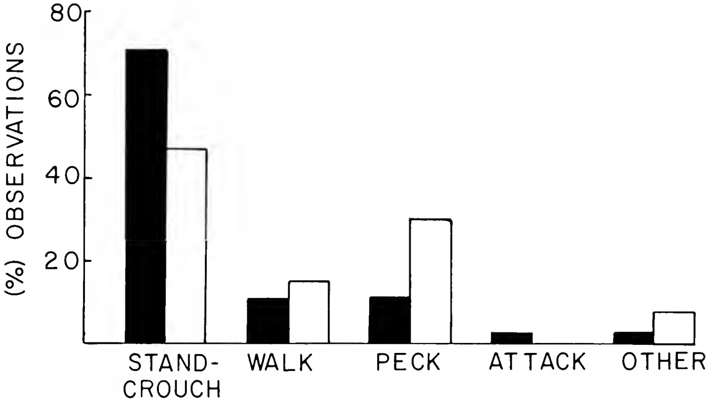


FIG. 1. The activity budget of male (shaded bars) and female (open bars) ptarmigan at Meade River, Alaska from 1–25 June 1976. N = 1620 observations for males, 715 for females. Chi-square for male vs female comparisons equals 240.8 (df = 4), $P < 0.005$.

We selected 3 habitats to examine the impact of ptarmigan on *Salix* spp. The first site was a disturbed area along the bluff of the Meade River where 5 species of willow occurred; netted willow (*Salix reticulata*), *S. pulchra*, *S. lanata*, *S. glauca* and Alaska Willow (*S. alexensis*). Except for *S. reticulata*, each species reached a height of 1 m or more. Situated along the margin of a drained lake, the second area was lower and wetter and was dominated by *S. pulchra*, although *S. reticulata* and *S. phlebophylla* were also present. Willows here were all under 0.5 m high. The third site lay along the banks of a small stream where only *S. pulchra* occurred, but it reached heights of 1 m. In August 1976, we chose twenty 1-m^2 plots for each site and constructed from hardware cloth exclosure cages over 10 of them. The cages prevented ptarmigan grazing and served as experimental plots (ungrazed); the 10 accessible plots served as controls (grazed). Each ungrazed plot and adjacent grazed plot was chosen such that the vegetation was similar in each. In mid-July of 1977, all catkins in each plot were collected, counted, dried (4 days at 65°C) and weighed. We found no evidence of other herbivores grazing on catkins on our study plots.

RESULTS

Activity budgets.—During June (1976) the activity budget of males was different from females (Fig. 1). Males often perched atop a small knoll within their territories, apparently observing their surroundings. Females spent more time feeding and walking than did males. By June 20, most females were incubating eggs, and the males became more secretive, making construction of a reliable activity budget difficult.

Composition of diet.—In June 1976, adult birds foraged on catkins and buds of *Salix* spp. (Table 1). Young *Salix* leaves (33.7%) and fruits (22.8%), and the flowers of mountain avens (*Dryas integrifolia*) comprised the major part of the diet in July. In August, *Salix* leaves and buds and the seeds of various grasses (*Luzula*, *Carex*, *Poa*) made up their diet. We

TABLE 1
A COMPARISON OF THE PERCENT DRY WEIGHT OF PLANT MATERIAL FOUND IN THE CROPS OF WILLOW PTARMIGAN ADULTS

	June N = 11		July N = 13		August N = 17	
Plant category	% dry wt.	No. of crops	% dry wt.	No. of crops	% dry wt.	No. of crops
Salix spp.						
leaves	1.7	5	33.7	12	47.2	17
buds/stems[1]	26.1	11	1.1	3	18.1	15
catkins	58.8	10	—	—	—	—
fruits	—	—	22.8	9	2.0	2
Dryas integrifolia						
flowers	—	—	21.5	5	—	—
Grasses						
seeds	—	—	0.4	1	8.0	5
Betula nana						
buds/stems	2.4	2	0.1	2	1.1	1
fruits	—	—	—	—	5.7	3
Cassiope tetragona						
flowers	—	—	5.4	7	—	—
fruits	—	—	0.7	5	7.4	6
Polygonum spp.						
flowers	—	—	2.1	2	—	—
bulbils	—	—	5.8	3	2.6	7
Eriophorum spp.						
flowers	2.5	6	—	—	—	—
Other	5.7	8	4.5	6	5.8	8
Unknown	2.8	4	1.9	6	2.1	8
Total dry wt. (g) =	18.3		8.1		9.4	

[1] Stems were usually attached to buds and undoubtedly were procured when the bud was plucked.

also obtained crops (N = 13) in August 1977 (not in Table 1). For this month we found that birds again concentrated on *Salix* buds (26%) and leaves (19%), but also took bearberry (*Arctostaphylos* spp.) fruits (32%).

In July 1976, chicks, averaging 68.2 g, often ate the leaves of *Salix* spp., but also consumed moss capsules, *Polygonum* bulbils, flowers of *D. integrifolia* and insects (Table 2). In August 1976, juvenile birds foraged on *Salix* leaves, bulbils of *Polygonum viviparum* and the seeds of grasses. We found young horsetail (*Equisetum*) sprouts in several crops. *Polygonum*

TABLE 2
A COMPARISON OF THE PERCENT DRY WEIGHT OF PLANT AND ANIMAL MATERIAL FOUND IN THE CROPS OF WILLOW PTARMIGAN CHICKS

	1976				1977			
	July N = 14		August N = 12		July N = 17		August N = 10	
Plant category	% dry wt.	No. of crops	% dry wt.	No. of crops	% dry wt.	No. of crops	% dry wt.	No. of crops
Salix spp.								
leaves	41.1	12	25.9	10	0.9	4	22.1	6
buds/stems	—	—	8.1	4	—	—	9.4	5
Polygonum spp.								
bulbils	7.6	5	10.3	9	89.3	16	0.2	3
Arctostaphylos								
fruits	—	—	3.0	4	2.4	1	20.5	4
Grasses								
seeds	0.7	1	10.3	6	—	—	19.9	4
Moss								
capsules	19.0	7	—	—	—	—	—	—
Fungi	1.1	1	—	—	+[1]	1	17.4	6
Saxifraga spp.								
bulblets	0.1	1	10.1	4	—	—	—	—
Dryas integrifolia								
flowers	0.2	1	4.5	1	—	—	—	—
fruits	8.4	3	—	—	—	—	—	—
Equisetum spp.	—	—	7.9	5	+	1	1.9	1
Cassiope tetragona								
fruits	5.1	4	3.0	3	0.3	1	—	—
Cardamine pratensis								
leaves	—	—	4.4	1	—	—	—	—
Insect gall	—	—	4.0	2	—	—	—	—
Oxytropis spp.–*Astragalus* spp.								
leaves	—	—	—	—	3.6	6	—	—
Pedicularis spp.								
leaves	3.1	2	—	—	—	—	0.3	3
fruits	—	—	3.1	3	—	—	—	—
Betula nana								
Insects	6.4	13	0.7	5	0.6	8	—	—
Other	3.7	7	1.8	5	1.3	7	5.2	6
Unknown	3.5	5	2.9	8	1.6	8	3.1	6
Total dry wt. (g)	1.2		2.4		3.7		3.2	

[1] + = values < 0.5%.

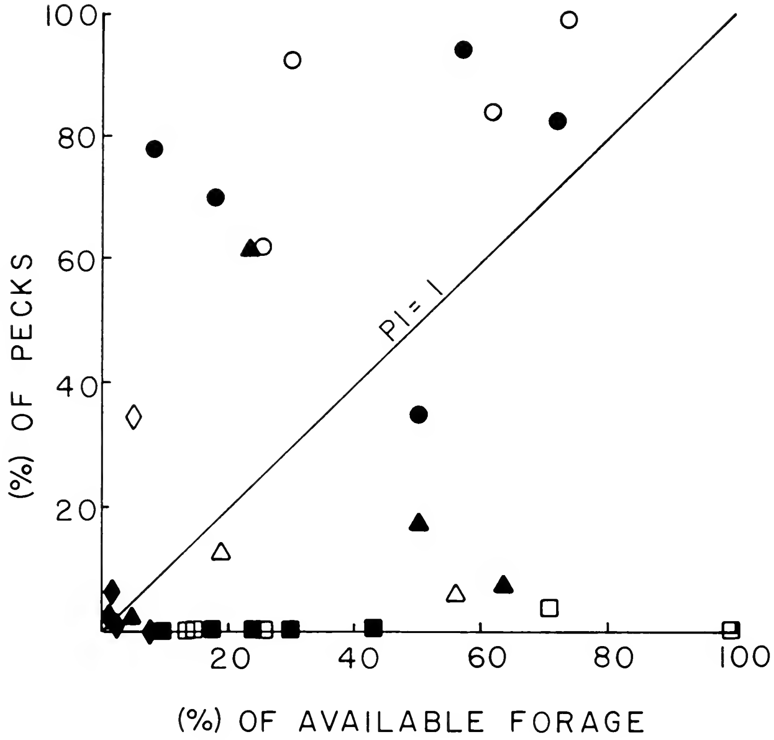


FIG. 2. Preferences of Willow Ptarmigan for monocots (squares), forbs (diamonds), deciduous shrubs (circles) and evergreen shrubs (triangles). Open symbols represent data from 1976 on juvenile birds; closed symbols represent data from 1977 on an adult female. The line represents a preference index (PI) of 1, where the proportion of pecks divided by the proportion of the plant type available equals unity. Values above the line indicate selective foraging. Statistics are in Appendix A.

bulbils dominated the diets of chicks, now averaging 73.0 g, during July 1977, much more than in 1976 (89% vs 8%), and *Arctostaphylos* berries and fungi were more important in August 1977 than in 1976 (20% vs 3% and 17% vs 0%, respectively).

Foraging trials.—For this analysis, we categorized plants consumed by ptarmigan into monocots (grasses and sedges such as *Carex aquatilis*, *Eriophorum* spp. and *Poa arctica*), forbs (herbaceous dicots such as louseworts [*Pedicularis* spp.], *Petasides frigidus* and *Polygonum* spp.), deciduous shrubs (*Salix* spp., dwarf birch [*Betula nana*] and *Arctostaphylos* spp.) and evergreen shrubs (Lapland Cassiope [*Cassiope tetragona*], Labrador tea [*Ledum palustre*] and mountain cranberry [*Vaccinium vitis-idaea*]). Results showing the percent of pecks on each plant species vs the

TABLE 3

MEAN NUMBER AND DRY WEIGHT OF *SALIX* CATKINS (±1 SE) FOUND IN PLOTS WITH AND WITHOUT PTARMIGAN GRAZING (N = 10 FOR EACH TREATMENT AT EACH LOCATION)

	Mean number of catkins		Mean dry weight (g)	
Location	Grazed	Ungrazed	Grazed	Ungrazed
Streamside	15.6 ± 4.7	85.7 ± 32.3[1]	1.1 ± 0.4	6.9 ± 2.3[1]
Disturbed area	106.1 ± 20.3	260.3 ± 48.7[1]	6.9 ± 1.4	17.4 ± 3.7[1]
Marsh margin	28.3 ± 8.3	37.8 ± 7.3	0.77 ± 0.2	0.8 ± 0.2

[1] $P < 0.05$; Wilcoxon paired sample test.

percent of each plant species available have been relegated to Appendix A.

Leaves of *Salix* and other deciduous shrubs comprised most of the diet of birds in our foraging trials (Fig. 2) (Appendix A). The adult female also selected the leaves of *D. integrifolia*, an evergreen shrub, in the dry bank habitat. Interestingly, birds avoided the leaves of evergreen shrubs such as *L. palustre*, *C. tetragona*, *Empetrum nigrum* and *V. vitis-idaea*, but readily foraged on the fruits of these species when available. Also, birds shunned the leaves of monocot grasses and when confined to pure patches of *C. aquatilis*, they did not feed.

Exclosure experiments.—Ptarmigan grazing appeared to affect the production of *Salix* catkins in 2 of the 3 habitats that we tested (Table 3; Wilcoxon paired sample test, $P < 0.05$). Where willow shrubs were more arborescent (streamside and disturbed area), we found catkin numbers to be significantly reduced in the grazed plots. But in the lake margin habitat, where *Salix pulchra* is somewhat decumbent, we found no significant differences between ungrazed and grazed plots. Thus, the impact of ptarmigan foraging on willows appears greater in habitats with taller willows, which would be above the snow earlier in spring and later in autumn.

DISCUSSION

Activity budgets for birds during June indicated that males spent a considerable amount of time in territorial surveillance and that females foraged more than males prior to nesting (Fig. 1). West (1968) showed that female Willow Ptarmigan required significantly more energy during late spring than any other time period. Moss (1972, 1977) thought female Red Grouse (*L. l. scoticus*) selected foods because of high nutrient content rather than for energy in the spring. The greater time spent foraging by females suggests that they were meeting increased physiological demands for either nutrients or energy, or both.

The diet of Alaskan Willow Ptarmigan during winter has been well documented and is composed principally of *Salix* buds and twigs (Bent 1932, West and Meng 1966, Weeden 1969). However, only 1 previous study has been done on their summer diet on the North Slope. From 23 crops collected at Umiat during June–August, West and Meng (1966) reported *Salix* leaves and *Equisetum* were the main constituents of the diet of this species (42.9% and 15.7% by dry weight, respectively). Since they lumped data for the 3 months, seasonal changes could not be determined. At Meade River birds concentrated their foraging on *Salix* catkins in June. We interpret this use of catkins as indicative that they are relatively high in nutritional value at this time. West and Meng (1966) found a marked increase of energy content in catkin buds of *Salix* just prior to flowering. Chapin et al. (unpubl.) found that the concentration of nitrogen and phosphorous of *Salix* catkins at Meade River reached a peak in mid-June and dropped linearly through the summer. In July, adults foraged more on young *Salix* leaves and maturing seed capsules. *Salix* leaves in July have a caloric value similar to wintering buds (West and Meng 1966), but the concentration of nitrogen and phosphorous in *Salix* leaves is highest at this time (Chapin et al., unpubl.). The lack of *Salix* buds in diets of ptarmigan in July may be because buds are relatively low in caloric content at this time (West and Meng 1966), or because buds are small and developing during July.

Because early June 1977 was relatively warm at Meade River (4.4°C mean temperature vs 2.7°C in 1976), plants were phenologically advanced by about 2 weeks, compared to the previous summer. Ptarmigan diets for August 1977 showed *Arcostaphylos* berries were favored, although *Salix* leaves and buds were still important. *Arctostaphylos* berries were still small and green when we left in mid-August 1976. We suspect that during September of normal years berries become important in ptarmigan diets because they are a readily available source of carbohydrates and nutrients (Gardarsson and Moss 1970, Moss and Parkinson 1975), and because *Salix* leaves have lost much of their nitrogen and phosphorous by translocation by this time (Chapin et al., unpubl.).

Chicks of gallinaceous birds often rely on arthropods as an important source of food (Ford et al. 1938, Christiansen and Kraft 1953, Pendergast and Boag 1970). Bent (1932) wrote that Willow Ptarmigan chicks are primarily insectivorous, but more recent studies indicate that insects comprise only 5–30% of the diets of ptarmigan chicks (Weeden 1969, Gardarsson and Moss 1970, Savory 1977). In this study chicks used a wide variety of flowers, fruits and seeds in addition to willow leaves in July 1976, but concentrated almost entirely on *Polygonum* bulbils during July 1977. We collected insufficient data to compare diets of very young chicks with older ones in July to see if young chicks concentrated more on insects.

But crops of 6 young chicks (<30 g) that we collected all contained more plant material than insects and never exclusively insects. Food items taken early in life by chicks (fruits, seeds, moss capsules) may be more digestible and/or more nutritious than *Salix* leaves, thus chicks would be able to obtain more energy and nutrients from them (Savory 1977). Gardarsson and Moss (1970) reported that *P. viviparum* spikes and bulbils comprised 62% of the diets of Icelandic ptarmigan chicks and that these foods were relatively high in nitrogen and phosphorus. Additionally, they found that bulbils were more easily digested (in vitro digestibility) than leafy materials. Moss and Parkinson (1975), using captive adult Rock Ptarmigan (*L. mutus*), ascertained that bulbils of *P. viviparum* were a good source of metabolizable energy, protein and phosphorus. Hence, this diet may provide juveniles with more needed protein for growth than would leaves. As chicks mature, their cecal flora probably develops, making leaves more digestible, and they begin to eat the leaves of *Salix* and other plants (McBee and West 1969, Gassaway et al. 1975). Part of the difference in chick diets between years perhaps can be attributed to the fact that 1977 was a warmer summer and thus seed and bulbil development was earlier.

Our grazing experiments documented the strong preference of Willow Ptarmigan for the leaves of deciduous shrubs, especially *Salix*, in all habitat types at Meade River. Batzli (unpubl.) found that leaves of *S. pulchra* and other *Salix* species contain tannins which are secondary metabolic products found in plants that form complexes with proteins rendering them indigestible (Feeny 1970). Apparently Willow Ptarmigan have evolved a mechanism which makes this line of defense in *Salix* ineffective.

Ptarmigan avoided the leaves of most evergreen shrubs (*C. tetragona*, *E. nigrum*, *L. palustre*), but did forage on the leaves of *D. integrifolia* in the dry bank edge habitat. Batzli (unpubl.) found that microtine rodents at Meade River (brown lemming [*Lemmus trimucronatus*], Greenland collared lemming [*Dicrostonyx groenlandicus*] and tundra vole [*Microtus oeconomus*]) also did not eat leaves of any evergreen shrubs except *Dryas*. Moreover, he showed that the leaves of evergreen shrubs contained a greater variety of chemical defenses (tannins, alkaloids, anthraquinones) than monocots, forbs, or deciduous shrubs. That leaves of evergreen shrubs at Meade River are highly protected by secondary metabolic products conforms to the suggestion of Rhoades and Cates (1976) that the most highly defended leaf tissue in plants should be the mature leaves of long-lived, common, evergreen, climax woody perennials.

SUMMARY

On a study area near Atkasook, Alaska, in the early summer, male Willow Ptarmigan spent more time in apparent territory surveillance, while females foraged more, possibly to meet the increased physiological demands of egg-laying. Diets of adult birds consisted pri-

marily of *Salix* catkins and buds in June, of young *Salix* leaves and maturing fruits in July, and of *Salix* leaves and buds, and the seeds of grasses in August. In addition to *Salix* leaves, chicks foraged on fruits, flowers and various insects. Foraging trials in various habitat types demonstrated the strong preference of Willow Ptarmigan for *Salix* leaves, and showed that these birds avoided the leaves of certain evergreen shrubs, perhaps because they possess chemical defenses. With exclosure experiments, we showed that ptarmigan reduce catkin numbers more along streams where willows are more aborescent.

ACKNOWLEDGMENTS

This study is part of the Research on Arctic Tundra Environments (RATE) program sponsored by the National Science Foundation. We wish to express appreciation to Dr. Steve McLean and his group for help with the ptarmigan exclosure experiments. Drs. George Batzli, Don Spailing and John Roseberry made helpful comments on an earlier draft.

LITERATURE CITED

BATZLI, G. O. AND J. BROWN. 1976. Research on arctic tundra environments (RATE). The influence of grazing on arctic tundra ecosystems. Arctic Bull. 2:153–160.

BENT, A. C. 1932. Life histories of North American gallinaceous birds. U.S. Natl. Mus. Bull. 162.

CHRISTIANSEN, B. AND A. KRAFT. 1953. Lirypekyllingenes naering. The food of Willow Grouse chicks. Norges Jeger-og Fisker-Forbunds Tidsskrift. Nr. 4. Cited in Peters, S. S. 1958. Food habits of Newfoundland Willow Ptarmigan. J. Wildl. Manage. 22:384–394.

FEENY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581.

FORD, J., H. CHITTY AND A. D. MIDDLETON. 1938. The food of partridge chicks (*Perdix perdix*) in Great Britain. J. Anim. Ecol. 7:251–265.

GARDARSSON, A. AND R. MOSS. 1970. Selection of food by Icelandic ptarmigan in relation to its availability and nutritive value. Pp. 47–71 *in* Animal populations in relation to their food resources, (A. Watson, ed.). Oxford Univ. Press, Oxford, England.

GASSAWAY, W. C., D. HOLLEMAN AND R. G. WHITE. 1975. Flow of digesta in the intestine and cecum of the Rock Ptarmigan. Condor 77:467–474.

IRVING, L., G. C. WEST, L. J. PAYTON AND S. PANEAK. 1967. Migration of Willow Ptarmigan in Arctic Alaska. Arctic 20:77–85.

KERSHAW, K. A. 1974. Quantitative and dynamic plant ecology. American Elsevier Pub. Co., New York, New York.

MCBEE, R. H. AND G. C. WEST. 1969. Cecal fermentation in the Willow Ptarmigan. Condor 71:54–58.

MOSS, R. 1972. Food selection by Red Grouse (*Lagopus lagopus scoticus*) in relation to chemical composition. J. Anim. Ecol. 41:411–428.

———. 1977. The digestion of heather by Red Grouse during spring. Condor 79:471–477.

——— AND J. A. PARKINSON. 1975. The digestion of bulbils (*Polygonum viviparum*) and berries (*Vaccinium myrtillus* and *Empetrum* sp.) by captive ptarmigan (*Lagopus mutus*). Br. J. Nutr. 33:197–206.

ORIANS, G. 1961. The ecology of Blackbird (Agelaius) social systems. Ecol. Monogr. 31:285–312.

PENDERGAST, B. A. AND D. A. BOAG. 1970. Seasonal changes in diet of Spruce Grouse in central Alberta. J. Wildl. Manage. 34:605–611.

RHOADES, D. F. AND R. G. CATES. 1976. Toward a general theory of plant antiherbivore chemistry. Pp. 168–213 *in* Biochemical interactions between plants and insects, (J. W. Wallace and R. L. Mansell, eds.). Plenum Press, New York, New York.

SAVORY, C. J. 1977. The food of Red Grouse chicks *Lagopus l. scoticus*. Ibis 119:1–9.

WEEDEN, R. B. 1969. Foods of Rock and Willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86:271–281.

WEST, G. C. 1968. Bioenergetics of captive Willow Ptarmigan under natural conditions. Ecology 49:1035–1045.

——— AND M. S. MENG. 1966. Nutrition of Willow Ptarmigan in northern Alaska. Auk 83:603–615.

WIENS, J. A., S. C. MARTIN, W. R. HOLTHAUS AND F. A. IWEN. 1970. Metronome timing in behavioral ecology studies. Ecology 51:350–352.

NATURAL SCIENCE DEPT., PEPPERDINE UNIV., MALIBU, CALIFORNIA 90265 (JBW, CW) AND WILDLIFE ECOLOGY, UNIV. WISCONSIN, MADISON, WISCONSIN 53706 (DB). (PRESENT ADDRESS JBW: DEPT. BIOLOGY, JOSEPH LEIDY LABORATORY OF BIOLOGY G7, UNIV. PENNSYLVANIA, PHILADELPHIA, PENNSYLVANIA 19104.) ACCEPTED 25 JUNE 1979.

APPENDIX A

PLANT AVAILABILITY (% COVER) AND THE PERCENTAGE OF OBSERVED PECKS BY PTARMIGAN ON THE PLANT SPECIES WITHIN 2 × 2 M PENS PLACED IN VARIOUS HABITAT TYPES[1]

1976			1977		
Plant species	Availability	% pecks	Plant species	Availability	% pecks
		Upland tundra—P_L			
Carex aquatilis	99.0	—	*Ledum palustre*	28.0	—
Eriophorum spp.	1.0	—	*Carex aquatilis*	22.3	—
		0	*Vaccinium vitis-idaea*	19.0	16.7
			Salix pulchra	15.0	49.0
			Eriophorum spp.	6.8	—
			Salix phlebophylla	3.7	21.0
			Cassiope tetragona	2.6	1.5
			Other	6.0	11.5
					(2863)[2]
		Upland tundra—P_H			
Ledum palustre	30.0	—	*Vaccinium vitis-idaea*	34.8	8.8
Salix phlebophylla	29.2	92.3	*Ledum palustre*	29.0	0.1
Carex bigelowii	13.2	—	*Eriophorum vaginatum*	11.6	—
Vaccinium vitis-idaea	10.6	—	*Carex bigelowii*	10.0	—
Diapensia lapponica	8.8	—	*Rubus chameamorus*	3.5	—
Cassiope tetragona	7.0	5.6	*Salix phlebophylla*	3.0	—
Eriophorum vaginatum	0.8	—	*Salix pulchra*	2.5	55.1
Pedicularis capitata	—	—	*Betula nana*	2.0	2.4
		(551)	*Poa arctica*	1.5	—
			Other	1.5	12.6
					(2666)

APPENDIX A

CONTINUED

1976			1977		
Plant species	Avail-ability	% pecks	Plant species	Avail-ability	% pecks
		Moist lake margin			
Carex aquatilis	69.5	3.6	*Salix pulchra*	56.5	94.0
Salix pulchra	25.0	61.0	*Carex aquatilis*	37.0	—
Pedicularis sudetica	3.2	35.3	*Eriophorum* spp.	4.0	—
Caltha sp.	2.1	—	*Polygonum viviparum*	1.1	6.0
		(1097)	Other	1.0	—
					(1700)
		Streamside shrub			
Salix pulchra	58.3	90.8	*Salix pulchra*	63.0	74.7
Carex spp.	23.4	—	*Betula nana*	9.0	7.7
Betula nana	15.9	9.0	*Petasides frigidus*	5.5	0.1
Calamagrostis holmii	1.5	—	*Calamagrostis holmii*	5.0	0.2
Petasides frigidus	0.7	—	*Carex* spp.	4.5	0.1
		(503)	*Vaccinium vitis-idaea*	4.5	3.8
			Pyrola grandifolia	3.0	—
			Other	4.0	13.4
					(1941)
		Dry bank edge			
Arctostaphylos sp.	53.1	21.5	*Arctostaphylos* sp.	38.3	11.8
Dryas integrifolia	17.4	13.0	*Dryas integrifolia*	22.7	62.2
Carex spp.	14.2	—	*Carex* spp.	15.6	—
Salix phlebophylla	9.5	62.5	*Salix phlebophylla*	11.6	23.2
Artemesia sp.	2.3	—	*Eriophorum vaginatum*	2.5	—
Diapensia lapponica	1.5	—	*Artemesia* sp.	1.5	0.2
Other	2.0	2.7	*Cassiope tetragona*	1.5	—
		(752)	*Salix pulchra*	1.0	0.1
			Polygonum bistorta	1.0	0.7
			Stellaria laeta	1.0	—
			Other	3.0	1.8
					(8717)

---

[1] Chi-square values for 1976 equal 100 (df = 1), 507.5 (df = 7), 1134.7 (df = 3), 534.8 (df = 4), 69.8 (df = 6) for upland tundra—low center polygons (P_L), upland tundra—high center polygons (P_H), moist lake margin, streamside shrub, and dry bank edge, respectively. In 1977 for the adult female, Chi-square values equal 2551.1 (df = 7), 3759.7 (df = 9), 1494.6 (df = 3), 446.2 (df = 7), and 5138.3 (df = 10) for the same sequence of habitats. $P < 0.005$ in all cases.

[2] Numbers in parentheses equal the total number of observed pecks.

Wilson Bull., 92(3), 1980, pp. 352–361

NESTING DENSITY, HABITAT STRUCTURE AND HUMAN DISTURBANCE AS FACTORS IN BLACK GUILLEMOT REPRODUCTION

David Cairns

Seabirds probably choose inaccessible islands and cliffs for breeding sites to counteract predation, but colony size and distribution are related more closely to food habits (Lack 1967). Thus, species of seabirds which feed inshore tend to form small colonies, while species which feed offshore often form large concentrated colonies, less often along the coast. The Black Guillemot (*Cepphus grylle*) differs from most alcids in feeding inshore, and its colonies are generally small and dispersed. But unlike other inshore feeders, guillemots nest in crevices which protect their clutches from avian predation at least. Breeding dispersion in other inshore feeders is affected by predation, so this protection may permit guillemots to respond to other selective pressures affecting nest spacing.

Breeding success of the Black Guillemot has been related to habitat quality and nesting density (Divoky et al. 1974, Preston 1968). In the latter case, low breeding success and a high rate of intraspecific aggression in 1 high density nesting area suggested that the Black Guillemot is not well adapted for colonial nesting.

The purpose of this study was to investigate the relations among habitat structure, nesting density, breeding success and behavior in the Black Guillemot. I also evaluated the possible influence of observer interference on breeding success, such as has been documented for Common Murres (*Uria aalge*) (Johnson 1938), Double-crested Cormorants (*Phalacrocorax auritus*) (Ellison and Cleary 1978) and gulls (*Larus* spp.) (Hunt 1972, Robert and Ralph 1975, Gillett et al. 1975).

STUDY AREA AND METHODS

This study was conducted on Brandypot Island (47°52′N, 69°41′W) in the estuary of the St. Lawrence River in 1976, and on the St. Mary's Islands (50°18′N, 59°39′W) on the north shore of the Gulf of St. Lawrence in 1977. Brandypot Island comprises 3 wooded islets underlain by quartzite and conglomerate bedrock. In quartzite areas the shores are generally smooth and regular, but the conglomerate shores are fissured deeply with cracks and caves and in several places are fronted by cliffs or jumbles of large boulders. On the St. Mary's Islands vegetation is limited to tundra-like communities and on wide bands around the islands' peripheries the metamorphosed igneous bedrock is exposed. The shorelines of St. Mary's West and Middle islands, where the study was carried out, vary from stepped terraces and low cliffs to gently sloping beaches of bare or stone-covered bedrock.

Common Murres, Razorbills (*Alca torda*) and Atlantic Puffins (*Fratercula arctica*) nested in small colonies throughout the St. Mary's study area, and Razorbills bred in small numbers on Brandypot. Detailed physical and avifaunal descriptions of these islands can be found in Reed (1973) for Brandypot, and Bédard (1969) for St. Mary's.

I found nests through repeated ground searches. I checked nests every 1–5 days on Brandypot, and daily (in the heavily disturbed zone) or every 4 days (in the lightly disturbed zone) on St. Mary's. In assessing the effect of my visits I considered a "visit" to be whenever I passed within 15 m of a nest.

Measurements of the types listed below were taken on all occupied nests, and on unoccupied holes on Brandypot which seemed to be suitable for nests.

(1) Particle size—the longest dimension of the largest particle on the surface of the nest cup.

(2) Nest diameter—the smallest dimension of the nest cavity, measured either vertically or horizontally.

(3) Nest depth—the distance between the nest bed and nest entrance. The nest entrance was defined as the deepest point able to be reached by a disc 25 cm in diameter oriented perpendicular to the nest.

(4) Overall shelter—the ratio of luminosity in the nest cavity to ambient exterior luminosity. Readings were taken with a Gossen Luna-pro meter (Berkey Marketing Co., Woodside, New York), equipped with a remote release. Measurements were made on overcast days so that the ambient light would be diffuse and uniform.

(5) Neighbor distance—mean distance between nests and their nearest neighbors.

(6) Nest density—number of nests per 50 m of coast. On Brandypot densities were determined from a continuous transect system set up from a randomly determined point of departure. Densities on St. Mary's were established from transect systems set up separately for each subcolony because the coast was irregular and nests were clumped.

Unoccupied holes on Brandypot were considered arbitrarily as potential nest-sites if their physical measurements fell within the central 90% of the frequency distributions of measurements of occupied sites for that island (except for particle size). In the case of particle size, the smallest 90% of measurements were included.

Hatching dates were determined by nest checks or estimated from growth curves of weight and wingspan (Cairns 1978). Behavioral observations on Brandypot were made in the morning when the birds assembled on the rocks during the rising tide, between 23 May and 23 June. The frequency of agonistic behavior was expressed as the number of agonistic interactions per bird-min. Agonistic interactions were defined as encounters in which the behavior of 1 bird induced the retreat of another.

RESULTS

I located 165 Black Guillemot nests on Brandypot and 143 on St. Mary's; these probably represent nearly all the nests in the study areas. My data on breeding success are complete for 90 and 122 nests in the 2 areas, respectively.

Nesting on Brandypot was restricted to areas of conglomerate bedrock. Nesting occurred in vertical and oblique fissures, under rock overhangs, under boulders and in earth-lined holes with ceilings of tree roots or rock. All occupied sites were bedded with either soil, small stones, or organic matter.

On St. Mary's most guillemots nested in natural crevices in the bedrock, although nests were also found among the small boulders of raised beach-

TABLE 1

SITE CHARACTERISTICS OF BLACK GUILLEMOT NESTS, AND THEIR CORRELATIONS WITH BREEDING SUCCESS

			St. Mary's			
	Brandypot N = 90		Lightly disturbed N = 72		Heavily disturbed N = 50	
Characteristic	$\bar{x} \pm SD$	t^a	$\bar{x} \pm SD$	t	$\bar{x} \pm SD$	t
Particle size (mm)	11.8 ± 11.4	-0.21^b	19.3 ± 12.0	0.16	21.4 ± 12.2	−0.003
Nest diameter (cm)	14.5 ± 5.0	−0.042	13.4 ± 3.6	−0.037	15.2 ± 12.1	−0.074
Nest depth (cm)	102 ± 51.6	−0.095	75.1 ± 27.8	0.092	79.7 ± 26.4	0.062
Overall shelter (ratio)	0.0072 ± 0.018	−0.087	0.040 ± 0.041	−0.032	0.045 ± 0.048	-0.34^c
Neighbor distance (m)	6.3 ± 11.2	0.094	32.1 ± 46.2	−0.13	16.9 ± 14.6	−0.016
Nest density (nests/50 m)	16.7 ± 11.9	0.005	3.44 ± 2.25	0.081	6.0 ± 1.6	0.16

[a] Kendall's rank-order coefficient of correlation between breeding success, ranked on a 1–6 scale, and site characteristics.

[b] $P \leq 0.01$.

[c] $P \leq 0.002$.

TABLE 2

BLACK GUILLEMOT NESTING SUCCESS IN 3 HABITATS

		St. Mary's	
	Brandypot N = 90	Lightly disturbed N = 72	Heavily disturbed N = 50
Eggs laid/nest	1.79[a]	1.94[a]	1.96
Eggs hatched/nest	1.11	1.31[b]	0.64[b]
Chicks fledged/nest	0.64	0.97[c]	0.38[c]
Eggs hatched/eggs laid	0.59	0.66[d]	0.32[d]
Chicks fledged/chicks hatched	0.59	0.71	0.61

[a] $P < 0.025$, $G = 8.7$.
[b] $P < 0.005$, $G = 16.2$.
[c] $P < 0.01$, $G = 14.3$.
[d] $P < 0.005$, $G = 16.5$.

es, under rock slabs and blocks splintered from the bedrock, and in earth-lined holes under boulders. As on Brandypot no eggs were found laid on bare rock, and fine gravel was the most common nest-bed material.

Mean values of nest characteristics are presented in Table 1. The most consistent parameter was nest diameter, its mean varied only from 13.4–15.2 cm in the 3 areas. Particle size of nest-bed material was larger on St. Mary's than on Brandypot, although nest-bed particles on Brandypot tended to be more sharp-edged and jagged than the rounded pebbles of St. Mary's. In general, nest-sites on Brandypot were more sheltered than those on St. Mary's, as indicated by their greater depth and lower light penetration.

Razorbill and guillemot nests were interspersed on Brandypot, but the Razorbills used crevices that were much less sheltered and I only once found eggs of the 2 species in the same hole. On St. Mary's the alcid dispersion pattern was not uniform, and nests were grouped by species and habitat. The highest densities were those of Common Murres nesting in large crevices and caves, and puffins nesting in burrows on turf slopes. Razorbills and crevice-nesting puffins tended to nest together, with large holes being occupied by Razorbills and smaller ones by puffins. Black Guillemot pairs nested individually and in small groups along the coast, and were generally absent from areas occupied by other alcids.

Nest density was considerably higher on Brandypot than on St. Mary's (Table 1). Potential nest-sites were available in excess in both study areas, but they were mapped and measured only on Brandypot. This was because puffins occupied many such sites on St. Mary's and tended to nest deep within them where they could not be detected. The Brandypot colony was divided into high and low density areas in order to give equivalent sample

TABLE 3

MEAN PARTICLE SIZE AND OVERALL SHELTER OF BLACK GUILLEMOT NEST-SITES, ACCORDING TO BREEDING SUCCESS OF NESTS

	Nests with clutch of:		Nests with hatching success of:			Nests with fledging success per hatched chick of:		
Variable and study area	1	2	0	0.5	1	0	0.5	1
Particle size (mm) Brandypot	13.5	11.1[a]	16.8	12.1	7.6[b,c]	7.2	4.4	11.4[d]
Overall shelter (ratio) St. Mary's heavily disturbed	0.034	0.049[e]	0.073	0.015	0.026[f]	0.025	0.0038	0.028[g]

[a] $P > 0.05$, F = 0.66.
[b] $P < 0.005$, F = 5.99.
[c] Values not significantly different are underscored (*a priori* test).
[d] $P > 0.05$, F = 2.34.
[e] $P > 0.05$, F = 0.18.
[f] $P < 0.025$, F = 4.25.
[g] $P > 0.05$, F = 0.54.

TABLE 4

DENSITY, REPRODUCTIVE VARIABLES AND FREQUENCY OF AGONISTIC BEHAVIOR IN 2 BLACK GUILLEMOT SUBCOLONIES ON BRANDYPOT ISLAND

	Subcolony	
	Aggregated	Dispersed
Number of nests	38	13
Density (nests/50 m of coast)	54.5	6.0
Occupation rate of potential sites	86%	76%[a]
Young fledged/nest	0.52	0.83[b]
Hatching date: $\bar{x}$	28 June	27 June
SD	±11.9	±13.4[c]
Agonistic interactions/bird-min	0.0312	0.0218[d]
Mean number of birds under observation	7.6	11.1
Total observations (bird-min)	4437	4078

[a] $P > 0.05$, G = 0.29.
[b] $P > 0.05$, G = 1.3.
[c] $P > 0.05$, F = 1.27.
[d] $P < 0.01$, G = 6.87.

sizes in the 2 density categories. The occupancy rate of available sites was significantly higher in areas of high site density than in areas of low site density (84 vs 58%, $P < 0.005$, G = 18.8).

Overall nesting success was highest in the St. Mary's lightly disturbed area where 0.97 young per nest fledged (Table 2). This value was not significantly different from the success rate on Brandypot (0.64 chicks fledged per nest), but was significantly higher than the 0.38 young produced per nest in the St. Mary's heavily disturbed zone. Most of the difference between production rates in the St. Mary's heavily vs lightly disturbed areas was due to lowered hatching success in the heavily disturbed area; differences between the 2 areas were large and significant for eggs hatched per nest and eggs hatched per egg laid, but the difference between rates of chicks fledging per chick hatched was small and not significant (Table 2).

The relation between breeding success and observer disturbance on Brandypot was examined with a Kendall rank-order correlation between the number of nest visits and a ranked scale of breeding success. The scale assigned values of from 1–6 according to success achieved (i.e., 1 or 2 eggs laid, 1 or 2 eggs hatched, 1 or 2 chicks fledged). The Kendall coefficient was non-significant ($t = -0.08$, $P > 0.05$).

The same scale of breeding success was used to examine the relationship between site characteristics and success (Table 1). Only 2 significant relationships emerged: on Brandypot breeding success diminished with increasing particle size, and in the St. Mary's heavily disturbed area success was reduced in holes with decreasing overall shelter. In order to break down the influence of these site variables on each stage of nesting, I calculated their mean values according to the breeding success of the nest (Table 3). No significant difference in site characteristics was found for nests of varying clutch-size or fledging success per hatchling, but sites with different hatching successes differed significantly in their particle size (Brandypot) and overall shelter (St. Mary's heavily disturbed).

In order to determine the effects of observer interference on the condition of chicks at fledging, I calculated maximum weights attained and wingspans at fledging of chicks in the St. Mary's lightly and heavily disturbed habitats. Chicks in the heavily disturbed area were heavier, but did not have broader wingspans than chicks in the lightly disturbed zone (412 vs 370 g, $P < 0.001$, $F = 21.4$; 516 vs 508 mm, $P > 0.05$, $F = 1.8$).

Mean hatching dates were 26 June on Brandypot, and 14 and 18 July in the 2 St. Mary's zones. To examine the relation between breeding synchrony and nest dispersion, I calculated Pearson correlations between deviations from mean hatching dates, and neighbor distances and nesting densities. No statistically significant relations were found.

A comparison between rates of agonistic interactions between 2 Brandypot subcolonies with high and low nesting densities is presented in Table 4. Agonistic behavior was significantly more frequent in the aggregate subcolony, but there were no significant differences between hatching dates, breeding synchrony or breeding success.

DISCUSSION

Reproductive success of Black Guillemots nesting in the part of the St. Mary's colony subjected to daily visits was much lower than in the part visited once every 4 days. Unfortunately, the possibility that observer disturbance might have a detrimental impact on breeding success was not suspected during planning of the fieldwork, and the 2 St. Mary's study areas are not strictly comparable, as the nesting density in the heavily disturbed zone is much higher than in the lightly disturbed zone (Table 1).

There are good reasons to believe, however, that high nesting density could not be responsible for the drastic difference in productivity between the areas. In the first place, no significant relation between density and breeding success was detected (Tables 1 and 4). If high density reduces breeding success, then the Brandypot colony should have a success rate lower than that of the St. Mary's heavily disturbed area, since its density is much greater (Table 1). However, this is true neither for the Brandypot colony as a whole (Table 2), nor for a subcolony whose density is 9 times that of the St. Mary's heavily disturbed area (Tables 1 and 4).

A depressing effect of density on success seems to be absent in the colonies, so observer disturbance is the most probable cause of the low breeding performance in the St. Mary's heavily disturbed area. Most of the reproductive failure in this area was due to a reduced hatching rate, possibly induced through decreased incubation attentiveness, damage to eggs during panic departures from the nest, nest abandonment, or some combination of these. None of these factors was measured directly, because nest abandonment generally could not be confirmed until the normal incubation period was exceeded, by which time the eggs were too decayed to determine the cause of their death.

The significant negative correlations between particle size and overall shelter, and breeding success (Table 1) may also have been observer-induced. On Brandypot most nest beds were lined with conglomerate pebbles with sharp-edged concave faces, and it can be assumed that the larger the nest-bed particles, the greater the chances that eggs would be damaged by a bird departing suddenly. Breeding success was greatest in the darker, better sheltered holes in the St. Mary's heavily disturbed area. Birds in these sites may have been less inclined to flush in panic when an observer entered the area (observer presence was usually signalled by gull alarm calls). In the case of both particle size on Brandypot and overall shelter on St. Mary's, the main effects on breeding success occurred during the egg stage, since the means of these variables differed for nests with varying levels of hatching success, but not for nests of differing clutch-size and fledging success per hatchling (Table 3).

Despite the depression in success rates associated with observer interference, maximum weights attained by fledglings were considerably higher in the St. Mary's heavily disturbed area than in the lightly disturbed area. Those birds which succeeded in hatching their eggs in the face of daily disturbance may have been more attentive or more experienced as parents than the average successful nester in the lightly disturbed area. Robert and Ralph (1975) found a similar situation in a colony of Western Gulls (*Larus occidentalis*), where hatching success dropped with increasing disturbance, but chick survivorship rose.

Previous studies of the effects of human interference on seabird reproduction indicate that disturbance lowers breeding success by raising the susceptibility of eggs or young to intra- or interspecific predation (Johnson 1938, Hunt 1972, Gillett et al. 1975, Ellison and Cleary 1978). The directly harmful effects on parental care induced by human interference have been documented poorly in colonial seabirds, although the possibility of such effects has been suggested by several authors, including Bergman (1971) for Black Guillemots, and Nettleship (1975) for Gannets (*Morus bassanus*).

On both Brandypot and St. Mary's suitable nest-sites were available in excess. In other North American guillemot colonies studied by Preston (1968) and Divoky et al. (1974), lack of suitable habitat forced many birds into marginal sites where they suffered heavy nest losses. The fact that the Brandypot guillemots, when given a choice of habitat, tended to nest in a clumped distribution suggests that the species shares the gregarious nesting tendencies of other alcids, although this effect could have come about through colony tradition (Lack 1967).

Preston (1968) found breeding success to be lower in a guillemot subcolony with high nesting density, and concluded that higher aggression rates in the dense area were the cause. In this study agonistic behavior was more frequent in a high density subcolony, but no evidence for a relation between density and breeding success was found.

SUMMARY

Breeding success, breeding synchrony and condition of young at fledging were measured in 2 Black Guillemot colonies. Nest productivity was lower, but maximum chick weights were higher, in an area disturbed daily than in an area disturbed once every 4 days. Intraspecific agonistic behavior was more frequent in a high density subcolony, but nesting density was uncorrelated with breeding success and synchrony. No relationship was found between habitat structure and breeding success. The occupancy rate of available sites was greater in high density zones, suggesting a gregarious tendency in Black Guillemot nesting.

ACKNOWLEDGMENTS

This study was funded by grants from the National Research Council of Canada to J. Bédard, and by a Canadian Wildlife Service grant in aid of university research. I am indebted to J. Montreuil, J. Tremblay and especially G. Rochette for assistance in the field. The Ministry of Transport of Canada kindly allowed me the use of their facilities for personal lodging. G. Foreman and L. Chislett, lightkeepers on St. Mary's Island, greatly facilitated work there with their valuable material assistance and generous hospitality. I thank J. Munro, G. Fitzgerald and particularly, J. Bédard for reviewing the manuscript.

LITERATURE CITED

Bédard, J. 1969. Histoire naturelle du gode, *Alca torda*, L., dans le golfe Saint-Laurent, province de Québec, Canada. Can. Wildl. Serv. Rep. no. 7.

Bergman, G. 1971. Gryllteisten *Cepphus grylle* in einem Randgebiet: Nahrung, Brutresultat, Tagesrhythmus und Ansiedlung. Commentat. Biol. Soc. Sci. Fenn. 42:1–26.

Cairns, D. 1978. Some aspects of the biology of the Black Guillemot (*Cepphus grylle*) in the estuary and the Gulf of St. Lawrence. M.Sc. thesis, Université Laval, Québec, Québec.

Divoky, G. J., G. E. Watson and J. C. Bartonek. 1974. Breeding of the Black Guillemot in northern Alaska. Condor 76:339–343.

Ellison, L. N. and L. Cleary. 1978. Effects of human disturbance on breeding of Double-crested Cormorants. Auk 95:510–517.

Gillett, W. H., J. L. Hayward and J. F. Stout. 1975. Effects of human activity on egg and chick mortality in a Glaucous-winged Gull colony. Condor 77:492–495.

HUNT, G. L. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53:1051–1061.

JOHNSON, R. A. 1938. Predation of gulls in murre colonies. Wilson Bull. 50:161–170.

LACK, D. 1967. Interrelationships in breeding adaptations as shown by marine birds. Proc. XIV Int. Ornithol. Congr. 3–42.

NETTLESHIP, D. N. 1975. A recent decline of Gannets, *Morus bassanus*, on Bonaventure Island, Quebec. Can. Field-Nat. 89:125–133.

PRESTON, W. C. 1968. Breeding ecology and social behavior of the Black Guillemot, *Cepphus grylle*. Ph.D. thesis, Univ. Michigan, Ann Arbor, Michigan.

REED, A. 1973. Aquatic bird colonies in the Saint Lawrence estuary. Serv. de la faune du Québec, Bull. 18.

ROBERT, H. C. AND C. J. RALPH. 1975. Effects of human disturbance on the breeding success of gulls. Condor 77:495–499.

DÉPARTEMENT DE BIOLOGIE, UNIVERSITÉ LAVAL, QUÉBEC, QUÉBEC G1K 7P4, CANADA. (PRESENT ADDRESS: MACLAREN MAREX INC., BOX 9493, POSTAL STATION B, ST. JOHN'S, NEWFOUNDLAND A1A 2Y4 CANADA.)
ACCEPTED 1 MAY 1979.

Wilson Bull., 92(3), 1980, pp. 362–368

NEST PLACEMENT IN SAGE THRASHERS, SAGE SPARROWS AND BREWER'S SPARROWS

Terrell Rich

Aside from the obvious variation in nest placement among species (Preston 1946, Preston and Norris 1947, Cruickshank 1956), nest-site selection may vary among individuals of a population (Preston and Norris 1947) or between early and later nests in a population during 1 season (Nice 1937, Best 1978, Rich 1978). Factors affecting nest placement may be primarily ecological (Goddard and Board 1967, Holcomb and Twiest 1968, Burger and Shisler 1978, Evans 1978, McCrimmon 1978), geographical (Schaefer 1976) or related to the thermal environment (Ricklefs and Hainsworth 1969; Calder 1973, 1974; Austin 1974, 1976). Differential success of nests placed in different sites may influence the evolution of nest placement within a species (Goddard and Board 1967, Holcomb and Twiest 1968, Austin 1974, Caccamise 1977, Best 1978, Evans 1978).

In this paper I present preliminary information on nest placement in the Sage Thrasher (*Oreoscoptes montanus*), Sage Sparrow (*Amphispiza belli*) and Brewer's Sparrow (*Spizella breweri*). These 3 species are reported to require sagebrush (*Artemisia* sp.) habitat for successful breeding (Braun et al. 1976). Although more information on these species is becoming available (Trost et al. 1975; Reynolds and Rich 1978; Rich 1977, 1978) the continuing destruction of sagebrush habitat for agricultural purposes necessitates continuing study of their biology.

MATERIALS AND METHODS

The study was conducted on a 50-ha study area northwest of Blackfoot, Bingham Co., Idaho, from March to July of 1976 and 1977. Habitat on the study area is described by Kuchler (1964) as sagebrush steppe dominated by sagebrush (*A. tridentata*). The grasses, *Poa sandbergii*, *Sitanion hystrix* and *Agropyron spicatum*, were common.

Nests were found incidental to other research, which involved repeated and thorough traversing of the study area. For both active and old nests (when attributable to a specific bird species) from previous years 6 variables were measured: (1) height from ground to bottom of nest, (2) height of sage containing nest, (3) circumference of sage, (4) distance from the edge of nest sage to next 2 nearest sage, (5) location of nest in the study area, and (6) height from bottom of nest to top of sage containing the nest. The last variable was termed "cover height," though it is not strictly a measure of cover for Brewer's and Sage sparrows. These sparrows place their nests towards the edge of the sage so that the maximum sage height is not, necessarily, directly over their nests. To facilitate comparisons thrasher nests were considered as either ground nests or sage nests. A 1-way analysis of variance was then performed on each variable for the 4 groups. The Student-Newman-Keuls multiple range test for unequal sample sizes was used to compare means when a significant F value resulted

TABLE 1

MEAN (±SD) NEST, SAGE AND COVER HEIGHT

Species	N	Nest height (cm)	Sage height (cm)	Cover height (cm)
Sage Sparrow	14	19.6 ± 10.9[a]	67.1 ± 8.4	47.4 ± 9.2
Brewer's Sparrow	27	28.2 ± 7.7	66.9 ± 11.3[b]	38.7 ± 10.9
Sage Thrasher-ground	61	0.0 ± 0.0	69.2 ± 12.0[b]	69.2 ± 12.0
Sage Thrasher-sage	114	23.1 ± 9.9[a]	83.6 ± 14.4	60.5 ± 11.5

[a] Not significantly different at $P \leq 0.05$.

[b] Not significantly different at $P \leq 0.05$. (All other pairs within a category significantly different at $P \leq 0.05$.)

from the analysis of variance (Zar 1974). Simple linear regressions were computed for the relationship between the independent variable—sage height, and the dependent variables—nest and cover height. A Chi-square goodness-of-fit test to the Poisson distribution was made for the horizontal distribution of thrasher nests with units of 0.25 ha and 1.00 ha (Zar 1974). Distribution of Brewer's and Sage sparrow nests was not examined, due to their small sample sizes.

A vegetation profile was constructed from 165 sample points along a single transect which bisected the study area. A 2-m rod marked at 1 dm intervals was placed vertically every 3 m and the total number of contacts with dead and live vegetation was recorded. Percentage cover of plant species was determined according to Daubenmire (1959). Four 50-m transects were positioned so as to sample what appeared to be the most and least dense vegetation in the study area.

RESULTS

Nest and sage height.—All nests were found either in or beneath sage. Of the measurements taken only nest height, sage height and cover height had significant F values. Table 1 presents statistics for nest placement and the results of the multiple range tests. Sage Sparrow (SS), Brewer's Sparrow (BS) and thrasher nests on the ground (STg) were in sage of the same height but each was at a different height within the sage—STg being the lowest, SS intermediate and BS highest. Sage-nesting thrasher nests (STs) were placed in taller sage than SS nests, but nests of the 2 were placed at the same height above the ground. Cover height was significantly different for each group. Thus, each group selected a unique site vertically in the sage.

For BS, SS and STs there was a tendency for birds to nest higher in taller sage (Fig. 1). Increasing height of cover above the nest with higher nests was shown for STs and BS. Comparison of the 2 regression lines—cover height and nest height—for each species indicates a preference, not for a constant height but rather for a proportion of the sage height available. The above comparison also reveals the influence that sage height alone has on nest-site selection.

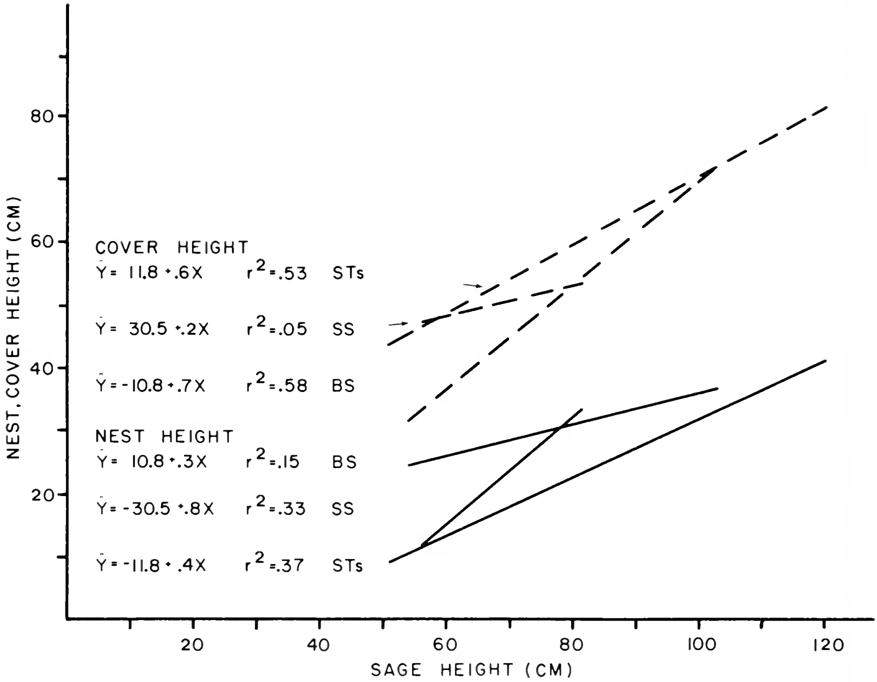


FIG. 1. Linear regressions of nest and cover height on sage height for Sage Sparrows (SS), Brewer's Sparrows (BS) and sage-nesting Sage Thrashers (STs).

Vegetation profile.—The resemblance between nest height frequency profile and vegetation profile suggests the importance to Sage Thrashers of having dense vegetation surround the nest (Fig. 2). Vegetation in the first interval was primarily grass, while the rest of the profile represents sage only. Both SS and STs nests were in the densest part of the sage, whereas BS nests were towards the edge of the densest portion. STg nests were placed in the relatively dense grass beneath the sage.

Horizontal distribution of thrasher nests.—To examine effects of larger scale differences in sage density and/or height on placement of nests I compared the number of nests in each 0.25 ha to the number in a random distribution. The nests were randomly distributed over the study area with a significant goodness-of-fit to the Poisson distribution (N = 164, χ^2 = 4.5584, df = 3, $P > 0.10$. The variance to mean ratio was 1.1528—close to the theoretical value of 1.0000. Similar results were obtained with units of 1.00 ha.

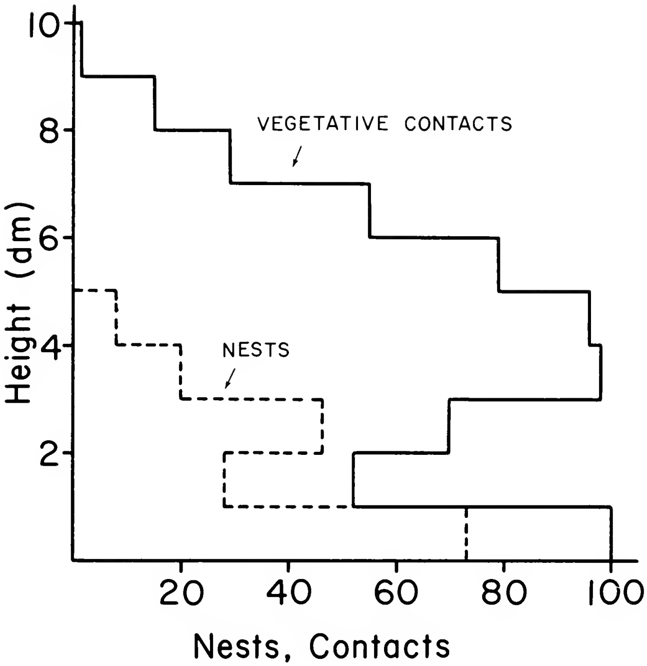


FIG. 2. Vertical vegetation density profile of the habitat and vertical frequency distribution of 175 Sage Thrasher nests.

DISCUSSION

Each of the 3 species, as well as the 2 subsets of thrashers, located their nests in a unique position vertically within the habitat. This may have been a result of interspecific competition for nest-sites (Burger and Shisler 1978), as the 3 species had broadly overlapping territories in the study area. However, the spacing of nests and density of sage did not suggest a shortage of sites. On the 50-ha study area there was about 1 nest per 1.25 ha for all species. The 4 vegetation transects revealed that sage covered from 11–44% of the study area, depending on the transect. Since the sage appeared rather evenly distributed each pair of birds had a computed 0.14–0.55 ha of "pure" sage in which to find a suitable site. Also, the breeding schedules for the 2 more abundant species did not overlap appreciably. Thrashers began laying in late April and early May, while Brewer's Sparrows did not begin laying until early June. Furthermore, if the random distribution of thrasher nests was not a sampling artifact at least this species seemed to find suitable sites everywhere in the study area.

Nest size.—Gross size of nests may have played a major role in vertical placement differences among the species. Thrashers built rather large nests of coarse sticks roughly 20 cm in diameter and 10 cm deep, requiring a site devoid of leaves and with substantial support. Ground nests benefited from both the support of the entire ground and the gap in foliage density (Fig. 2) which occurred slightly above the ground. Nests placed off the ground tended to be supported by the main branches of sage. The lack of large supporting branches higher in the sage may explain why frequency of nests decreased faster than vegetation density at greater heights (Fig. 2).

Sage Sparrows built smaller grass nests about 12 cm in diameter and 5 cm deep, which were supported by smaller branches. Although nests of this species were at the same mean height as STs nests they were placed more to the periphery of the sage where branches were smaller. Brewer's Sparrows built the smallest nests, about 8 cm in diameter and 4 cm deep. Their nests were located in the finest growth near the edge of the sage.

Vegetation and thermal environment.—For Sage Sparrows and certainly for thrashers it was important to maintain a certain density of vegetation around and above the nest (Fig. 2). This may have been variously related to wind protection, shading and heat loss. Overhead cover may also have been important in reducing heat loss from adults at night (Calder 1973) although this factor may not be as important as initially thought (Smith et al. 1974). Since Brewer's Sparrows nested in the most recent growth of individual sage there was less vegetation above their nests than above those of other species. Heat dissipation from the nest as a result of wind (Ricklefs and Hainsworth 1969, Austin 1974) may have been more important to Brewer's Sparrows. They nested relatively late in the year when air temperatures were at their maximum.

Of particular interest is H.W. Henshaw's (1875) observation of a platform of twigs placed 8 in above a thrasher nest so as ". . . to screen the setting bird from the rays of the almost tropical sun." I found 4 such platforms, 2 of which were almost certainly nests of a previous year. In the 2 other cases the platforms were too decomposed to permit identification. Only through direct observation would it be possible to claim that shading platforms were deliberately constructed for that purpose. More likely, sites which will benefit from the shade of a previous year's nest are selected.

Thrasher nest shifts.—Possibly, thrashers build later nests higher in the sage to benefit from cooler air temperatures off the ground and higher rates of wind-facilitated heat dissipation (Rich 1978). An increase in nest height as the season progresses has been reported for several other species (Best 1978, references in Welty 1975:272–3). This has been attributed to foliage development whereby the growth, e.g., of grass, provides cover at greater heights (Walkinshaw 1968). Best (1978) found this growth inadequate to explain the shift in Field Sparrow (*Spizella pusilla*) nests. In the present study the vertical growth of grass and forbs between the time of early and late nesting would not have been appreciable. Though sage is an evergreen species it does produce a growth of deciduous leaves each year (D. Wilde, pers. comm.). The chronology and extent of this growth are not known but could be important.

SUMMARY

Sage Sparrows, Brewer's Sparrows, ground-nesting and sage-nesting Sage Thrashers each selected a unique vertical position for nest placement in their sagebrush habitat. All nests were located in or beneath sagebrush. Each species nested higher in taller sagebrush. Sage-nesting thrashers and Brewer's Sparrows also had more cover over the nest in higher sage. This indicated their preference for placing a nest at a proportion of the sage height available, rather than at a constant height. Sage Thrashers and Sage Sparrows selected sites within the densest portion of the sage while Brewer's Sparrows selected sites above the densest portion. Sage Thrasher nest height frequency profile corresponded well with the vertical vegetation density profile. Though the species' territories overlapped extensively there seemed to be enough sage for each pair of birds so that interspecific competition for nest-sites did not have to occur. Nest size differences among the species may have been one of the most important factors influencing vertical placement.

ACKNOWLEDGMENTS

Data were collected incidental to research sponsored by the Frank M. Chapman Memorial Fund of the American Museum of Natural History in 1976 and 1977 and by a Grant-in-Aid of Research from the Society of Sigma Xi in 1977. I thank Charles H. Trost for unfailing assistance and several reviewers for valuable comments on earlier versions of this manuscript.

LITERATURE CITED

AUSTIN, G. T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. Condor 76:216–217.

———. 1976. Behavioral adaptations of the Verdin to the desert. Auk 93:245–262.

BEST, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95:9–22.

BRAUN, C. E., M. F. BAKER, R. L. ENG, J. S. GASHWILER AND M. H. SCHROEDER. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bull. 88:165–171.

BURGER, J. AND J. SHISLER. 1978. Nest site selection and competitive interactions of Herring and Laughing Gulls in New Jersey. Auk 95:252–266.

CACCAMISE, D. F. 1977. Breeding success and nest-site characteristics of the Red-winged Blackbird. Wilson Bull. 89:396–403.

CALDER, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. Ecology 54:127–134.

———. 1974. The thermal environment of a winter hummingbird nest. Condor 76:268–273.

CRUICKSHANK, A. D. 1956. Nesting heights of some woodland warblers in Maine. Wilson Bull. 68:157.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43–64.

EVANS, E. W. 1978. Nesting responses of Field Sparrows (*Spizella pusilla*) to plant succession on a Michigan old field. Condor 80:34–40.

GODDARD, S. V. AND V. V. BOARD. 1967. Reproductive success of Red-winged Blackbirds in north central Oklahoma. Wilson Bull. 79:283–289.

HENSHAW, H. W. 1875. Report upon the ornithological collections made in portions of Nevada, Utah, California, Colorado, New Mexico and Arizona during the years 1871, 1872, 1873 and 1874. Wheeler's Expl. Surv. West 100th Merid.

HOLCOMB, L. C. AND G. TWIEST. 1968. Ecological factors affecting nest building in Red-winged Blackbirds. Bird-Banding 39:14–22.

KUCHLER, A. W. 1964. Potential natural vegetation of the conterminous United States. Am. Geog. Soc. Spec. Publ. No. 36.

MCCRIMMON, D. A., JR. 1978. Nest site characteristics among five species of herons on the North Carolina coast. Auk 95:267–280.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. I. A population study of the Song Sparrow. Trans. Linn. Soc. N. Y. 4.

PRESTON, F. W. 1946. Nesting heights of birds building in shrubs. Ecology 27:87–91.

——— AND R. T. NORRIS. 1947. Nesting heights of breeding birds. Ecology 28:241–273.

REYNOLDS, T. D. AND T. D. G. RICH. 1978. Reproductive ecology of the Sage Thrasher (*Oreoscoptes montanus*) on the Snake River Plain in south-central Idaho. Auk 95:580–582.

RICH, T. D. G. 1977. Territorial behavior of the Sage Sparrow. M.S. thesis, Idaho State Univ., Pocatello, Idaho.

———. 1978. Nest placement in Sage Thrashers. Wilson Bull. 90:303.

RICKLEFS, R. E. AND F. R. HAINSWORTH. 1969. Temperature regulation in nestling Cactus Wrens: the nest environment. Condor 71:32–37.

SCHAEFER, V. H. 1976. Geographic variation in the placement and structure of oriole nests. Condor 78:443–448.

SMITH, W. K., S. W. ROBERTS AND P. C. MILLER. 1974. Calculating the nocturnal energy expenditure of an incubating Anna's Hummingbird. Condor 76:176–183.

TROST, C. H., T. D. REYNOLDS, M. S. REYNOLDS, P. G. RICH, T. G. RICH AND D. W. SHOREY. 1975. Preliminary draft environmental statement for the sodium-cooled class III design safety research experiment facility. Argonne National Laboratories, Argonne, Illinois.

WALKINSHAW, L. H. 1968. *Spizella pusilla pusilla*: Eastern Field Sparrow. Pp. 1217–1235 *in* Life histories of North American Cardinals, grosbeaks, buntings, towhees, finches and allies, Pt. 2, (O. L. Austin, Jr., ed.). U.S. Natl. Mus. Bull. 237.

WELTY, J. C. 1975. The life of birds. W. B. Saunders Co., Philadelphia, Pennsylvania.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

DEPT. BIOLOGY, IDAHO STATE UNIV., POCATELLO, IDAHO 83209. (PRESENT ADDRESS: P.O. BOX 204, 510 S. EDITH, SHOSHONE, IDAHO 83352.)
ACCEPTED 22 MAY 1979.

Wilson Bull., 92(3), 1980, pp. 369–375

WINTER HOME RANGES OF 4 CLANS OF RED-COCKADED WOODPECKERS IN THE CAROLINA SANDHILLS

Denise Moreau Sherrill and Verna Miller Case

The behavior and ecology of the Red-cockaded Woodpecker (*Picoides borealis*) have been of interest to ornithologists for a number of years (Murphy 1939). However, only recently have these aspects of the biology of the woodpecker been studied in any detail (Lay and Russell 1970, Ligon 1970, Thompson 1971, Hooper, Lennartz and Harlow [paper given at Wilson Soc. meeting 19–21 May 1977]). Red-cockaded Woodpeckers live in clans consisting of a mated pair, their offspring and associated helpers (Ligon 1970). Nesting and roosting cavities of these woodpeckers usually are constructed in living pine trees infected with red-heart disease (*Phellinus pini*) (Steirly 1957).

The amount of space used by Red-cockaded Woodpecker clans varies. Crosby (1971) found a mean of 17.2 ha for home ranges of 2 clans in March–June in northcentral Florida. The territory of 1 clan in Georgia was estimated to be 65.6 ha (Baker 1971). Skorupa and McFarlane (1976) studied seasonal variation in the foraging territories of 2 clans in South Carolina and found maximum territory sizes of 48.3 ha and 65.8 ha during the month of January. The mean winter territories of 6 clans in the coastal plains of South Carolina was 64.8 ha (Hooper et al., unpubl.) Nesbitt et al. (1978) reported an average range of 69.8 ha for 4 clans in central Florida during October–December.

The purpose of our study was to determine the area used by 4 clans of Red-cockaded Woodpeckers in the Carolina Sandhills during the winter of 1977–1978 and to examine the influence of clan size and interclan pressures on the spacing of the clans.

STUDY AREA AND METHODS

Four clans of Red-cockaded Woodpeckers were observed during December 1977, January and February 1978 at the Carolina Sandhills National Wildlife Refuge, South Carolina. The predominant habitat in the approximately 161.8-ha study area was longleaf pine (*Pinus palustris*) with a scrub oak (*Quercus laevis* and *Q. marilandica*) understory. The longleaf pine in the study area included sawtimber (DBH > 22.86 cm) and pulpwood (DBH = 10.16–22.60 cm). Approximately 8.00 ha contained only longleaf pine of sawtimber size and no understory. These 8.00 ha were centrally located. On the western border of the study area there were several bodies of water, 3 small ponds which ranged in size from 0.80–1.33 ha and one 12.14-ha lake. Wet areas containing pond pine (*Pinus serotina*) scattered longleaf pine and a dense hardwood understory (various spp.) surrounded the ponds and lake.

Clan members were uniquely color banded during the first week in January. Clan 1 consisted of 8 birds, with 5 males and 2 females banded. Clan 2 had 4 birds and 2 males were banded. During the majority of the observation period, clan 3 included a banded pair. On several days during January, 2 other Red-cockaded Woodpeckers were seen foraging with clan 3. No apparent agonistic encounters between the non-resident birds and the home pair were seen; however, the 2 non-resident birds never roosted within the range of clan 3. Clan 4 consisted of 4 birds, of which a male and female were banded.

On each day of observation, 1 clan was selected and followed for the remainder of the day. Total days and hours of observation for each clan were as follows: clan 1—10 days (39 h), clan 2—15 days (33 h), clan 3—14 days (37 h), and clan 4—11 days (40 h). Observation days for each clan were distributed randomly throughout the 3-month study. The time of day when a clan was observed depended on when the clan was first spotted and weather conditions. Location of the clan was plotted on a grid map at 5 min intervals throughout each observation period. Grid maps were made by placing a grid (1 block = 10 ha) over aerial photographs and other available maps of the refuge.

Observation points for all days were plotted on 1 map for each clan (clan 1—471 observation points; clan 2—451 observation points; clan 3—457 observation points; clan 4—488 observation points). The size of the area used by each clan during the duration of the study was then calculated by connecting all peripheral points and measuring the area within these points.

Locations of cavity trees within and adjacent to the home ranges were plotted. Distances from the peripheral cavity trees of a clan to the peripheral cavity trees of all adjacent clans were measured. Also, distances from the nest cavity of a clan to the nest cavities of adjacent clans were measured. Locations of nest cavities used by various clans in the spring of 1978 were determined, with the exception of clan 4, by observations of the refuge forester, David Robinson, and authors. The nest cavity used by clan 4 was not observed and there is a possibility that they may not have nested in 1978. However, from activities around the cavity trees during our study and from later observations by David Robinson we feel that the cavity tree circled (⊙) for clan 4 in Fig. 1 had the highest probability of being the 1978 nest cavity, if one was present. Finally, the agonistic interactions between clans were recorded and the locations of disputes were plotted on the maps. The agonistic encounters generally consisted of members of 2 clans giving the SHE-U call (Ligon 1970). A few instances of chasing and wing boxing were recorded.

Standard parametric statistical methods were used for computing means and standard deviations of distances among cavity trees of all clans. Simple linear correlations were computed to determine relationships between home range size and other parameters measured in the study (Steel and Torrie 1960:183).

RESULTS AND DISCUSSION

The mean home range of the 4 clans was 31.2 ha (clan 1—43.7 ha; clan 2—20.6 ha; clan 3—20.7 ha; clan 4—39.9 ha). A diagrammatic representation of the areas occupied by the 4 clans is shown on Fig. 1.

According to Wilson's (1975) classification of social spacing, a home range is an "area that an animal learns thoroughly and habitually patrols" and a territory is an "area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisment." Terminology used to describe the social spacing of Red-cockaded Woodpeckers has varied. Ligon (1970, 1971), Lay and Russell (1970)

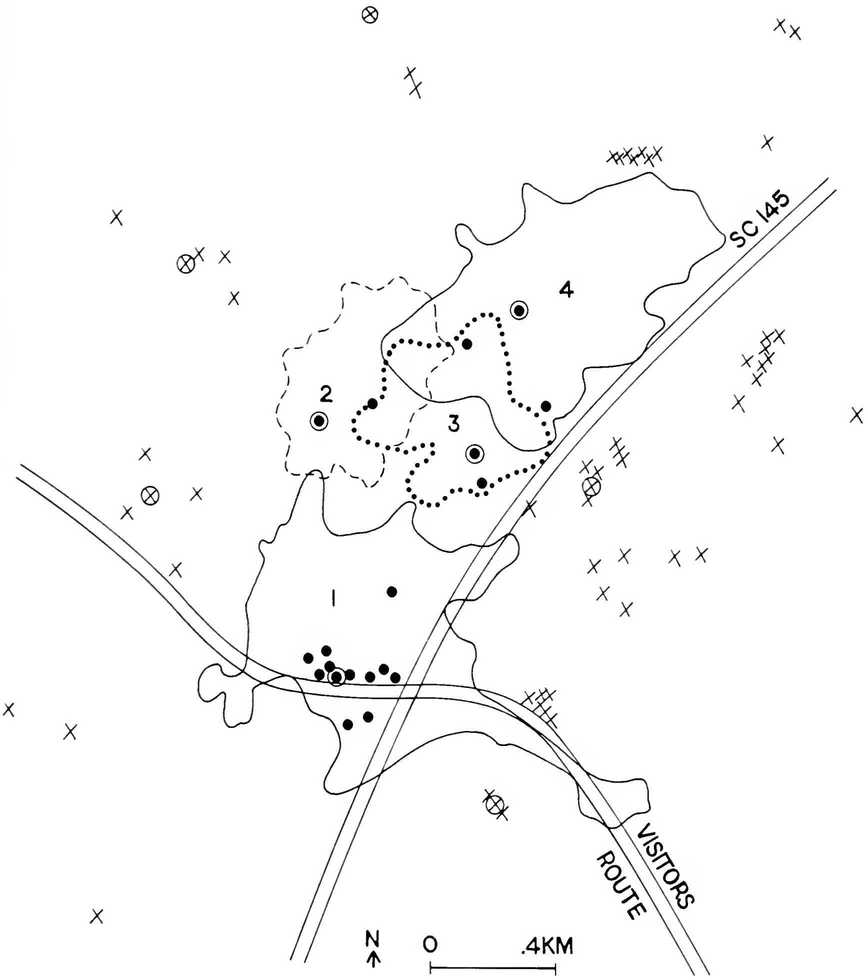


FIG. 1. Home ranges of 4 clans of Red-cockaded Woodpeckers. Symbols are as follows: ● = cavity trees, ⊙ = nest trees (1978), × = cavity trees of neighbors, ⊗ = nest trees of neighbors.

and Baker (1971) used the term "territory" to describe the red-cockaded's social spacing. Crosby (1971) appeared to use the terms home range and territory interchangeably, while Hooper et al. (unpubl.) distinguished between territories and home ranges of red-cockaded clans. They indicated that the home range was larger than the territory in all clans studied; however, the difference between the size of the home range and the territory was variable. We have classified the 4 areas occupied by the clans

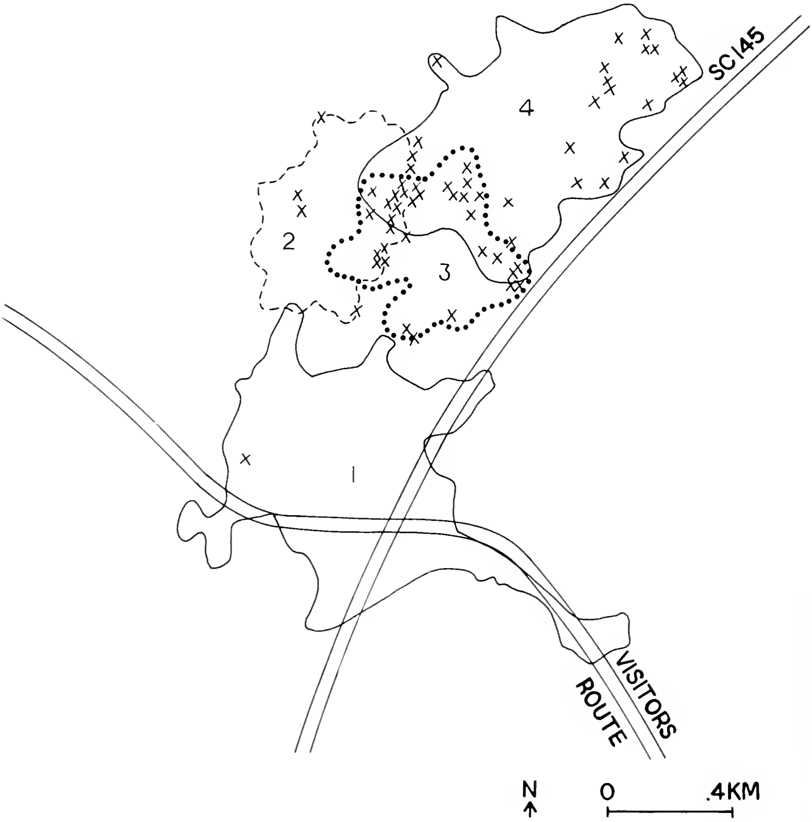


FIG. 2. Location of agonistic encounters of 4 clans of Red-cockaded Woodpeckers. X represents 1 agonistic encounter.

of this study as home ranges rather than territories for 2 reasons. First, the areas used by clans 2–4 overlap, indicating that parts of the ranges of these 3 clans are shared by 2 or more clans (see Fig. 1). Secondly, no well-defined defense perimeter was apparent in the 4 clans with the possible exception of clan 3 (Fig. 2). Therefore, the results of this study do not present sufficient evidence to justify classifying the areas occupied by the 4 clans as territories. Further study may indicate that these 4 clans occupy a home range and defend a smaller territory within the home range as reported by Hooper et al. (unpubl.) for clans at Francis Marion National Forest.

The average size of home ranges reported here is within the size variation of areas occupied by other Red-cockaded Woodpecker clans (Lay

TABLE 1

TOTAL AGONISTIC ENCOUNTERS OBSERVED IN 4 CLANS DURING STUDY

Clan Total h observation/clan	1 39	2 33	3 37	4 40
		No. agonistic encounters		
December	0	0	2	2
January	0	6	5	7
February	1	6	5	5
Total	1	12	12	14

and Russell 1970, Crosby 1971, Baker 1971, Skorupa and McFarlane 1976, Hooper et al., unpubl.). The closest correspondence was found between our results and the results for 4 clans located in predominantly longleaf pine areas at Francis Marion National Forest, which had winter home ranges of 22.6–28.7 ha (Hooper, pers. comm.).

As suggested by Hooper et al. (unpubl.), the size of the area used by a red-cockaded clan may be related to the size of the clan, interclan pressures and the type of habitat. We looked at some aspects of the first 2 factors in relation to home range size. No significant relationship was found between the number of birds in the 4 clans and the size of the home range used by each clan ($r = 0.75$, NS). Hooper et al. (unpubl.) also reported finding no striking relationship between clan size and territory size, but stated that more data were needed before any conclusions could be drawn.

We analyzed the influence of interclan pressures on the size of the home ranges of the 4 clans using 3 criteria: (1) agonistic encounters between clans (Table 1); (2) average distances to peripheral cavity trees of surrounding clans (Table 2); and (3) average distances to nest cavities of neighboring clans (Table 2).

During observations clan 1 was seen to be involved in only 1 agonistic

TABLE 2

MEANS AND SD OF DISTANCES TO NEIGHBORING CAVITY TREES AND NEST CAVITIES

	Ave. distances to neighboring cavity trees (m)	Ave. distances to neighboring nest cavities (m)
Clan 1	560 ± 133	770 ± 132
Clan 2	480 ± 153	590 ± 123
Clan 3	295 ± 106	500 ± 185
Clan 4	560 ± 284	720 ± 267

interaction with another clan, while clans 2, 3 and 4 were involved in 12, 12 and 14 encounters respectively. The sites of the agonistic encounters for each clan are shown in Fig. 2. No significant correlation was found between home range size and the number of agonistic encounters ($r = -0.55$, NS); however, there seems to be a tendency for clans with larger home ranges to be involved in fewer encounters. Also the greatest numbers of conflicts occurred where the home ranges overlapped (see Fig. 2).

No significant correlation was found when the home range sizes of the clans were compared to the average distances to peripheral cavity trees of neighboring clans ($r = 0.78$, NS). However, when home range sizes were compared to the average distances between the nest cavities of all surrounding clans, a significant relationship was found ($r = 0.95$, $P \leqslant 0.05$). Hence, it appears that the further away the nest cavities of neighboring clans, the larger the size of the home range.

One possible explanation for the relationship between the proximity of nest cavities and home range size is that aggression by members of a clan toward intruders decreases as the distance from their nest cavity increases. When nest cavities are close together, movements of a clan are limited by aggression encountered from neighboring clans in areas surrounding their respective nest cavities. When nest cavities of neighboring clans are not in close proximity, a clan can expand its home range over a larger area without encountering agonistic interactions. By comparing Figs. 1 and 2, we see that where home ranges of clans 2–4 extend toward the nest cavities of their neighbor clans, the number of agonistic encounters is high. The nest cavity of clan 1 is more isolated from neighboring nest cavities than the nests of clans 2–4 and this isolation may explain the small number of agonistic encounters recorded for this clan and its large home range. Hence, we feel that a clan's defense of its nest cavity is a major factor in limiting the range of adjacent clans. This hypothesis is congruent with the suggestion of Hooper et al. (unpubl.) that the territories, or defended areas, of 6 red-cockaded clans were smaller than their home ranges and would also strengthen the argument for the importance of the nest cavity as the central focus of the clan (Ligon 1971).

SUMMARY

The average size of the winter home ranges of 4 clans of Red-cockaded Woodpeckers in the Carolina Sandhills National Wildlife Refuge was 31.2 ha. Distance between nest cavities of clans appears to be significantly related to the sizes of the home ranges of the 4 clans. No significant relationship was found between home range size and clan size, agonistic encounters or distances to peripheral cavity trees. Future research involving a larger sample size will clarify whether these factors may play a role in influencing home range size. The relationship between nest cavity distances and home range size does indicate that interclan

pressure is a major factor influencing the home range size of 4 clans of Red-cockaded Woodpeckers in the Carolina Sandhills National Wildlife Refuge.

ACKNOWLEDGMENTS

The authors wish to thank Marvin Hurdle, David Robinson and George Haas, at the Carolina Sandhills National Wildlife Refuge, for supporting this research and providing information about the woodpeckers in the area. We are indebted to Robert Hooper and Michael Lennartz of the U. S. Forest Service at Clemson, South Carolina, for their suggestions of methods for observations, for their encouragement and advice, and for banding the Sandhill woodpeckers.

LITERATURE CITED

BAKER, W. W. 1971. Progress report on the life history studies of the Red-cockaded Woodpecker at Tall Timbers Research Station. P. 56 *in* Proc. Symp. Ecol. Manage. Red-cockaded Woodpecker, (R. L. Thompson, ed.). Bur. Sport Fish Wildl. and Tall Timbers Res. Stn.

CROSBY, G. T. 1971. Home range characteristics of the Red-cockaded Woodpecker in north-central Florida. Pp. 60–73 *in* Proc. Symp. Ecol. Manage. Red-cockaded Woodpecker (R. L. Thompson, ed.). Bur. Sport Fish Wildl. and Tall Timbers Res. Stn.

LAY, D. W. AND D. N. RUSSELL. 1970. Notes on the Red-cockaded Woodpecker in Texas. Auk 87:781–786.

LIGON, J. D. 1970. Behavior and breeding biology of the Red-cockaded Woodpecker. Auk 87:255–278.

———. 1971. Some factors influencing numbers of the Red-cockaded Woodpecker. Pp. 30–41 *in* Proc. Symp. Ecol. Manage. Red-cockaded Woodpecker (R. L. Thompson, ed.). Bur. Sport Fish Wildl. and Tall Timbers Res. Stn.

MURPHY, E. E. 1939. Red-cockaded Woodpecker. Pp. 72–79 *in* Life histories of North American woodpeckers, (A. C. Bent, ed.). U.S. Natl. Mus. Bull. 174.

NESBITT, S. A., D. T. GILBERT AND D. B. BARBOUR. 1978. Red-cockaded Woodpecker fall movements in a Florida flatwoods community. Auk 95:145–151.

SKORUPA, J. P. AND R. W. MCFARLANE. 1976. Seasonal variation in foraging territory of Red-cockaded Woodpeckers. Wilson Bull. 88:662–664.

STEEL, R. G. D. AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York, New York.

STEIRLY, C. C. 1957. Nesting ecology of the Red-cockaded Woodpeckeer in Virginia. Atl. Nat. 12:280–292.

THOMPSON, R. L., ed. 1971. Proc. Symp. Ecol. Manage. Red-cockaded Woodpecker. Bur. Sport Fish Wildl. and Tall Timbers Res. Stn.

WILSON, E. O. 1975. Sociobiology. Harvard Univ. Press, Cambridge, Massachusetts.

DEPT. BIOLOGY, DAVIDSON COLL., DAVIDSON, NORTH CAROLINA 28036. ACCEPTED 9 AUG. 1979.

GENERAL NOTES

Wilson Bull., 92(3), 1980, pp. 376–381

Growth and development of major body components in the Monk Parakeet.—The growth rates of a considerable number of bird species have been summarized (Ricklefs, Ibis 110:419–451, 1968; Ibis 115:177–201, 1973), yet among these there are few records for hole-nesting species and none for parrots. Caccamise and Alexandro (Wilson Bull. 88:495–497, 1976) have since published information on the growth rate of Monk Parakeets (*Myiopsitta monachus*), but they considered only age-specific changes in body weight. This paper provides information on egg size and nestling development and analyzes growth rates of major skeletal elements of Monk Parakeets.

While most species of parrots are hole or cavity nesters, Monk Parakeets are unique in building large enclosed stick nests, often communally (Caccamise and Weathers, Wilson Bull. 89:346–349, 1977; Forshaw, Parrots of the World, Doubleday and Co., New York, New York, 1973). These nests are occupied all year by mated pairs and by the young of the year for a considerable time beyond fledging (Alexandro, M.S. thesis, Rutgers Univ., New Brunswick, New Jersey, 1977). In a strict sense this species is not a true hole-nester since the nests are constructed of sticks. Considering the often massive size (200 kg) and sturdy construction of the nests (Roscoe et al., N. Y. State Fish and Game J., 1973), however, it is not surprising that this species demonstrates the large clutch-size (5–9 eggs) and slow growth rate common in many hole-nesting species (Lack, Ibis 90:25–45, 1946; Ricklefs 1968).

Methods.—Successive measurements were made on 2 young in 1975 and 3 young in 1976, that were reared in the outdoor flight cage described by Weathers and Caccamise (Oecologia 18:329–342, 1974). During both years the pair producing the young were part of a group of 6 birds collectively housed. I supplied freshly cut privit (*Ligustrum* sp.) twigs for nesting material. These birds used to construct the characteristic enclosed nest. The birds were provided with water, sunflower seeds, white bread and dry dog food ad libitum. Vitamins were added to the water, and fresh apples were placed occasionally in the cage. Though growth data were collected from nestlings in only 2 nests, 9 nests were under observation at various times during this study. One of these nests was built by free-living birds in New Jersey (Caccamise and Alexandro 1976). The others were the result of pairings by the remaining birds in the cage. Data were collected on rates of egg-laying and egg morphology from all nests.

In 1975, egg-laying was first observed during the first week in April when 2 eggs were discovered in the nest. This initial attempt failed, when the female of the pair died. After another pairing, a second clutch was begun on 3 May. Of the 5 eggs in this clutch only 3 hatched, 1 each day on 27, 28 and 29 May.

In 1976, the first nesting attempt began during the first week in April when 3 eggs were laid. This attempt failed when the pair undertook reconstruction of their nest on 13 April. The second clutch was begun on 5 May, with 8 eggs laid by 15 May. The first young hatched on 30 May. The other 3 eggs that hatched did so over the succeeding 3 days. One nestling (9 days old) died on 8 June.

Measurements of elements representing maximum perpendicular distance between articular surfaces of bones were taken regularly on live specimens throughout the growth period. They included bill width (at base where bill emerges from skin); bill length (tip of upper rhamphotheca to distal edge of cere); bill depth (perpendicular distance from distal edge of cere to ventral surface of lower mandible); and digit span (for this foot placed on flat surface and second and third toes aligned) which was recorded as the distance between distal ends of terminal phalanges of toes 2 and 3. Body length was the distance from the top of the head (with bill held perpendicular to the long axis of the body) to the posterior end of the pygostyle. Also, feather length was taken from the distal end to the point of emergence from the skin. Measurements also were taken from 9 caged adults.

Results.—Eggs from 3 nests were measured within 3 days of laying. For 28 eggs, the mean length (±SE) was 27.2 ± 0.20 mm (range 25.0–29.7 mm) and the mean width was 20.5 ± 0.15 mm (range 19.2–23.4 mm). The mean weight of 14 eggs was 6.10 ± 0.01 g (range 5.48–6.55 g).

Incubation apparently began with the first egg. During egg-laying females spend considerable time in the nest, occasionally leaving for very short feeding bouts (Alexandro 1977). Hatching is asynchronous, and a wide disparity in nestling size is typical.

At hatching, nestlings had only a sparse covering of yellowish down, were incapable of locomotion and were blind with eyelids fused. They did gape, but seemed unable to raise their heads. I first heard a nestling vocalize on day 2. That comprised a short 0.5 sec *see-ee-ep* given repeatedly at 0.25 sec intervals.

By day 4 nestlings showed limited coordinated activity, only able to squat with their ventral surface on the substrate. They commonly rolled their heads from side to side, using the bill as a pivot against the substrate, but I never saw a head lifted at this age.

About day 10 the eyelids began to open. Now nestlings could unsteadily hold up their heads. By day 16 nestlings held up their heads without wavering but, as their legs remained fairly weak and of limited coordination, they were capable of only limited locomotion. The rectrices were conspicuously emerged by this time but natal down still covered the remainder of the body. By day 18 the eyes were fully open, and primaries had begun to emerge. By day 20 nestlings were able to stand steadily and firmly grasp a perch with their feet. They were quite active and could use the bill for grasping.

The major feather tracts of the body were well delineated by day 24. The feathers of the head and wings were fully emerged, while many contour feathers of the body were still in sheaths. On day 27 I first heard a nestling emit an alarm call essentially similar to that of the adult. At this age the nestlings were very active, flapping their partially feathered wings and walking very quickly and strongly. At day 28 the body feathering was about half developed, although much natal down remained (except on the head).

By day 37 most contour feathering was complete, and little down remained. The flight feathers were still emerging from sheaths, being less than 50% of adult size at this time. The earliest fledging was observed on day 40.

For each body component growth was relatively uniform throughout the first 35 days of development, after which growth slowed considerably (Figs. 1, 2). Linear regressions of age (through day 35) and percent adult size (Table 1) were highly significant ($P < 0.01$). While the growth rate was probably not uniform throughout this period, as required for a truly linear relationship, the high r^2 values indicated that the deviations from linearity were small.

The slope of these regression equations provided an estimate of the overall growth rate during the initial stages of development (Table 1). With the exception of the tarsometatarsus, the skeletal elements grew at very similar rates of 2–2.5% per day. The tarsometatarsus grew at rates significantly lower than all other leg and wing elements except the tibiotarsus, which was intermediate in value. The bill dimensions grew more slowly at a rate of about 1.5% per day. Growth rates of the 10th primary and the innermost rectrix were taken, beginning from the time they emerged from the skin (day 10 and 18, respectively); thus the growth rates of these feathers did not correspond to the same period of development as the other measurements.

Estimates of relative levels of maturation at the end of the linear portion of the growth curve were indicated by the ratio of the mean nestling size at 35 days to the mean adult size (Table 1). In terms of linear dimensions, the wing was somewhat more developed than the

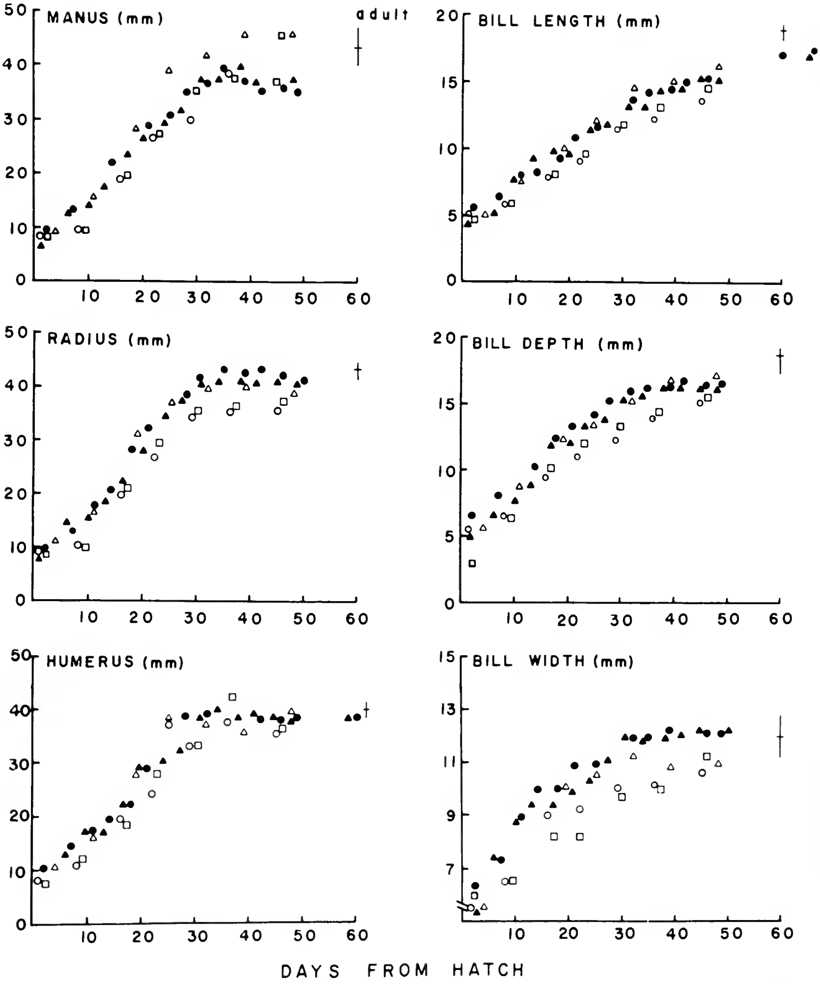


FIG. 1. Size of body components relative to the number of days from the date of hatching. Open symbols represent the 1975 brood, and closed symbols the 1976 brood. The mean and range are indicated for the adult measurements.

leg. For the leg and wing, both the proximal and the most distal segments most closely approached adult dimensions. The bill grew relatively slowly, and at 35 days it was still well below adult size in both length and depth, while width was 92% of adult size. By day 35 primary 10 and the inner rectrix were only 42% and 30% of adult size, respectively.

Discussion.—Based on studies of growth in 3 species of altricial passerines, O'Connor (Ibis 119:147–166, 1977) stated: ". . . resources are allocated at any time to the growth of the components with the currently highest functional priority, though with due regard for future needs." Monk Parakeets fledge at 35–40 days. At the younger end of this range, which

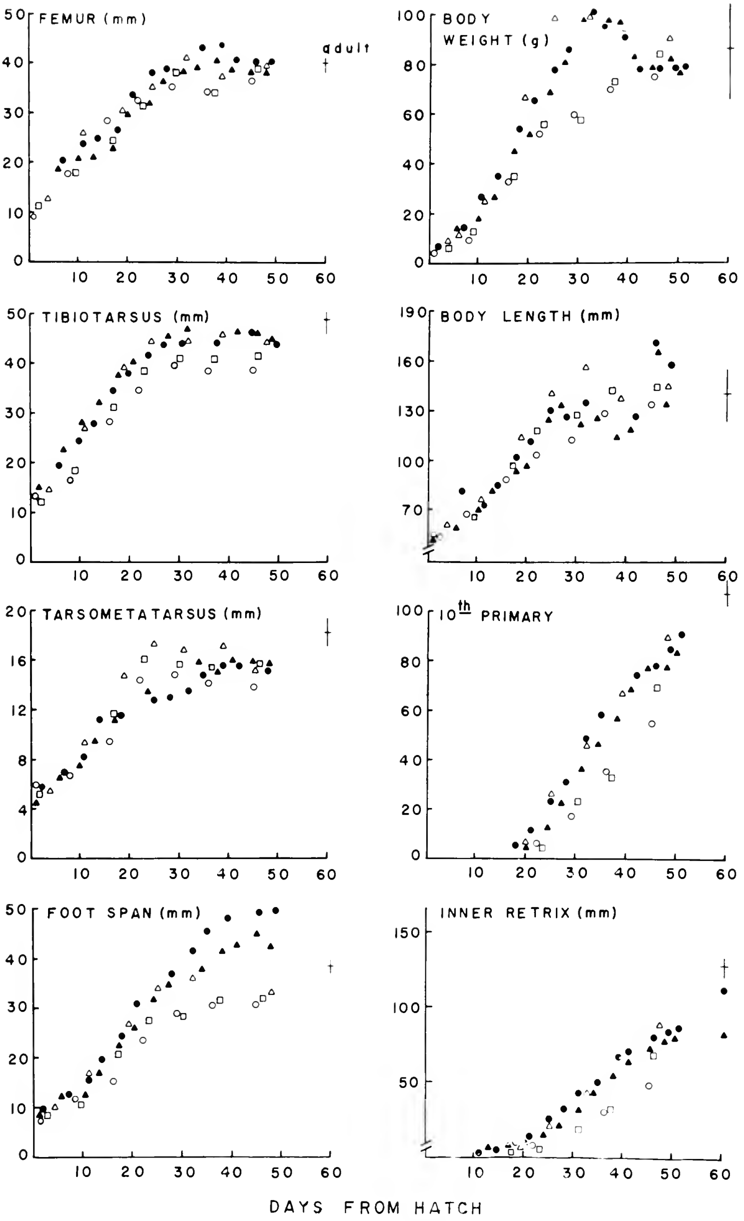


FIG. 2. Size of body components, body weight and feather lengths relative to the number of days from the date of hatching. Open symbols represent the 1975 brood, and closed symbols the 1976 brood. The mean and range are indicated for the adult measurements.

TABLE 1

REGRESSIONS OF BODY COMPONENT SIZE (PERCENT OF MEAN ADULT SIZE) ON AGE; PERCENT OF MEAN ADULT SIZE AT 35 DAYS

Body component	a[1]	b[2]	$S_{\bar{b}}$[3]	r^2*	% mean adult size at 35 days
Humerus	15.4	2.6	0.11	0.94	100
Radius	12.8	2.5	0.10	0.95	90
Manus	12.2	2.3	0.10	0.94	96
Femur	28.2	2.3	0.10	0.94	97
Tarsometatarsus	27.4	1.9	0.14	0.85	84
Tibiotarsus	27.4	2.2	0.11	0.92	89
Toe span	13.2	2.6	0.14	0.92	99
Bill length	22.3	1.5	0.06	0.96	71
Bill width	49.4	1.5	0.12	0.82	92
Bill depth	26.6	1.8	0.08	0.93	82
Tenth primary	−50.0	2.7	0.31	0.82	42
Inner rectrix	−20.9	1.4	0.16	0.79	30
Body length	32.3	2.1	0.12	0.91	99

[1] a = Y-intercept from the regression equation.

[2] b = slope from regression equation.

[3] $S_{\bar{b}}$ = standard error of the slope.

* All $r^2 = P \leq 0.01$.

corresponds with the age of maximum weight, the body components of greatest functional priority, and hence greatest survival value would be expected to be the most nearly full grown. Comparisons of the percent mean adult size with nestlings at an age of 35 days provide an indication of the state of maturation, at least in terms of size, at about the time of fledging.

Since this species is an arboreal nester, fledging age is probably a function of the attainment of flight capabilities. By day 35 both lengths of body and wing components were either of adult size, or nearly so. By comparison, major leg bones had not attained adult length even though these elements at hatching were considerably more advanced than the wing bones. This is evidenced by the much higher Y-intercepts for regressions of leg bone length on age (Table 1).

O'Connor (1977) suggested that early development of the leg, particularly the tarsometatarsus, is important in some altricial species because the nestlings must have the ability to orient and extend themselves towards the adult during begging and feeding. In contrast to the Monk Parakeet, in which leg growth and coordination is late, altricial species discussed by O'Connor (1977) hatch synchronously and are fed by the parents in response to begging behavior. Though feeding of Monk Parakeet nestlings in the nest has not been observed, it seems unlikely that begging is of primary importance in this species, at least early in development, since the young appeared unable to raise their heads until after day 8. In addition, asynchronous hatching of eggs in Monk Parakeets results in a wide disparity in age among the nestlings. Assuming that 1 egg hatches per day, with a 9-egg clutch there would be a considerable disparity in age and size between the oldest and youngest nestling. If begging alone elicited feeding behavior by the parents, the youngest nestling would be at a severe disadvantage under all circumstances, except when all the older siblings were satiated.

By day 35 foot span already averaged 99% of adult size. Rapid attainment of adult foot size likely reflects the importance of the many tasks the foot performs (e.g., perching, climbing, feeding).

At hatching, bill width was already 49.4% of adult size, although, at day 35, bill width was closer to adult size than length or depth. This was the result of a more rapid development in width before hatching, since the growth rates of all bill dimensions were about the same throughout nestling development. Since bill width was measured at the base of the bill, it is about equivalent to gape width. The rapid increase of gape width in other species (Dunn, Condor 77:431–438, 1975; Holcomb, Nebraska Bird Rev. 36:22–32, 1968; Holcomb and Twiest, Ohio J. Sci. 68:277–284, 1968; Royama, Ibis 108:313–347, 1966) has been interpreted (O'Connor, Ibis 119:147–166, 1975) as important in increasing parental feeding efficiency because it allows the young to consume larger food items. Young Monk Parakeets are fed by regurgitation. This material was described as a white, milky fluid (Alexandro 1977). Accordingly, the ability to consume large food items may be of little value to nestlings. Since food is provided by the parents in a rather processed form, there would be little advantage in rapid bill growth for the purpose of processing food items. Fledglings, too, are fed by regurgitation, although they soon begin to do some foraging for themselves. Yet, as Portmann (Proc. 11th Int. Ornithol. Congr. 138–151, 1955) has shown, as the brain develops early, the skull must develop similarly to accommodate it. Thus, the greater maturity in bill width may simply reflect the need for early skull development.

Acknowledgments.—For their contributions throughout the course of this study I wish to thank Thelma Arculin, Peter J. Alexandro, Susan Ford and Charles Wagg. This is a paper of the Journal Series, New Jersey Agricultural Experiment Station, Cook College, Rutgers, The State University of New Jersey, New Brunswick, New Jersey.—DONALD F. CACCAMISE, *Dept. Entomology and Economic Zoology, Rutgers, The State Univ. New Jersey, New Brunswick, New Jersey 08903.* *Accepted 1 June 1979.*

Wilson Bull., 92(3), 1980, pp. 381–389

The influence of agriculture on avian communities near Villavicencio, Colombia.—Destruction of natural vegetation to meet demands for increased agricultural production has restricted the distribution of certain avian species in Colombia, while benefiting others (Olivares, Smithson. Contrib. Zool. No. 26:77–87, 1970; Munves, Auk 92:307–321, 1975). In regions where a systematic conversion to agriculture is occurring, studies of the avifauna adapted to the altered habitats would have predictive value. Blydenstein (Ecology 48:1–15, 1967) described a recent westward extension of the savanna as forests were cleared at the western edge of the Llanos Orientales, implying changes in avian community composition. This paper examines habitat usage by bird species on a representative agricultural area in this region and asks: how do present land-use trends affect species abundance and distribution?

Study area.—The western sections of the Department of Meta and the Intendencia of Casanare were formerly covered by a piedmont rain forest which extended eastward from the Andean foothills, gradually merging with the savanna and gallery forests typical of the Colombian Llanos (Bates, Geogr. Rev. 38:555–574, 1948). During the last 3 decades, forests have been diminished greatly in the vicinity of Villavicencio, Meta, and the land converted to the production of rice and cattle. Fieldwork was conducted at the Hacienda La Corocora (3°57′N, 73°24′W; elev. 310 m) 35 km SE of Villavicencio. Detailed descriptions of vegetation and climate in this region are given by Bates (1948) and Blydenstein (1967). Annual precipitation averages 2600 mm, distributed mostly April through October. Following the clearing of forest, ricefields and pasture now comprise the large majority of the Hacienda's 3500 ha.

Methods.—Habitats on the Hacienda were defined and classified as increasing in area, decreasing, or stable, in accordance with observed land-use trends. Each habitat was censused for bird species an average of 1 h per week from 3 December 1976–10 November 1977, and from 12 May–4 August 1978. Permanent and seasonally resident species recorded were classified as to relative abundance in each habitat: (1) common, almost always observed in the habitat, frequently in large numbers; (2) regular, observed on at least 50% of trips to the habitat, but not in large numbers; (3) uncommon, observed on less than 50% of trips; and (4) scarce, observed on only a few occasions. Classifications for seasonal residents reflect periods of peak abundance. Transient species remaining on the study area for less than a week were not included. Assumptions regarding trends in species abundance and distribution are based on observed species-habitat associations.

Results.—Eight habitats were defined on the Hacienda:

(1) remnant forest—largely in thin (<200 m) strips along streams;

(2) morichales—stands of Moriche Palms (*Mauritia*) beside permanent pools of water and slow-moving sections of streams;

(3) second growth—thick herbaceous growth, large woody shrubs, and small trees, often forming a transition between forest and open areas;

(4) marshes—shallow standing or slow-moving water with floating and emergent vegetation, increasing considerably in area during the wet season;

(5) ricefields—lots of 10–90 ha with a layer of water usually less than 10 cm deep;

(6) early-successional fields—low herbaceous growth invading ricefields following harvest and drainage of water. Fields are grazed by cattle for about 7 months, after which weeds are burned and the lots are returned to rice production. Rice is planted in different lots at different times so that rice and cattle production continue simultaneously. During the grazing stage, the vegetation typifies savanna conditions. At any given time, habitats 5 and 6 combined comprise about 65% of the total study area.

(7) pasture—short-grass permanent pasture with succession arrested by heavy grazing pressure;

(8) residential areas—buildings and grounds with small gardens, shade and fruit trees.

Habitats 5–8 reflect agricultural land-use and can be considered increasing throughout the region, while 1 and 2 most clearly represent original vegetation decreasing due to development. Habitats 3 and 4 are considered essentially stable. Although the latter areas are frequently cleared to increase the amount of land involved in crop production, the rate of depletion is seemingly balanced by the rapid rate at which these habitats are produced.

Habitat usage and abundance of 159 resident and 40 seasonally resident species are summarized in Table 1.

Discussion.—Presumably, species most directly benefited by land alteration would be those whose habitat usage is confined to increasing habitats or both increasing and stable habitats. The 57 resident species (36% of total residents) in this category are characterized by raptors associated with open areas (e.g., vultures, Savanna Hawk, caracaras, Burrowing Owl), doves (e.g., ground-doves, Eared Dove, Pale-vented Pigeon), small finches (e.g., seedeaters, yellow-finches, Yellow-browed Sparrow), as well as various icterids, flycatchers, hummingbirds and others. Most of these species were recorded principally in early-successional fields; few resident species (e.g., Burrowing Owl, Double-striped Thick-knee, Scaled Dove, Carib Grackle) were primarily supported by pastures or residential areas. No resident species were found exclusively or predominately in ricefields. Relatively few of the species associated with increasing habitats were considered uncommon or scarce, implying rapid niche-exploitation and population expansion by open-area species as these habitats become available.

TABLE 1

HABITAT USAGE AND RELATIVE ABUNDANCE OF 199 SPECIES AT HACIENDA LA COROCORA, META, COLOMBIA

Species	Habitat usage[a]							
	1	2	3	4	5	6	7	8
Cinereous Tinamou (*Crypturellus cinereus*)	S[b]	–	S	–	–	–	–	–
Undulated Tinamou (*C. undulatus*)	–	–	S	–	–	–	–	–
Anhinga (*Anhinga anhinga*)	–	S	–	–	–	–	–	–
White-necked Heron (*Ardea cocoi*)	–	–	–	U	–	–	–	–
Great Egret (*Casmerodius albus*)*	–	U	–	C	C	–	–	–
Snowy Egret (*Egretta thula*)*	–	–	–	R	R	–	–	–
Little Blue Heron (*Florida caerulea*)*	–	–	–	U	U	–	–	–
Striated Heron (*Butorides striatus*)	–	–	–	C	R	–	–	–
Cattle Egret (*Bubulcus ibis*)**	–	–	–	C	C	C	C	–
Whistling Heron (*Syrigma sibilatrix*)*	–	–	–	C	–	–	–	–
Capped Heron (*Pilherodius pileatus*)	U	U	–	–	–	–	–	–
Black-crowned Night-Heron (*Nycticorax nycticorax*)	–	–	–	R	–	–	–	–
Stripe-backed Bittern (*Ixobrychus involucris*)*	–	–	–	R	R	–	–	–
Pinnated Bittern (*Botaurus pinnatus*)*	–	–	–	U	S	–	–	–
Bare-faced Ibis (*Phimosus infuscatus*)*	–	–	–	C	C	C	–	–
White Ibis (*Eudocimus albus*)*	–	–	–	R	R	–	–	–
Scarlet Ibis (*E. ruber*)*	–	–	–	C	C	–	–	–
Roseate Spoonbill (*Ajaia ajaja*)*	–	–	–	R	R	–	–	–
Fulvous Whistling-Duck (*Dendrocygna bicolor*)*	–	–	–	R	–	–	–	–
White-faced Whistling-Duck (*D. viduata*)*	–	–	–	C	R	–	–	–
Black-bellied Whistling-Duck (*D. autumnalis*)*	–	–	–	C	R	–	–	–
Brazilian Duck (*Amazonetta brasiliensis*)*	–	–	–	U	–	–	–	–
Masked Duck (*Oxyura dominica*)*	–	–	–	C	–	–	–	–
Black Vulture (*Coragyps atratus*)	–	–	C	–	–	C	C	–
Turkey Vulture (*Cathartes aura*)	–	–	–	–	–	C	C	–
Lesser Yellow-headed Vulture (*C. burrovianus*)	–	–	–	–	–	C	C	–
White-tailed Kite (*Elanus leucurus*)	C	–	C	R	–	C	–	–
Pearl Kite (*Gampsonyx swainsonii*)	–	–	S	–	–	–	–	–
Plumbeous Kite (*Ictinia plumbea*)	R	–	R	–	–	R	–	–
White-tailed Hawk (*Buteo albicaudatus*)	R	–	R	–	–	R	–	–
Zone-tailed Hawk (*B. albonotatus*)	–	–	–	U	U	–	–	–
Roadside Hawk (*B. magnirostris*)	C	–	C	–	–	C	–	–
Gray Hawk (*B. nitidus*)	U	–	R	–	–	R	–	–
Savanna Hawk (*Heterospizias meridionalis*)	–	–	–	–	C	C	–	–
Laughing Falcon (*Herpetotheres cachinnans*)	S	–	–	–	–	–	–	–
Black Caracara (*Daptrius ater*)	U	U	–	–	–	–	–	–
Yellow-headed Caracara (*Milvago chimachima*)	–	–	–	–	C	C	C	–
Crested Caracara (*Polyborus plancus*)	–	–	–	–	–	C	C	–
Bat Falcon (*Falco rufigularis*)	S	–	S	–	–	S	–	–
Aplomado Falcon (*F. femoralis*)	–	–	–	–	U	U	–	–
American Kestrel (*F. sparverius*)	–	–	–	–	–	R	R	–
Speckled Chachalaca (*Ortalis guttata*)	U	–	–	–	–	–	–	–

TABLE 1
CONTINUED

Species	Habitat usage[a]							
	1	2	3	4	5	6	7	8
Crested Bobwhite (*Colinus cristatus*)	–	–	–	–	–	C	–	–
Hoatzin (*Opisthocomus hoazin*)	R	R	–	–	–	–	–	–
Spotted Rail (*Rallus maculatus*)*	–	–	–	U	–	–	–	–
Gray-necked Wood-Rail (*Aramides cajanea*)	U	–	–	–	–	–	–	–
Ash-throated Crake (*Porzana albicollis*)*	–	–	–	R	–	–	–	–
Yellow-breasted Crake (*P. flaviventer*)*	–	–	–	R	–	–	–	–
Gray-breasted Crake (*Laterallus exilis*)*	–	–	–	S	S	–	–	–
Purple Gallinule (*Porphyrula martinica*)**	–	–	–	C	C	–	–	–
Azure Gallinule (*P. flavirostris*)*	–	–	–	C	R	–	–	–
Wattled Jacana (*Jacana jacana*)	–	–	–	C	C	–	–	–
Southern Lapwing (*Vanellus chilensis*)**	–	–	–	R	R	C	C	–
Pied Lapwing (*Hoploxypterus cayanus*)*	–	–	–	U	–	–	–	–
Collared Plover (*Charadrius collaris*)*	–	–	–	R	–	–	–	–
Solitary Sandpiper (*Tringa solitaria*)*	–	–	–	C	C	–	–	–
Lesser Yellowlegs (*T. flavipes*)*	–	–	–	C	C	–	–	–
Greater Yellowlegs (*T. melanoleuca*)*	–	–	–	C	C	–	–	–
Spotted Sandpiper (*Actitis macularia*)*	–	–	–	C	C	–	–	–
Buff-breasted Sandpiper (*Tryngites subruficollis*)*	–	–	–	–	–	–	C	–
Common Snipe (*Gallinago gallinago*)*	–	–	–	C	R	–	–	–
Common Stilt (*Himantopus himantopus*)*	–	–	–	C	C	–	–	–
Double-striped Thick-knee (*Burhinus bistriatus*)	–	–	–	–	–	–	U	–
Large-billed Tern (*Phaetusa simplex*)	–	–	–	S	–	–	–	–
Yellow-billed Tern (*Sterna superciliaris*)	–	–	–	S	–	–	–	–
Pale-vented Pigeon (*Columba cayennensis*)	–	–	R	–	–	R	–	–
Rock Dove (*C. livia*)	–	–	–	–	–	–	–	C
Eared Dove (*Zenaida auriculata*)	–	–	–	–	–	C	–	–
Plain-breasted Ground-Dove (*Columbina minuta*)	–	–	–	–	–	C	–	C
Ruddy Ground-Dove (*C. talpacoti*)	–	–	–	–	–	C	–	–
Blue Ground-Dove (*Claravis pretiosa*)	S	–	S	–	–	–	–	–
Scaled Dove (*Scardafella squammata*)	–	–	–	–	–	–	–	R
White-tipped Dove (*Leptotila verreauxi*)	U	–	U	–	–	–	–	–
Red-bellied Macaw (*Ara manilata*)	–	C	–	–	–	–	–	–
Brown-throated Parakeet (*Aratinga pertinax*)	–	–	C	–	–	–	–	–
Spectacled Parrolet (*Forpus conspicillatus*)	–	–	C	–	–	–	–	–
Yellow-headed Parrot (*Amazona ochrocephala*)	U	–	U	–	–	–	–	–
Orange-winged Parrot (*A. amazonica*)	U	–	U	–	–	–	–	–
Mealy Parrot (*A. farinosa*)	S	–	S	–	–	–	–	–
Yellow-billed Cuckoo (*Coccyzus americanus*)*	–	–	S	–	–	–	–	–
Dark-billed Cuckoo (*C. melacoryphus*)	–	–	S	–	–	–	–	–
Squirrel Cuckoo (*Piaya cayana*)	R	–	R	–	–	–	–	–
Little Cuckoo (*P. minuta*)	U	U	U	–	–	–	–	–
Smooth-billed Ani (*Crotophaga ani*)	–	–	C	–	C	C	C	–

TABLE 1
CONTINUED

Species	Habitat usage[a]							
	1	2	3	4	5	6	7	8
Striped Cuckoo (*Tapera naevia*)	–	–	R	–	–	R	–	–
Barn Owl (*Tyto alba*)	–	–	–	–	U	R	R	–
Tropical Screech-Owl (*Otus choliba*)	R	–	R	–	–	–	–	R
Burrowing Owl (*Speotyto cunicularia*)	–	–	–	–	–	–	R	–
Striped Owl (*Rhinoptynx clamator*)	–	–	S	–	–	–	–	–
Great Potoo (*Nyctibius grandis*)	S	–	–	–	–	–	–	–
Common Potoo (*N. griseus*)	R	R	–	–	–	–	–	–
Lesser Nighthawk (*Chordeiles acutipennis*)	–	–	C	–	–	C	C	–
Nacunda Nighthawk (*Podager nacunda*)	–	–	–	–	–	C	C	–
Pauraque (*Nyctidromus albicollis*)	–	–	–	–	–	C	C	–
Spot-tailed Nightjar (*Caprimulgus maculicaudus*)	–	–	S	–	–	–	–	–
White-collared Swift (*Streptoprocne zonaris*)	C	C	C	R	–	C	R	C
Short-tailed Swift (*Chaetura brachyura*)	C	C	C	–	–	–	–	–
Fork-tailed Palm-Swift (*Reinarda squamata*)	–	C	–	–	–	–	–	–
Rufous-breasted Hermit (*Glaucis hirsuta*)	–	–	U	–	–	U	–	–
Long-tailed Hermit (*Phaethornis superciliosus*)	–	–	R	–	–	R	–	–
Littler Hermit (*P. longuemareus*)	–	–	S	–	–	S	–	–
Black-throated Mango (*Anthracothorax nigricollis*)	–	U	–	U	–	–	–	U
White-tailed Goldenthroat (*Polytmus guainumbi*)	–	–	–	C	–	R	–	–
Ringed Kingfisher (*Ceryle torquata*)	–	–	–	S	–	–	–	–
Green Kingfisher (*Chloroceryle americana*)	–	–	–	U	–	–	–	–
Pygmy Kingfisher (*C. aenea*)	–	–	–	S	–	–	–	–
Blue-crowned Motmot (*Momotus momota*)	S	–	–	–	–	–	–	–
Russet-throated Puffbird (*Hypnelus ruficollis*)	–	–	U	–	–	–	–	–
Swallow-wing (*Chelidoptera tenebrosa*)	–	–	S	–	–	–	–	–
Chestnut-eared Araçari (*Pteroglossus castanotis*)	R	–	–	–	–	–	–	–
Scaled Piculet (*Picumnus squamulatus*)	–	–	C	–	–	–	–	–
Spot-breasted Woodpecker (*Chrysoptilus punctigula*)	R	–	R	–	–	–	–	–
Lineated Woodpecker (*Dryocopus lineatus*)	R	–	R	–	–	–	–	–
Yellow-tufted Woodpecker (*Melanerpes cruentatus*)	U	–	–	–	–	–	–	–
Little Woodpecker (*Veniliornis passerinus*)	U	–	U	–	–	–	–	–
Crimson-crested Woodpecker (*Campephilus melanoleucos*)	S	–	–	–	–	–	–	–
Straight-billed Woodcreeper (*Xiphorhynchus picus*)	U	–	–	–	–	–	–	–
Pale-breasted Spinetail (*Synallaxis albescens*)	–	–	–	R	–	C	–	–
Plain-crowned Spinetail (*S. gujanensis*)	–	–	U	–	–	U	–	–
Black-crested Antshrike (*Sakesphorus canadensis*)	S	–	U	–	–	–	–	–

TABLE 1
CONTINUED

Species	Habitat usage[a]							
	1	2	3	4	5	6	7	8
Barred Antshrike (*Thamnophilus doliatus*)	R	–	R	–	–	–	–	–
White-bellied Antbird (*Myrmeciza longipes*)	–	–	U	–	–	–	–	–
White-winged Becard (*Pachyramphus polychopterus*)	–	–	U	–	–	–	–	–
Black-tailed Tityra (*Tityra cayana*)	U	–	–	–	–	–	–	–
White-bearded Manakin (*Manacus manacus*)	S	–	–	–	–	–	–	–
Pied Water-Tyrant (*Fluvicola pica*)	–	–	–	C	–	–	–	–
White-headed Marsh-Tyrant (*Arundinicola leucocephala*)	–	–	–	C	–	–	–	–
Cattle Tyrant (*Machetornis rixosus*)	–	–	–	–	–	R	R	–
Sirystes (*Sirystes sibilator*)	S	–	S	–	–	–	–	–
Fork-tailed Flycatcher (*Muscivora tyrannus*)	–	–	–	–	–	C	–	–
Eastern Kingbird (*Tyrannus tyrannus*)*	–	–	S	–	–	–	–	–
Tropical Kingbird (*T. melancholicus*)	–	C	C	–	–	C	–	C
Boat-billed Flycatcher (*Megarhynchus pitangua*)	U	–	U	–	–	–	–	–
Streaked Flycatcher (*Myiodynastes maculatus*)	–	–	U	–	–	–	–	–
Rusty-margined Flycatcher (*Myiozetetes cayanensis*)	–	C	C	C	–	C	–	C
Social Flycatcher (*M. similis*)	–	–	C	–	–	–	–	–
Great Kiskadee (*Pitangus sulphuratus*)	C	C	C	R	–	R	–	C
Lesser Kiskadee (*P. lictor*)	–	–	U	–	–	U	–	–
Short-crested Flycatcher (*Myiarchus ferox*)	–	–	S	–	–	–	–	–
Brown-crested Flycatcher (*M. tyrannulus*)	–	–	R	–	–	U	–	–
Dusky-capped Flycatcher (*M. tuberculifer*)	–	–	R	–	–	U	–	R
Yellow-breasted Flycatcher (*Tolmomyias flaviventris*)	–	–	U	–	–	–	–	–
Painted Tody-Flycatcher (*Todirostrum chrysocrotaphum*)	S	–	–	–	–	–	–	–
Common Tody-Flycatcher (*T. cinereum*)	R	–	R	–	–	–	–	–
Slate-headed Tody-Flycatcher (*T. sylvia*)	–	–	U	–	–	–	–	–
Pale-eyed Pygmy-Tyrant (*Atalotriccus pilaris*)	–	–	S	–	–	–	–	–
Yellow-bellied Elaenia (*Elaenia flavogaster*)	–	–	C	C	–	–	–	–
Lesser Elaenia (*E. chiriquensis*)	–	–	R	–	–	–	–	–
Southern Beardless Tyrannulet (*Camptostoma obsoletum*)	–	–	U	–	–	–	–	–
Blue-and-white Swallow (*Notiochelidon cyanoleuca*)*	–	–	–	–	C	C	–	–
Rough-winged Swallow (*Stelgidopteryx ruficollis*)	–	–	–	U	U	–	–	–
Barn Swallow (*Hirundo rustica*)*	–	–	C	C	C	C	C	C
Violaceous Jay (*Cyanocorax violaceus*)	U	–	–	–	–	–	–	–
Bicolored Wren (*Campylorhynchus griseus*)	R	C	–	–	–	–	–	–
Rufous-breasted Wren (*Thryothorus rutilus*)	C	–	C	–	–	–	–	–

TABLE 1
CONTINUED

Species	Habitat usage[a]							
	1	2	3	4	5	6	7	8
House Wren (*Troglodytes aedon*)	–	–	–	–	–	–	–	R
Tropical Mockingbird (*Mimus gilvus*)	–	–	–	–	–	C	–	C
Black-capped Mockingthrush (*Donacobius atricapillus*)	–	–	–	C	–	–	–	–
Black-billed Thrush (*Turdus ignobilis*)	–	–	U	–	–	–	–	–
Bare-eyed Thrush (*T. nudigenis*)	U	–	U	–	–	–	–	–
Yellowish Pipit (*Anthus lutescens*)	–	–	–	–	–	R	–	–
Red-eyed Vireo (*Vireo olivaceus*)	C	–	R	–	–	–	–	–
Shiny Cowbird (*Molothrus bonariensis*)	–	–	U	R	–	–	–	R
Giant Cowbird (*Scaphidura oryzivora*)	U	–	U	–	–	–	–	–
Crested Oropendula (*Psarocolius decumanus*)	R	C	–	–	–	–	–	–
Yellow-rumped Cacique (*Cacicus cela*)	R	–	R	–	–	–	–	–
Yellow-billed Cacique (*C. holosericeus*)	–	–	U	–	–	–	–	–
Carib Grackle (*Quiscalus lugubris*)	–	–	–	–	–	–	–	U
Yellow-hooded Blackbird (*Agelaius icterocephalus*)	–	–	–	C	C	–	–	–
Oriole Blackbird (*Gymnomystax mexicanus*)	–	–	C	R	–	C	–	–
Red-breasted Blackbird (*Leistes militaris*)	–	–	–	–	R	C	C	–
Eastern Meadowlark (*Sturnella magna*)	–	–	–	–	–	R	C	–
Bobolink (*Dolichonyx oryzivorus*)*	–	–	–	–	C	C	–	–
Blackpoll Warbler (*Dendroica striata*)*	R	–	R	–	–	–	–	–
Masked Yellowthroat (*Geothlypis aequinoctialis*)	–	–	–	C	–	–	–	–
Bananaquit (*Coereba flaveola*)	–	–	C	–	–	–	–	C
Swallow-tanager (*Tersina viridis*)	–	–	S	–	–	–	–	–
Orange-bellied Euphonia (*Euphonia xanthogaster*)	–	–	U	–	–	–	–	–
Burnished-buff Tanager (*Tangara cayana*)	–	–	C	–	–	–	–	–
Blue-gray Tanager (*Thraupis episcopus*)	C	R	C	–	–	–	–	C
Palm Tanager (*T. palmarum*)	C	C	–	–	–	–	–	C
Silver-beaked Tanager (*Ramphocelus carbo*)	–	–	C	–	–	–	–	–
White-lined Tanager (*Tachyphonus rufus*)	–	–	U	–	–	U	–	–
Magpie Tanager (*Cissopis leveriana*)	–	–	U	–	–	–	–	–
Black-faced Tanager (*Schistochlamys melanopis*)	–	–	R	–	–	–	–	–
Buff-throated Saltator (*Saltator maximus*)	–	–	R	–	–	–	–	–
Grayish Saltator (*S. coerulescens*)	–	–	C	–	–	–	–	–
Blue-black Grassquit (*Volatinia jacarina*)	–	–	–	–	–	C	–	–
Gray Seedeater (*Sporophila intermedia*)	–	–	–	–	–	C	–	–
Lined Seedeater (*S. lineola*)*	–	–	S	–	–	S	–	–
Yellow-bellied Seedeater (*S. nigricollis*)*	–	–	S	–	–	S	–	–
Ruddy-breasted Seedeater (*S. minuta*)	–	–	–	–	–	C	–	–
Large-billed Seed-Finch (*Oryzoborus crassirostris*)	–	–	–	C	–	–	–	–
Lesser Seed-Finch (*O. angolensis*)	–	–	–	U	–	U	–	–
Saffron Finch (*Sicalis flaveola*)	–	–	–	–	–	R	–	R

TABLE 1
CONTINUED

Species	Habitat usage[a] 1	2	3	4	5	6	7	8
Grassland Yellow-Finch (*S. luteola*)	–	–	–	–	–	R	–	–
Black-striped Sparrow (*Arremonops conirostris*)	–	–	R	–	–	–	–	–
Yellow-browed Sparrow (*Myospiza aurifrons*)	–	–	–	–	–	C	–	–
Wedge-tailed Grass-Finch (*Emberizoides herbicola*)	–	–	–	–	–	R	–	–
Total species	53	19	88	60	36	62	21	19
Species unique to habitat	13	3	33	21	0	11	3	4

[a] 1 = Remnant forest, 2 = morichales, 3 = second growth, 4 = marshes, 5 = ricefields, 6 = early-succesional fields, 7 = pasture, 8 = residential areas.

[b] C = Common, R = Regular, U = Uncommon, S = Scarce—as defined in text.

* Seasonal resident.

** Mostly seasonal, with small numbers resident all year.

Twenty-two species (14% of total residents) were confined to decreasing habitats and should be the most negatively affected by habitat change. These include species requiring large trees for cavity nest-sites (e.g., Chestnut-eared Araçari, woodpeckers, Straight-billed Woodcreeper, Black-tailed Tityra), large branches for cover or nesting (Speckled Chachalaca, potoos, Crested Oropendula) and wooded streams or pools (Capped Heron, Hoatzin, Gray-necked Wood-Rail). Although few species use morichales, at least 2 (Red-bellied Macaw, Fork-tailed Palm-Swift) apparently require stands of palm trees for nesting. The extent to which forests might limit the abundance of certain species most closely associated with other habitats is uncertain. An additional 48 species (30% of total residents) use decreasing habitats to some degree, many of which undoubtedly depend upon factors such as the availability of cavity nest-sites (e.g., parrots) or forest-edge perches (e.g., Bat Falcon, kites).

Ricefields supported very few resident species, but provided the preferred habitat for most of the seasonally resident herons, ibis, rails and shorebirds. Most of the migrants recorded were wetlands species which breed either in North America (shorebirds) or other regions of Colombia and occur commonly in ricefields, mainly between November and June. The majority occupied early-stage ricefields (until about 10 weeks following germination), although a few (bitterns, gallinules, Bobolink) were most often found in maturing ricefields. According to local farmers, Purple Gallinules have increased considerably in abundance coincident with the overall increase in ricefield area. This species occupied the study area throughout the wet season (with some individuals remaining all year) and was the only bird to nest commonly in the rice. Little is known regarding the movements of migratory species in Colombia, and many of the Hacienda's seasonally resident species have seldom been reported from the Villavicencio region (Meyer de Schauensee, Caldasia 5:251–1214, 1948–52). Since large expanses of ricefields are a fairly recent development in the Llanos Orientales, and offer excellent habitat to numerous migrants, it is possible that some of these species may be extending their ranges in response to this creation of favorable habitat.

Among the agricultural practices which benefit certain species, the alternation of rice and cattle culture on plots of land is clearly the most important. This process maintains large sections of savanna vegetation in a region where the amount of rainfall would induce the regrowth of forest if succession were allowed to proceed. The effect of this practice is shown by the relatively large proportion of species associated with the early-successional field habitat. The rice stage supports large numbers of seasonally resident species. Forests occupy a small area of the Hacienda, but were used to some extent by about one-third of the resident species observed. The comparatively low usage of pastures and residential areas indicates that creating these habitats by clearing forests greatly decreases species richness on a given area. Of the 60 species recorded in decreasing habitats, 32 (53%) were considered either uncommon or scarce, further underscoring the importance of forest conservation in contributing to avian community composition in this region.

This survey was conducted during a study of avian agricultural damage, sponsored by the Colombian Agricultural Institute (ICA). I am grateful for the assistance of La Corocora Ltda., D. Valencia G., D. Leal and E. Barriga B.—WALLACE D. MCKAY (deceased), *Smithsonian-Peace Corps Environmental Program, U.S. Embassy, Bogotá, Colombia.* *Accepted 20 Apr. 1979.*

Wilson Bull., 92(3), 1980, pp. 389–393

Three more probable hybrids of *Larus hyperboreus* and *L. argentatus*.—Although widespread hybridization between Glaucous (*Larus hyperboreus*) and herring (*L. argentatus*) gulls has taken place in Iceland and Eurasia (Ingolfsson, Ibis 112:340–362, 1970), there are few reports of its presumed natural occurrence in North America (Jehl and Frohling, Auk 82:498–500, 1965; Ingolfsson 1970; Jehl, Calif. Birds 2:27–32, 1971). Smith (Ornithol. Monogr. no. 4, 1966) was able to induce hybridization by experimental manipulation of eye-ring color and wing-tip pattern.

Of the 3 new presumed hybrids, 1 was found by Arthur Clark, Arthur Schaffner and me on 7 November 1976, on the Niagara River near its mouth off Niagara-on-the-Lake, Ontario. We collected it (BSNS 7057) on 13 November 1976. The other 2 were secured by Richard Poulin in Ontario at the Ottawa dump in Gloucester Township on 23 November 1974 (NMC 61982), and at Beare Road dump, Dunbarton, Ontario Co. (now Durham RM), on 25 October 1975 (NMC 65619). The Niagara bird was probably in its second year, the Ontario specimens in first-year plumage. All 3 birds in most measurements are intermediate between Glaucous and Herring gulls (Table 1). The Niagara specimen is quite whitish, but has dark markings on wings and tail, unlike any plumage of Glaucous Gull. The Ontario birds are generally brownish and white and markedly paler overall than Herring Gulls of corresponding age.

The Niagara River specimen's plumage is not worn. The head, neck and under-parts are white with medium to dark brown streaks on crown, nape, sides of neck and throat; the lower breast and belly are tinged pale brown with some darker brown markings, and undertail coverts are barred with medium brown. Mantle is whitish with scattered tan, medium brown and gray feathers (Pallid Neutral Gray of Ridgway, Color standards and color nomenclature, 1912) are evident, especially on scapulars and back. Outer 5 primaries are Hair Brown on outer vane, paler on inner with "tongues" of white on inner vane of primaries 6 to 9. Primary shafts are buffy-white and there is a narrow, whitish, approximately 15 mm-long area on the outer vane of each 10th primary about 17 mm from the tip. Outer webs of secondaries are also Hair Brown, some slightly mottled with whitish, the inner webs paler brown, except for proximal ones which are whitish peripherally. Terminal half of tail is Hair Brown blending into mottled pale brown on white and then to white. Bill was pale whitish, the terminal third black. Iris was pale brownish-gray, the orbital ring whitish-gray, and the legs and feet flesh color. All soft part colors were noted immediately after collecting.

In general coloration our specimen resembles a probable *L. hyperboreus* × *L. argentatus* hybrid (AMNH 468816) collected by Jehl and Frohling (1965) in New Jersey except that ours

TABLE 1

MEASUREMENTS OF MALE GULLS OF *L. HYPERBOREUS* AND *L. ARGENTATUS* FROM DWIGHT (1925), AND THOSE OF 4 PROBABLE HYBRIDS FROM ONTARIO AND NEW JERSEY

	L. hyperboreus (N = 11) Range + $\bar{x}$	BSNS[1] 7057	NMC[2] 61982	NMC[2] 65619	AMNH[3] 468816	*L. argentatus* (N = 19) Range + $\bar{x}$
Wing (chord)	435–477 (459.1)	440	463	442	440	405–460 (433.8)
Tail	180–210 (196.6)	182	191	185	184	151–190 (175.2)
Tarsus	69–77 (72.6)	69.4	69	65	73	60–74 (67.8)
Exp. culmen	57–67 (62.6)	62.5	62.5	57.5	54	49–62 (57.0)
Bill (depth at base)	20–24 (21.8)	23	23.7	20.9	19.0	17–22.5 (19.5)
Bill (depth at gonys)	21–25 (22.4)	21	20.2	18.6	18.9	18–22 (20.3)

[1] BSNS—Buffalo Society of Natural Sciences.
[2] NMC—National Museum of Canada.
[3] AMNH—American Museum of Natural History.

has more brown on head, neck and underparts and more brown and less gray on the mantle. In addition to the possible plumage variations in immature hybrid gulls, the fact that the Niagara bird was secured in November and the New Jersey bird in February could also partially account for these differences between the 2 birds. Soft parts are about the same colors in both specimens.

It is possible that the Niagara bird is an aberrantly plumaged Glaucous Gull, but I think that this is very unlikely, and have not seen any individuals of this species in the field or in collections with primary and tail coloration and the overall plumage pattern of this specimen. Also, I have seen no plumage of a dark-mantled species in which such a combination of colors appears. Jehl and Frohling could not match their specimen with any in several large collections. Our bird's primary shafts are whiter than those of the New Jersey specimen. However, they are not the cream color of *L. hyperboreus* primary shafts. Those of *L. argentatus* are dark brown or blackish. Fig. 1 shows the spread wing and tail of the probable Niagara hybrid compared to the wing and tail of a second year *L. hyperboreus* specimen (BSNS 7058). Note the considerably darker shade of the secondaries, primaries and rectrices of the former, as well as its darker wing coverts.

The Niagara specimen is smaller than the mean for *L. hyperboreus* males in all dimensions except bill depth at base (Table 1). Its wing, tail, tarsus, and bill depth at gonys are in the overlap zone between *L. hyperboreus* and *L. argentatus*. Unlike AMNH 468816, whose bill is smaller than the mean for *L. argentatus*, our bird's bill is quite large, near the mean measurements for *L. hyperboreus*. Its testes measured (right) 4.5 × 1.9 mm, (left) 5.0 × 2.3 mm and it weighed 1931.2 g. Our specimen was about 200 g heavier than the New Jersey bird, and the latter, Jehl and Frohling state, was more than 300 g heavier than any male Herring Gull in the University of Michigan (Ann Arbor) collection.

Considering the most probable origin of the Niagara gull as eastern North America, it

---

→

FIG. 1. Wing and tail of probable Niagara River hybrid *Larus hyperboreus* × *L. argentatus* (lower wing and tail to the right) compared to those of *L. hyperboreus*.

seems most likely that *L. hyperboreus* was the lighter parent and that 1 of the 3 dark-mantled forms sympatric there with the Glaucous Gull (Great Black-backed [*L. marinus*], Herring, and Thayer's [*L. thayeri*] gulls) was the darker parent. Our bird is unlike Lonnberg's (Arkiv för Zoologi 12:1–22, 1919) description of a zoo-bred immature *L. marinus* × *L. hyperboreus* cross, which is much more similar to a young *L. marinus*, especially in dark pattern of back, wings, and tail, than to the pale *L. hyperboreus* of a similar age. Also, though its bill is near the mean measurements for Glaucous Gull, its wing, tail, and tarsus are close to the minimum size for that species.

It is not possible to determine from coloration or size of the Niagara specimen which of the other 2 dark-mantled species is the likely darker parent because their plumages and sizes differ only slightly. However, it seems more likely that it was the Herring Gull for its eye and orbital ring color is very like that of the Glaucous Gull, unlike that of *L. thayeri*, and Smith (1966) has shown that orbital ring color may act as an isolating mechanism in these gulls. Also, the Herring Gull appears to be extending its range northwards and individuals on the edge of the range might mate more readily with a different species than those well within the range (Jehl and Frohling 1965).

The brown and white pattern of the 2 Ontario specimens resembles Herring Gull plumage of corresponding age. Underparts are generally plain brown with some white streaking on throat and upper breast and mottling on abdomen. Upperparts are brown with whitish fleckings on feathers forming a mottling on back, rump and wings and a more streaked appearance on head and nape. However, they are noticeably paler overall than the Herring Gull with less contrast between light and dark color, particularly on the back. The Ottawa bird is slightly paler overall than the Dunbarton specimen, with whitish areas more extensive and brown portions lighter. The brown outer primaries and the rectrices of the 2 specimens are considerably paler than the Fuscous, Fuscous-Black, or Clove Brown of average Herring Gull primaries and rectrices. In shade they fall between these colors and the Hair Brown of the Niagara bird. As in the latter, inner vanes of outer primaries have "tongues" of white and are paler than the outer vanes. Primary shafts are paler than those of Herring Gulls, but they do not approach the buffy white shafts of the Niagara bird. Tails of these 2 Ontario specimens are largely brown with whitish frecklings basally. They are generally similar in pattern to that of a first-year Herring Gull, except that they have more frecklings on outer vanes of the 2 outer rectrices than has the latter.

Data on the Ottawa specimen are: weight—1734.1 g; iris—medium brown; eye ring—buff; bill—basal ⅔ flesh, tip dusky; tarsus—dull pink; and on the Dunbarton specimen weight—1623.3 g; iris—light brown; eye ring—buff; bill—base pinkish flesh, tip dusky; tarsus—dusky flesh.

The generally pale coloration of these 2 specimens most closely resembles some first-year Thayer's Gull plumages. They are lighter shades of brown on breast and belly and have slightly darker brown primaries and tails than 2 first-year *L. thayeri* specimens in our collection. Their 2-tone bills are unlike the largely dark bills of these young *L. thayeri*.

In all measurements except bill depth at gonys the Ottawa specimen falls within the range given by Dwight (Bull. Am. Mus. Nat. Hist. 52, 1925) for *L. hyperboreus*. It exceeds his maxima for *L. thayeri* in all measurements and *L. argentatus* in all except tarsus and bill depth at gonys. Unlike the Niagara bird, only tarsal length is intermediate to *L. hyperboreus* and *L. argentatus*. As large as this bird is, it is still about 200 g lighter than the Niagara individual. The Dunbarton bird is smaller than the Ottawa specimen and falls within the range of *L. argentatus* but exceeds the mean of that species in wing, tail, exposed culmen and bill depth at base. However, only in tarsus and bill depth at gonys is this bird less than the minimum measurements of *L. hyperboreus*, its other measurements being in the lower range for the latter species (Table 1). In all except these 2 dimensions it exceeds maxima for *L. thayeri* and falls within the overlap zone between *L. hyperboreus* and *L. argentatus*.

I do not recall specifically seeing any gulls in the field or in collections that match these 2 birds. Despite their resemblance to *L. thayeri* in overall coloration and shading and the fact that first-year Thayer's Gulls exhibit a rather wide range of plumage variation, I think that the larger size and different bill coloration of these 2 Ontario birds preclude the possibility that they are this form. Their soft part colors and general plumage coloration are unlike that of first-year *L. glaucescens*, a species with which they are somewhat comparable in size. I believe that these 2 birds are also hybrids, that *L. hyperboreus* was most probably the lighter parent, and a Herring Gull the darker parent.

Although populations of *L. argentatus* and *L. hyperboreus* have apparently been sympatric for some time in parts of North America and allopatric in western Europe until this century when widespread contact occurred, there is considerable hybridization in the latter area and apparently very little in the former. This may be owing to the opportunity for development of isolating mechanisms in the New World between these 2 species as Ingolfsson (1970) suggested, but also may involve some aspects of the breeding biology. Certainly more study on this whole subject is needed, particularly in western North America where the distribution of gull colonies is not well known and the 4 large gull species, though largely allopatric in breeding ranges (Jehl 1971), show cases of hybridization in the wild and in specimens where overlap occurs.

I thank John Farrand, Jr., for the loan of the specimen from the American Museum of Natural History and Henri Ouellet for the loan of the 2 specimens from the National Museum of Natural Sciences at Ottawa, Ontario, Canada—ROBERT F. ANDRLE, *Buffalo Museum of Science, Humboldt Parkway, Buffalo, New York 14211.* *Accepted 1 June 1979.*

Wilson Bull., 92(3), 1980, pp. 393–394

A Paint-billed Crake in Virginia.—On 15 December 1978, Charles and Kay James observed a strange rail wandering in a surburban area in western Henrico County near Richmond, Virginia, and after a short chase were able to capture it. The bird, which I subsequently identified as a Paint-billed Crake (*Neocrex erythrops*), was alive but obviously not in good health when I first examined it. It died overnight and I preserved the specimen by freeze-drying. Although the wings, tail and nails of the specimen were not worn and therefore showed no indications that the bird had been in captivity, I assumed the occurrence represented an artificial introduction. However, the first United States record for this species (Arnold, Auk 95:745–746, 1978) and the unusual occurrences of the Spotted Rail (*Pardirallus macultatus*) (Parkes et al., Am. Birds 32:295–299, 1978) prompted me to investigate the bird further. Richard C. Banks and Storrs Olson of the U.S. National Museum confirmed the species identification and Banks tentatively suggested that the specimen represents *N. e. olivascens*, rather than the nominate race, but very limited comparative material is available. The occurrence of *olivascens* is geographically far more probable than *N. e. erythrops* since the latter is found only in a relatively restricted area on the Pacific slope of Peru south of Lima, while the former exists at a wide variety of locations in northern South America (Blake, Manual of Neotropical Birds, Univ. Chicago Press, Chicago, Illinois, 1977:510–511). The specimen was donated to the collections of the U.S. National Museum (USNM 575802) and Olson believes that the skeleton contained within the dried body may be the only 1 of the genus preserved (other than a partial skeleton; see Arnold 1978).

As pointed out by Arnold (1978) and confirmed by Banks (pers. comm.), there is no importation record for this species and it apparently never occurs in zoos or animal exhibits. We canvased local residents and pet dealers and contacted local birders through the Richmond Audubon Society chapter's newsletter, but no potential source was located.

Neocrex erythrops is known from widely scattered sites east of the Andes in Venezuela, Colombia, eastern Brazil, Paraguay, northwestern Argentina, Bolivia, Surinam and Ecuador (Meyer de Schauensee, The Species of Birds of South America and their Distribution, Livingston, Narberth, Pennsylvania, 1966:68–69; Blake 1977; Ripley, Rails of the World, David R. Godine, Boston, Massachusetts, 1977:228–229; Meyer de Schauensee and Phelps, Birds of Venezuela, Princeton Univ. Press, Princeton, New Jersey, 1978:63). From the northern part of its range, the rail would have to travel more than 3200 km to reach the Richmond area. Because of the curvature of the earth and the position of the continents, this is a shorter distance than the Texas specimen must have traveled. I know of no weather conditions which might have brought the bird to Virginia, although the winter prior to the discovery of the bird was unusually warm. As Arnold (1978) suggests, the importance and credibility of extralimital records of such unusual birds depends upon repeated occurrences. Even though rails are noted for their extralimital occurrences, the recent rash of foreign rail sightings indicates that some unusual phenomenon may be at work in stimulating such wide dispersal. If the present record does represent a natural occurrence, and at this point I have no reason to believe it does not, this constitutes the second specimen for the United States.

I am grateful to Richard Banks and Storrs Olson for their assistance in identifying the specimen and for sharing information regarding the species.—CHARLES R. BLEM, *Dept. Biology, Academic Division, Virginia Commonwealth Univ., Richmond, Virginia 23284.* *Accepted 14 June 1979.*

Wilson Bull., 92(3), 1980, pp. 394–398

House Sparrows kleptoparasitize digger wasps.—Interspecific stealing of food, or kleptoparasitism, is a specialized feeding pattern for a few birds (Arnason and Grant, Ibis 120:38–54, 1978; Hatch, Ibis 117:357–365, 1975; Meinertzhagen, Pirates and Predators, Oliver and Boyd, London, England, 1959; Nelson, Living Bird 14:113-155, 1975) and an occasional source of food for many opportunistic species (Brockmann and Barnard, Anim. Behav. 27:487–514, 1979). I know of only 1 brief reference to birds stealing prey from digger wasps. Ristich (Can. Entomol. 85:374–386, 1953) observed House Sparrows (*Passer domesticus*) and American Robins (*Turdus migratorius*) stealing the katydid prey of great golden digger wasps (*Sphex ichneumoneus*) at a large nesting aggregation on the campus of Cornell University. The birds chased wasps that were carrying prey to their nests, causing them to drop the food, which the birds then retrieved and ate. In this paper I describe observations of House Sparrows systematically stealing prey from great golden digger wasps at a nesting site in Minnesota. I also speculate on the possible origins of this behavior.

Background.—The great golden digger wasp is a large (2–3.5 cm), solitary species found throughout the United States. The female digs a burrow in the ground with a terminal chamber which she provisions with food for her offspring. After constructing the burrow she flies from the nesting area to open fields where she hunts any of a number of species of the smaller, locally available katydids (Orthoptera, Tettigoniidae) and occasionally a tree cricket (Gryllidae). After stinging and paralyzing the katydid, the wasp returns to her nest with the prey clasped beneath her. If the prey is small she flies directly to the nest, but if large, the wasp either walks across the ground or climbs trees and launches herself in a descending

TABLE 1

THE FREQUENCY AND SUCCESS OF DIFFERENT KINDS OF KLEPTOPARASITIC BEHAVIOR

Kleptoparasitic behavior of sparrow	No. (%) of prey stolen by this method	Numbers of attempts	Success of this method (catches/attempts)
(1) Flies directly at flying wasp	46 (58%)	58	79%
(2) Flies at wasp dragging prey over ground	2 (3%)	2	100%
(3) Pursues wasp through shrubbery	25 (32%)	61	41%
(4) Forages on ground in nesting area	6 (8%)	17[a]	35%
TOTAL	79	138	57%

[a] Number of times sparrows were observed foraging on ground in nesting area.

flight to the next tree. A wasp often lands in shrubbery or a tree near her nest before flying to the burrow she has prepared. Even when the katydid is relatively small, it is easy to recognize the laborious flight of a wasp returning with prey. When the wasp lands at her burrow, she sets the paralyzed katydid down and enters the nest leaving the prey outside and unattended for 10–20 sec before she pulls it into the chamber below (Bohart and Menke, Univ. Calif. Publ. Entomol. 30:91–182, 1963; Brockmann, Ph.D. diss. Univ. Wisconsin, Madison, 1976; Frisch, Am. Midl. Nat. 18:1043–1062, 1937).

For a variety of reasons, these solitary wasps often nest locally in sizeable aggregations (Brockmann, Ecol. Entomol. 3:211–224, 1979; Fernald, Ann. Entomol. Soc. Amer. 38:458–460, 1945). From mid-July to mid-August I observed the behavior of individually marked wasps at 3 different sites as follows: (1) an aggregation of 8–50 wasps nesting in a flower planter on the campus of the University of Michigan-Dearborn from 1972 through 1975; (2) 33 wasps on a lawn in Exeter, New Hampshire in 1975; and (3) 136 wasps on the campus of Carleton College, Northfield, Minnesota in 1976. Each nesting site was a sunny open location with little or no surface vegetation.

Observations.—Before 1976 I observed only isolated cases of birds stealing prey from digger wasps. In New Hampshire a male Scarlet Tanager (*Piranga olivacea*) flew directly at a flying wasp causing her to drop her prey. The tanager landed nearby, but then flew off without picking up the paralyzed katydid. On 3 successive days, I saw a juvenile Brown-headed Cowbird (*Molothrus ater*) walking in the New Hampshire nesting area. The bird flew up (observed 7 times) at incoming wasps causing them to drop their prey, which I once observed the bird to eat. Similarly at the Minnesota site, I once saw a Starling (*Sturnus vulgaris*) flying at a digger wasp causing her to drop her prey. The Starling then landed, picked up the dropped prey and flew off. Although House Sparrows, Starlings, cowbirds and American Robins were common around the Michigan site, kleptoparasitism was never observed. House Sparrows occasionally entered the nesting area, but they never flew at passing wasps nor ate prey found on the ground.

The pattern of kleptoparasitism was very different at the Minnesota site. I arrived in early July after the wasps had been nesting for about 2 weeks (also true of the New Hampshire site, but not true of the Michigan site) and saw House Sparrows repeatedly stealing the katydid prey of the digger wasps. I noted 79 thefts (or 25% of the total prey taken by wasps) between 8 and 27 July. Although I remained at the site until 6 August, the sparrows ceased their activity at the nesting area after 27 July (reason unknown).

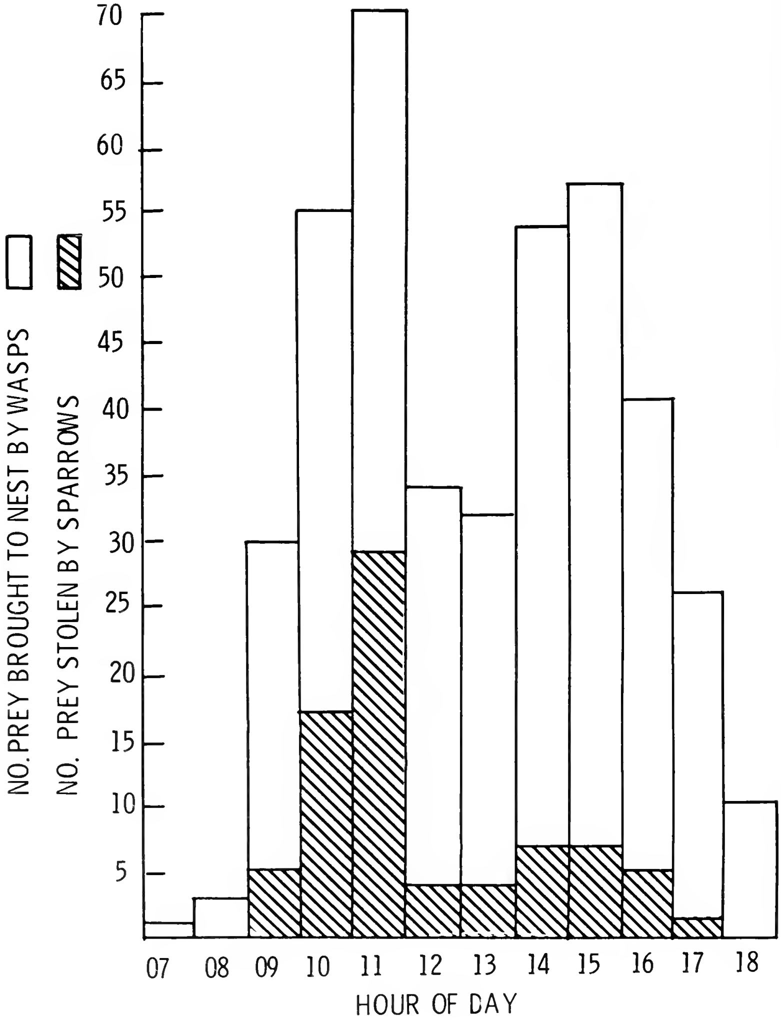


FIG. 1. A comparison between the frequency with which wasps brought prey to the nesting area at different times of the day and the frequency with which sparrows stole these prey (79 thefts).

The sparrows used several different methods to steal prey from the wasps. From 1–5 sparrows sat in a large tree or at the tops of dense shrubbery overlooking the nesting area. When in the tree, the sparrows often pecked at leaves and appeared to be feeding, but when in the shrubs nearer the nesting area, they sat alertly upright. When a wasp returned with prey, the sparrows used 1 of 4 kleptoparasitic methods (Table 1).

(1) The most common method was for the sparrow to fly rapidly and directly at the flying wasp, usually causing the wasp to drop her prey. During some thefts (20% of attempts) the

bird pursued the wasp 50 m or more and once in a while (9% of attempts) a sparrow flew under the wasp forcing her upward until she dropped her prey. Only twice did I see a sparrow chasing a wasp with no prey.

(2) Rarely, a sparrow flew at a wasp that was dragging her prey across the ground toward her nest, causing her to fly up and leave the paralyzed insect for the sparrow.

(3) A sparrow frequently pursued a prey-laden wasp through the dense shrubbery in which she landed until she was frightened off her prey. Often (55% of attempts) the sparrow hovered first before landing on a limb near the wasp. This method is clearly less successful (χ^2 test, $P < 0.001$) than the outright pursuit of method 1.

(4) Occasionally, sparrows foraged on the ground in the nesting area, picking up paralyzed katydids left outside a burrow entrance while the wasp inspected the chamber below. The frequency of attempts varied for the 4 different methods (Table 1), due largely to differences in numbers of opportunities.

Sparrows either acted alone or in groups of 2–5 (generally 2 or 3) adult males and females and occasionally juveniles. Often a katydid was so large that the sparrow had to land on the ground and repeatedly peck at the paralyzed insect, dismembering it before eating. When in a group the sparrows fought over the prey item, pursuing the individual carrying the katydid and when the bird stopped to feed, lunging and grappling (57% of groups engaged in extended chasing or fighting over stolen prey). Occasionally a begging juvenile followed an adult and once I saw an adult female feeding a paralyzed katydid to a juvenile.

The sparrows did not usually begin to sit in the trees and shrubs near the nesting area until 10:00. Most of the kleptoparasitism (61% of attempts) occurred between 10:00 and 12:00, a peak period for wasp hunting (Fig. 1). Although wasps showed a second hunting peak between 14:00 and 16:00, the sparrows rarely appeared in the nesting area at this time and only a small number of thefts occurred.

After being robbed of her prey, a wasp either departed (80% of thefts) or flew tight circular loops around the posterior end of the bird as it flew off or she swooped back and forth around its head if the sparrow was on the ground. The wasps' behavior never deterred the sparrows in any way: a sparrow never moved away from nor altered its path in the face of a wasp buzzing around nearby (these solitary wasps do not use the sting as a defensive weapon but only to paralyze their prey).

Discussion.—The kleptoparasitic behavior of the sparrows was almost certainly learned and may be a traditional pattern similar to that described by Fisher and Hinde (Br. Birds 42:347–357, 1949). Although the sparrows were not individually marked, 1 female that I frequently observed stealing katydids had 2 white tail feathers. Kleptoparasitism was probably confined to a small group of sparrows that worked the densest aggregation of wasps around the Minnesota site. The fact that this behavior was found at only 1 of 3 nesting areas suggests that it is a novel, localized pattern (see also Ristich 1953).

How might a pattern of stealing from wasps begin? Digger wasps in a large concentration bringing in such numbers of large prey make themselves particularly vulnerable to attack and a profitable source of food for birds. No other species of digger wasps are known to be harassed by birds in this way (H. E. Evans, pers. comm.). Predator-prey interactions are a common source of kleptoparasitism among many bird species (Brockmann and Barnard 1979). Stomach analyses of House Sparrows, Starlings and American Robins indicate that they do not normally feed on wasps (Bent, U.S. Natl. Mus. Bull. 196:25–33, 1949; Bent, U.S. Natl. Mus. Bull. 197:195, 1950; Bent, U.S. Natl. Mus. Bull. 211:13–443, 1958; Kalmbach, U.S. Dept. Agric. Tech. Bull. 711:1–66, 1940), although they regularly feed on orthopterans. Cowbirds, on the other hand, are known to prey on Hymenoptera. Occasionally House Sparrows and Starlings have been seen to catch large flying insects (Atkinson, Br. Birds 60:57, 1967; Bent 1958; Summers-Smith, The House Sparrow, Collins, London, England, 1963). Such chases might, from time to time, result in a large paralyzed katydid being dropped by the pursued insect. It seems possible then, that species which hunt large flying insects may occasionally encounter and chase digger wasps, picking up dropped prey; in addition, House Sparrows and other ground-foraging birds such as robins are likely to enter a wasp nesting area where they may find large paralyzed katydids lying on the ground near a burrow entrance. It is not difficult to cause a wasp to abandon her prey. A short lunge or run at a wasp dragging a katydid over the ground might yield a large food item.

There are 2 characteristics of sparrows which no doubt play an important role in the appearance of kleptoparasitic behavior in 2 separate populations of this species. First, the House Sparrow is a particularly opportunistic and adaptable species, easily exploiting new and abundant sources of food (Potter, Condor 33:30, 1931; Richardson, Condor 40:126–127, 1938; Fisher and Hinde 1949; Wilson, Emu 54:69, 1954; Hobbs, Emu 55:202, 1955; Mountfort, Br. Birds 50:311–312, 1957; Purser, Br. Birds 52:199–200, 1959; Summers-Smith, 1963). Kleptoparasitism appears to be a secondary source of easy food on which sparrows specialize at certain times of the day. Secondly, House Sparrows forage in flocks which increases the opportunities for learning the chance discoveries of others. Kleptoparasitic behavior could easily arise by trial and error and observational learning in a species known for its catholic tastes and opportunistic feeding habits (Kalmbach 1940; Kendeigh, Ornithol. Monogr. 14:1–2, 1973; Summers-Smith 1963).

Acknowledgments.—I thank Richard Dawkins, Malte Andersson, Chris Barnard and Suzanne Hamilton for reading the manuscript. I am also indebted to Gary Wagenbach and Carleton College, Northfield, Minnesota, for providing the study site.—H. JANE BROCKMANN, *Dept. Zoology, Univ. Florida, Gainesville, Florida 32611.* *Accepted 29 July 1979.*

Wilson Bull., 92(3), 1980, pp. 398–399

Ruby-throated Hummingbirds feed at night with the aid of artificial light.—Hummingbirds feed frequently throughout the day, from before dawn to after sunset (Grant and Grant, Hummingbirds and Their Flowers, Columbia Univ. Press, New York, New York, 1968). We have found no reference to nocturnal feeding by hummingbirds, other than in aviaries (Scheithauer, Hummingbirds, T. Y. Crowell Co., New York, New York, 1966). Typically, at night, hummingbirds may become torpid, and by lowering metabolic rate conserve energy at a time when they are unable to feed (Grant and Grant 1968). Recent results indicate that torpor is used only in "energy emergency" situations at a minimum "threshold" of energy reserves and not to reduce noctural energy expenditures when net gains during the day were sufficient for overnight expenditures (Hainsworth, Collins and Wolf, Physiol. Zool. 50:215–222, 1977).

A Ruston, Louisiana homeowner, Mrs. Agnes Lewis, had observed noctural feeding by Ruby-throated Hummingbirds (*Archilochus colubris*) during September 1977. The birds, never observed during the day, were observed at night when the flower beds were illuminated. Noctural activity occurred from dusk to sometime just before 24:00 CDST in the presence of a single, nearby (within 7 m) carport light and distant streetlights. Sunset occurs from about 19:45–19:59 CDST during September in northern Louisiana.

The yard contained a lawn, trees, hedges and flowers, including marigolds (*Tagetes* spp.), red cannas (*Canna* sp.) and white four-o-clocks (*Mirabilis* sp.). No artificial hummingbird feeders were present in the neighborhood.

We made observations to verify the noctural feeding activity of Ruby-throated Hummingbirds (not moths), as follows: (1) flower beds were observed from 21:15–21:45 on 22 September 1977; temperature 24°C; 1 male and 1 female Ruby-throated Hummingbird were observed feeding on *Mirabilis* for about 5 min at 21:30; carport light on; and (2) flower beds were observed from 20:45–22:00 on 27 September 1977; temperature 20°C; a male began feeding on *Mirabilis* at 20:57; a female appeared at 21:09; both continued to feed until 21:25 when they were frightened; they did not return; the carport light was on.

The white tubular flowers of *Mirabilis* were open only late in the day and at night; they were the only flowers known to have been used. Grant and Grant (1968) mention that flowers in North America favored by birds are characteristically open throughout the day and yield large quantities of nectar. Our observations indicate that *Mirabilis* not only offered the hummingbirds a source of nectar late in the day, but with the aid of artificial light, a source of nectar that was used well into the night. During the cooler nights of October (observations on evenings of 3 and 11 October) all of the *Mirabilis* flowers remained closed with most of the blooms showing signs of deterioration by the middle of the month. No hummingbirds were present during these last 2 observations.

To what extent resident or migratory hummingbirds make use of artificial man-made light sources to feed at night is poorly documented, but this type of nocturnal feeding may be more common than realized in the presence of illumination and certain night blooming flowers around human domiciles and cities in general.—JOHN W. GOERTZ, ANGELA S. MORRIS AND STEPHEN M. MORRIS, *Dept. Zoology, Louisiana Tech Univ., Ruston, Louisiana 71272.* *Accepted 18 July 1979.*

Wilson Bull., 92(3), 1980, pp. 399–402

Response to novel food in captive, juvenile Mockingbirds.—Simple feeding experiments were made with handreared, juvenile Mockingbirds (*Mimus polygottos*) to test 2 hypotheses: (1) birds would not increase eating efficiency with regard to new foods; and (2) birds would not eat brightly-colored (and possibly distasteful) insects that are found in their habitat. These hypotheses have not been tested in Mockingbirds, although many studies have been made on aspects of their biology (Horwich, Wilson Bull. 81:87–93, 1969; Howard, Evolution 28:428–438, 1974; Barrows, Avicult. Mag. 84:51–56, 1978) and on bird avoidance of distasteful foods (Alcock, Am. Midl. Nat. 89:307–313, 1973, and references therein).

Nine nestling Mockingbirds were obtained within 32 km of Washington, D.C.; 2 birds were nestmates. Birds were handreared, and when at least 17 days old, they were individually maintained in wire and cardboard cages that were about 0.2 m^3. When birds could feed themselves, they were given liberal amounts of chopped fruits, vegetables and dog food and provided with bowls of water. Birds were between 2 and 9 months (juvenile status starts at 40 days, adulthood at 9 months [Horwich 1969]) when they were presented with novel foods. Some insects used in experiments were killed by freezing and defrosted to room temperature before presentation to birds. Fruits and dead insects were presented on white cardboard discs 10 cm in diameter. One investigator presented a given experimental food (Table 1). Live cockroaches (*Blattella*) were presented in glass bowls (6 cm deep and 12 cm in diameter) lined with white filter paper and coated with petroleum jelly on their sides to prevent escape. *Desmodium* loment articles (sections with 1 seed, 4 × 7 mm) were also presented. During food presentations, observers were 1 m from birds. A contact was recorded when a bird pecked at, or picked up, a food item. Stopwatches were used to time behavior.

Each of 9 birds was presented with *Viburnum* fruits 5 times. Presentations were made

TABLE 1
NOVEL FRUITS AND INSECTS WHICH WERE PRESENTED TO JUVENILE MOCKINGBIRDS

Fruits

Desmodium sp., tick-trefoil (Fabaceae)
Vaccinium macrocarpon, cranberry (Ericaceae)
Viburnum opulus, Guelder-rose (Caprifoliaceae)

Insects

Blattella germanica, German cockroach (Blattellidae)[1]
Chauliognathus pennsylvanicus, soldier beetle (Cantharidae)
Coccinella novemnotata, ladybird beetle (Coccinellidae)
Cycloneda munda, ladybird beetle (Coccinellidae)
Deloyala guttata, tortoise beetle (Chrysomelidae)
Diabrotica undecipunctata howardi, cucumber beetle (Chrysomelidae)
Metriona bicolor, tortoise beetle (Chrysomelidae)
Murgantia histrionica, harlequin bug (Pentatomidae)
Oncopeltus fasciatus, milkweed bug (Lygaeidae)
Tenebrio molitor, mealworm beetle (Tenebrionidae)[1]

[1] All but *Blattella germanica* and *Tenebrio molitor* were brightly colored species.

between 2- and 4-day intervals and for 5 min, or until birds ate fruits, whichever period was shorter. Birds usually swallowed fruits whole after first pecking at them. They ate fruits in 39 of 45 presentations, and particular birds ate from 2–5 fruits ($\bar{x} = 4.1 \pm 1.00$). In last presentations, during which they ate fruits, birds contacted them fewer times and ate them in less time than in first presentations (Table 2).

Seven birds were presented with orange-color-phase, dead *Metriona* beetle adults (Barrows, Coleopterists' Bull. 33:9–16,1979) for from 5–10 times on different days during a 41-day period, and presentations were made for up to 5 min. Each of 5 birds ate beetles in from 4–8 presentations. In last presentations, during which birds ate beetles, they contacted them less frequently before eating them compared to first presentations (Table 2). In eating these beetles and other insects, birds usually squeezed them in distal areas of their bills 1 or more times before moving them to their mouths and swallowing them. They often first pecked off and ate small pieces before they swallowed the remainder.

Active *Tenebrio* larvae were presented 5 times to each of 9 birds; 2–4 days elapsed between presentations. Birds always ate larvae, which they squeezed from end to end before swallowing. In last presentations, birds ate larvae in less time and contacted them fewer times before eating than in first presentations (Table 2).

Thus, after limited exprience with *Viburnum* fruits, *Tenebrio* and *Metriona*, birds ate them more efficiently by showing shorter eating times, making fewer preliminary contacts, or both. Perhaps learning, maturation of their motor coordination, or both, enabled birds to feed more efficiently on novel foods with so little experience. Quick, increased efficiency in consumption of new, palatable foods would seem advantageous to omnivorous birds.

Birds did not show increased efficiency in eating *Vaccinium*, *Desmodium*, or *Blattella*. Each bird was presented with 1 of these foods once a day for 5 days, and 2–3 days elapsed between presentations. Birds might show increased feeding on such foods if they were given more experience with these foods.

TABLE 2

MOCKINGBIRD RESPONSES TO NOVEL FOODS

Food	No. birds tested	No. contacts made with food before eating[1]		Time (sec) taken to eat food[1]	
		1st presentation	last presentation	1st presentation	last presentation
Viburnum	9	2.1 ± 0.78[2] (1–3)	1.1 ± 0.33[2] (1–2)	61.9 ± 34.52[2] (22–127)	18.6 ± 11.02[2] (7–41)
Tenebrio larvae	9	19.0 ± 23.23[3] (2–74)	3.1 ± 2.26[3] (1–6)	139.2 ± 50.31[2] (73–236)	19.6 ± 14.91[2] (3–49)
Metriona adults	7	16.6 ± 14.66[2] (2–37)	2.0 ± 1.53[2] (1-5)	—	—

[1] Mean, SD and range.

[2] $P < 0.01$, Wilcoxon's matched-pair test.

[3] $P < 0.05$, Wilcoxon's matched-pair test.

To test bird response to certain brightly-colored insects, we presented each of 7–9 birds with 1 of each of the species listed in Table 1. It is assumed that birds tasted insects if they picked them up and squeezed them in their bills. From 1–4 birds which tasted each insect species ate them. Based on frequency of consumption, no insect species was shown to be significantly distasteful. However, if distastefulness is related to vigorous head-shaking after tasting (Alcock 1973), birds found *Cycloneda*, *Coccinella* and *Oncopeltus* distasteful. Seven of 8 birds showed head-shaking after tasting *Coccinella*, but not when they ate *Tenebrio* on days before and after they were presented with brightly-colored insects. All 6 birds which tasted *Oncopeltus* displayed head-shaking, as did 4 of 6 that tasted *Cycloneda*. None of the birds was observed to vomit after eating any of the presumably distasteful insects. *Oncopeltus fasciatus* (Duffey, Science 169:78–79, 1970; Duffey and Scudder, J. Insect Physiol. 18:63–78, 1972) and the lady-bird beetle (*Coccinella undecimpuctata*) (Rothchild et al., Insect Biochem. 2:334–343, 1972) store poisonous cardenolides, and generally may be avoided by experienced birds. Although Mockingbirds did not appear to find *Murgantia* distasteful, Red-winged Blackbirds (*Agelaius phoeniceus*) avoid other pentatomid stinkbugs (Alcock 1973).

Further study is required to ascertain why the birds ate presumably distasteful insects. One or more of the following reasons may account for this behavior. (1) Some brightly-colored insect species tested might not be distasteful or only slightly distasteful to Mockingbirds. The beetle *Chauliognatus pennsylvanicus* (specimens from Chicago, Illinois), had no cardenolides (Rothschild and Reichstein, Nova Acta Leopoldiana, Suppl. 7:507–550, 1976). It was not reported whether or not they are distasteful to predators. (2) Juvenile Mockingbirds may change their perceptions of distastefulness as they mature. (3) Individual Mockingbirds or populations may vary in this perception. (4) Birds may be able to eat safely at least some species of "protected" prey, as do other bird species, and highly omnivorous birds should be tolerant of ill-tasting substances, or else they might avoid nutritious foods (Alcock, Behaviour 40:1–9, 1971). (5) Eating such insects may be necessary for birds to learn to avoid them. (6) Exploratory eating of novel foods is likely to have adaptive value to highly omnivorous birds such as Mockingbirds, especially during apparently stressful post-fledgling periods as in Red-winged Blackbirds (Alcock 1973) and during seasonal change in food availability. Mockingbirds are primarily insectivorous in May, and vegetarians in December and January (Horwich, Wilson Bull. 77:264–281, 1965). Red-winged Blackbirds show similar behavior (Alcock 1973). Thus, in juveniles and young adults, a period of exploratory feeding combined with some tolerance to unpleasant-tasting prey probably gives them familiarity with many possible food types and enables them to learn to avoid many poisonous foods.

We thank many persons who helped with this study. J. Alcock, J. C. Barlow, D. H. Morse, R. B. Payne and T. Rich made important suggestions on a preliminary manuscript. R. E. White and R. D. Gordon (USDA, Washington, D.C.) identified tortoise and ladybird beetles, respectively. W. R. Kensinger (US Fish and Wildlife Service, Glen Burnie, Maryland) helped us obtain a permit for maintaining native birds in the laboratory. Birds were located with the use of an "Action Alert" notice in the Washington Star Newspaper. The following persons helped collect and maintain birds: R. S. Blanquet, J. M. Brown, N. W. Eisenhower, M. Guy, Mrs. H. R. Murdock, J. Proctor, Mrs. V. J. Riley and Mrs. K. E. Townsend.—EDWARD M. BARROWS, A. P. ACQUAVELLA, P. J. S. WEINSTEIN AND R. E. NOSAL, *Dept. Biology, Georgetown Univ., 37th and O Streets, N.W., Washington, D.C. 20057.* *Accepted 5 Apr. 1979.*

Wilson Bull., 92(3), 1980, p. 402

Bull snake kills and attempts to eat Long-eared Owl nestlings—On 22 June 1976, we were attracted by loud shrieks to a dense stand of ponderosa pine (*Pinus ponderosa*) in Big Horn County, Montana. There we saw a pair of Long-eared Owls (*Asio otus*) hovering over their nest located 7.4 m up in a ponderosa pine. During the next several minutes, we saw a 1-m long bull snake (*Pituophis melanoleucus*) kill and attempt to swallow 2 owlets. However, the snake seemingly found them too large to swallow and so rejected them. The adult owls alternately fluttered above the nest and perched 3–10 m away for 20 min and then left the area. Neither adult approached closer to the snake than 1 m, and the snake did not visibly respond to their presence. The snake remained in the nest, but was only partly visible, until we left 1 h after the start of this observation. Examination of the nest early the next morning revealed 4 dead 15- to 18-day-old owlets. Feather disturbance suggested all 4 had been partially swallowed headfirst and then rejected.

On 3 June 1977, at another Long-eared Owl nest in Big Horn County, we found 2 dead 13- to 16-day-old owlets. One owlet was found dead in the nest 6.8 m up in a ponderosa pine and the other at the base of the nest tree. Appearance of both owlets was similar to those found the previous year, indicating attempted snake predation.

Rat snakes (*Elaphe* sp.) and racers (*Coluber* sp.), as well as bull snakes, have frequently been reported as predators of birds, their eggs and young (Uhler et al., Trans. N. Am. Wildl. Conf. 4:605–622, 1939; Imler, J. Wildl. Manage. 9:265–273, 1945; Laskey, Wilson Bull. 58:217–218, 1946; Clapp and Abbott, Wilson Bull, 78:321, 1966; Jackson, Wilson Bull. 82:329–330, 1970; Niedrach, Wilson Bull. 83:317–318, 1971; Best, Condor 79:509, 1977). Although Strange, Cunningham and Goertz, (J. Wildl. Manage. 35:786–793, 1971) and Kalmbach (Trans. N. Am. Wildl. Conf. 4:591–604, 1939) reported snake predation on Wood Ducks (*Aix sponsa*) and medium sized ground nesters, most available information relates to predation on small species which are probably incapable of effective defense against snake-sized predators. The killing of a bull snake by Turkeys (*Meleagris gallopavo*) (Beasom and Pattee, Wilson Bull. 87:281–282, 1975) is the only report we could find of an encounter between a snake and a more formidable bird than the owls. Our report is apparently the first of snake predation on a raptorial species.—STEVEN C. AMSTRUP AND TERRENCE P. MCENEANEY, *Fish and Wildlife Service, P. O. Box 916, Sheridan, Wyoming 82801.* *Accepted 28 July 1979.*

Wilson Bull., 92(3), 1980, p. 403

Herring Gull predation on Red-breasted Merganser ducklings.—It has been suggested that gulls can seriously reduce duckling survival of island-nesting ducks by preying upon the ducklings as they enter the water (Vermeer, Wilson Bull. 80:78–83, 1968; Dwernychuk and Boag, Can. J. Zool. 50:559-563, 1972). During a study of island-nesting Red-breasted Mergansers (*Mergus serrator*) in Lake Michigan we observed Herring Gull (*Larus argentatus*) predation on merganser ducklings. The Wisconsin population of Red-breasted Mergansers nests primarily on a few islands off the Door County peninsula; these islands also support major nesting colonies of Herring Gulls. The observations we list below facilitate understanding the impact these gulls have on reproductive success of this limited and important population of mergansers.

On 22 June 1977, near Spider Island, a Herring Gull attacked a brood of 6 Red-breasted Merganser ducklings in the water, but the female was able to ward off several attacks by raising herself partly out of the water and striking toward the gull. She then safely led her brood toward the mainland about 1 km away.

A Herring Gull attacked 4 unattended ducklings on 6 July near Hog Island, but the ducklings dived simultaneously to avoid the gull. Shortly thereafter, these 4, plus 5 additional ducklings, joined a female nearby and headed toward the mainland. The female had to strike at swooping gulls several times to protect her young, but did safely lead them out of the area of gull activity. On 7 July, we saw a Herring Gull that was flying over Hog Island swallow a Red-breasted Merganser duckling it had been holding in its bill.

On 22 July, while watching 9 Red-breasted Merganser ducklings and 3 adults swimming close to Spider Island, we saw a Herring Gull fly in, grab 1 of the ducklings and fly off with it over the island. A few minutes later a gull swooped twice toward the young, but did not catch any. However, about 20 min later a gull carried off another duckling, only momentarily startling a female swimming next to the duckling.

During the course of our study we also saw Herring Gulls carry off 2 Mallard (*Anas platyrhynchos*) ducklings. On 3 occasions, we saw Red-breasted Merganser ducklings swimming in full view of many gulls, but no attacks occurred.

Collier (Ibis 4:490–512, 1904) saw a Greater Black-backed Gull (*L. marinus*) pick up and swallow 2 Red-breasted Merganser ducklings from a brood, and Mills (The Wildfowl Trust 13:79–92, 1962) observed the species taking a young Red-breasted Merganser. We have not read of Herring Gulls preying upon Red-breasted Merganser ducklings, but they have been reported to prey upon young Common Eiders (*Somateria mollissima*) (Minot, M.S. thesis, Univ. Maine, Orono, Maine, 1976) and Shelducks (*Tadorna tadorna*) (Spaans, Ardea 59:73–188, 1971).

Although our limited data do not permit a good estimation of the success rates of Herring Gulls preying on Red-breasted Merganser ducklings, it does appear that when gulls choose to attack and do so persistently they sometimes do succeed in killing ducklings. Why attacks occur at some times and not others remains an important question that might be approached by studying such factors as food availability, size of gull chicks in the colony and whether only a few Herring Gulls in each colony have learned to prey on ducklings or whether all will do so occasionally. It is already apparent that both adult and young Red-breasted Mergansers are aware of the threat posed by Herring Gulls and respond appropriately to attacks by defensive action.—BARBARA M. BRAUN, *Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, Laurel, Maryland 20811;* PATRICIA A. HEINZ, *Route 2, Box 256, Laurel, Maryland 20811;* AND GARY H. HEINZ, *Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, Laurel, Maryland 20811. (Present address BMB: Dept. Ecology and Evolutionary Biology, Univ. California, Irvine, California 92717.)* *Accepted 10 May 1979.*

Wilson Bull., 92(3), 1980, pp. 404–408

Factors affecting the incidence of distress calls in passerines.—The response of small birds to capture by predators varies greatly, both among and within species. A captured bird may fight back, struggle to escape, give distress calls, or remain motionless and silent. It may also do some, or all of these, in sequence. Distress vocalizations, which are distinct from the mobbing and alarm calls of free birds, are typically harsh and easily located (Stefanski and Falls, Can. J. Zool. 50:1513–1525, 1972).

Norris and Stamm (Bird-Banding 36:83–88, 1965) found that in most species of small landbirds captured in mist nets, some individuals gave distress calls when handled; the percentage of callers differed widely among species. Balph (Wilson Bull. 89:325–327, 1977) reported more female Evening Grosbeaks (*Hesperiphona vespertina*) calling when handled than males. Driver and Humphries (Ibis 111:243–244, 1969) suggested that calling startles a predator into loosening its grip. Rohwer et al. (Am. Midl. Nat. 96:418–430, 1976) proposed and tested 3 more hypotheses about the functions of distress calls: (1) the call attracts helpers who attack, harrass or distract the predator enough to make it release the prey; (2) the call warns other potential prey of the location of a predator; and (3) the call attracts another predator, which may attack the first predator to kill or rob it, allowing the original prey to escape. This paper reevaluates and extends the latter work. I analyze the problem in 2 ways, dealing with both the risks and benefits of calling.

Risks of calling.—Both calling and struggling must alert a predator that its prey is still alive. Silence and motionlessness in the prey can cause the predator to loosen its grip and even put the prey down (Sargeant and Eberhardt, Am. Midl. Nat. 94:108–119, 1975), or shift its attention elsewhere and thus allow the prey to escape. For example, small birds taken from mist nets most often escape while being handled if they are still and quiet, because this behavior may lead a person to hold them loosely. Whereas active attempts to escape may succeed for prey that are nearer to their predator in size, strength or weaponry. Thus, more birds of larger and stronger species should struggle with their predator. Birds that struggle forego the benefit of feigning death and should incur no added risk by calling. Thus, a greater proportion of birds that do struggle than birds that do not should give distress calls.

Benefits of calling.—(1) *The distress call is a call for help.*—If this hypothesis is true, free birds should respond to distress calls with distraction displays, swoop dives or actual attacks directed at the predator. In fact distress calls of fledglings and juveniles of many species elicit the above responses from their parents (Stefanski and Falls, Can. J. Zool. 50:1501–1512, 1972; Curio, Anim. Behav. 23:1–115, 1975). Parents and offspring of many species stay together for a time after the juveniles fledge. Because parental defense of juveniles seems more likely than the reverse, more juveniles than adults of the same population should give distress calls.

Aside from the case of parents and offspring, we can assume helpers are either kin of the captured bird, or reciprocators. Kin selection can favor helping and the prerequisite distress calling only if kin of the captured bird are likely to be within earshot. That is, kin groups must be cohesive. Reciprocation requires cohesive groups of unrelated birds. Proof of cohesiveness requires observations of groups of marked birds of known parentage. However, kin groups in nonmigratory populations are probably more cohesive than in species that migrate at night, because the great majority of nocturnal migrants fly alone and presumably independently of their kin (Balcomb, Auk 94:479–488, 1977). Therefore, the nepotism hypothesis predicts higher proportions of callers in nonmigratory species than in nocturnal migrant species wintering in the same area, while the reciprocation hypothesis predicts no difference (Rohwer et al. 1976). Both predictions assume that the average degree of cohesiveness of winter social groups is equal in migrant and nonmigrant species.

(2) *The distress call warns other birds of the exact location of a predator.*—Birds so alerted may flee, hide, or approach the caller, but do not help the caller escape. Warned individuals may be kin of the caller or reciprocators, but can be reciprocators only if callers survive.

(3) *The distress call attracts a second predator to attack the first predator to kill or rob it, which gives the prey a chance to escape.*—This hypothesis predicts no correlation between the cohesiveness of kin or reciprocator groups and the frequency of callers. It should work best if large predators are attracted to the call.

(4) *The distress call startles the predator into loosening its grip on the prey.*—Like the predator attraction hypothesis, the startle hypothesis predicts no correlation between the cohesiveness of kin or reciprocator groups and caller frequency. To be effective, the call should be abrupt, explosive and brief. A startle effect cannot be the only function if the call is long and continuous.

Methods.—Hypotheses about risks and benefits of calling were tested with wintering birds at Point Reyes Bird Observatory (PRBO), Marin Co., California, from 15 December 1977 to 21 March 1978. Birds were captured in mist nets (N = 343) and walk-in traps baited with grain (N = 81). Included in the analysis were 11 American Robins (*Turdus migratorius*) and 27 Cedar Waxwings (*Bombycilla cedrorum*) netted in King Co., Washington, in September 1977.

I recorded the behavior of each bird as I approached the net or trap, during removal from the net or trap, and during subsequent handling. Each bird was handled in the same way in sequence: (a) held by the body and legs, with 2 fingers encircling the neck, with the palm of the same hand enclosing the torso; (b) held firmly by the legs only; and (c) released. Birds were held each way for a period varying from about 10–60 sec. For each stage of handling I recorded: (a) whether the bird called; (b) the kind of call, whether distress or other; (c) bouts of struggling, including wing flapping, squirming, biting or pecking; (d) static displays, including erection of crown feathers, partial opening of wings or spreading of tail feathers; or (e) silence and motionlessness.

Distress calls of 1 hand-held Varied Thrush (*Ixoreus naevius*) and 1 Brown Towhee (*Pipilo fuscus*) were played back from a Sony TC-11OB portable tape recorder, with frequency response range 50–10,000 Hz. I chose these species for their loud voices. I matched playback volume to the natural level or slightly louder. Each original cut was duplicated several times in sequence to produce a continuous playback of about 5 min duration. Playbacks were transmitted through the hand-held recorder in 7 cases and through an amplifier in 8 cases. In the latter playbacks a mounted Sharp-shinned Hawk (*Accipiter striatus*) was placed next to the amplifier and I sat 5–20 m away. All playbacks took place within 11 km of the recording site at PRBO, in sites occupied by the species whose calls were used. For each playback I noted (a) all bird vocalizations, by species and call type, within about 50 m of the tape player during the playback and in the 5 min interval preceding and 10 min interval following the playback, and (b) the tendency of birds to approach the source of the call, depart or remain stationary in the same interval. Playbacks lasted 30 sec–5 min, sometimes with pauses. Status of birds as migrant or resident was determined from a 12-yeaı summary of seasonal distribution and abundance prepared from PRBO banding records.

Results.—(1) *Frequency of calling in relation to body size and struggling.*—Struggler frequency and body size were compared with Spearman rank correlation tests. All species with 8 or more individuals represented were included in the analysis (Table 1). For 7 species of nocturnal migrants the frequency of strugglers within a species correlated positively with body size ($P < 0.05$), as predicted. Among 7 nonmigrant species size and struggler frequency were uncorrelated ($P > 0.50$).

The frequency of calling in relation to struggling was recorded for the birds listed in Table 1 and for 92 birds of 26 other species as well, totalling 378. Thirty-seven percent of 284

TABLE 1

STRUGGLING FREQUENCY AND CALLING FREQUENCY IN NONMIGRANT AND NOCTURNAL MIGRANT SPECIES CAPTURED IN TRAPS AND MIST NETS[a]

Species	Mean weight (g)[b]	N	Struggling frequency (%)	Calling frequency (%)
Nonmigrants				
Robin	80	11	91	85
Song Sparrow	19	8(7)	100	0
Oregon Junco	17	21	64	0
Wrentit	13	24(2)	88	8
Pine Siskin	11	8	25	0
Chestnut-backed Chickadee	9	36	94	44
Bushtit	5	23	78	70
Nocturnal migrants				
Varied Thrush	76	11	91	57
Fox Sparrow (*Passerella iliaca*)	33	14(9)	79	0
Golden-crowned Sparrow (*Zonotrichia atricapilla*)	31	28(25)	86	11
Hermit Thrush (*Catharus guttatus*)	23	10	90	10
Townsend's Warbler	9	9	67	0
Ruby-crowned Kinglet	5	29	38	17
Golden-crowned Kinglet	5	54	53	17

[a] Mist net captures in parentheses.

[b] Weights are of lean birds (little or no fat in the furculum) at time of capture.

strugglers and 9% of 94 nonstrugglers called. Thus, a significantly greater proportion of strugglers than nonstrugglers called ($\chi^2 = 45.16$, df = 1, $P < 0.01$), as predicted. Of the 110 callers, 101 struggled, 6 gave static displays interpretable as threat displays and 3 Ruby-crowned Kinglets (*Regulus calendula*) remained still. Thus, in every species except this kinglet, all or nearly all, callers struggled, as predicted.

Four Golden-crowned Kinglets (*Regulus satrapa*) were captured more than once. Two were silent in each of 2 and 3 captures, respectively. One called once in 2 captures and 1 called once in 4 captures, and thus they varied in behavior.

(2) *Nepotism versus reciprocation.*—Both the warning and call-for-help hypotheses assume the existence of stable social groups. The nepotism model predicts that the proportion of callers in a population should increase with the proportion of related individuals in the group. This proportion should be larger, on the average, in nonmigratory species than in nocturnal migrants. Because almost all callers struggle and struggler frequency increases with body size among nocturnal migrants, species of similar size should be compared. Three such comparisons were possible between nonmigrant and migrant species.

The sedentary Bushtit (*Psaltriparus minimus*) showed a significantly higher proportion of callers than either of 2 migratory species, the Golden-crowned Kinglet ($\chi^2 = 15.27$, df = 1, $P < 0.01$) and Ruby-crowned Kinglet ($\chi^2 = 9.77$, df = 1, $P < 0.01$). The sedentary Chestnut-backed Chickadee (*Parus rufescens*) called more than Townsend's Warbler (*Dendroica townsendi*), a nocturnal migrant, though the difference was not significant ($\chi^2 = 2.47$, df = 1, NS). The American Robin, nonmigratory in western Washington, called more than the

Varied Thrush, a nocturnal migrant ($\chi^2 = 5.54$, df = 1, $P < 0.05$). All 3 cases support the nepotism model.

(3) *Call-for-help hypothesis.*—Because parental defense of juveniles seems more likely than the reverse, more juveniles than adults should give distress calls. This held true for the 2 species examined. Significantly more juveniles than adults called among House Finches (*Carpodacus mexicanus*) ($\chi^2 = 10.78$, df = 1, $P < 0.01$) and Cedar Waxwings ($\chi^2 = 9.95$, df = 1, $P < 0.01$). Ten percent of 215 adult and 25% of 67 juvenile House Finches called (data from S. A. Rohwer, Univ. Washington). One of 5 adult and 18 of 22 juvenile waxwings called. One adult waxwing was captured and mouthed by a cat until the cat was forced to release it. The bird was silent and still while held by the cat.

Responses of small birds to playbacks of distress calls of Varied Thrush and Brown Towhee in January, February and March 1978 were similar in all 15 experiments. Playbacks failed to attract conspecifics. Birds of all species either continued with previous activity, e.g., singing or feeding, or became quieter during playbacks. There were 2 exceptions, both using a hand-held recorder and no stuffed hawk. Two Scrub Jays (*Aphelocoma coerulescens*) approached the speaker, calling loudly during a playback. Once 2 Wrentits (*Chamaea fasciata*) and a Bewick's Wren (*Thryomanes bewickii*) approached 1 min after a playback had stopped.

(4) *Warning hypothesis.*—Distress calls indicate the exact location of a predator and small birds can use this information for their own protection. The warning hypothesis predicts that more birds with kin within earshot than birds without kin nearby will call and is supported by the data from the Bushtit, kinglets, Chestnut-backed Chickadee, Townsend's Warbler, American Robin and Varied Thrush.

(5) *Predator attraction hypothesis.*—This hypothesis assumes that distress calls attract predators of small birds and perhaps larger, second-order predators as well. Playbacks confirmed this. Of 7 trials with a hand-held recorder, playbacks attracted a Cooper's Hawk (*Accipiter cooperii*) once, 2 Sharp-shinned Hawks once (the first bird to arrive chased the second one), and Great Horned Owls (*Bubo virginianus*) twice, once in mid-afternoon and once at dusk. Of 8 trials using a stuffed Sharp-shinned Hawk, playbacks attracted a Cooper's Hawk once and a Sharp-shinned Hawk once. In 4 of 5 cases the accipiters appeared within 10 sec of the onset of the playbacks, approached to within 10 m or less of the speaker, perched overhead in vegetation and peered in the direction of the sound source and at the observer who sat nearby. The Great Horned Owls appeared within 30 sec and 3 min of the start of the playbacks and approached to within 15 and 6 m, respectively.

(6) *Startle hypothesis.*—This hypothesis assumes that the distress call surprises the predator by its sudden and explosive occurrence. If the call continues, its later portions cannot be startling and must serve another purpose, if any. Of 110 birds that called, 59% continued to call through more than 1 stage of handling. For these birds the startle hypothesis seems inadequate.

Discussion.—Nearly all captured birds that gave distress calls struggled in the hand. Among nocturnal migrants larger species struggled more often than smaller species, and this suggests that the propensity to struggle increases with physical strength. Differences in tendency to struggle among individuals of a species may also be based on differences in strength, perhaps due to hormone levels or general health. The lack of correlation of size and struggler frequency among 7 nonmigrant species is unexplained.

Birds more likely to be within earshot of kin, called more than species of similar size who were probably not with kin. This result supports the nepotism hypothesis, which construes the call as a warning, a cry for help, or both. Rohwer et al. (1976) also found callers to be more common in nonmigrant than nocturnal migrant species. In the present study 3 of 7 nonmigrant species, Pine Siskin (*Spinus pinus*), Oregon Junco (*Junco hyemalis oreganus*) and Song Sparrow (*Melospiza melodia*), yielded no callers. This can be taken either as evidence that these 3 species do not have cohesive kin groups or as evidence against the nepotism hypothesis. One should avoid assumptions about kinship and stability of social groups unless observing marked birds of known parentage.

Distress calls of fledglings and juveniles of some species attract their parents, who attack or distract the predator. This confirms the nepotism model for this case. Accordingly, more juveniles than adults of 2 species (House Finch and Cedar Waxwing) gave distress calls when handled. However, for 2 species of wintering birds playbacks of distress calls failed to elicit responses that could lead to helping. They did attract predators of birds, usually within a few seconds of the start of the playback. Such rapid arrival could find a captured bird still sufficiently unharmed that it could escape during a struggle between predators. Bent (U. S. Natl. Mus. Bull. 170, 1938) described an instance in which the scream of a meadowlark (*Sturnella* sp.) caught by a Prairie Falcon (*Falco mexicanus*) seemed to attract a Golden Eagle (*Aquila chrysaetos*), and when the eagle approached, the falcon released its prey, who then flew away.

Whether a distress call can startle a predator is unclear. Observations of captures by natural predators are needed. Naive predators should be the most susceptible because the behavior is new to them. The protracted calling of many captured birds implies that startling is not the sole function of the call.

Except in the case of parental defense of juveniles, altruism may be entirely absent from the distress call phenomenon in birds. The altruistic basis of calling (i.e., the risk incurred by the caller) is to alert the predator that the prey is still alive. However, nearly all captured birds that call also struggle, and the struggle itself suffices to tell the predator the condition of the prey. Thus, as long as a bird struggles it can call at no added risk to itself.

There are also 2 unexplained results. First, because silence confers no identifiable benefit on strugglers, it is odd that only 37% of strugglers called. Perhaps such birds were silent because their kin were absent, though this point is untestable without direct knowledge of kinship. Second, 2 Golden-crowned Kinglets differed in behavior between captures, sometimes calling and other times not. This suggests that calling frequencies may be affected by the capture and handling techniques, including the following. (1) The conditions of capture and handling are not consistent, e.g., length of time a bird spends in the net or trap and amount of time taken to remove a bird vary. Birds confined or handled for long periods may tire and switch to a different behavior. Perrone and Paulson (Condor, 81:423-424, 1979) found differences between observers in the incidence of distress calls of mist-netted birds, apparently due to differences in handling methods. (2) Mist nets and traps are not natural predators and may induce abnormal responses, e.g., a few birds caught in nets gave distress calls as I approached them and before I began to untangle them. This situation of being caught and yet not caught must have few parallels in nature. (3) Birds may habituate to capture by human and not regard it as predation. Balph (1977) reported that Evening Grosbeaks are less likely to call in successive recaptures than when first handled.

In conclusion, this work shows that outside the nesting season at PRBO, distress calls do not summon help or even attract small birds, but warning occurs inevitably and predator attraction often occurs. The swift approach of accipiters to the source of the call may explain why small birds do not approach—it is dangerous for them to do so. The predator attraction and startle hypotheses are not incompatible with the warning and call-for-help hypotheses. Studies must be done to assess their relative importance for individual species and different seasons.

Acknowledgments.—I thank the staff and volunteers of the Point Reyes Bird Observatory for their help, especially Bruce Sorrie. Julienne Lemoine taught me to tape-record bird calls. Anne Clark, Steven Fretwell, Gordon Orians, Dennis Paulson, Sievert Rohwer and Raymond Stefanski provided valuable reviews of the manuscript.—MICHAEL PERRONE, JR., *Zoology Dept., Univ. Washington, Seattle Washington 98195.* (Present address: *HDR Sciences, 804 Anacapa St., Santa Barbara, California 93101.*) *Accepted 15 Feb. 1979.*

Wilson Bull., 92(3), 1980, p. 409

Novel rape avoidance in the Mallard.—Rape in the Mallard (*Anas platyrhnchos*) has been well described by Lebret (Ardea 49:97–158, 1961). Rape attempts are readily distinguishable by: (1) resistance on the part of the female in the form of struggling and/or escape behavior; and (2) absence of pre-copulatory displays characteristic of normal, non-forced pair bond copulations (see Barash, Science 197:788–789, 1977). Female Mallards use a variety of tactics to avoid rape, including hiding, diving under water, evasive flight and fighting with the rapists (Weidmann, Z. Tierpsychol. 13:208–271, 1956; Titman and Lowther, Can. J. Zool. 53:1270–1283, 1975; Barash 1977). I now present what I believe to be previously undocumented mechanism by which females avoid rape.

Mallards were observed for a total of 40 h along the Yahara River in Madison, Wisconsin, from 16 March–3 May 1976. The population consisted of approximately 100 partially tame birds occupying a 50 m stretch of river and bank where they were fed regularly by visitors. Censusing on 12 April showed a 54:45 sex ratio favoring males.

At 16:00 on 12 April a female was approached by 3 males. One male grabbed her at the nape and attempted mounting. Breaking free, the female ran and flapped along the water. She then flew up, circled and glided, landing on a horizontal tree limb 7 m above the water. The group of males congregated below her, exhibiting "grunt-whistle" displays accompanied by an occasional call, which was either a "slow" *raehb* or *räb räb* call. The female remained static on the limb except when giving a "decrescendo" call. For the rest of the day this type of rape avoidance behavior, perching in trees, was witnessed 3 more times. A different female was involved each time and at one point, 4 females were aligned on the same limb.

I had not witnessed this behavior prior to 12 April, although rape attempts were regularly seen. I did not observe this behavior again. However, my next observation was on 25 April when half the birds were gone, and nesting, presumably, had begun. Mallards nest in trees so the sight of a perched Mallard is not uncommon during the nesting season. Perching per se may not be new to these birds, but the context in which it is used might be.—VERNER P. BINGMAN, *Dept. Zoology, Univ. Wisconsin, Madison, Wisconsin 53706.* (Present address: *Dept. Biology, SUNY Albany, Albany, New York 12222.*) *Accepted 29 July 1979.*

Wilson Bull., 92(3), 1980, pp. 409–412

Sunbathing behavior of the Pied-billed Grebe.—In their review of sunbathing in grebes, Storer, Siegfried and Kinahan (Living Bird 14:45–57, 1975) state that, although sunbathing postures are widespread among species of Podicipediformes, sunbathing is unknown in Pied-billed Grebes (*Podilymbus podiceps*). Likewise, concentrations of dark pigments in the skin and feathers have not been reported for this species. Wetmore (Auk 37:221–247, 1920), however, briefly described a sunbathing posture in pied-bills. Our paper presents behavioral and morphological evidence of sunbathing in Pied-billed Grebes in Iowa.

We watched Pied-billed Grebes from 23 April–21 July 1977, from blinds at Smith's Slough and Dewey's Pasture, Clay Co., and from the shores of Hottes Lake, Dickinson Co. All are state-owned marshes in northwest Iowa. We used a 15–60× spotting scope or 7 × 35 binoculars to observe orientation and posture of individual pied-bills while they were between foraging dives or loafing. Orientation was recorded relative to both the direction of incident solar radiation and wind, and posture was designated as sunbathing or not sunbathing. Description of the postures came from field notes and photographs. Skin and feather pigmentation were determined from museum specimens and carcasses.

Pied-billed Grebes assumed sunbathing postures closely resembling those of the Least

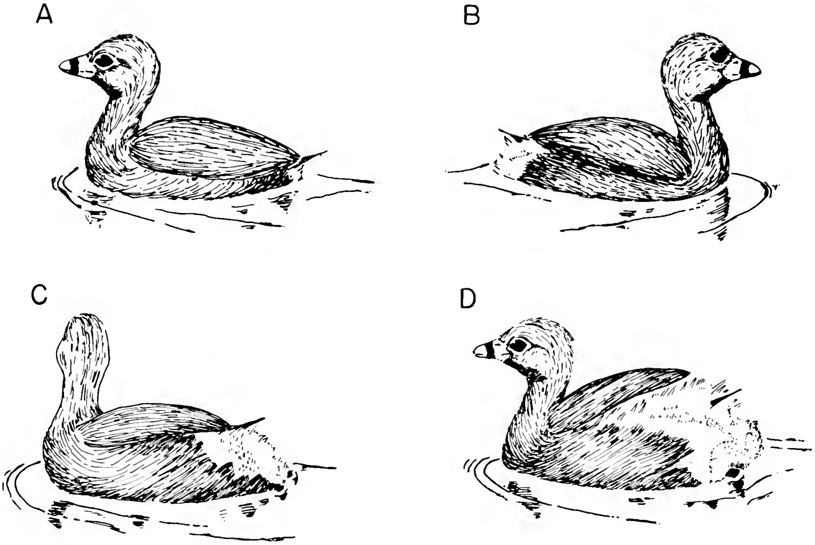


FIG. 1. A. Non-sunbathing posture of Pied-billed Grebes. B-D. Sunbathing postures of pied-bills, from least to greatest intensity.

Grebe (*Podiceps* [=*Tachybaptus*] *dominicus*) as described by Storer et al. (1975). Posturing varied in intensity and duration (Fig. 1). In the least intense display, pied-bills slightly erected their white rump feathers and undertail coverts. This behavior graded into a more intense display in which they raised the wings to a 30–45° angle above the back and exposed fluffed, silky white feathers from the axillary region along the flanks to the rump and undertail coverts. Occasionally, they would raise the backs of the legs above water level. Preening did not regularly precede or follow sunbathing.

The most intense display was maintained for several sec up to 25 min and was seen most often between foraging dives in open areas. Sunbathing bouts between dives averaged 11.1 ± 0.9 sec (N = 21). Storer et al. (1975) reported sunbathing bouts between foraging dives of approximately 10 sec for the Dabchick (*Tachybaptus ruficollis*). Pied-bills also sunbathe while loafing near emergent vegetation.

Adult males and females, and juveniles were seen sunbathing. Females were observed sunbathing between 103 of 107 (96%) foraging dives, but males were observed sunbathing between only 68 of 136 (50%) ($\chi^2 = 61.45$, df = 1, $P < 0.001$).

We obtained 231 independent observations of orientation to incident sunlight for Pied-billed Grebes displaying sunbathing postures. The birds faced away from the sun much more often than would be expected on the basis of chance ($\chi^2 = 105.28$, df = 3, $P < 0.001$) (Fig. 2). We also examined orientation relative to incident sunlight by pied-bills that were not in sunbathing postures, and found that their orientation was random ($\chi^2 = 5.03$, df = 3, N = 182, $P > 0.10$) (Fig. 2). Presumably, when pied-bills are in sunbathing postures they position themselves to maximize solar input.

Storer et al. (1975) found that in sunbathing Least Grebes this orientation away from the sun occurred contrary to the common avian habit of facing into the wind. We tested orien-

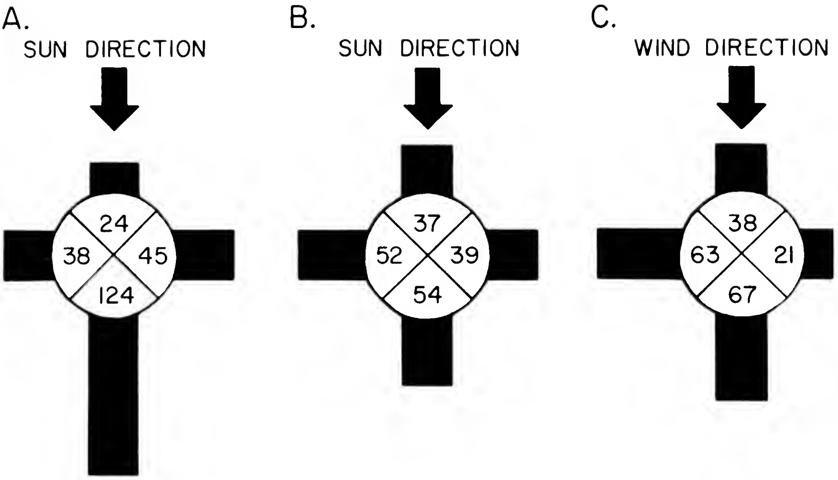


FIG. 2. Orientation frequency of Pied-billed Grebes. A. Position of sunbathing pied-bills relative to incident solar radiation. B. Position of non-sunbathing birds with respect to incident solar radiation. C. Orientation of pied-bills to wind direction. Direction of incident sunlight and wind is from the top of the circles, and the birds are facing outward from the circle.

tation of sunbathing Pied-billed Grebes to wind, and found that they faced not into the wind, but significantly away from or perpendicular to it ($\chi^2 = 29.90$, df = 3, N = 184, $P < 0.001$) (Fig. 2). The lack of random bearing relative to wind direction is probably a function of the relationship between sun and wind direction. Prevailing winds either came from the same direction as the sun or perpendicular to it, but were rarely from the opposite direction.

Pied-billed Grebes have skin and feather pigmentation resembling that described by Storer et al. (1975) for the Least Grebe. Two long patches of silky white feathers running from the axillary region to rump, where they converge around the legs and under the tail, are exposed and erected during sunbathing. Dark grey feathers of the dorsal tract run between these 2 patches to the tail. When not sunbathing, pied-bills cover most of the white feathers with their wings and long, dark scapular and flank feathers.

The posterior ⅓ of the body, especially between and dorsal to the legs and around the tail, is the area most exposed to the sun during sunbathing. Feathers in the anterior ⅓ of the 2 white patches are mostly white with the proximal ¼–⅛ darkly pigmented (Fig. 3). Posterior to the convergence of these 2 patches the feathers are progressively darker grey. Under the tail and at the base of the legs the feathers have only the distal ¼–⅛ white. The skin underlying the dark-based white feathers is much more darkly pigmented than the rest of the skin (Fig. 3). No patch of dark skin occurs on the nape as in the Least Grebe (Storer et al. 1975), although feathers in this area may be fluffed during sunbathing.

Mueller (Z. Tierpsych. 30:253–258, 1972) thought heat conservation an unlikely function of sunbathing in most birds. Based upon our observations of pied-bills, we agree with Storer et al. (1975) that heat conservation is the most important, if not the only function of sunbathing in grebes.

A larger surface-to-volume ratio and greater susceptibility to heat loss makes it more

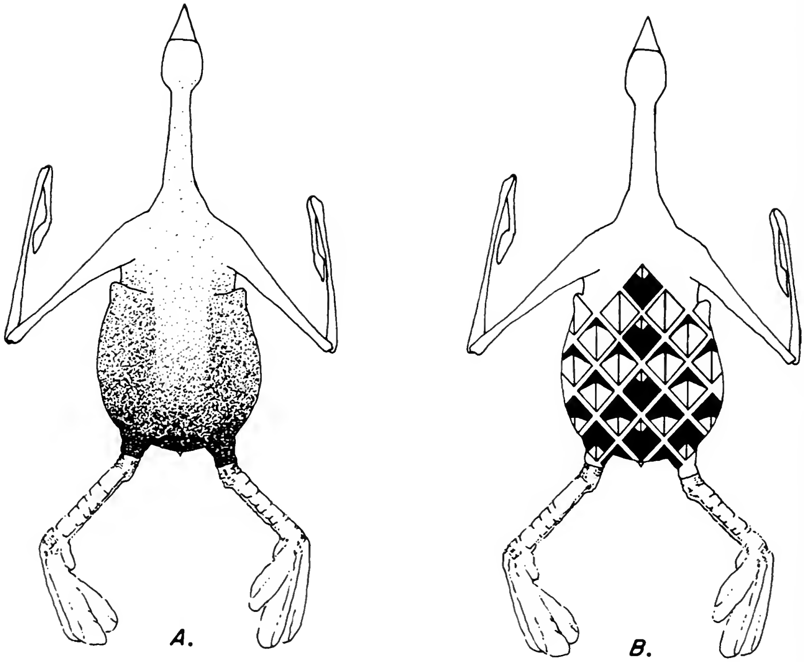


FIG. 3. Pied-billed Grebe skin (A) and feather (B) pigmentation, dorsal view. Diamonds represent individual feathers showing relative pigmentation; anterior ends of the diamonds are proximal ends of feathers. (After Storer et al. 1975.)

beneficial for a small bird to have a supplemental heat source than a large bird. Storer et al. (1975) demonstrated sunbathing in grebe species averaging less than 350 g, and in heavier montane species. Pied-billed Grebes may not need to sunbathe as much as smaller species such as the Least Grebe. This may explain why Storer et al. (1975) did not see the behavior in pied-bills when Least Grebes were sunbathing.

Storer et al. (1975) give a mean weight of 396 g for Pied-billed Grebes, but there is considerable sexual dimorphism in size in this species. Adult females range in weight between 281 and 435 g, adult males between 485 and 559 g (Handbook of North American Birds, Vol. 1, Palmer, ed., Yale Univ. Press, New Haven, Connecticut, 1962:106). This size differential may be related to the significant difference in sunbathing frequency we observed for the sexes.

Acknowledgments.—We thank L. B. Best, J. J. Dinsmore, R. A. Ryder, R. W. Storer and an anonymous reviewer for many valuable suggestions on an earlier draft of this note. R. W. Storer assisted the senior author in examining a freshly collected specimen for skin and feather pigmentation. J. J. Dinsmore provided additional study skins and preserved specimens. The senior author was partially supported during this study by the Department of Animal Ecology, Iowa State University, and by grants from the Frank M. Chapman Memorial Fund, American Museum of Natural History, and the Society of Sigma Xi. This is contribution No. 2 of the Avian Research Laboratory, Department of Animal Ecology.—MARK R. RYAN AND PATRICIA A. HEAGY, *Dept. Animal Ecology, Iowa State Univ., Ames, Iowa 50011.* *Accepted 9 Aug. 1979.*

Wilson Bull., 92(3), 1980, p. 413

Back carrying of young by Trumpeter Swans.—Although Black-necked (*Cygnus melanocoryhus*), Mute (*C. olor*) and to a lesser extent, Black swans (*C. atratus*) are known to carry young on their backs, back-carrying is almost unknown among northern swans (Johnsgard and Kear, Living Bird 7:89–102, 1968). Johnsgard (Waterfowl of North America, Indiana Univ. Press 81, Bloomington, Indiana, 1975) stated the young of Trumpeter Swans (*C. buccinator*) have never been seen riding on a parent's back. During aerial surveys of Trumpeter Swans on the Kenai National Moose Range, Alaska, cygnets from 2 separate broods of swans were observed to climb on a parent's back as we passed over them at low altitude to determine brood size.

On 13 June 1978, 2 adult and 4 cygnets approximately 1-week-old were observed swimming closely together on the Moose River about 1.6 km east of Swan Lake. When we passed about 60 m overhead the swans made no attempt to flee, but on the second approach, about 45 m above the swans, 3, perhaps 4, of the cygnets were observed (by Bailey) climbing upon a parent's back between the adult's left wing tip and tail. Although the cygnets appeared alarmed, the parent made no obvious attempt to help the cygnets climb aboard. There was little available cover for escape in the 4-m-wide river at this location because of the stream's steep banks.

On 16 June 1978, Bangs observed identical behavior, as the same aircraft, a Piper Supercub, passed 45 m over 2 adults and 4 week-old cygnets on a small lake south of Bay Lake, 45 km from the Moose River location. The family of swans was swimming about 100 m from shore, cover for escape was present, but not dense; the behavior was also observed during the second lower flight over the swans.

We are unaware of any reports of back-carrying of young by wild, arctic-breeding Trumpeter Swans. King and King (First Int. Birds in Captivity Symp., Seattle, Washington, 8–12 Mar. 1978) observed young climbing on the back and hiding under a wing of a captive Trumpeter Swan on a nest, but not while the parent was on water. Back-carrying of young Trumpeter Swans has been observed in an introduced, temperate-breeding population. Hammer (Wilson Bull. 82:324–325, 1970) observed and photographed a cygnet on the back of an adult at Lacreek National Wildlife Refuge in South Dakota, and refuge manager H. Burgess (pers. comm.) observed cygnets of at least 2 families on the backs of parents several times during a period of 6 years. Johnsgard and Kear (1968) speculated that northern swans did not carry young because there were few underwater predators where northern swans nested, the long wings of northern swans made back climbing by cygnets too difficult and cygnets grew so rapidly and spent so much time feeding that climbing and resting on the parents' backs was not important.

Our observations suggested the cygnets we observed may have climbed on their parents' backs as an escape response initiated by the approaching low flying aircraft and perhaps the lack of adequate adjacent cover for escape. Predators observed near or believed responsible for destroying swan eggs or cygnets on the Kenai National Moose Range include otters (*Lutra canadensis*) and coyotes (*Canis latrans*), but mink (*Mustela vison*), bears (*Urus arctos*, *U. americanus*), wolverine (*Gulo gulo*) and Bald Eagles (*Haliacetus leucocephalus*) are also present and may be possible predators. No large predatory fish live in lakes used by nesting swans. Our observations suggest young cygnets of Trumpeter Swans may instinctively climb on their parents' backs and possibly hide under their wings (King and King 1978) when endangered. This response of cygnets to danger has seldom been observed because young cygnets of Trumpeter Swans have rarely been intensively studied in areas in the wild where the impact of predators on cygnet survival may be significant.—THEODORE BAILEY, EDWARD BANGS AND VERNON BERNS, *U.S. Fish and Wildlife Service, Kenai National Moose Range, Box 2139, Soldotna, Alaska 99669. Accepted 29 July 1979.*

Wilson Bull., 92(3), 1980, p. 414

Canvasback tolerance of Redhead parasitism: an observation and an hypothesis.—At 09:00 on 24 May 1978, while observing waterfowl from a blind 10 km NE of Minnedosa, Manitoba, I saw a Canvasback (*Aythya valisineria*) return to her nest, which was in sparse bulrush (*Scirpus* sp.) cover about 90 m away and visible through a 60× spotting-scope. At 09:05 a Redhead (*A. americana*) hen, which had been feeding with a drake immediately in front of the Canvasback nest for 1 h, approached the nest. The Canvasback moved to the side of the nest and the Redhead settled in the middle of the nest, facing in my direction. For 15 min, while the Redhead made pulsating movements, the Canvasback, facing in the opposite direction, sat pressed against the Redhead; she occasionally preened herself or rested her bill on the Redhead's back, but never showed aggression such as that seen by Weller (Ecol. Monogr. 29:333–365, 1959) and McKinney (Wilson Bull. 66:146–148, 1954). When the Redhead left, the Canvasback rearranged the eggs with her bill and then resettled on them. At 09:27, I flushed her and found 8 Redhead and 4 Canvasback eggs. On the afternoon of 28 May, the nest contained 10 Redhead and 3 Canvasback eggs; 1 egg of each was outside the nest. The nest was found destroyed on 31 May.

Besides the Canvasback's non-aggressive behavior, 2 points are worth emphasizing. First, the Redhead's intrusion was as other authors have described—in particular, she spent a long time in the vicinity of the Canvasback nest before intruding (Weller 1959, McKinney 1954). Second, considerable parasitism was sustained (11 Redhead:4 Canvasback eggs) without nest desertion, which can result from numerous parasitic intrusions (Weller 1959).

Although Canvasbacks accept foreign eggs (Weller 1959), tolerance of Redhead intrusions has not been reported. This is not an isolated case, however, as R. Sayler (pers. comm.) observed such behavior in his detailed studies of Canvasback-Redhead interactions at Delta Marsh. As parasitism is detrimental to the host (see below), its tolerance seems curious, although parasitism may benefit some hosts (Smith, Nature 219:690–694, 1968). Can tolerance of parasitism benefit a Canvasback?

Post-hatch costs of harboring parasitic young are relatively small for precocial species. Canvasbacks do not distinguish their young from Redhead young, although some interspecific aggression and segregation occurs in mixed broods after 3–4 weeks (Weller 1959). Thus, post-hatch costs of parasitism may not be great enough to select for consistent defence of the nest. However, as aggressive nest defence does occur, why is it shown only sometimes (or by some females)?

Pre-hatch costs of parasitism to Canvasbacks (Weller 1959) include: (1) reduced clutch-size because Canvasbacks are indeterminate layers; (2) egg losses from (a) inability to incubate too many eggs; (b) eggs rolling from nests containing very large clutches, even during normal movements; and (c) possibly increased predation due to eggs being outside the nest; (3) nest desertion and (4) increased egg breakage or spillage during aggressive encounters between host and parasite. Thus, parasitism is probably always costly to Canvasbacks; but as Redheads attempt parasitic laying in spite of host aggression, parasitized Canvasbacks may recoup some of their losses in 2 ways. First, of the pre-hatch costs of parasitism, the fourth may be the most easily "remedied" in an evolutionary sense if tolerance behavior, by reducing egg breakage or spillage, reduces the overall costs of parasitism by more than that resulting from aggressive nest defence. Second, tolerance may enhance the post-hatch survival of Canvasback ducklings in mixed broods due to a "selfish herd" effect (Hamilton, J. Theoret. Biol. 31:295-311, 1971) if the probability that a Canvasback duckling being taken by a predator from a mixed brood is reduced. This may help explain why many Canvasback nests contain more Redhead eggs than Canvasback eggs (Weller 1959).

I am grateful, as usual, to C. D. Ankney for stimulating discussions and to B. F. Bietz, J. McA. Eadie, D. G. L. Innes, R. D. Sayler, D. M. Scott, W. L. Vickery and M. W. Weller for criticisms of earlier versions of this note.—THOMAS D. NUDDS, *Dept. Zoology, Univ. London, Ontario N6A 5B7 Canada.* *Accepted 24 July 1979.*

Wilson Bull., 92(3), 1980, p. 415

Eggless Canada Goose raises foster broods.—It is generally recognized that birds complete their breeding cycle under the stimulation of photo-period and other environmental influences and under the control of the endocrine system. Abnormal cycles have rarely been reported for wild birds living in their normal environment. Heusmann and Pekkala (Wilson Bull. 88:148–149, 1976) recorded a Wood Duck (*Aix sponsa*) incubating for 3 consecutive breeding seasons on an empty nest in Massachusetts. In the third year she was given eggs which she successfully hatched. Fjetlund (Wilson Bull. 90:456–457, 1978) also recorded a Canada Goose (*Branta canadensis*) incubating on an empty nest at the Seney National Wildlife Refuge, Schoolcraft Co., Michigan.

On 23 November 1975, I caught and color banded (F13) a wild female Canada Goose on a small artificial pond at Aurora, Ontario. In the spring of 1976 this bird returned and was seen forming a pair bond with an unbanded wild male. On 7 April and 28 April the pair were seen copulating. On 12 April the female was discovered sitting on a nest on an island. On 19 April she moved to a small island nearby and was again seen sitting on a nest and defending the site with her mate. On 1 May she had moved back to the first nest-site and incubated without eggs until after 5 May. (When the male of this pair was flightless that June, I caught and color banded him F16.)

In 1977 the pair copulated on 19 March and the female was found on 11 April sitting on a new nest at her traditional site. She, like normal breeding females, had become very fat and continued to sit on the empty nest until 23 April when she was given 5 dummy eggs. On 25 May she was given 7 partially incubated goose eggs from a captive pair, 5 of which hatched on 3–4 June. She had been sitting on the nest for 53 days. By 12 June the pair had lost 1 gosling, but succeeded in raising the remaining 4 goslings to maturity.

In 1978, F13 again became exceedingly fat and was found sitting at her traditional site on an empty nest on 19 April when she was given dummy eggs. These were replaced with 6 fresh eggs from a captive pair on 22 April, at which time little down was in the nest, but by 28 April a large amount was present. Three goslings hatched on 28 May and were successfully raised.

The behavior of this pair of geese did not differ from that of a normal pair except for failure to lay eggs. It is possible to work out part of the female's cycle for 1978. Although given eggs on 22 April she probably did not start to incubate steadily until 1–2 May. There was therefore a period of 12 days from the time (19 April) she was first found sitting to the time she started to incubate. Assuming a 36 h laying cycle, she probably had enough time to lay a clutch of up to 8 eggs.

Since the goose completed her breeding cycle normally, except for production of eggs, it seems likely that endocrine deficiencies were not the cause of failure to lay. There are 2 possible physical causes for such failure. Huston and Nalbandov (Endocrinol. 52:149–156, 1953) have shown that a foreign body, even as small as a thread, lodged in the lumen of the magnum can inhibit ovulation. They suggested that a neural link exists between the oviduct and the pituitary gland. An egg or a foreign body in the lumen may inhibit the secretion of luteinizing hormone peaks which are probably necessary to trigger ovulation.

Sturkie (Avian Physiology, 2nd ed; Springer-Verlag, New York, New York, 1965:450) reported that failure of the infundibulum to engulf the ovum from the ruptured follicle results in its discharge into the body cavity where it is rapidly absorbed. The bird appears to be laying, but never actually does.

It is therefore possible that the Canada Goose in question may have an obstruction or tumor in the lumen which inhibits ovulation or it may possess a defective infundibulum. This is Ontario Ministry of Natural Resources, Wildlife Branch, Wildlife Research Section Contribution No. 79-3.—H. G. LUMSDEN, *Ontario Ministry of Natural Resources, P. O. Box 50, Maple, Ontario L0J 1E0. Accepted 30 July 1979.*

ORNITHOLOGICAL LITERATURE

Wilson Bull., 92(3), 1980, pp. 416–424

THE GANNET. By Bryan Nelson. Buteo Books, Vermillion, South Dakota, 1978:336 pp., 62 figs., 32 tables, 32 plates and numerous line drawings. $25.00.—Bryan Nelson, who erased any doubts that he is the world authority on sulids by publishing The Sulidae: Gannets and Boobies, has favored us with a less imposing and perhaps more useful volume on his favored sulids, the gannets. The bulk of the book is about North Atlantic gannets (*Sula* [*bassana*] *bassana*), but available information on Australasian and African forms (*S. serrator* and *S. capensis*) is incorporated extensively. After a brief introduction to the basic gannet and its nomenclature, 7 chapters describe the birds in much more detail—recount distribution and numbers, analyze breeding behavior and ecology in a chapter each, follow gannets at sea, compare members of the order and family to which gannets belong, and chronicle relationships between gannets and humans.

Descriptions include distinctions among the 3 gannet species and, for the North Atlantic form, useful details of both the sequence and variability found in subadult plumages.

All known counts of the 34 currently active and several defunct North Atlantic gannetries are discussed. Numbers of Australasian and African gannets are tabulated without discussion. It is encouraging to learn that most European gannetries are growing and that several new ones have been found in recent times. Western Atlantic populations, unfortunately, appear to be retarded by chemical contaminants in their recovery from severe human exploitation. Nelson's estimate of around half a million North Atlantic gannets is unarguably one of the most accurate for a major sea bird, and the details given provide basic data for future studies.

Nelson's long experience with Bass Rock gannets provides the basis for his analysis of breeding behavior and ecology. He carefully interprets morphological and behavioral adaptations that have enabled North Atlantic gannets to live in cold waters on seasonally abundant, relatively large fish. Examples of these adaptations are: the gannet's large size, which enables it to handle large fish and requires that it nest on cliffs; its strongly seasonal and closely synchronized breeding seasons; and its slow sexual maturation. Breeding synchrony is reinforced by social stimulation, which accounts for the evolution of dense nesting colonies and complex behaviors, including intense aggression, that occur there. Information on gannets at sea is far less complete, but Nelson integrates data from band returns, direct observations and the scanty knowledge of fish populations and distribution to complete his discussion of the ecology of the largest sea-going plunge diver. A brief but comprehensive review of the order and family to which gannets belong sharpens the contrast between Atlantic gannets and their near relatives, which inhabit warmer waters and feed on smaller prey. The overview of the other sulids, including fossil forms, is no substitute for the larger book on the family, but it should serve as a good introduction. A number of excellent figures and tables summarize comparisons.

The chapter titled "The gannet and man" is a mix of history, literature, sociology and aesthetics. Missing is any mention of scientific uses of gannets, such as Donald Griffin's exploitation of their gleaming white plumage, an adaptation for communal feeding, in his efforts to learn how they navigate by following displaced birds as they made their way homeward from interior Maine. Human threats to gannets have changed from exploitation for meat and eggs to dangers from oil spills, fish nets and overzealous birders. The future may see competition with man as North Atlantic fish stocks are depleted.

Outright errors are few, but the statement (page 69) "Black-browed Albatrosses are the most likely member of their redoubtable family to be met in the northern hemisphere . . ."

should read, ". . . North Atlantic . . ." in deference to the 3 resident North Pacific albatrosses. Also erroneous is the statement (page 254) that Brown Boobies (*Sula leucogaster*) never rear twins (see Atoll Res. Bull. 192:221–222, 1976).

John Busby's superb line drawings, the watercolor on the jacket and the sequential plunge dive on the spine highlight the book. The excellent black and white photographs add measurably to the text, but are difficult to correlate because they are not referred to by number, and not all are in sequence with the text. Reference to a plate of Bonaventure Island (page 79) seems to have survived a cut which eliminated the plate itself.

In addition to numbered references, there is a chronologically arranged "Annotated select bibliography" of 35 early works, some of them also listed as references. An additional 3 page bibliography lists works not referred to in the text. The book is adequately indexed and each chapter, except the last, has a useful summary.

I suspect that Nelson's hope ". . .that many copies will even see a gannetry in the flesh," will have been realized long since. No better guide to the seeming confusion and turmoil of a seabird colony can be imagined than the sympathetic insights of Bryan Nelson.—PHILIP C. SHELTON.

GREENSHANKS. By Desmond and Maimie Nethersole-Thompson. Buteo Books, Vermillion, South Dakota, 1979:379 pp, 44 color plates, drawings, photographs, sonagrams. $27.50.—In 1932, Desmond Nethersole-Thompson began his studies of one of Britain's most elusive birds. In 1950, after 17 years of fieldwork, appeared The Greenshank, by any measure the most detailed monograph on any wader, and one which seemingly answered every question that might be asked about the species. He then turned his attention elsewhere, but in 1964, with the collaboration of his wife, Maimie, and large family, resumed his studies. The present book, published in 1979, nearly 5 decades (!) after the start of his investigations, is a revision as well as a supplement to the original. It is the impressive culmination of more than 30 years of active field studies on a single species—a remarkable event—and will become an essential reference for shorebird biologists.

Greenshanks (*Tringa nebularia*) are hard to study, and a less diligent person would have long since given up in total frustration. Just finding the nest may require days of concentrated effort. The male chooses a nesting area which may be up to 2½ miles from his courting territory, where pairing occurs. The female is led to the nesting area, where she selects among the scrapes previously prepared by the male and takes over defense of the territory. Incidentally, this seems an unequivocal case of mate selection based solely on sexual characters and having nothing to do with a presumed "assessment" of the "quality" of the nesting territory. The male accompanies the female when the first egg is laid; both share incubation, the female incubating by day, the male by night and nest relief occurs only once at 2 times each day. Parents remain with the brood for about 4 weeks, after which time the female departs.

The strength of the book lies in the wealth of detailed information that has been gathered over a sufficently long period that variability can be appreciated. Data on mate and nest-site tenacity, behaviors which are far commoner in birds than is generally recognized, are exceptional. Interestingly, the same nest scrape may be reoccupied after a hiatus of several years by birds new to the region, showing that certain habitat configurations are sufficiently superior—even for a ground-nesting species—to be selected de novo. The nature of the desirable characteristics remains to be worked out.

Population fluctuations of significant magnitude occur regularly. In one area, the number of breeding pairs varied from 6–7 to 20–23 over 14 years, though there was no apparent explanation for the changes. No species will experience an unbounded series of "good" years, and increases as well as declines are normal events. This seems to have been forgotten by an increasing number of people who consider any decrease as grounds for federal intervention.

The detail of the fieldwork is well exemplified by the data on brood dispersal, which are almost impossible to find in other studies. In some shorebirds (e.g., Common Snipe [*Gallinago gallinago*]) the parents are alleged to divide the brood, each taking 2 young; this is usually interpreted as an adaptive response that acts to minimize the risks of predation. I have never been convinced about either the evidence of that event or its explanation, and the Nethersole-Thompsons' observations reinforce my skepticism. If hatching is prolonged, one parent may wander away with the early-hatching chicks, while the other remains with the pipping eggs. Later, however, the family will reunite. Thus, in the Greenshank at least the "brood division" is only apparent—a temporary consequence of the normal hatching pattern.

Good research requires the gathering of detailed information, but good writing does not require that all of the data be presented. The book's major shortcoming is that it lacks synthesis or analysis. Basically, it is a compendium of descriptions, a book for reference but not for reading. Constantly I found myself wishing for a chapter summary or the author's interpretation of the average condition of some event. It has long been known, for example, that the shapes and coloration of eggs may be sufficiently distinctive to allow the identification of individual hens. Yet the Nethersole-Thompsons present many examples and descriptions, when a single statement would suffice. An entire chapter is devoted to vocalization, with descriptions and sonagrams of 59 calls of everything from the sound of a pipping chick to the variety of adult notes. Yet, there is no attempt at analysis or to use the sonagrams to study the ontogeny of vocalizations. One gets the impression that the sonagram is a wonderful new toy, its scientific application unappreciated. Tabular material (mostly raw data and superfluous to the presentation) and appendices compose 43 pages (17% of the book).

There is no doubt that this is a classic book, both in the exhaustive coverage of the subject and in the personal flavor of much of the narrative. It is a monument to dedication and probably represents the end of an era in field studies. I cannot conceive that anyone will ever deliberately undertake further studies of this duration. It will be sufficient if someone will take up the challenge to make a short term comparative study of the Greater Yellowlegs (*Tringa melanoleuca*), the Greenshank's new world counterpart.— J. R. JEHL, JR.

THE ROLE OF INSECTIVOROUS BIRDS IN FOREST ECOSYSTEMS. By James G. Dickson, Richard N. Connor, Robert R. Fleet, Jerome A. Jackson and James C. Kroll (eds.). Academic Press, Inc., New York, New York, 1979:381 pp., with figs. and tables. $24.00.—This book results from a symposium held in July 1978. It reached print in less than 1 year, using the "rapid manuscript reproduction" technique. This requires a camera-ready typescript, and the end result will be as professional as the material provided by the contributors. Unfortunately, frequent typos (or, perhaps genuine spelling errors) occur throughout. In other places corrections have been made without lining them up to the rest of the page. The overall result is a product that often does not look very professional.

The stated purpose of the volume was to provide information on the ecology of insectivorous birds and their roles in forest ecosystems. It consists of 20 papers, divided into an introduction, censusing techniques, sampling prey populations, foraging strategies, ecology and conclusions. The references are in abbreviated form, meaning that there are no titles for the research papers cited, a format that will no doubt disappoint some, as will the absence of an index.

How successful is this book in accomplishing its stated purpose? In general, it is a distinct disappointment; some papers are only marginally appropriate to the stated theme (e.g., Coulson et al.'s paper on bark beetles), while others are so superficial as to be of limited value. Whiting's paper on feeding niche partitioning of chickadees (*Parus*) and titmice attempts to cover a problem that has already been explored by several others in far greater detail. He tries to draw detailed conclusions from a data set that is far too small for meaningful analysis (it could have been gathered in 1 afternoon). Whiting concludes that his birds are more specialized in their foraging than has generally been believed. Using the minute data set presented, however, it is unlikely that he could have come to any other conclusion. In general, this study more closely resembles a pilot run than a polished scientific contribution. Other papers share these shortcomings to varying degrees. Several appear to be dumped sections of theses, not appropriate for a symposium volume (at least in their present form) and others show duplication to varying degrees. McClelland's contribution on Pileated Woodpeckers (*Dryocopus pileatus*) includes 3 full-page studio photographs (2 of Pileated Woodpeckers, 1 of a Screech Owl (*Otus asio*) that are inappropriate to this type of presentation. Perhaps the editors or convenors of the symposium are as much to blame as the authors for letting many of these papers be published in their present form.

Having commented thus far on what this compilation is not, let me dwell on what I consider to be bona fide contributions to the literature. A few papers make substantial contributions of high quality. My measure of quality is that a paper would pass the editors of either a major ornithological or ecological journal with little modification. Jackson provides an interesting discussion of the structure of bark and its consequent qualities as a colonizing site for insects and foraging site for birds. Grubb makes the sensible point that optimal foraging theory, about which there is currently so much ballyhoo, may be most useful in forming a behavioral baseline against which observed foraging patterns can be compared. In the few other places where this trendy new theory is brought up in the book, one does not usually see a similarly critical approach. Pinkowski makes some interesting comparisons of bluebird (*Sialia*) foraging patterns as a function of foliage changes that take place over the period of a breeding season. He makes a plea for studies that take place in more than 1 area and for more than 1 year; some of the best advice that could be given to workers in foraging ecology. However, Pinkowski makes assumptions about competition for food between different bluebird species in areas of geographical overlap that seem open to alternative explanations, particularly for species that are hole-nesters. In an unjustifiably long paper of 43 pages, Dahlsten and Copper report on the demography of Mountain Chickadees (*Parus gambeli*). They got this species to use nest boxes with high frequency in comparison to levels expected from chickadees and titmice in eastern North America. In fact, their success approximates that reported from Europe and the British Isles for Great Tits (*P. major*) and Blue Tits (*P. caeruleus*). Thus, they are able to provide some of the first life-table information for North American parids. Most of the values are very similar to those of their European cousins. However, recovery of nestlings is much lower than for the European systems, presumably a consequence of the large contiguous areas about the study area, as opposed to the isolated woodlots generally studied in England or the Netherlands. This paper badly needs editing. At one point the reader encounters 7 consecutive pages of largely unreduced data. Most of this spread treats stomach contents, which in the absence of other data on prey availability, are of limited significance.

Although certain papers in this book note that birds' greatest significance in forest ecosystems may lie in helping to keep insects at low levels, the overall argument presented leaves one with the unmistakable impression that the contributors believe birds to be of major importance in controlling insects. Since this symposium was about birds, this conclusion is probably not surprising. At this point a balanced review attempting to evaluate the relative roles of birds, parasitoid insects and other possible biological factors in controlling numbers of forest insects would have been of great value. Many entomologists and even ecologists will probably be surprised at the importance implicitly accorded to birds here as controlling factors.

In sum, in spite of the scholarship of certain contributions, I cannot recommend this book. The papers taken as a whole raise serious doubts about the wisdom of publishing entire symposia, regardless of the merit of the individual parts. Perhaps part of the responsibility should fall on the shoulders of the editors. If so, the contributors should know of this in advance of preparing their presentations.—DOUGLASS H. MORSE.

SAMPLING DESIGN AND STATISTICAL METHODS FOR ENVIRONMENTAL BIOLOGISTS. By Roger H. Green. John Wiley & Sons, New York, 1979:257 pp., 64 numbered text figures, 15 tables. $19.95.—As the title suggests, this is primarily a handbook to guide environmental biologists through decisions about the design, analysis, and presentation of the results of studies of the effects of man-originated changes on the environment. But it is also a valuable reference for ecologists in general. For the skeptics who are concerned that statistical methods may sometimes be used to extract differences that do not really exist in nature, the book is a good introduction to an alternative view. Properly applied statistical methods can save us from claiming that our favorite theory is substantiated by observations that do nothing of the sort, and in addition they can identify complex patterns in nature that are not obvious from mere examination of large data sets. Since the world is neither all chaos nor all order, insightful analyses based on probability theory are our best hope for clarifying relationships. If birds are rarely mentioned, that is at least partly because imaginative experimental design and data analysis are hard to find in the ornithological literature.

The book has 4 well-organized sections: Introduction, Principles, Decisions, and Sequences. In the first section the author presents principles of inference, sampling and statistical design, hypothesis formulation and testing. Section 2, Decisions, gives a key to five broad categories of environmental studies and specific decisions that must be made about the design, analysis and display of results. Ten principles give rules of sampling strategy, emphasizing such procedures as replicates, controls, the importance of preliminary sampling, stratified versus random sampling, tests for error variation, and transformations. Section 3, Sequences, gives examples from the literature and discusses them in detail. The examples are mostly in aquatic systems, reflecting the author's experience.

One of the most valuable features of the book is its comprehensive bibliography, cross-referenced to the text, and keyed by types of methods and environments studied. This covers the general ecological literature in addition to the literature on environmental studies. In combination with the 1978 edition of T. R. E. Southwood's Ecological Methods and statistical texts such as Biometry by R. R. Sokal and F. J. Rohlf and An Introduction to Quantitative Ecology by R. W. Poole, we now have excellent up-to-date summaries of the state of the art in ecological research.

Green emphasizes that the options for data analysis are greater than most people realize. Certainly ornithologists have been overlooking tools such as contingency tables, nonparametric ranking procedures, and time series analysis. He warns that the properties and assumptions of a model must be considered critically. Clustering routines will make patterns out of random numbers. Arbitrary compounds of independent variables such as indices and importance values should be avoided unless their interpretive sense is very clear. Most ecologists have abandoned the H′ information theoretic diversity index as not having any biological significance. In his plea for robust but conservative methods Green recalls that when Watson and Crick described the double helix structure of DNA they said it had "novel features of considerable biological interests" (Nature 171:737–738, 1973).

Some of the author's positions reflect his personal taste. In the section on the form of data he recommends that with presence-absence data, quantitative densities, or rank abundances one should use transformations so that linear models can be used rather than "fleeing" to nonparametric methods. In the section on ratios he follows Atchley in recommending analysis of covariance. In addition, he totally ignores species-area effects and discredits the rarefaction procedure. These are points on which we disagree. But I found the book rich in its treatment of the overall subject, very well-written, and I recommend it highly.—FRANCES C. JAMES.

ANALYSIS OF ECOLOGICAL SYSTEMS. By David J. Horn, Rodger D. Mitchell and Gordon R. Stairs (eds.). Ohio State Univ. Press, Columbus, Ohio, 1979:ix + 312 pp. $27.50—This volume of contributed papers is the result of a colloquium held at Ohio State University in 1976. The 9 chapters include: "Fitness, survival, and optimality," by R. C. Lewontin; "Darwinian analysis: the new natural history," by R. D. Mitchell and M. B. Williams; "The ecology of colonizing species, with special emphasis on animal invaders," by D. G. Embree; "Niche segregation in desert lizards," by E. Pianka et al.; "Development of theory in insect-plant interactions," by L. E. Gilbert; "On the theory of central place foraging," by G. H. Orians and N. E. Pearson; "Quantitative plant ecology," by P. C. Miller; "Population models: experimental tools for the analysis of ecosystems," by R. G. Wiegert; and "Parasitoid ecology and biological control in ephemeral crops," by D. J. Horn and R. V. Dowell.

As in any symposium with various participants, there is a great difference in coverage given to particular topics. For example, Lewontin presents an interesting cautionary tale on the dangers of assuming that some particular organismal trait is optimized by natural selection. He points out that many selective forces, and many genes, affect particular phenotypic characteristics, and that optimizing 1 specific process might be detrimental to other equally important organismal functions. Pianka, Huey and Lawlor present a long chapter comparing desert lizard niches in Australia, Africa and the United States. They show that the species of a particular guild differ in one or another niche component, but that they do not necessarily differ along the same niche parameter in the different deserts. Also, the greater the species diversity in a particular site, the lower the niche overlap (presumably because of diffuse competition). Orians and Pearson present a theoretical optimality model for central place foraging. They support their model weakly with a bit of data on foraging blackbirds, and note that most of their ideas are still waiting to be tested. The papers of Miller and Wiegert are synthetic approaches to broad ecosystematic topics.

By and large these papers are interesting, though they approach ecosystems from very different points of view. One has to ask whether 9 papers are worth the high cost of the book. They may be to a seminar group, although even this is debatable. Probably a book like this belongs in a library rather than on one's own bookshelf.—MICHAEL A. MARES.

WORKING BIBLIOGRAPHY OF OWLS OF THE WORLD WITH SUMMARIES OF CURRENT TAXONOMY AND DISTRIBUTIONAL STATUS. By Richard J. Clark, Dwight G. Smith and Leon H. Kelso. National Wildlife Federation Scientific/Technical Series No. 1, Washington, D.C. 1978:319 pp., soft cover. $9.00.—Owls have been widely studied, but the results have appeared in such a diversity of publications that students of strigiforms sometimes miss important work as they survey the literature. This book is therefore of practical value to many avian biologists. The coverage of the literature, which took 11 years to survey, is remarkably extensive. The master list, arranged chronologically by author, cites 6590 references that deal with owls to a substantial degree. General papers on raptorial birds that incorporate a discussion on owls are included, but popular and photographic articles, and faunal studies, are not. There is a 172 page bibliography, plus 3 chapters of summaries and cross-references. Master numbers (relating to the master list) are arranged by geography, subject category and genus. The first chapter organizes the literature geographically, with the master numbers arranged by genus in each subheading. The second chapter subdivides all genera into the categories of anatomy, behavior, ecology, physiology, taxonomy, conservation, general information and distribution. The third chapter simply lists reference numbers by genus, a seemingly redundant feature given the information in the previous chapter. To find references for a particular species, one must examine either the geographic or the generic reference list, or both. Certainly these 3 chapters save the researcher a great deal of time, and justify the title "working bibliography."

This work is also a valuable general reference. The authors present a summary of owl taxonomy and a synopsis of genera from recent checklists. This is helpful because it minimizes any problems one might encounter owing to the past use of more than 1 scientific name for a particular species. The authors should be commended for their exceptional coverage of common names, spanning 54 languages, which are listed both alphabetically and under scientific names. For example, 60 common names are given for *Asio flammeus* alone. Another tabularized summary, covering 133 species, incorporates information on the approximate number of races, distribution, habitat and a section of general remarks.

Although in general this volume is exceptionally well done, a few aspects require critical comment. As the authors warn, a careful reading of the introduction is necessary to make the best use of the bibliography because it is in the introduction that the methods of compilation and scope of the text are outlined. I was overwhelmed at times by the amount of information in this book, and sometimes found it difficult to locate a particular section quickly. Rapid location of specific information is not enhanced by the narrow page margins or the rather cryptic demarcation of chapters. Computer page generation of the summary reference lists has created some problems, e.g., incomplete cross-references. Laboratory studies are categorized by the location of the experiment, rather than by the species under examination. This practice could result in users overlooking some papers. Care must also be taken in interpreting the subject categories used in the generic reference list as they are rather loosely defined.

The book is a bargain considering the amount of information that it contains, and its value in circumventing the anguish commonly associated with literature searches. It may be ordered from the Raptor Information Center, National Wildlife Federation, 1412 16 St., N. W., Washington, D.C. 20036.—GARY BORTOLOTTI.

Rare and Endangered Biota of Florida, Vol. 2: Birds. By H. W. Kale, II (ed.). Univ. Presses of Florida, Gainesville, Florida 1978:xix + 121 pp., 1 color, 35 black-and-white photographs, 1 line cut, 67 range maps; paper. $7.00.—This authoritative publication was prepared by 26 separate contributors; the lion's share was written by W. B. Robertson, H. W. Stevenson, H. W. Kale, J. C. Ogden, or O. T. Owre, but many others supplied from 1–3 accounts. The book covers 74 taxa: species, subspecies and 1 color morph (Great White Heron [*Ardea herodias occidentalis*]) that either are resident in, or migrate through, Florida. The birds are grouped into 7 categories, by their status in the state: 11 species that are endangered, 13 threatened, 11 rare, 29 "of special concern," 5 whose status could not be determined (*Falco columbarius*, 3 rails and 1 ssp. of seaside sparrow [*Ammospiza maritima*]), 3 recently extirpated, and 2 extinct. Of the 11 listed as endangered in Florida (7 breeding species, 4 endemics), only 9 are also so designated on Federal lists; the other 2 (Wood Stork [*Mycteria americana*] and Florida Grasshopper Sparrow [*Ammodramus savannarum floridanus*]) have undergone recent serious population declines or are poorly known and probably have vanishingly small numbers. The categories of threatened, rare and species of special concern include a mixture of a few otherwise common species with peripheral breeding populations in Florida (e.g., American Redstart [*Setophaga ruticilla*] which breeds only in the northwestern panhandle); some that are literally threatened (the only colony of Magnificent Frigatebird [*Fregata magnificens*] lies on the edge of a Navy artillery range); many herons, shorebirds and terns that may not be "individually" endangered but whose habitats are rapidly disappearing; some that are truly rare but still too numerous to be classified as endangered; and the Eastern Brown Pelican (*Pelecanus occidentalis carolinensis*) and Southern Bald Eagle (*Haliaetus l. leucocephalus*) that are Federally listed as endangered, but that have healthy enough Florida populations to be classified here as just threatened.

The book begins with brief descriptions of the major terrestrial and wetland habitats of Florida, followed by the species accounts grouped by status. Each of the accounts takes from 1–4 pages, and contains a description of the species and its range (both within and outside of Florida), a range map, habitat notes, and sections dealing with its life history and ecology, specialized or unique characteristics, the basis for its status classification, recommendations, selected references, and usually a photograph of the bird and/or its habitat. My only negative note about the book as a whole is that it is awkward for a reader to find any given species account quickly: the list of taxa included is rather buried on pp. xviii-xix, contains no page references, and there is no index.

Throughout, one finds strong emphasis on population declines as the result of habitat destruction, and the need to preserve habitats if the birds are to be preserved. In many instances concrete recommendations are offered that would improve the species' condition. The main objective of the Florida Committee on Rare and Endangered Plants and Animals, and its Special Committee on Birds that produced this exhaustive inventory, is to increase public awareness of the damage (sometimes unwitting) to natural habitats through unregulated development. It is heartening indeed, to have this publication written by highly competent local scientists—both amateur and professional—and produced through the joint efforts of private environmental organizations, 2 industrial interests, a private wildlife foundation and state and federal agencies. Florida is to be congratulated on this fine (and continuing) effort; I can only hope that this is the first in a series of equally thorough floral and faunal inventories by other states. It is not only of academic interest, but should serve as an important planning tool in the future.—Mary H. Clench.

MY WORLD OF BIRDS: MEMOIRS OF AN ORNITHOLOGIST. By George J. Wallace. Dorrance & Co., Philadelphia and Ardmore, Pennsylvania, 1979:345 pp., 28 pp. photos. $10.00.—How many ornithologists have started their careers armed only with a Reed bird guide, with inadequate or more likely no binoculars, but with the seemingly endless energy and intense enthusiasm of youth? George Wallace, like many others, followed this path while growing up on a farm in Vermont. It is difficult in this age with its plethora of bird guides to imagine a time when Reed's "Land Birds East of the Rockies" and "Water and Game Birds" were the only guides small enough to be slipped into a pocket and taken into the field. The shapes of all the species illustrated, especially in the land guide, were somewhat similar, and the colors in the later printings of the book apt to be distorted. It still remained a necessity for any youth wishing to identify birds. Binoculars were both costly and difficult to obtain, so few had them. In retrospect, one can see that the training resulting was of great value. To observe a bird closely, it was necessary to approach slowly and quietly, blending as much as possible with the background. For how many did a red-letter day arrive when they slowly approached that first Scarlet Tanager (*Piranga olivacea*)? Without binoculars, one became more aware of other features of the landscape such as flowering plants, trees, and mammals, giving an early awareness of the habitat preferences of various species of birds. Starting on the home farm and then to areas within hiking distance, Wallace extended his bird lists. In later years, he was able to note the difference between the bird life in the unsprayed orchards, fields, and woods of his youth and those drenched with pesticides. Thus he became a crusader against the use of D.D.T. and the indiscriminate use of other toxic poisons.

Eventually the University of Michigan became his choice for college years, partly because the hard-to-obtain tuition was only $93 per year. In order to get to Ann Arbor, he hitchhiked from Vermont to Michigan. After graduation, he undertook graduate work at the University of Michigan, selecting for a thesis the life history of the *bicknelli* form of the Gray-cheeked Thrush (*Catharus minimus*). This meant summers back in Vermont, living far up on the slopes of Mt. Mansfield. Later, he went as Warden to the Pleasant Valley Sanctuary in the Berkshires. Finally in 1942, he joined the teaching staff in the Department of Zoology at Michigan State University, where he was to remain until retirement in 1972. The first section of the book relates his experiences growing up and later as professor, and affords revealing glimpses into the lives of other ornithologists such as Josselyn Van Tyne, the Craigheads, Maurice Broun, Harold Peters, and others.

The latter part of the book deals with trips taken to various sections of the United States, and with trips to South America (Colombia, during a sabbatical year), Europe, India and surrounding areas, East Africa, Australia, and New Zealand. These chapters are a trip into nostalgia for those who have visited the areas, and can be used as a guide by those planning to visit these regions. Appended to each chapter is a list of species of birds seen with dates and locations.

George Wallace has written many articles for technical journals, and in 1955 he published the first edition of his "Introduction to Ornithology." One wishes that his autobiography had a more in-depth discussion of his research and related problems.

The extensive bibliographies at the end of each chapter are an important asset for any reader wishing to delve further into the subjects that have been mentioned in the book. An index would have been of further assistance.—MARGARET H. HUNDLEY.

This issue of *The Wilson Bulletin* was published on 7 October 1980.

THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "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 (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss 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.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Dr. Robert C. Whitmore, Division of Forestry, West Virginia University, Morgantown, West Virginia 26506.

CONTENTS

GENERAL NOTES

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 92, NO. 4 DECEMBER 1980 PAGES 425–562

The Wilson Ornithological Society

Founded December 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

The Wilson Bulletin is sent to all members not in arrears for dues.

The Josselyn Van Tyne Memorial Library

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.

The Wilson Bulletin

(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and esewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

Female Guayaquil Woodpecker *[Campephilus (Phloeoceastes) gayaquilensis]* at nesting cavity on 29 May 1978 in the western foothills of the Andes in the Department of Lambayeque, Peru (photo: M. D. Williams).*

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 92, No. 4 DECEMBER 1980 PAGES 425–562

Wilson Bull., 92(4), 1980, pp. 425–438

TERRITORIAL BEHAVIOR OF THE SAGE SPARROW: SPATIAL AND RANDOM ASPECTS

TERRELL RICH

The territorial behavior of birds is often easily observable and has been extensively studied since it was first treated by Howard (1920). Several recent authors (Yamagishi 1971, Post 1974, Koeppl et al. 1975, Zach and Falls 1978) have used spatial analysis to reveal basic patterns of territorial behavior. The purpose of this paper is to examine certain aspects of the territorial behavior of male Sage Sparrows (*Amphispiza belli*), an uncommon breeding bird of the intermontane west. I have concentrated on vocal behavior of a few males, stressing distribution of song perches in the territory, number of songs per bout and orientation of singing males. I made no specific attempt to quantify subtle interactions between males or influences of female activity on males. Interactions between birds were rare due to both the secretiveness of females and the large territories which often left neighboring males separated by several hundred meters. I have also combined data from different stages of the breeding cycle. Thus, several important influences on behavior have not been specifically evaluated.

STUDY AREA AND METHODS

The study was conducted from 9 April to 19 July 1976, and from 16 March to 3 June 1977, 14 km northwest of Blackfoot, Bingham Co., Idaho. The 30-ha study area was gridded with 2-m stakes at 50-m intervals and marked with colored flagging. I studied 4 neighboring territorial males each year who were not marked, but could be identified by song. Males are referred to in this paper by numbers. Two of these, males 1 and 3, were studied in both years, and are identified by a 2-digit number, the second digit being the year studied. All males were mated except male 1-6. Data for male 6 were insufficient to include in some of the following analyses.

Each day I followed a male around his territory from sunrise until at least 4 h after sunrise. The location of song perches, number of songs per perch and compass orientation of the

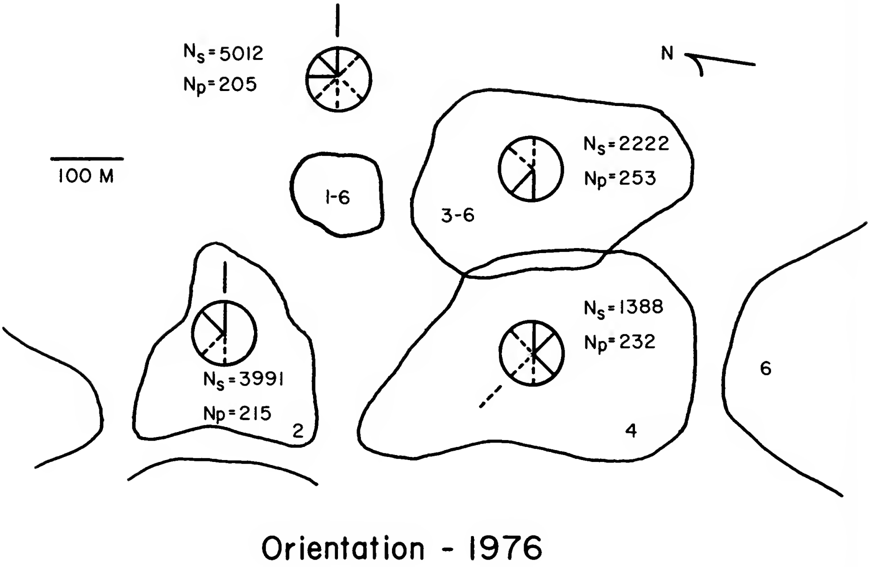


FIG. 1. Orientation of males on song perches in 1976. Solid lines indicate directions of more songs and perches than expected by chance. Dashed lines indicate directions of fewer and no line indicates values near expected (see Methods). Lines inside the circle in each territory are the orientation of songs while the outer lines give orientation of perches. N_s is the number of songs and N_p the number of perches used in the analysis for each male.

singing male (direction he was facing) were recorded. Orientation of each male on each perch was classified into 1 of 8 compass directions. I analyzed 2 types of orientation. First, I counted the total number of songs sung in each of the 8 directions for the entire study period (song orientation). Second, I counted only the orientation of the male regardless of how many songs were sung (perch orientation). Thus, for perch orientation, if a male faced direction 1 (east) and sang 100, 20 or 1 song each case would be equal, i.e., each is scored 1 perch in direction 1. If the male changed orientation during a given song bout the appropriate proportions of songs and perches were assigned to each direction. Song and perch orientation for each male was analyzed by a Chi-square goodness-of-fit test to an expected even distribution. In those instances where the Chi-square value exceeded χ^2, $P = 0.05$, df $= 7$, I examined subgroups of directions to define those that contributed most to the total Chi-square value. In Figs. 1 and 2, lines indicate directions which contributed most to the Chi-square value; solid lines note directions with greater than expected frequencies and dashed lines, less. No lines indicate the subgroups which did not differ from the expected even distribution at $P \leq 0.05$. A complete description of this technique is given in Snedecor and Cochran (1967).

I used the distribution of song perches to calculate 2 centers of each territory following the methods of Post (1974). First, the coordinates of each song perch were weighted by the number of songs at that point (song center). Second, no weighting factor was used (perch center). Territory size was determined by connecting outer perches with straight lines.

An annulus of perch concentration was determined from the number of perches in each

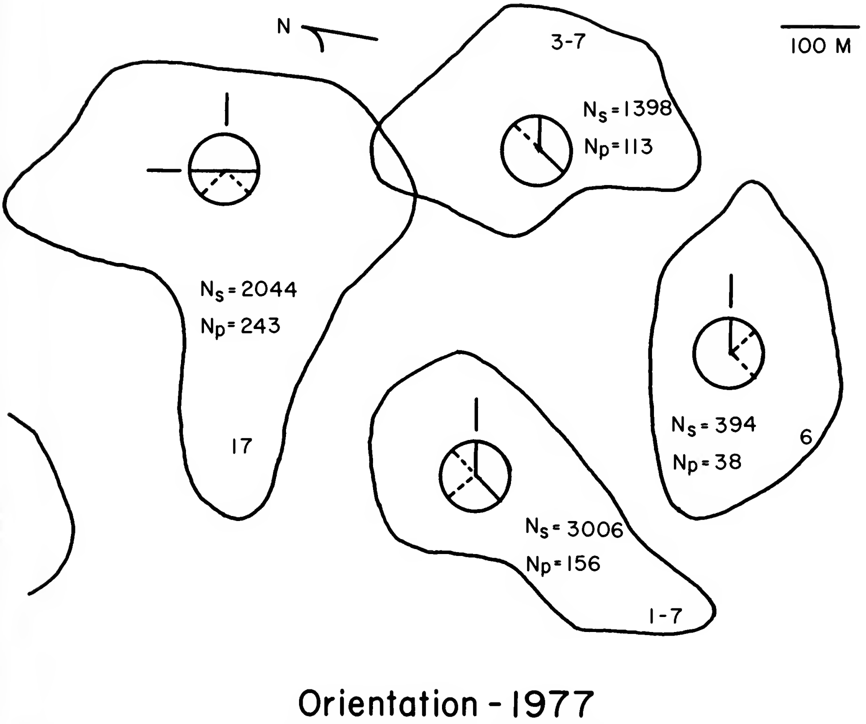


FIG. 2. Orientation of males on song perches in 1977. Symbols are explained in Fig. 1.

successive annulus of 25-m width. Following adjustment for the increasing area of each annulus the distribution was compared to that expected in a uniform distribution by Chi-square goodness-of-fit.

I then wanted to determine how much of the territory of each male could be adequately described by random movements of the territorial male. The data in Table 1 were obtained by counting the number of perches in each 25 × 25 m plot (subdivisions of the 50 × 50 m grid intervals) in each territory with a value of 0 assigned only if the plot were bordered on 3 sides by plots with at least 1 perch. Other plots with no perches were not considered part of the territory. Then plots with large numbers of perches were successively removed until the remaining distribution of frequencies was not significantly different from the Poisson distribution at $P \leq 0.05$.

A 1-way analysis of variance was applied to the data on songs per bout in Fig. 6. Since a significant F ratio resulted, the Student-Newman-Keuls multiple range test was applied to slopes of the log-transformed data. All statistical techniques were taken from Zar (1974).

The vegetation was sampled according to Daubenmire (1959). Two parallel transects were established 50 m apart through each of the 4 territories in 1976. Percentage cover was recorded for each plant species at every 1.5-m interval for a total of 40 points per transect. Vocalizations were recorded with a Dan Gibson Electronic Parabolic Microphone and Uher 4000 Report L recorder. Sound spectrograms were prepared on a Kay Electric Company Sona-Graph, model 6061-B.

TABLE 1

DISTRIBUTION OF SONG PERCHES PER 25 × 25 M PLOT IN THE TERRITORIES OF MALE SAGE SPARROWS

Male	N[a]	Total[b]	$\bar{x}$	$S^2/\bar{x}$	Random[c]	$\bar{x}$	$S^2/\bar{x}$	%[d]	N[e]
1-6	237	0–35	9.12	14.55	0–10	2.89	0.89	69	53
2	278	0–18	5.67	4.81	0–8	2.97	2.08	73	111
3-6	322	0–23	5.61	4.46	0–6	2.77	1.14	70	123
4	309	0–13	3.96	3.39	0–7	2.45	1.18	82	158
1-7	189	0–16	3.05	4.90	0–8	2.40	1.63	91	96
3-7	146	0–15	1.95	3.21	0–6	1.57	1.12	96	104
17	300	0–15	3.55	2.89	0–8	2.61	1.32	92	229

[a] Total perches in the territory.
[b] Range of frequency of occurrence of songs per plot.
[c] Range of only those frequencies which yield a goodness-of-fit to the Poisson distribution.
[d] Percent of the 25 × 25 m plots in the territory described by random perch locations.
[e] Perches remaining in the random distribution.

RESULTS

Habitat.—As for most species, structural parameters of habitat influence Sage Sparrow foraging sites, choice of song perches, height of perches and orientation of singing. Habitat may, therefore, have an important effect on the spatial territory. Sagebrush (*Artemisia tridentata*), the dominant species, varied from 11–44% cover, depending on the transect, and the most abundant grass (*Poa sandbergii*) from 4–15% cover. Two other grasses, *Sitanion hystrix* and *Agropyron spicatum* varied from 3–11% cover. *Phlox longifolia* covered from 1–5% of the study area. Only the percent cover of sage varied appreciably, but in a gradual and uniform manner. The habitat appeared homogeneous.

Territory establishment.—Sage Sparrows seem atypical among passerines because 7 of 8 males arrived already paired (see Hilden 1965). Arrival dates were 18 March 1976 and 16 March 1977. Males sang little or not at all at first. Initially, pairs mostly foraged together as their territories were delineated. Males 3 and 6 established territories in the same area in both years. In 1977, male 1 established a territory somewhat west of his 1976 territory. The 1977 territory was in the area to which he moved later in 1976 after failing to mate in that year. Identities of males were verified by comparing spectrograms of their songs from both years.

Territory size.—Territories varied considerably in size and shape both daily and seasonally with the progress of breeding. Similar variation has been reported for other species (Yarrow 1970, Robins 1971, Yamagishi 1971, Catchpole 1972, Potter 1972, Welsh 1975). Mean territory size for 8 male Sage Sparrows was 4.43 ha ± 1.86 (range 1.06–7.06 ha) and is larger than the known size for other North American sparrows (see Potter 1972, Rich 1977).

General behavior.—Behavior of all males in the morning consisted of single bouts of song from tops of sage, interspersed with foraging. Males seemingly moved randomly through the sage flying up to sing from nearby perches. Typically, a male sang, dropped abruptly and directly to the ground, foraged for some time and then flew directly up to a new perch. Males only rarely foraged above surface in sage or other vegetation. This pattern seemingly reflects the relationship of territorial behavior, foraging, habitat configuration and probably food distribution.

Territorial behavior.—Song was the outstanding feature of territorial behavior. There was almost no fighting or visual displaying, a pattern observed in other sparrows (Cartwright et al. 1937, Robins 1971, Potter 1972), and little chasing. I rarely saw physical responses between males. I saw virtually no sentinel behavior in Sage Sparrows. However, such behavior has been reported for Savannah Sparrows (*Passerculus sandwichensis*) (Welsh 1975), Twites (*Acanthis flavirostris*) (Marler and Mundinger 1975) and Black Rosy Finches (*Leucosticte atrata*) (pers. obs.).

Perched males typically sang at 8–10 sec intervals. One song bout per perch was the rule as perches were always changed immediately after the bout had ceased, and the next bout began within seconds of landing on a new perch. Rarely did males sing while foraging, and then only at intervals of 30–90 sec. Males did not have favorite song perches though they had preferred areas. Some species prefer certain perches (Potter 1972, Catchpole 1972, Welsh 1975), whereas Bewick's Wren (*Thryomanes bewickii*) (Gorton 1977) also shows no preference.

Song variation.—Each male uttered a single song type which rarely varied throughout the breeding season except by omission of 1 or 2 of the final syllables. This stereotypy of the primary song has also been observed in other sparrows (Walkinshaw 1939, Borror and Reese 1954, Borror 1959, Goldman 1973, Heckenlively 1976). Males 1, 3 and 6 did not change their songs even slightly between 1976 and 1977 as verified by spectrograms. Martin (1977) reported that some Fox Sparrows (*Passerella iliaca*) also sing identical songs from year to year. Fig. 3 presents songs of 6 male Sage Sparrows.

Conspicuousness of singing males.—Males on perches were visible from the front but often difficult to locate from behind. The white breast plumage contrasted with the color of sage, whereas dorsal plumage was cryptically colored. The low pitch of the song combined with abrupt beginnings and endings of most syllables and their short duration maximized locatability of the singer (Thorpe 1956). When singing a male elevated his bill and turned his head from side-to-side throughout each song. All of the

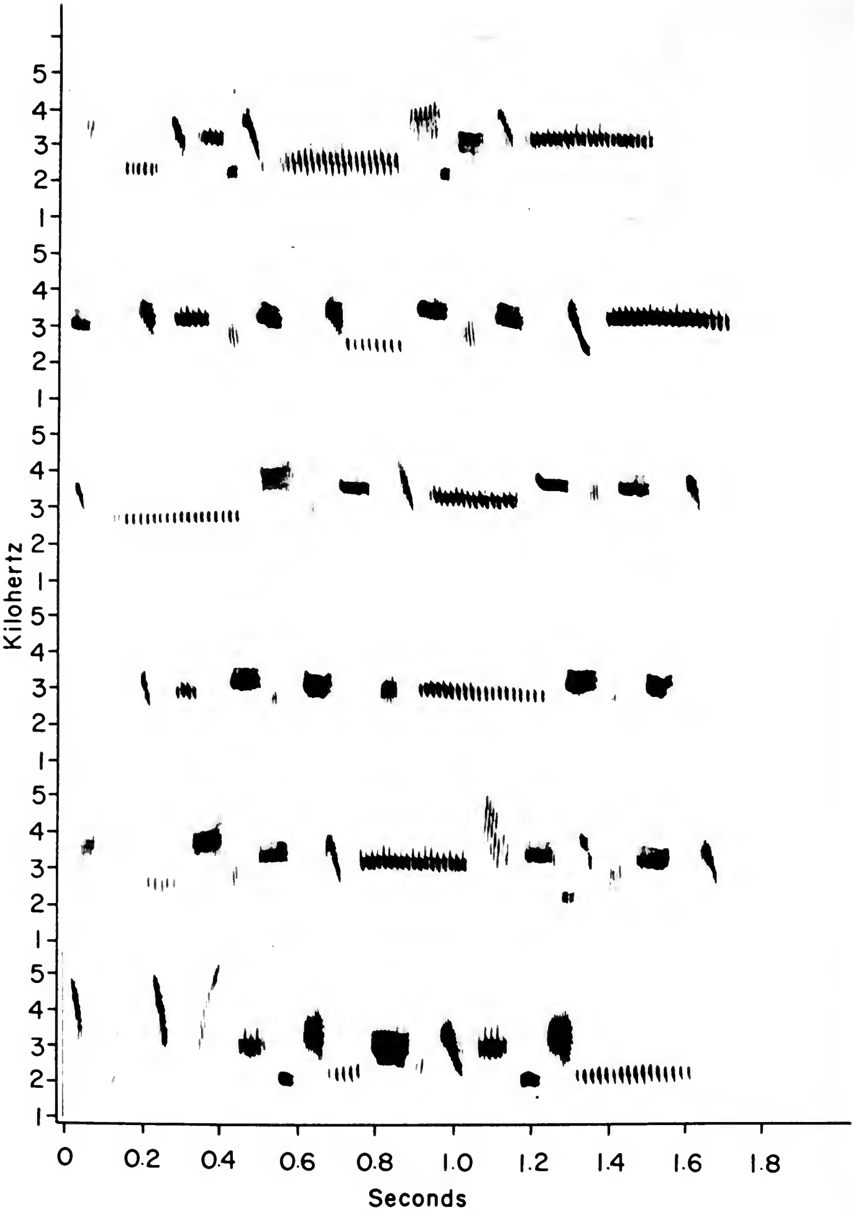


FIG. 3. Sound spectrograms of 6 territorial male Sage Sparrows' songs, (males 1, 2, 3, 4, 17, and 6).

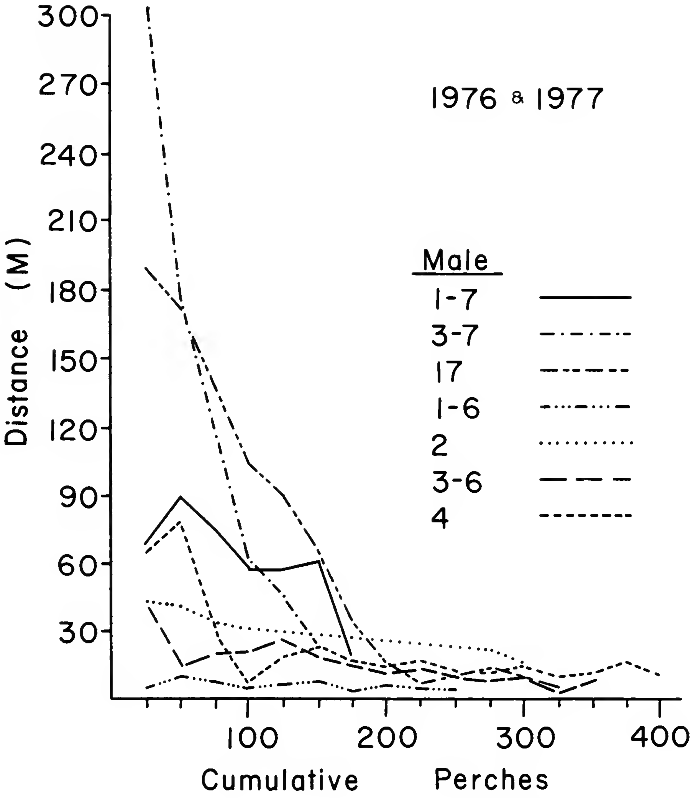


FIG. 4. Distance between the song center of the territories and the perch center after the accumulation of every 25 perches (see text).

above factors facilitated rapid location of singing males when they were facing the observer. Thus, orientation of the male is an important aspect of territorial behavior.

Song orientation.—Males did not show evenly distributed song orientation in 1976 (Fig. 1). Males 1-6 and 2 tended to face east and away from neighboring males. Males 3-6 and 4 sang towards each other and male 4 also sang towards male 6. In 1977 (Fig. 2), there was also a preference for certain directions. Males 1-7, 3-7 and 6 sang facing east and unoccupied habitat. Male 1-7's easterly orientation was also towards male 3-7, though a wide buffer zone separated their territories. Only rarely could I hear the 1 male while in the other's territory. Male 17 faced north, a patch of unoccupied habitat and male 3-7. Male 3-7 also faced male 6.

Perch orientation.—Perch orientation of the males seemed more random than song orientation (Figs. 1 and 2). Males 3-6 and 3-7 had even orientation. Males 1-6, 1-7, 4 and 6 had uneven orientation due mainly to an excess or deficiency of perches in only 1 direction. Males 1-6, 1-7, 2, 6 and 17 all faced east and unoccupied habitat. Male 17 also faced north and unoccupied habitat. Male 4 had fewer perches facing northwest and a neighboring male.

Center of territory.—Fig. 4 presents the distance between the perch center and song center of the territories after the accumulation of every 25 song perches. The 2 centers nearly coincided when points for the entire period were considered. For example, for male 4 the distance between the 2 centers was about 80 m after 50 perches and only 10 m after 400 perches. The exception to this trend occurred for male 1-6 where the distance was 4 m after 25 perches and only slightly less than 4 m after 250 perches. This constant displacement revealed that male 1-6 sang more songs on those perches on the side of his territory nearest the rising sun. Both song and perch orientation were also towards the east. Perhaps the stimulus of the rising sun influenced the strong eastward orientation of this male.

Distribution of perches.—The variance to mean ratio of perch frequencies (Table 1) revealed that perches were clustered in the territories of each male except male 6 for which there were insufficient data. After the few plots with large numbers of perches were removed from the analysis (see Methods) the remaining distribution of perching frequency was not statistically different from the Poisson distribution and was, therefore, random. The importance of this difference in the distribution of perches (depending on the way the data are treated) is that plots where perches were distributed randomly made up the largest portion of each male's territory. Thus, perches were randomly distributed over 69% of the territory of male 1-6 and 96% of the territory of male 3-7. Percentages for other males fell between these 2 values.

Annulus of song concentration.—Males 1-6 and 4 had most of their songs in the center of their territories (Fig. 5). Male 1-6 and 9.4 times the number expected in the center while male 4 had 4.4 times that expected. Males 1-7, 2 and 3-6 sang most in the third annulus, male 3-7 in the fourth annulus and male 17 in the fifth. The median of song concentration was the third annulus while the median of territory radius was the twelfth.

Songs per bout.—The males sang between 1 and 118 songs per bout. The mean number of songs per bout varied from 4.76–18.08. The frequency distribution of songs per bout revealed a preponderance of 1-song bouts and a decline in the number of bouts with more songs. I analyzed only the frequency of observations of bouts between 1 and 20 songs, which provided a continuous distribution for all males. Fig. 6 gives the cumulative distribution and slopes of the lines obtained from the log-transformed

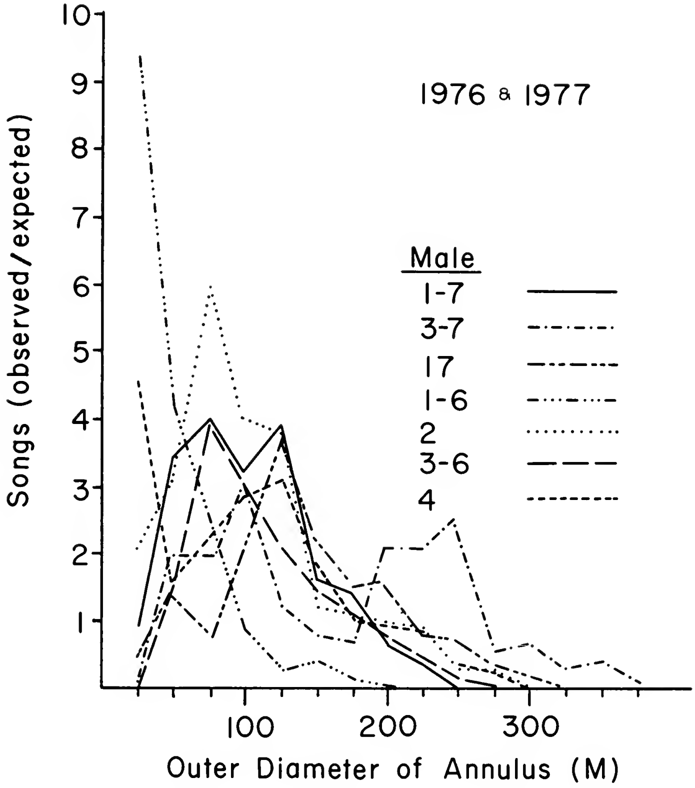


FIG. 5. Distribution of songs in each 25-m annulus from the center of the territories.

data. There are 3 things to notice in this figure. First, the slope of each line is the probability that a male will leave the perch after singing a given number of songs. Second, that probability was similar for all males, ranging from 0.18–0.28. The probabilities were not significantly different for either male 1 or male 3 in both years. Third, the probability was approximately constant for each male. Thus, the probability of leaving the perch after singing the first song was about the same as that of leaving the perch after singing the nineteenth song.

DISCUSSION

Habitat.—In many territorial species irregularities of habitat provide limiting points (e.g., attractive perch sites, obstructions) for males as they move about the territory singing and foraging (Cartwright et al. 1937, Potter 1972, Welsh 1975). This influence was particularly pronounced in Sa-

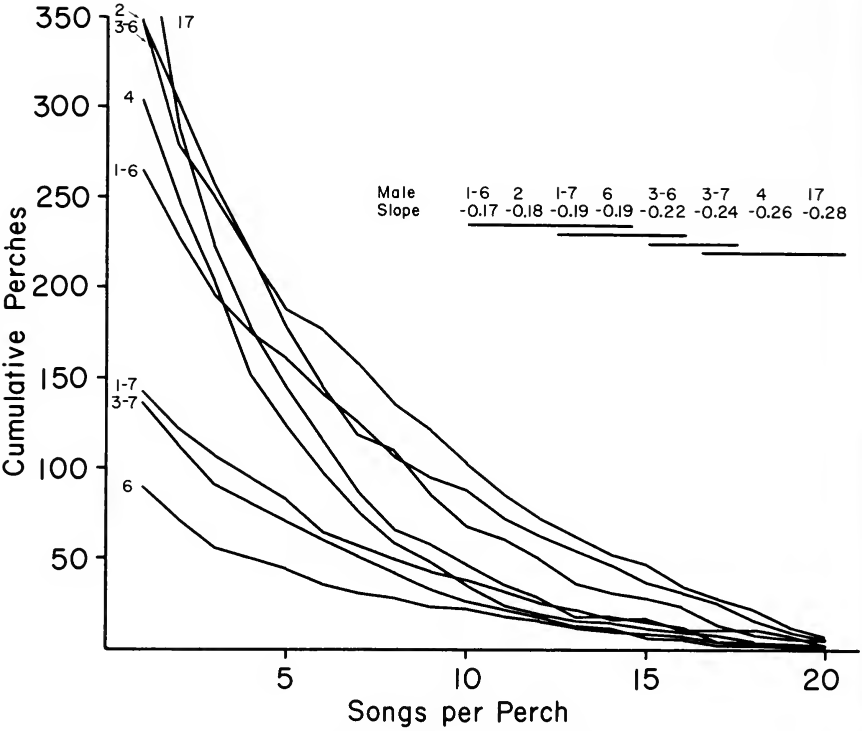


FIG. 6. Relationship between songs per bout and cumulative bouts for each male. Subsets of equivalent slopes derived from the log-transformed data are given.

vannah Sparrows who used fence posts as perches and barbed wire fences as territorial boundaries (Potter 1972). The habitat of the Sage Sparrow varied gradually and, I believe, placed virtually no restrictions on where the males may have moved and perched. The males were free to respond to other factors in the distribution of perches.

Orientation.—There were 3 important aspects of orientation. First, males 3-6, 3-7, 4 and 17 sang facing neighbors, but for all males there were several possible directions facing neighbors that did not show excessive singing. Furthermore, males 1-6, 1-7, 2 and 17 sang appreciably fewer songs facing some neighbors. This could be taken to support the idea that males know their neighbors (Weeden and Falls 1959, Falls 1969, Emlen 1971, Wiley and Wiley 1977) and are not sufficiently stimulated to expend energy advertising in their directions.

Verner (1977) predicted from his super-territory hypothesis that the space between territories should be defended if those spaces were large enough to support a breeding pair. The orientation of males 1-7, 2, 3-6 and 4 towards gaps between territories and the orientation of all 8 males towards unoccupied habitat suggests the latter possibility. Orientation away from neighbors might also serve to reduce the stress between males. Nesting Adelie Penquins (*Pygoscelis adeliae*) orient to inter-nest spaces rather than towards each other (Spurr 1975). But where neighboring Sage Sparrow territories overlapped males oriented towards each other—males 3-6 and 4 towards each other and male 17 towards male 3-7. Also, male 4 faced male 6 in 1976. Male 6 arrived late and persistently sang near the boundary of male 4's territory.

Second, when only perch orientation is considered, none of the directions of excess orientation were towards other males. In fact, 5 of 8 males perched facing east and all males except 3-6 had either song orientation, perch orientation or both to the east. There are at least 3 possible explanations for orientation to the east that may relate to the rising sun. (1) Males may enhance reflection of light from light-colored breast feathers. This may maximize conspicuousness as to reinforce their physical location in the habitat. Conspicuousness would also increase the chances for each male to evaluate the local population size and/or density for which there are apparently minimum requirements in some territorial species (see Hilden 1965:61). (2) The sun may provide early morning warmth. If this were the only consideration it seems that the darker colored back would absorb more radiant energy. Also, males did not fluff feathers as if to conserve heat. (3) Males may orient towards the sun simply because it is the most outstanding stimulus in the environment. The validity of these suggestions could be addressed by observing orientation before sunset and on cloudy days.

Finally, there was a large difference between the number of noted song directions and perch directions. All males showed greater evenness of perch orientation than of song orientation. Recalling the alternating sequences of foraging and singing, it appears as if males flew up to a perch at nearly random directions. Once on a perch the number of songs depended largely on what the bird happened to be facing. This suggests that, except for an orientation towards the sun, males were not reacting to a specific external stimulus when they flew up to a perch. This focuses attention on gross environmental stimuli and internal mechanisms controlling timing and orientation patterns in males. This control of the orientation is further clarified by male 1-6. This unmated male was the only bird showing substantially more or fewer songs in 7 of 8 directions. He sang almost all of his songs in direction 6, 7 or 8 and very few songs in the other 5 directions. His orientation was more predictable and may represent the basic pattern of male orientation that becomes modified upon mating.

Center of territory and probability of singing another song.— As more points were added in the calculation of the song center the more closely the song center approached the perch center, as expected in a random system of an infinite number of points. This suggests that for at least 6 of the males the song bout lengths were randomly distributed among the perch locations. The frequency distribution of songs per bout showed that the longer the bout the less likely it was to occur. However, once a distribution of bouts was defined, the spatial distribution of bouts could probably not be predicted. This removes importance from the number of songs in a bout and places more significance with the simple existence of a bout.

The similarity of the distribution of songs per bout for all males and the constant probability of singing 1 more song implies that song bout length is largely under the control of internal mechanisms. A similar distribution was found for calls per bout in Black-capped Chickadees (*Parus atricapillus*) (Ficken et al. 1978). If males sang particular numbers of songs in response to particular stimuli I would expect the frequencies to cluster at 1 or more values. Or if they simply sang until something interrupted them the distribution should have been random.

Annulus of perch concentration.—Post (1974) found that there was a difference in the distribution of activity points from the territory centers in Seaside Sparrows (*Ammospiza maritima*) having ungrouped as opposed to grouped territories and was able to ascribe possible selective significance to the observation. Weeden (1965) found that Tree Sparrows (*Spizella arborea*) concentrated their activity in the center of the territory with outer zones of progressively diminishing use. Smith (1963) stated that Grasshopper Sparrows' (*Ammodramus savannarum*) song perches were clustered on the periphery of territories as were those of 2 vireos (*Vireo* spp.) (Barlow and Rice 1977). Bonelli's Warbler (*Phylloscopus bonelli*) follows a circuit around its territory which varies little (Bremond 1976). Yamagishi (1971) reported that male Meadow Buntings (*Emberiza cioides*) have 2 centers of activity—one near the nest and another between the nest and the center of the territory. Sage Sparrows have a few plots where many perches are clustered between the edge and center of the territory and closer to the latter. But the remaining perches were scattered randomly throughout the largest part of the territory. Without knowledge of nest locations it is difficult to be certain that the data have been interpreted to best advantage. But when these 2 patterns, random placement and concentration annulus, are observed together, they may represent an optimal placement of songs to convey all the information—species, sex, location, individual identity, motivation—the song of the Sage Sparrow must serve (Marler 1956). Identification of such basic patterns of behavior facilitate recognition and interpretation of variations which occur in Sage Sparrows in different habitat or of other species in similar habitat.

SUMMARY

The distribution of song perches over territories, songs per bout and compass orientation of males on song perches were studied for 8 male Sage Sparrows. Each male had 1 nearly invariable song whose physical characteristics facilitated location of the singer. The uniformly varying habitat did not restrict the males' foraging and perching sites. For 6 males, song bouts of various lengths were distributed randomly among perch locations. Song perches were also randomly distributed in most of the male's territory, although a few 25 × 25 m plots had clustered perches. There was a constant probability that a male would sing 1 more song during any bout. All males showed perch orientation, song orientation or both towards the east and rising sun. Males also tended to sing towards unoccupied habitat and away from neighbors except where they approached too closely or consistently. Gross environmental stimuli, the uniform habitat and internal mechanisms may be important influences on the patterns considered.

ACKNOWLEDGMENTS

I am grateful to the Frank M. Chapman Memorial Fund of the American Museum of Natural History for support in 1976 and 1977 and to the Society of Sigma Xi for support in 1977. The Department of Biology, Idaho State University provided equipment and supplies. Charles H. Trost was an endless source of stimulation. William Saul, Edson Fichter, Jack Griffith and Barry Keller helped at various points during the research. I thank Mike Mahoney, Tim Reynolds, Jim McIver and Jim Perry for ideas on various aspects of the work. A special thanks goes to my wife, Pat, for her patience and understanding.

LITERATURE CITED

BARLOW, J. C. AND J. C. RICE. 1977. Aspects of the comparative behavior of Red-eyed and Philadelphia vireos. Can. J. Zool. 55:528–542.

BORROR, D. J. 1959. Songs of the Chipping Sparrow. Ohio J. Sci. 59:347–356.

——— AND C. R. REESE. 1954. Analytical studies of Henslow's Sparrow songs. Wilson Bull. 66:243–252.

BREMOND, J.-C. 1976. Specific recognition in the song of Bonelli's Warbler (*Phylloscopus bonelli*). Behaviour 58:99–116.

CARTWRIGHT, B. W., T. M. SHORTT AND H. D. HARRIS. 1937. Baird's Sparrow. Trans. Roy. Can. Inst. Pt. 2. 21:163–197.

CATCHPOLE, C. K. 1972. A comparative study of territory in the Reed Warbler (*Acrocephalus scirpaceus*) and Sedge Warbler (*A. schoenobaenus*). J. Zool. Lond. 166:213–231.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43–64.

EMLEN, S. T. 1971. The role of song in individual recognition in the Indigo Bunting. Z. Tierpsychol. 28:241–246.

FALLS, J. B. 1969. Functions of territorial song in the White-throated Sparrow. Pp. 207–232 *in* Bird vocalizations: their relation to current problems in biology and psychology, (R. A. Hinde, ed.). Cambridge Univ. Press, Cambridge, England.

FICKEN, M. S., J. P. HAILMAN AND R. W. FICKEN. 1978. A model of repetitive behaviour illustrated by chickadee calling. Anim. Behav. 26:630–631.

Goldman, P. 1973. Song recognition by Field Sparrows. Auk 90:106–113.

Gorton, R. E., Jr. 1977. Territorial interactions in sympatric Song Sparrow and Bewick's Wren populations. Auk 94:701–708.

Heckenlively, D. B. 1976. Variation in cadence of Field Sparrow songs. Wilson Bull. 88:588–602.

Hilden, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2:53–75.

Howard, H. E. 1920. Territory in bird life. John Murray, London, England.

Koeppl, J. W., N. A. Slade and R. S. Hoffman. 1975. A bivariate home range model with possible application to ethological data analysis. J. Mammal. 56:81–90.

Marler, P. 1956. The voice of the Chaffinch and its function as a language. Ibis 98:231–261.

——— and P. C. Mundinger. 1975. Vocalizations, social organization and breeding biology of the Twite *Acanthus flavirostris*. Ibis 117:1–17.

Martin, D. J. 1977. Songs of the Fox Sparrow. I. Structure of song and its comparison with song in other Emberizidae. Condor 79:209–221.

Post, W. 1974. Functional analysis of space-related behavior in the Seaside Sparrow. Ecology 55:564–575.

Potter, P. E. 1972. Territorial behavior in Savannah Sparrows in southeastern Michigan. Wilson Bull. 84:48–59.

Rich, T. D. G. 1977. Territorial behavior of the Sage Sparrow. M.S. thesis, Idaho State Univ., Pocatello, Idaho.

Robins, J. D. 1971. A study of Henslow's Sparrow in Michigan. Wilson Bull. 83:39–48.

Smith, R. L. 1963. Some ecological notes on the Grasshopper Sparrow. Wilson Bull. 75:159–165.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. Iowa State Univ. Press, Ames, Iowa.

Spurr, E. B. 1975. Orientation of Adelie Penguins on their territories. Condor 77:335–337.

Thorpe, W. H. 1956. The language of birds. Sci. Am. 195:128–138.

Verner, J. 1977. On the adaptive significance of territoriality. Am. Nat. 111:769–775.

Walkinshaw, L. H. 1939. Notes on the nesting of the Clay-colored Sparrow. Wilson Bull. 51:17–21.

Weeden, J. S. 1965. Territorial behavior of the Tree Sparrow. Condor 67:193–209.

——— and J. B. Falls. 1959. Differential responses of male Ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76:343–351.

Welsh, D. A. 1975. Savannah Sparrow breeding and territoriality on a Nova Scotia dune beach. Auk 92:235–251.

Wiley, R. H. and M. S. Wiley. 1977. Recognition of neighbor's duets by Stripe-backed Wrens *Campylorhynchus nuchalis*. Behaviour 62:10–34.

Yamagishi, S. 1971. A study of the home range and the territory in Meadow Bunting (*Emberiza cioides*): I. Internal structure of home range under a high density in breeding season. Misc. Rept. Yamashina Inst. Ornithol. 6:356–368.

Yarrow, R. M. 1970. Changes in Redstart breeding territory. Auk 87:359–360.

Zach, R. and J. B. Falls. 1978. Bivariate normal song territories in Ovenbirds. Can. J. Zool. 56:2088–2092.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

DEPT. BIOLOGY, IDAHO STATE UNIV., POCATELLO, IDAHO 83209. (PRESENT ADDRESS: P.O. BOX 204, 518 S. ALTA, SHOSHONE, IDAHO 83352.) ACCEPTED 14 NOV. 1979.

Wilson Bull., 92(4), 1980, pp. 439–451

INTERSEXUAL NICHE PARTITIONING IN DOWNY WOODPECKERS

Joseph B. Williams

Rand (1952) proposed that sexual dimorphism facilitated attraction between males and females, inhibited mismating, and in some situations permitted differential niche use reducing dietary overlap and thus competition. Selander (1966) demonstrated a relationship between the degree of sexual dimorphism and sexual divergence in foraging behavior in 2 melanerpine woodpeckers, the insular Hispaniolan Woodpecker (*Melanerpes striatus*) and the continental Golden-fronted Woodpecker (*M. aurifrons*). He hypothesized that in continental avian communities the extent of sexual divergence in niche use would be limited owing to the relative richness of the avifaunas (see also Wallace 1974).

Since Selander's (1966) seminal paper, several investigators have quantified foraging differences in continental areas between sexes, especially in the Picidae (Jackson 1970, Kilham 1970, Willson 1970, Kisiel 1972, Grubb 1975, Williams 1975, Jenkins 1979). Foraging differences are not always associated with morphological divergence (Ligon 1968, Jackson 1970, Kisiel 1972). In this study, I examine the relationship between sexual dimorphism and intersexual niche partitioning of Downy Woodpeckers (*Dendrocopos pubescens*) living in different habitats and in different competitive environments. Further, I report a controlled experiment testing the premise that foraging differences between sexes are reduced by increased interspecific competition.

STUDY AREAS AND METHODS

Hart Memorial Woods, situated along the Sangamon River near Mahomet, Champaign Co., Illinois contained 2 distinct types of woodland—a relatively dry upland area (9.6 ha), and a wetter floodplain (3.4 ha). My third study site, an upland forest called Monen Woods (5.9 ha), was separated from Hart upland by a lowland strip 100 m wide. Analysis of vegetation composition and vertical structure for each area is presented in Williams (1977). Hart and Monen uplands are dominated by black (*Quercus velutina*), red (*Q. rubra*) and white (*Q. alba*) oaks; the lowland by silver maple (*Acer saccharinum*). Relative availability based on basal area of each tree species is presented in Table 2. With a density of 553.7 and 565.3 trees/ha, respectively, Hart and Monen uplands were similar. The floodplain, with 239.9 trees/ha, had an open canopy owing to loss of many large elms (*Ulmus* sp.) 15 years earlier (Root et al. 1971).

Habitat use was measured by 4 variables: (1) tree species occupied; (2) height of bird in tree; (3) condition of substrate (dead or alive); and (4) limb diameter. Observations were recorded on activity of the bird and habitat use at 10 sec signals given by an electronic metronome as suggested by Wiens et al. (1970). I collected data an average of 10 days each month. After a bird was located, I allowed several min for habituation to my presence, timed the bird for no longer than 5 min and then found a new bird. This method reduced the sample size somewhat, but it also reduced bias by including observations from as many different individuals as possible.

Activities were categorized as follows (modified from Ficken and Ficken 1966, Jackson 1970, Willson 1970): (1) perch—no observable behavior taking place; (2) scale—pedal movement (horizontal or vertical), usually in search of food; (3) peck—repeated pecking in same location in tree; (4) bark probe—poking bill into cracks and crevices of bark; (5) fly—bird in flight; (6) ground forage—walking or hopping on ground, usually in search of food; (7) unknown—behavior unobservable at the signal; and (8) other—any other activity, such as display, preen, etc.

Foraging activity graphs were constructed using relative amounts of time spent on different foraging tactics. Perching is included in these graphs because birds stop during a foraging bout and study the bark surface.

Visual estimates of height were made for each bird; occasionally height estimates were checked with a forester's altimeter. For determinations of limb diameters I used the size of the bird being observed as a reference.

Niche breadths (B_i), or tendencies to specialize along a particular resource dimension, were calculated using the formula of Levins (1968). To simplify comparison of niche breadth values where different numbers of categories were involved, I scaled the values (Fager 1972) so that $B_{max} = 1$ and $B_{min} = 0$.

Overlap values on each niche dimension were calculated using Schoener's index (1968). Total overlap along a dimension yields a value of 1, complete separation yields a value of 0.

In addition to a monthly census of each area, I kept detailed notes on movements by individual Downy Woodpeckers. Thus, I estimated that 4 different individuals occupied Hart upland and lowland during both winters. In Monen upland, at least 4 different birds were observed during the winters of 1974–1975 and 1975–1976.

Morphological measurements were taken following Baldwin et al. (1931). Tongues were measured fully extended from the tip to the distal edge of the glottis (Lucas 1895). Methods for assessment of foods eaten by male and female Downy Woodpeckers are given in Williams and Batzli (1979a).

Elsewhere (Williams and Batzli 1979b), I have shown that the aggressive actions of Red-headed Woodpeckers (*M. erythrocephalus*) cause Downy Woodpeckers to forage lower in the canopy in upland habitats. During the winter of 1973–1974, oak trees produced few acorns and Red-headed Woodpeckers vacated my study areas, but during the winter of 1974–1975 with a relatively large acorn crop, Red-headed Woodpeckers dominated both Hart and Monen upland (for similar circumstances see Graber and Graber 1979). Only 2 Red-headed Woodpeckers established territories in Hart lowland during the winter of 1974–1975. This natural experiment allowed me to examine intersexual niche partitioning in an upland forest under 2 different competitive environments. Further, in early January 1975, I removed all Red-headed Woodpeckers from Monen upland and subsequently monitored the foraging of male and female Downy Woodpeckers in both Monen and Hart uplands. Red-headed Woodpeckers remained in Hart upland which served as a control area.

RESULTS

To determine the degree of sexual dimorphism, I compared mean values for 7 characters from 18 males and 12 females taken in central Illinois in 1975. Unlike Willson (1970), I did not find a significant difference in bill

TABLE 1

INTERSEXUAL COMPARISON OF MENSURAL CHARACTERS (MM) FOR MALE AND FEMALE DOWNY WOODPECKERS IN CENTRAL ILLINOIS

	DW-M	DW-F		DW-M	DW-F
N	18	12	Tongue length	38.8 ± 0.78	35.0 ± 0.51*
Weight (g)	27.8 ± 0.45[a]	27.0 ± 0.42	Wing length	125.2 ± 1.1	126.6 ± 1.6
Bill length	14.0 ± 0.16	13.8 ± 0.22	Span of foot	26.8 ± 0.22	26.4 ± 0.23
Bill width	5.2 ± 0.15	5.0 ± 0.20	Tarsal length	14.4 ± 0.23	13.9 ± 0.34

[a] $\bar{x}$ ± SE.

* Difference between sexes significant at $P < 0.05$ level.

length between sexes. Interestingly, tongue length for males and females was significantly different (Table 1).

Foraging activity patterns of males and females diverged in Hart upland and lowland for both winters (Fig. 1, $P < 0.01$ in all cases). Males pecked for prey items more than females, whereas females probed bark crevices more. When Red-headed Woodpeckers were experimentally removed from Monen upland, divergence patterns between the sexes were similar in the experimental and control areas. Males pecked for food more, but females bark-probed more often.

Males and females selected different tree species on both study areas of Hart Woods during both winters (Table 2, $P < 0.01$ in all cases). When Red-headed Woodpeckers emigrated from Hart upland, males preferred black and red oaks, whereas females selected the morphologically distinct white oak most of the time. The shift of both males and females to understory trees in this area in 1974–1975 was in part because Red-headed Woodpeckers controlled the upper canopy and compelled both sexes to forage lower (Williams and Batzli 1979b). In Hart lowland, females favored maple more than did males for both years, but males chose fallen logs and standing dead trees most often during the winter of 1973–1974. The following winter, when only 2 Red-headed Woodpeckers established territories in the lowland, males foraged more often on maples and honey locust (*Gleditsia triacanthos*) trees. Comparing data from the experimental and control areas, both sexes used white oaks in the control area less, which was probably a result of decreased availability of that species (Table 2). In addition, both sexes used understory trees more in the control area because they were compelled to forage lower in the canopy.

Sexual divergence along the foraging height dimension was disparate between years and habitats (Fig. 2, $P < 0.01$ in all cases). During 1973–1974, when Red-headed Woodpeckers were absent from the upland, male

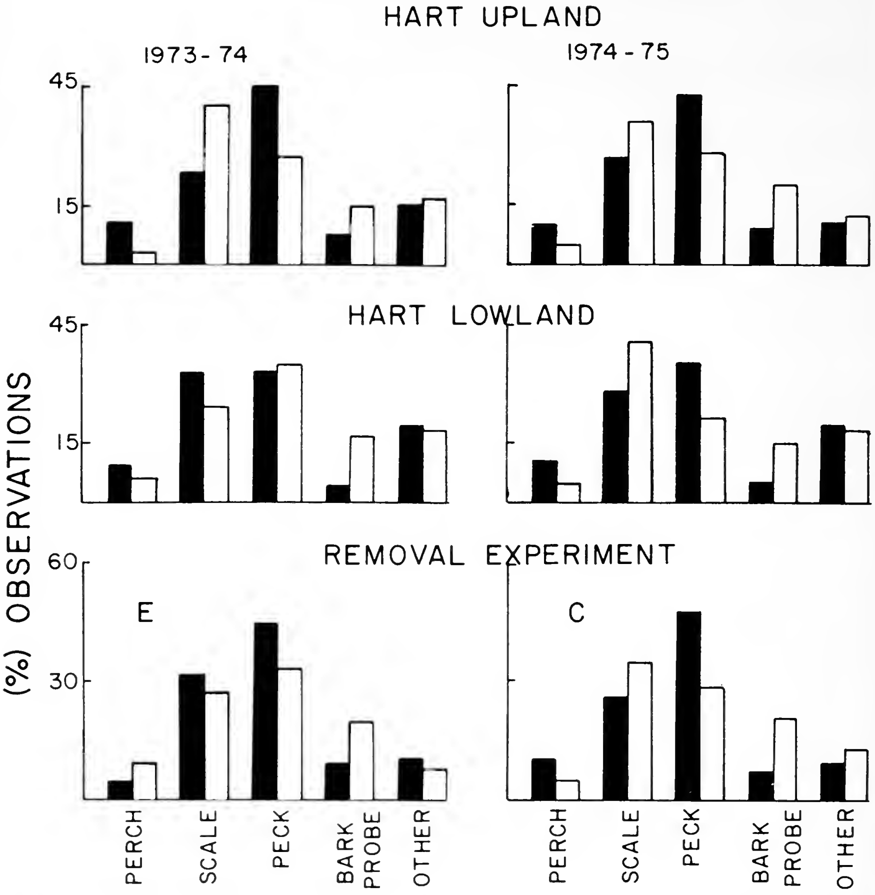


FIG. 1. Foraging acitivity graphs for male (solid bars) and female (open bars) Downy Woodpeckers from 2 habitats and during an experiment in which Red-headed Woodpeckers were removed from the experimental area (E), but allowed to remain in the control area (C). Sample sizes are the same as in Table 2.

and female Downy Woodpeckers foraged in the upper canopy most of the time, but when Red-headed Woodpeckers were present the following year, males and females more often exploited the lower portions of the canopy. In addition, males and females seemed to diverge more along the height dimension in the presence of Red-headed Woodpeckers. Because of the low numbers of Red-headed Woodpeckers in the lowland during 1974–1975, the impact of their dominance on foraging patterns of Downy Woodpeckers was slight. Males tended to ground forage more in this area during

TABLE 2

TREE SPECIES USED BY BOTH SEXES OF DOWNY WOODPECKERS DURING 2 WINTERS AND DURING AN EXPERIMENT IN WHICH RED-HEADED WOODPECKERS WERE REMOVED

Tree species	Availability[a]	1973–1974 DW-M	1973–1974 DW-F	1974–1975 DW-M	1974–1975 DW-F
Hart upland					
		(730)[b]	(652)	(172)	(791)
Black and red oak	0.55	0.36	0.08	0.40	0.12
White oak	0.33	0.46	0.88	0.24	0.66
Bitternut hickory (*Carya cordiformis*)	0.02	0.04	—	0.13	†
Understory trees	0.03	0.06	0.02	0.19	0.09
Fallen logs	0.06	—	—	—	0.03
Shagbark hickory (*C. ovata*)	†	0.03	†	0.02	0.08
Standing dead	†	0.02	—	†	†
Other	†	0.02	0.02	0.01	†
Hart lowland					
		(339)[b]	(302)	(551)	(629)
Silver maple	0.26	0.14	0.36	0.30	0.33
Logs	0.24	0.38	0.33	0.03	0.09
Bur oak (*Quercus macrocarpa*)	0.13	—	—	0.02	0.32
Green ash (*Fraxinus pennsylvanica*)	0.11	0.07	0.04	0.12	0.08
Standing dead	0.07	0.16	0.06	0.06	0.03
Hackberry (*Celtis occidentalis*)	0.06	0.09	0.03	0.06	0.01
Black walnut (*Juglans nigra*)	0.03	—	0.02	†	0.01
American and red elm	0.03	0.05	†	0.10	0.07
Bitternut hickory	0.02	†	—	0.03	—
Hawthorns (*Crataegus* sp.)	0.02	—	—	—	—
Sycamore (*Plantanus occidentalis*)	0.01	—	0.04	—	0.02
Honey locust	0.01	0.02	0.04	0.23	—
Other oaks	†	0.08	0.02	†	0.02
Other	†	†	0.05	0.04	0.02

Removal experiment

Tree species	Experiment	Control	Experiment	Experiment	Control	Control
			(370)[b]	(725)	(378)	(647)
Black, red oak	0.47	0.55	0.55	0.11	0.69	0.10
White oak	0.39	0.33	0.45	0.84	0.14	0.66
Understory trees	0.02	0.03	—	0.05	0.10	0.10
Fallen logs	0.07	0.06	—	—	—	0.04
Shagbark hickory	†	†	—	—	0.01	0.09
Standing dead	0.05	†	—	—	0.02	†
Other	†	0.01	—	—	0.04	0.01

[a] Availability index based on basal area/ha.

[b] Number of observations.

† Trace.

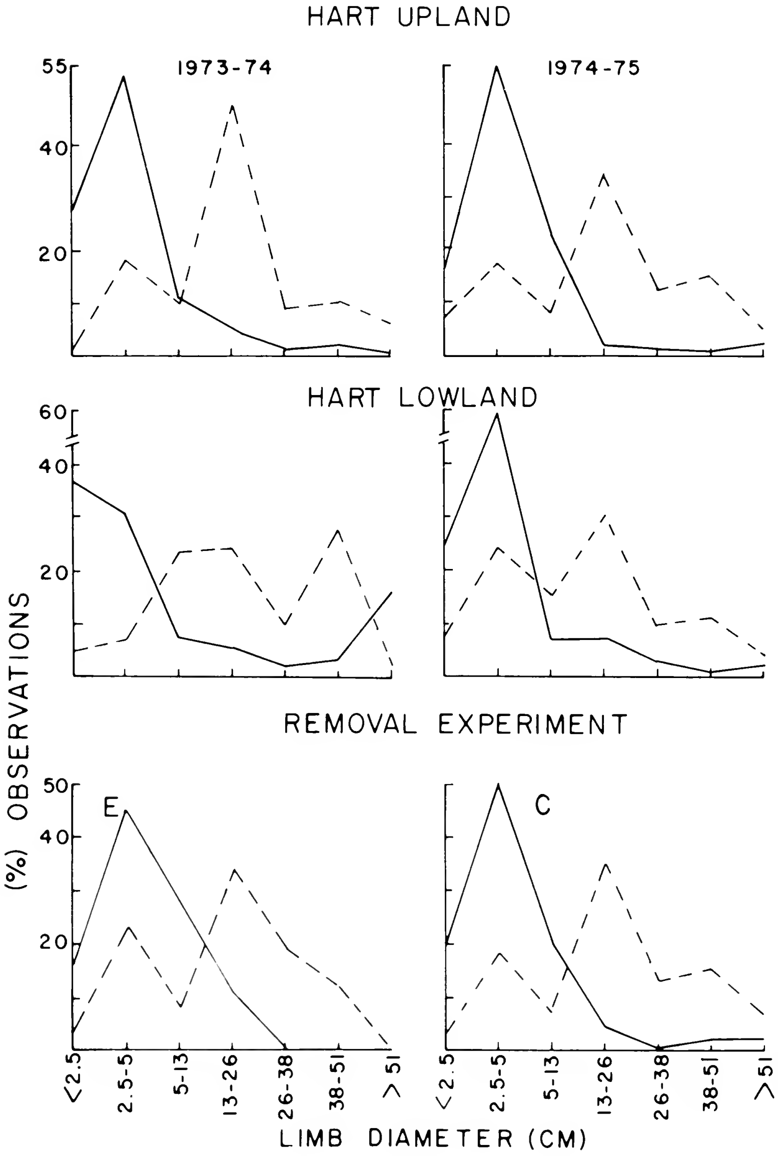


FIG. 2. The use of heights by male (solid lines) and female (dashed lines) Downy Woodpeckers in 2 habitats and during an experiment in which Red-headed Woodpeckers were removed from the experimental area (E), but allowed to remain in the control area (C). Sample sizes are the same as in Table 2.

both winters. In the experimental area both sexes shifted to higher portions of the canopy, but in the control area males diverged from females by foraging both high and low in the canopy.

Selection of living versus dead substrate by males varied, but was always different from females ($P < 0.05$ in all cases). Females foraged over living substrate more often in both areas for both years. I found no apparent shift in substrate use by the sexes between experimental and control areas.

For limb diameter use, males consistently hunted for prey on smaller limbs than did females (Fig. 3). Males selected smaller limbs than females regardless of their foraging height distribution. Even though males and females altered their foraging height patterns in the experimental area, no observable shift was noted in limb diameter use. In harmony with previous data, males perused small limbs for prey more often than did females in both the experimental and control area.

Niche breadth values showed males and females using tree species more evenly when Red-headed Woodpeckers were present in the upland (Table 3). Males tended to be more generalized than females on tree species in all areas in the presence or absence of Red-headed Woodpeckers. Males were more specialized for limb diameters in all situations. A noticeable shift in niche breadth patterns in the experimental area occurred for both sexes along the height dimension. Males and females were more generalized in the presence of a competitor. Also, males and females exploited live and dead substrate more evenly in the experimental area, although relative substrate availability was not measured in either area. Females were more specialized in tree species use in the experimental area.

Overlap values revealed that sexes separated more along the tree species and height dimensions when Red-headed Woodpeckers occupied the upland (Table 4). Comparing experimental and control areas, sexes showed less overlap along the foraging activity, tree species, height and limb diameter dimensions in the control area where dominant Red-headed Woodpeckers were present.

Because of a mast crop failure in the fall of 1975, Red-headed Woodpeckers emigrated from my experimental area (Monen upland). To examine how male and female Downy Woodpeckers would forage when Red-headed Woodpeckers were naturally removed from this area, I observed their feeding behavior during January and February of 1976 (56 observations for males, 423 for females). I noted consistent patterns compared to the previous winter when Red-headed Woodpeckers were experimentally removed. Males excavated more than females, but females bark-probed more. Females concentrated on white oaks but males preferred black, red

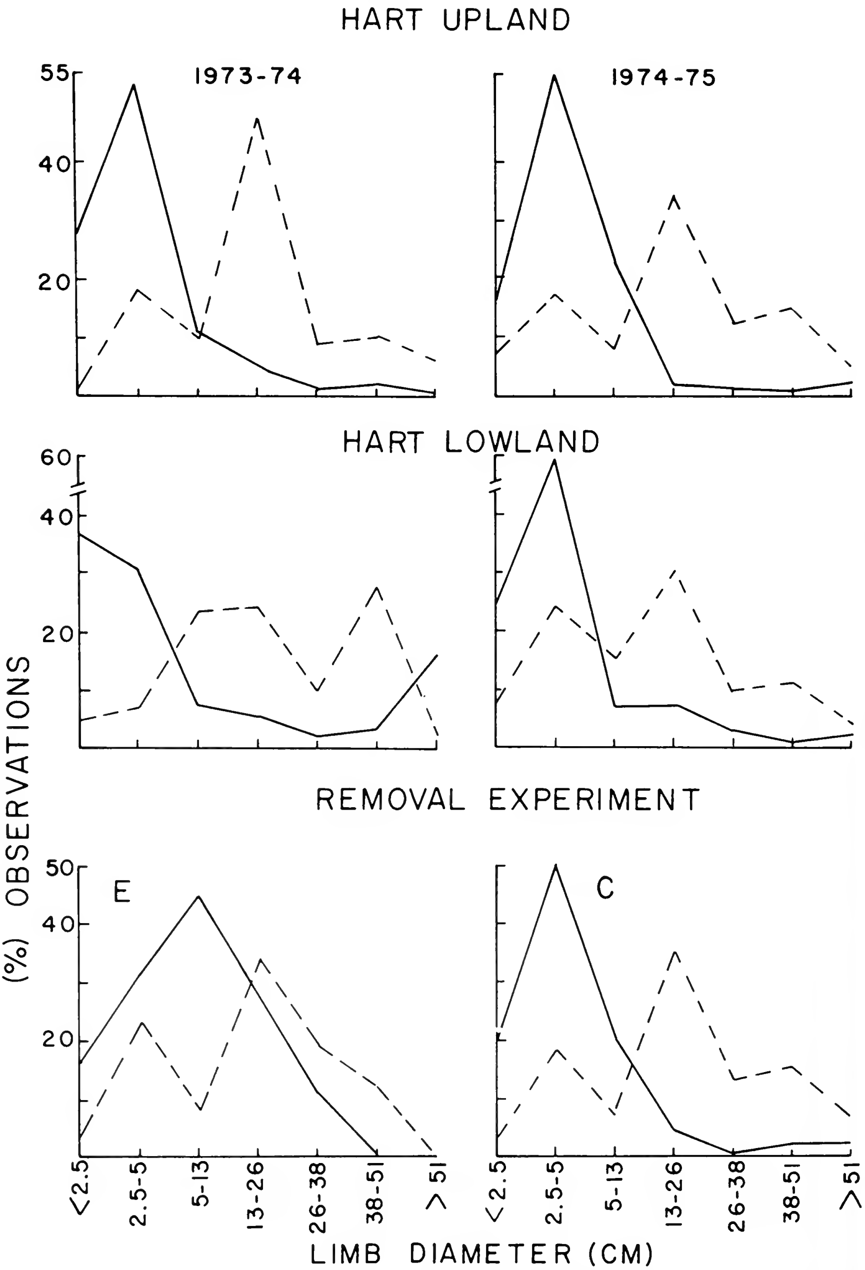


FIG. 3. The use of limb diameters by male (solid lines) and female (dashed lines) Downy Woodpeckers in 2 habitats and during an experiment in which Red-headed Woodpeckers were removed from the experimental area (E), but allowed to remain in the control area (C). Sample sizes are the same as in Table 2.

TABLE 3

NICHE BREADTH VALUES FOR MALE AND FEMALE DOWNY WOODPECKERS DURING 2 WINTERS AND DURING AN EXPERIMENT IN WHICH RED-HEADED WOODPECKERS WERE REMOVED

	Hart upland				Hart lowland				Removal experiment			
	1973–1974		1974–1975		1973–1974		1974–1975		Experiment		Control	
Category	M	F	M	F	M	F	M	F	M	F	M	F
Activity	0.34	0.35	0.36	0.44	0.57	0.45	0.42	0.40	0.55	0.79	0.56	0.77
Tree species	0.19	0.03	0.29	0.12	0.29	0.23	0.35	0.25	0.16	0.07	0.16	0.20
Height	0.76	0.48	0.67	0.79	0.22	0.55	0.79	0.79	0.16	0.58	0.67	0.67
Dead or alive	0.99	0.63	0.98	0.63	0.72	0.99	0.55	0.65	0.64	0.24	0.96	0.82
Limb diameter	0.28	0.40	0.27	0.68	0.49	0.64	0.25	0.67	0.36	0.57	0.29	0.64
Mean	0.51	0.38	0.51	0.53	0.46	0.59	0.47	0.55	0.37	0.45	0.53	0.62

and white oaks. Patterns for height and limb diameter use duplicated those from the experimental site for the previous winter.

The diet of Downy Woodpeckers in central Illinois during winter collectively consists of about 60% animal material (Williams and Batzli 1979a), but significant differences existed between males and females (χ^2, $P < 0.005$). Males consumed more Hymenoptera (mostly Formicidae) (22% vs 12%), corn (*Zea mays*) (23% vs 15%), and poison ivy (*Rhus radicans*) seeds (9% vs 4%); females had more homopterans (5% vs 11%), spiders (Araneida) (1% vs 10%), and wheat (*Triticum aestivum*) (1% vs 5%) in their diets. Intersexual overlap values for the food, calculated to be

TABLE 4

NICHE OVERLAP VALUES ALONG 5 DIMENSIONS FOR MALE AND FEMALE DOWNY WOODPECKERS DURING 2 WINTERS AND DURING AN EXPERIMENT IN WHICH RED-HEADED WOODPECKERS WERE REMOVED

	Hart upland		Hart lowland		Removal experiment	
Category	1973–1974	1974–1975	1973–1974	1974–1975	Experiment	Control
Activity	0.70	0.78	0.76	0.73	0.82	0.76
Tree species	0.57	0.49	0.65	0.57	0.56	0.36
Height	0.63	0.58	0.59	0.78	0.60	0.53
Alive or dead	0.73	0.71	0.79	0.96	0.56	0.76
Limb diameter	0.36	0.38	0.32	0.49	0.46	0.36
Mean	0.60	0.59	0.62	0.71	0.60	0.55

0.61, were not appreciably greater than interspecific comparisons for the bark-foraging guild during winter (Williams and Batzli 1979a).

DISCUSSION

The hypothesis that the sexes of Downy Woodpecker partition the overall niche of the species into subniches is supported by the data in this report. The pattern which emerges, that males forage more by pecking, use a wider array of tree species and search smaller limbs, appears to be consistent regardless of habitat or competitive environment. Where Downy Woodpeckers forage along the vertical dimension depends not only on habitat type but also the competitive environment. Grubb (1975) has suggested that weather factors may also influence the vertical foraging patterns of Downy Woodpeckers.

Other investigators have witnessed similar patterns. Kisiel (1972), collecting data for Downy Woodpeckers in maple-beech-hemlock forests of eastern New York, wrote that males excavated more than females and that they were more frequently observed on smaller limbs. Recording observations in Brownfield woods during winter in central Illinois, Willson (1970) wrote that males chose small limbs significantly more than did females. She did not observe differences in foraging technique. From data taken in Kansas, Jackson (1970) also observed males more often on smaller limbs. In an earlier paper, I noted foraging patterns during early spring consistent with those discussed in this presentation (Williams 1975).

Kilham (1970) speculated that male Downy Woodpeckers foraging higher in the canopy signified dominance over females. My data do not support this hypothesis, but rather suggest that vertical foraging patterns in both sexes are influenced by a complex set of variables such as habitat structure, food availability at various heights and the competitive environment. However, males do consistently peck on smaller limbs for food items than do females. Perhaps selection has acted to separate males from females by choosing male genotypes which are more efficient at extracting (by pecking) prey items from smaller limbs. Their longer tongues may indicate that males take prey from deeper within the foraging substrate. Conversely, females may be more efficient at probing for insects within bark crevices.

Tree species selection may simply be a reflection of foraging efficiencies of the respective genotypes. If female genotypes are more efficient at bark-probing, then one would expect them to choose more rough-barked tree species (i.e., white oaks), which almost certainly harbor more insects than do smooth-barked species.

Dietary analysis for the sexes of Downy Woodpecker during winter does indicate that differential foraging techniques allow acquisition of different food resources, thus reducing competition. I have shown elsewhere that Brown Creepers (*Certhia familiaris*) eat mostly small homopterans during winter and that they forage by probing crevices in bark on trunks and larger branches (Williams 1977). I suggest here that in upland forests female Downy Woodpeckers consume more homopterans and spiders because they probe more in bark crevices. Conversely, males take more ants by pecking into small limbs and removing them with a longer tongue.

Selander (1966) posited that greater intersexual structural dimorphism and behavioral divergence occurs for insular woodpeckers compared to mainland forms because of a reduced competitive environment on islands. With fewer competitors, insular populations increased and subsequently expanded their niches. When food became limiting, selection favored establishment of subniches for the sexes. These ideas are based on long-term evolutionary responses of populations under different competitive regimes. My data point out short-term niche shifts by both sexes of the Downy Woodpecker under different competitive environments. In upland forests with increased interspecific competition, both sexes decreased overlap along several niche dimensions. If food is most likely to be in short supply during this period (see Williams 1977), then when Downy Woodpeckers are restricted to the lower canopy by interference from Red-headed Woodpeckers, perhaps sexes diverge to reduce competition for food. When the competitor was removed (Red-headed Woodpeckers) both males and females shifted to higher zones in the canopy. Since more limbs and branches occur in the upper zones (Williams 1977), food may have been more abundant there, allowing greater overlap in space between sexes.

SUMMARY

I studied intersexual niche partitioning of a relatively monomorphic population of Downy Woodpeckers in central Illinois during 3 winters and in 2 different habitats. By comparing the foraging patterns of male and female Downy Woodpeckers during the winters of 1973–1974 and 1975–1976 when Red-headed Woodpeckers were absent, to their foraging patterns during the winter of 1974–1975 when Red-headed Woodpeckers were present, I examined the influence of competition on intersexual niche partitioning in upland habitats. Additionally, I observed the foraging of males and females in an upland area where Red-headed Woodpeckers were experimentally removed and compared those differences to patterns in a control area where Red-headed Woodpeckers remained. Results showed that male Downy Woodpeckers usually pecked for food on small limbs, but females more often probed bark crevices of trunks and larger branches regardless of habitat or competitive environment. In upland forests, males chose black, red and white oaks, but females preferred white oak. In the lowland females more often selected maples, whereas males more often foraged on fallen logs and standing dead trees during the winter of 1973–1974. Males shifted to maples and honey locust trees during the winter of 1974–1975. When Red-headed Woodpeckers occupied

the upland forest, both sexes foraged lower in the canopy and more often used understory trees. Sexes diverged more along the height dimension in the presence of Red-headed Woodpeckers, seemingly reducing interspecific competition. Analysis of diets revealed that males consumed more ants, whereas females ate more homopterans.

LITERATURE CITED

BALDWIN, S. P., H. C. OBERHOLSER AND L. G. WORLEY. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Nat. Hist., Cleveland, Ohio.

FAGER, E. W. 1972. Diversity: a sampling study. Am. Nat. 106: 293–310.

FICKEN, R. W. AND M. S. FICKEN. 1966. A review of some aspects of avian field ethology. Auk 83:637–661.

GRABER, J. W. AND R. R. GRABER. 1979. Severe winter weather and bird populations in southern Illinois. Wilson Bull. 91:88–103.

GRUBB, T. C. 1975. Weather–dependent foraging behavior of some birds wintering in a deciduous woodland. Condor 77:175–182.

JACKSON, J. A. 1970. A quantitative study of the foraging ecology of Downy Woodpeckers. Ecology 51:318–323.

JENKINS, J. M. 1979. Foraging behavior of male and female Nuttall Woodpeckers. Auk 96:418–420.

KILHAM, L. K. 1970. Feeding behavior of Downy Woodpeckers. I. Preference for paper birches and sexual differences. Auk 87:544–556.

KISIEL, D. 1972. Foraging behavior of *Dendrocopos villosus* and *D. pubescens* in eastern New York state. Condor 74:393–398.

LEVINS, R. 1968. Evolution in changing environments. Monogr. Pop. Biol. Princeton Univ. Press, Princeton, New Jersey.

LIGON, D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. Auk 85:203–215.

LUCAS, F. A. 1895. The tongues of woodpeckers. Bull. U.S. Dept. Agric. 7:35–45.

RAND, A. L. 1952. Secondary sexual characters and ecological competition. Fieldiana—Zool. 34:65–70.

ROOT, T. W., J. W. GEIS AND W. R. BOGGESS. 1971. Woody vegetation of Hart Memorial Woods, Champaign County, Illinois. Trans. Ill. State Acad. Sci. 64:27–37.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151.

SCHOENER, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726.

WALLACE, R. A. 1974. Ecological and social implications of sexual dimorphism in five melanerpine woodpeckers. Condor 76:238–248.

WIENS, J. A., S. C. MARTIN, W. R. HOLTHAUS AND F. A. IWEN. 1970. Metronome timing in behavioral ecology studies. Ecology 51:350–352.

WILLIAMS, J. B. 1975. Habitat utilization by four species of woodpeckers in a central Illinois woodland. Am. Midl. Nat. 93:354–367.

———. 1977. Community organization in a bark-foraging guild in central Illinois. Ph.D. thesis, Univ. Illinois, Urbana, Illinois.

——— AND G. O. BATZLI. 1979a. Winter diet of a bark-foraging guild of birds. Wilson Bull. 91:126–131.

——— AND ———. 1979b. Competition among bark-foraging birds in central Illinois: experimental evidence. Condor 81:122–132.

WILLSON, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:129–132.

DEPT. NATURAL SCIENCE, PEPPERDINE UNIV., MALIBU, CALIFORNIA 90265. (PRESENT ADDRESS: DEPT. BIOLOGY, JOSEPH LEIDY LABORATORY OF BIOLOGY G7, UNIV. PENNSYLVANIA, PHILADELPHIA, PENNSYLVANIA 19104.) ACCEPTED 6 JULY 1979.

Errata.—Vol. 92, No. 1, "Bi-parental care in Killdeer: an adaptive hypothesis" by Sarah Lenington. On p. 18 the scientific name for Great Knot should read *Calidris tenuirostris* and the scientific name for Green Sandpiper should read *Tringa ochropus.*

"The selection and use of fruit by birds in an eastern forest" by John W. Baird. On p. 69 the scientific name for Red-bellied Wooodpecker should read *Melanerpes carolinus.*

"Spatial and temporal distribution of rails in Colorado" by Herman J. Griese, Ronald A. Ryder and Clait E. Braun. On p. 96 the scientific name for Yellow Rail should read *Coturnicops novaboracensis.*

"Food habits of White Pelicans during 1976 and 1977 at Chase Lake National Wildlife Refuge" by Gary R. Lingle and Norman F. Sloan. On p. 124 the scientific name for fathead minnow should read *Pimephales promelas.*

Vol. 92, No. 2, "Nest predation by the speckled king snake" by Charles F. Facemire and Stephen D. Fretwell. On p. 250 the scientific name for Red-winged Blackbird should read *Agelaius phoeniceus.*

Credit for the photograph for the Frontispiece of the Magellanic Oystercatcher (*Haematopus leucopodus*) should go to Dr. Joseph Jehl, Jr.

Vol. 92, No. 3, "Nest placement in Sage Thrashers, Sage Sparrows and Brewer's Sparrows" by Terrell Rich. On p. 263, Table 1, the first value under Sage height (cm) should read 67.1 ± 8.4^b.

"A Paint-billed Crake in Virginia" by Charles R. Blem. On p. 393 the scientific name of the Spotted Rail should read *Paradirallus maculatus.*

"The influence of agriculture on avian communities near Villavicencio, Colombia" by Wallace D. McKay. On p. 384 the common name of *Forpus conspicullatus* should read Spectacled Parrotlet.

"Back carrying of young by Trumpeter Swans" by Theodore Bailey, Edward Bangs and Vernon Berns. On p. 413 the scientific name of Black-necked Swan should read *Cygnus melanocoryphus.*

Wilson Bull., 92(4), 1980, pp. 452–457

IMPLICATIONS OF JUVENILE HARASSMENT IN PURPLE MARTINS

Charles R. Brown and Erik J. Bitterbaum

Juvenile Purple Martins (*Progne subis*) are frequently harassed by mature martins, both before fledging and afterwards. On their initial flights juveniles are chased and pecked by nonparental birds in the colony, and if nonparental birds encounter a fledged brood in a grouping area (see Brown 1978a), they continue to harass the juveniles and chase them away. Birds engaging in this behavior were termed "raiders" by Brown (1978a). Parents have never been seen harassing their own young.

Brown (1978a) suggested that harassment could improve juveniles' awareness and reflexes and make them more noticeable to parents during brood assembly. But these possible advantages do not seem selectively important enough to maintain this behavior, which appears maladaptive at first glance. In this paper we offer a new hypothesis to explain juvenile harassment, report certain observations that have important bearing on our hypothesis and discuss the implications of harassment.

METHODS

Studies of Purple Martin nesting biology and breeding behavior were conducted by CRB at a maximum of 36 colony locations in Sherman, Grayson Co., Texas, from 1968–1979 (Brown 1978a,b; 1979). During 1974–1979, all juveniles and 30–50% adults per year at 1 main study colony were marked with color-painted aluminum bands and colored plastic bands. The number of martin pairs occupying this study colony averaged 26 each year, with a similar average number of broods annually. Birds were captured as nestlings or (with more limited success) as adults using the technique of Klimkiewicz and Jung (1976). EJB made observations on martin behavior at 3 colony locations in Gainesville, Alachua Co., Florida, in 1977 and 1978. All adult birds in Florida (14 pairs in 1977 and 16 in 1978) were color-banded and marked with paints as they entered cavities; no juveniles were marked in Florida. Studies in both Texas and Florida emphasized direct observation of birds.

THE HYPOTHESIS

Purple Martins are specialized secondary hole nesters and face severe intraspecific (Nice 1957, Johnston and Hardy 1962) and interspecific (Brown 1977, 1978c) nest-site competition. We hypothesize that juvenile harassment is a strategy of breeding birds to reduce potential nest-site competition in subsequent years. Nesting birds chase juveniles away from colonies to insure that the juveniles will not become imprinted upon these sites, lessening the probability that juveniles will return there the following year to compete with the raiders.

RESULTS

Our hypothesis is based, in part, on the presumed ability of juvenile Purple Martins to learn the location of nest-sites. Observations at a Sherman martin colony indicate that juveniles may possess the ability to learn site locations in late summer. At this colony in 1977–1979, Purple Martins raised 3 second broods and an unusually late first brood. It now appears that double broods in martins are somewhat rare, but regular in Grayson County colonies, and are not always associated with unusual population increases (see Brown 1978d). Table 1 contains the dates on which these broods fledged. At these late dates other martins in the colony had completed breeding. Few, if any, nonparental birds were present to act as raiders.

In these cases, the juveniles returned to sleep in the nest for an extended period (Table 1). The female parents of all 4 broods led the juveniles to the nest for the first 6–7 days on which they returned, but after that time the juveniles had apparently learned the location of their nest-site within the colony and often appeared there in the late afternoons before their parents arrived. In Brood A's and Brood D's case, the female parent disappeared during the time of returning, but by then the juveniles had learned the location of their nests and returned in each case an additional 6 days without parental accompaniment. No male parents were associated with these late first and second broods in 1977–1979 after the juveniles fledged (unlike in 1976, see Brown 1978d). In addition, Brown (1978e) reported post-breeding nest defense by juveniles that had been out of the nest no more than 6–7 weeks. These individuals also learned the location of nest-sites and returned there repeatedly each day. Finlay (1971) and Brown (1978a,e) suggested that post-breeding nest defense might imprint the location of future nest-sites. These observations suggest to us that juveniles, if given perhaps a 10–15 day period, can learn the location of sites, implying that raiders may indeed realize an advantage by harassing and chasing them away.

In contrast to the late broods of 1977–1979, Purple Martin broods that fledge in late May and early June in Sherman, Texas, return to sleep in the nest a mean of only 4.85 days after fledging (Brown 1978a). We think that 4.85 days is insufficient time for juveniles to learn the location of sites, because the juveniles of Broods A–D never appeared to be capable of finding their nest on their own until at least the sixth or seventh day of returning. Since most Purple Martins in Sherman, Texas, fledge young prior to 15 July (Brown, unpubl.), it is likely that only a few (very late) broods ever learn the location of their nest-sites.

How effective are raiders at reducing, through harassment, possible

TABLE 1
TIME LATE PURPLE MARTIN BROODS IN SHERMAN, TEXAS RETURNED TO SLEEP IN NESTS, 1977–1979

	Late broods			
	A[1]	B[1]	C[2]	D[1]
Year	1977	1977	1978	1979
Total number of martin pairs in colony	13	13	29	39
Size of colony in rooms	42	42	66	90
Size of brood	4	3	2	5
Date brood fledged	19 July	10 Aug.	9 Aug.	4 Aug.
Date brood returned to sleep last time	28 July	28 Aug.	23 Aug.	19 Aug.
No. of days returned to nest	10	19	15	16

[1] Second broods.
[2] First brood.

nest-site competition from juveniles in subsequent years? Indirect evidence comes from banding studies by CRB and S. D. Wolfe (unpubl.), who banded 2016 Purple Martins, primarily nestlings, in Grayson County, Texas colonies 1974–1979. The results of this work suggest that raiders may be remarkably efficient at reducing potential competition. Fewer than 1% of nestlings banded have been recovered (dead, recaptured, or via sight records) the following year in their natal colony, and only about 8% of the juveniles have returned to any colony within the 6 km^2 area where most of the martin colonies and banding efforts were concentrated. We suspect that the 1% which returned the following year to their natal colony did so by accident. In contrast, among nesting mature birds (which, of course, are not subjected to harassment), approximately 35% of the residents exhibited site tenacity between years (Brown and Wolfe, unpubl.).

DISCUSSION

Other, though less direct, evidence supports our hypothesis. First, yearling males are most often raiders (Brown 1978a; Bitterbaum, pers. obs.). Since male Purple Martins generally return to colonies before females and establish territories, it is to their advantage to minimize future competition. Females search for territories with attending males and rarely establish territories where no male is present, seeking male-site combinations (Johnston and Hardy 1962, pers. obs.). There may be less selective pressure for females to be raiders because, unlike males, they do not engage in strict nest-site competition. Furthermore, Rohwer and Niles (1977) suggested that all females in a population breed, whereas not all males do.

If this suggestion is true, it supports our idea that selective pressures for males to be raiders are greater than similar pressures for females.

Second, it is likely that yearling males have more to gain by being raiders than do adult birds. As an adult male becomes older, there is less potential competition from juveniles since old males arrive earlier when cavities are relatively easy to obtain. A yearling conceivably could face appreciable competition from juveniles the following year. CRB observed approximately 15 instances in which a banded second-year bird (the preceding year's yearling) and unbanded yearlings (the preceding year's juveniles) arrived essentially simultaneously in the spring. Although these yearlings were not raised the preceding year at the main study colony, they nevertheless competed with the second-year birds for nest-sites.

A reduced time of returning to the nest to sleep for May and June Purple Martin broods as opposed to August broods is related, we believe, to increased juvenile harassment in the early part of the nesting cycle. Broods that fledge in late June and early July frequently do not return to sleep at all (Brown 1978a), possibly because at that time large numbers of post-breeding male raiders loaf near colonies. When raiders depart for the premigratory roosts in late July and August, broods that fledge and return to sleep then do so without harassment. Because raiders contribute to a scattering of broods (Brown 1978a), it is possible, though unproven, that survival rates of unharassed late broods before migration may be greater than similar survival rates of earlier broods.

Presumably it is advantageous for broods to return to the nest to sleep, and presumably harassment by raiders is disadvantageous to juveniles. Thus, it might seem that selection would favor late nesting to counteract raider effects. By nesting late, as these double-brooded birds did, their young were able to return to sleep for longer periods than were early broods. Furthermore, the late broods were not scattered by raiders, and the juveniles likely learned the location of potential future nest-sites.

However, Purple Martins in north Texas begin migration in early to mid-August, and late broods may not have the time available to early broods for increasing fat reserves and becoming proficient at foraging before migration. Given the probable rigorous stresses in migration, the advantages in early broods of having an extended period to accumulate fat during summer outweigh the advantages in late broods of having no juvenile harassment. And although we have no proof, late second broods probably suffer high mortality in migration, and thus double-broodedness is not selected for in populations (despite the lack of juvenile harassment of double broods). Conflicting energetic requirements of parents who raise second broods at a time when molt is initiated also may limit double-broodedness, probably by causing greater mortality of these parents during migration.

To test our hypothesis further, it would be desirable to compare return rates to the natal colony of unharassed late broods and harassed early broods. If late broods learn the location of nest-sites, as we believe, they would be expected to return the following spring more often than would early broods. This test would be feasible if one could find and band enough late first and second broods for adequate returns, but unfortunately, in Texas and Florida, we were unable to locate very many. Comparison of return rates for late- and early-reared broods would also be useful in elucidating whether or not late broods suffer heavy mortality in migration as we hypothesize.

SUMMARY

We suggest that nonparental Purple Martins (i.e., raiders) harass unrelated juveniles to disperse them, thus preventing juveniles from learning the location of nest-sites. Observations indicate that if given a period of perhaps 10–15 days post fledging, juvenile martins can learn site locations. Harassment prevents site learning in all broods except late-reared ones that fledge after most other martins have left the nesting colonies. Juvenile harassment, brought about by intense intraspecific and interspecific nest-site competition, is selectively advantageous (especially for males) in that it minimizes future potential competition from juveniles. Late first and second broods suffer little harassment from raiders, but selection still does not favor second broods, possibly because of high mortality of late-reared juveniles in migration.

ACKNOWLEDGMENTS

We thank John William Hardy for reading the manuscript and Rebecca Dellinger, who provided most pleasant company during the period in which we generated this hypothesis.

LITERATURE CITED

Brown, C. R. 1977. Purple Martins versus Starlings and House Sparrows in nest site competition. Bull. Texas Ornithol. Soc. 10:31–35.

———. 1978a. Post-fledging behavior of Purple Martins. Wilson Bull. 90:376–385.

———. 1978b. Clutch size and reproductive success of adult and subadult Purple Martins. Southwestern Nat. 23:597–604.

———. 1978c. On early spring arrival of Purple Martins. Bird-Banding 49:130–133.

———. 1978d. Double-broodedness in Purple Martins in Texas. Wilson Bull. 90:239–247, 657.

———. 1978e. Juvenile Purple Martins: field identification and post-fledging nest defense. Bull. Texas Ornithol. Soc. 11:25–27.

———. 1979. Territoriality in the Purple Martin. Wilson Bull. 91:583–591.

Finlay, J. C. 1971. Post-breeding nest cavity defense in Purple Martins. Condor 73:381–382.

Johnston, R. F. and J. W. Hardy. 1962. Behavior of the Purple Martin. Wilson Bull. 74:243–262.

KLIMKIEWICZ, M. K. AND P. D. JUNG. 1976. A new banding technique for nesting adult Purple Martins. N. Am. Bird Bander 2:3–6.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.

ROHWER, S. AND D. M. NILES. 1977. An historical analysis of spring arrival times in Purple Martins: a test of two hypotheses. Bird-Banding 48:162–167.

2601 TURTLE CREEK, SHERMAN, TEXAS 75090 AND DEPT. ZOOLOGY, UNIV. FLORIDA, GAINESVILLE, FLORIDA 32611. ACCEPTED 15 NOV. 1979.

SPECIAL ISSUE OF RAPTOR RESEARCH DEVOTED TO GOLDEN EAGLES

The Raptor Research Foundation, Inc., will devote the spring 1982 issue of Raptor Research to publishing significant new research on Golden Eagles. Full length manuscripts, as well as shorter communications, are being actively solicited. The deadline for receipt of manuscripts is 1 August 1981. For further information, please contact Richard L. Knight, Washington Eagle Study, Washington Department of Game–Nongame Program, 600 North Capitol Way, Olympia, Washington 98504.

REQUESTS FOR ASSISTANCE

Eastern Bluebird study.—During the spring and summer of 1980, the Muddy Run Ecological Laboratory conducted an Eastern Bluebird banding project at the Muddy Run Project Area, near the towns of Holtwood and Drumore, Lancaster Co., Pennsylvania. Bluebirds were banded with numbered, colored leg bands of either red, yellow, green or blue, in addition to the standard Fish and Wildlife Service leg bands. Observers of these birds are asked to report such details as sex, exact location, date, time of day, number of bluebirds in the flock, number (if possible), color and position of bands, e.g. left leg green over metal or left leg green, right leg metal. Please report sightings, along with your name, address and telephone number, to the Bird Banding Laboratory, Laurel, Maryland 20811, with a copy to Robert M. Schutsky, Muddy Run Ecological Laboratory, P.O. Box 10, Drumore, Pennsylvania 17518 (717-548-2121). All reports will be fully acknowledged.

Translations of research studies.—The Pacific Seabird Group is compiling translations of foreign seabird, shorebird and waterfowl research. Every group that studied these birds seems to have a file of translated papers yellowing with age and neglect; translations are often duplicated elsewhere. To counter this, we request all ornithologists who have translations to contact us. Originals sent to us will be copied and returned; copies will be deposited in the Josselyn van Tyne Library of The Wilson Ornithological Society for the use of all researchers. All translations sent will be cited in the PSG Bulletin. For more information, please contact: Douglas Siegel-Causey, PSG Committee on Foreign Research, Dept. Ecology, University of Arizona, Tucson, Arizona 85721.

Wilson Bull., 92(4), 1980, pp. 458–465

NESTLING FOODS AND FORAGING PATTERNS IN THE CLAY-COLORED SPARROW

RICHARD W. KNAPTON

The Clay-colored Sparrow (*Spizella pallida*) is a common breeding bird of central North America (Bent 1968, Erskine 1977), but little is known of its feeding ecology. In this paper, I report on nestling foods, on foraging behavior and on locations where prey was gathered, and I compare prey items brought to young among different pairs and between males and females within each pair. The Clay-colored Sparrow is an appropriate study animal as it is relatively easy to catch, its nests are not difficult to find, it readily accepts blinds close to the nest and it is easy to observe in the low shrub communities and surrounding meadows, marshes and pastures which it inhabits.

METHODS

The study was carried out in extreme southwestern Manitoba near the town of Lyleton. Two study areas were chosen, each incorporating extensive stands of low shrubs, primarily snowberry (*Symphoricarpos occidentalis*) and silverberry (*Elaeagnus commutata*), with small areas of grass and of trembling aspen (*Populus tremuloides*). Study area 1 was a 5.86-ha plot about 2 km west of Lyleton, and study area 2 comprised 5.67 ha 14 km northwest of Lyleton (for further details see Knapton 1979). Daily observations were made during the breeding seasons of 1974–1976.

Adult and immature Clay-colored Sparrows were captured in mist nets and nestlings were banded at about 5 days of age. Each bird received an aluminum band plus 2 colored plastic bands in different combinations for individual recognition.

I observed individual sparrows in areas around the nesting habitat (the low shrub communities) during May and early June. I noted the identity of each bird, where it was foraging, and whether it was foraging alone or close (within 5 m) to another bird. From 15 June to 17 July 1976, I spent 65 h observing 7 pairs of Clay-colored Sparrows that were feeding nestlings. Observation periods were usually about 2-h long, and were carried out between 06:00 and 12:00 from blinds located 5–10 m from the nest. Pairs appeared to accept the presence of blinds, and no nest under observation was deserted or lost to predators. Information was recorded on portable tape recorders and later transcribed.

The parent's line of flight on leaving the nest was recorded as 1 of 8 possible compass directions. Locations to which the parent birds flew to forage were recorded, and the distances determined by plotting the foraging locations on aerial photographs and measuring the distance to the nest. It was relatively easy to observe how far individuals flew before alighting, as the low height of the vegetation permitted an extensive panoramic view of surrounding areas.

I obtained information on prey items brought to the young by 2 methods. I used a portable Sony Videocorder equipped with a 230 mm lens, and filmed parent birds carrying food items in their beaks. Characteristically, each parent bird returning with prey perched conspicuously for several seconds before dropping down into the shrubbery to the nest; this allowed several seconds of film footage to be taken per prey item. The video tapes were later analyzed on closed-circuit television, a still switch on the videocorder allowing close analysis of individual frames. It was possible to identify most prey items at least to order.

I also obtained actual samples of food delivered to nestlings in 4 other nests using the neck-band method. I attached ligatures around the necks of young Brown-headed Cowbirds (*Molothrus ater*), 1 cowbird in each nest, each cowbird from 5–7 days old. Each young cowbird was in a Clay-colored Sparrow nest in which the sparrow's own young were no longer present. The ligatures were left on the young cowbirds for about 1 h at a time. Ligatures were not placed on young Clay-colored Sparrows because concurrent information was being collected on survival rates of the young sparrows, and repeated visits to their nests within 1 day might have influenced predation rates. Also, nestling Clay-colored Sparrows 6 days or older cannot be easily returned to the nest-bowl, and handling often causes nest departure prematurely.

The ligature method is not without potential error, as small prey items can slip through the ligature or else food can be coughed up and eaten by the parents (Orians 1966). The similarity in results (see below) between the videocorder and the ligature methods suggest that errors were not large.

RESULTS

Foods presented to nestlings.—Adult Clay-colored Sparrows fed their young a wide variety of invertebrates (Table 1). Predominant foods were lepidopteran larvae, orthopteran nymphs and various types of Odonata. These 3 groups comprised 76% of the total number of prey items recorded. A similar breadth of diet is evident in the sample of prey items collected from the nestling cowbirds (Table 1), mainly lepidopteran larvae and orthopteran nymphs, indicating that adult sparrows brought the same sorts of food to young cowbirds as they did to their own young.

There were large differences between pairs in foods presented to nestlings (Table 2). Pair 5, whose territory was close to a pond overgrown with smartweed (*Polygonum* spp.), fed their young almost exclusively on narrow-winged damselflies (Coenagrionidae), apparently taking advantage of a readily available and abundant food source localized around the pond. Pair 6 fed their young mostly short-horned grasshoppers (Acrididae), whereas lepidopteran larvae predominated in the food of the remaining 5 pairs.

Males and females brought the same type of prey items to their young in roughly the same proportions (Table 2). Horn's (1966) measure of overlap, C, is given by

$$C = \frac{2 \sum_{i=1}^{s} X_i Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where X_i and Y_i are the proportions of prey species i for males and fe-

TABLE 1
FOOD ITEMS BROUGHT TO 11 CLAY-COLORED SPARROWS' NESTS[1]

	Videocorder information		Ligature information	
Prey group	Number	Percent	Number	Percent
Orthoptera	108	18.1	11	29.7
Neuroptera	11	1.8		
Lepidoptera (adult)	23	3.8		
(larvae)	256	42.8	15	40.5
Odonata	93	15.6	3	8.1
Coleoptera	12	2.0	4	10.8
Hemiptera	1	0.1		
Diptera	58	9.7	4	10.8
Araneida	4	0.7		
Unidentified	32	5.4		
Total	598	100	37	100

[1] Food was recorded at 7 nests by videocorder and at 4 nests by ligatures on young cowbirds (28 samples).

males, respectively. A value of 0% means no overlap, a value of 100% means total overlap. For Clay-colored Sparrows, C is 96%, indicating there is no difference between males and females within each pair in prey items presented to nestlings.

There was a noticeable change in the relative importance of major food items during the breeding season. Proportionately more lepidopteran larvae were taken in June, Odonata increased in July, and there tended to be a general increase in the relative numbers of orthopteran nymphs over the breeding season. These trends are similar between males and females (Knapton 1978a).

Foraging behavior.—Observations throughout the breeding season on several pairs of banded Clay-colored Sparrows indicated that the birds did not obtain food for themselves or for their young in their territories. Up to mid-May, male Clay-colored Sparrows sometimes fed in grassy areas adjacent to their territories, possibly because they were reluctant to fly far from their territories before territorial boundaries were firmly established. After mid-May, foraging and food-gathering for the young occurred away from the breeding areas, in arable and pasture land, weedy fields and around the edges of sloughs and marshes.

Between territory establishment and the nestling stage of the reproductive cycle, males of adjacent territories foraged at about the same time of day (late morning and late afternoon) off the breeding areas. No overt aggressive interactions were observed between males foraging off territory during 15 h of observation from 6 May to 2 June 1976, although on 9

TABLE 2

FOODS PRESENTED TO NESTLINGS BY EACH OF 7 PAIRS OF CLAY-COLORED SPARROWS

	Pair 1		Pair 2		Pair 3		Pair 4		Pair 5		Pair 6		Pair 7		Total	
Prey group	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Orthoptera	9	6	5	2	13	10	10	8	1	0	27	17	0	0	65	43
Neuroptera	3	0	0	1	0	1	0	4	0	1	0	1	0	0	3	8
Lepidoptera																
(adult)	0	0	4	0	4	3	6	2	0	0	1	3	0	0	15	8
(larvae)	21	24	26	18	38	30	23	26	0	1	2	6	23	18	133	123
Odonata	4	8	5	2	0	1	0	2	30	36	1	2	2	0	42	51
Coleoptera	1	4	0	0	0	0	3	3	0	0	1	0	0	0	5	7
Hemiptera	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Diptera	16	6	5	7	0	5	2	7	0	0	1	0	4	3	30	28
Araneida	0	0	0	0	1	3	0	0	0	0	0	0	0	0	1	3
Unidentified	4	2	6	4	2	1	1	1	1	1	3	2	2	1	19	13

occasions males from adjacent territories were observed within 5 m of each other in the foraging areas. Furthermore, although individual males seemed to forage in specific locations, there was no indication that males defended feeding territories.

Flight lines.—Parents were not observed to gather food for their young within the confines of the territory nor over the breeding habitat as a whole. I therefore recorded the lines of flight which the birds followed between the nest and the foraging locations.

There were no major differences between members of a pair in the direction flown from a nest towards the foraging locations (Knapton 1978a). In general, a male and a female of a pair, whether leaving the nest singly or together, flew predominantly in one and the same direction towards the foraging locations.

Pairs 1 and 5 held peripheral territories, and they used feeding areas adjacent to their territories. Pairs holding central territories flew to probably the closest available foraging locations. Pairs 3 and 4, which held adjacent territories and were feeding nestlings at the same time, consistently flew to the southwest on leaving their nests, and both pairs foraged in and around a large pond overgrown with vegetation. This suggests that neighboring birds might be following each other to preferred feeding locations. However, the pond was probably the closest foraging location to both nests, and hence evidence for following remains inconclusive.

Distances foraged from the nest.—Pair 7 is omitted from this analysis as these birds frequently flew around an intervening clump of trees on leaving the nest, and hence went out of sight. Foraging distances (Table 3) varied

TABLE 3

DISTANCES (M) FROM THE NEST THAT MALE AND FEMALE CLAY-COLORED SPARROWS FLEW TO FORAGE

	Male		Female	
Pair no.	No. foraging trips	$\bar{x} \pm$ SD	No. foraging trips	$\bar{x} \pm$ SD
1	26	46.2 ± 18.6	21	29.9 ± 20.1
2	41	89.9 ± 15.6	32	78.9 ± 13.6
3	38	56.2 ± 6.8	34	51.6 ± 5.8
4	29	75.3 ± 12.4	32	67.5 ± 8.8
5	30	32.5 ± 6.0	31	31.1 ± 5.4
6	18	94.7 ± 8.1	22	77.3 ± 20.2

between pairs, and this was partially due to the location of the territory. Pairs 1 and 5, holding territories on the periphery of the nesting habitat, flew shorter distances, presumably because foraging locations were closer than the other 4 pairs, which held territories in the middle of the nesting habitat.

The mean distances from the nest to the foraging areas were compared between mates for each direction flown (Fig. 1), and were found to be significantly different for all pairs combined ($G = 13.28$, $P < 0.005$ [goodness-of-fit test, Sokal and Rohlf 1969]). Within most pairs, the male flew farther, on average, from the nest to the foraging locations than the female. This was particularly evident when the pair left the nest together; the female alighted first and closer to the nesting area than the male, who flew farther on and alighted. This suggests that there is spatial partitioning of the foraging areas between members of a pair.

DISCUSSION

Clay-colored Sparrows presented a wide variety of prey items to their young, and they collected the prey in a variety of foraging locations off territory. Different pairs brought different prey items in different proportions to their young.

A change in proportion of prey items in the nestling diet as the young grow older has been indicated in some passerines (Betts 1955, Royama 1970, Robins 1971, Best 1977). In the Clay-colored Sparrow, similar-aged nestlings did not receive the same foods. For example, the oldest nestlings in nests 1, 4 and 6 were about the same age (6 days old), yet orthopteran nymphs were more prominent in pair 6's prey items, whereas lepidopteran larvae predominated in the other two. Moreover, the oldest nestlings in nests 2, 5 and 7 were about 5 days old; Odonata were the chief food at

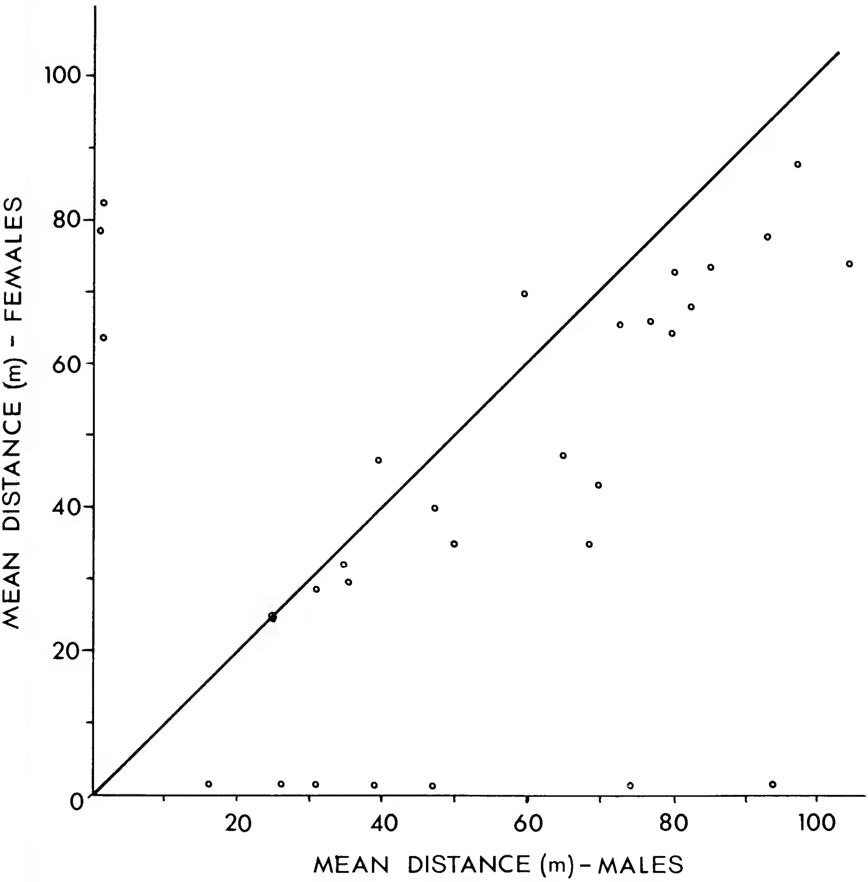


FIG. 1. Comparison of foraging distances between males and females in 6 pairs of Clay-colored Sparrows in 1976. Each point plots the mean distance flown in 1 direction by a male against that flown by his mate. Number of directions flown by each pair ranged from 2–6. Points lying below the line (slope of 1) indicate that males flew farther; points above the line that females flew farther.

nest 5 and lepidopteran larvae at the other two. This suggests that the birds were not selectively choosing prey according to age of the nestlings. However, nestlings of pair 3, the youngest nestlings under observation at about 3 days old, were the only ones to receive spiders, which is consistent with Royama's (1970) suggestion that spiders have special nutritional value important for nestling growth at an early age.

Males and females within a pair did not differ either in type or proportion of prey items presented to their young (Table 2). Hence, the sexes did not appear to select different food items in order to reduce intersexual competition. This is perhaps not surprising as the sparrows are essentially monomorphic in culmen depth and length, and in length of tarsometatarsus (Knapton 1978b). Although males and females used essentially the same types of food, they appeared to spatially partition the food gathering areas. Within a pair, the male, on average, foraged at a slightly greater distance from the nest than the female, a tendency reported in other passerines (Morse 1968, Wiens 1969, Robins 1971, Busby 1978). In the Clay-colored Sparrow, it is not known if this is a mechanism to reduce intersexual competition for food, or is a result of a greater tendency in females to be more nest oriented than males.

SUMMARY

Feeding ecology of the Clay-colored Sparrow was studied in 2 banded populations in southwestern Manitoba. Adults brought to their young a wide variety of prey items which they collected off territory and away from the breeding habitat. There were large differences between pairs in proportions of prey items collected, and each pair was probably exploiting whatever suitable foods were seasonally available. There were no major differences between members of a pair in food items brought to the young, or in the direction of foraging flights. However, within each pair, the male foraged at greater distances from the nest than the female, suggesting spatial partitioning of foraging areas.

ACKNOWLEDGMENTS

I thank Roger M. Evans for his advice and constructive criticisms during the study. Jon C. Barlow, Peter Lowther, Spenser G. Sealy and Robert C. Whitmore offered helpful comments, and Kenneth DeSmet, David Duncan and David Ross gave valuable assistance in the field. My study was supported by National Research Council grants to Roger M. Evans and by University of Manitoba fellowships to myself.

LITERATURE CITED

Bent, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and their allies. U.S. Natl. Mus. Bull. 237.

Best, L. B. 1977. Nestling biology of the Field Sparrow. Auk 94:308–319.

Betts, M. M. 1955. The food of titmice in oak woodland. J. Anim. Ecol. 24:282–323.

Busby, D. G. 1978. Feeding ecology of a dense population of nesting Yellow Warblers. M.Sc. thesis, Univ. Manitoba, Winnipeg, Manitoba.

Erskine, A. J. 1977. The first ten years of the co-operative breeding bird survey in Canada. Can. Wildl. Serv. Rep. 42.

Horn, H. S. 1966. Measurement of overlap in comparative ecological studies. Am. Nat. 100:419–424.

Knapton, R. W. 1978a. Behavioural ecology of the Clay-colored Sparrow, *Spizella pallida.* Ph.D. thesis, Univ. Manitoba, Winnipeg, Manitoba.

———. 1978b. Sex and age determination in the Clay-colored Sparrow. Bird-Banding 49:152–156.

———. 1979. Birds of the Gainsborough—Lyleton Region (Saskatchewan and Manitoba). Sask. Nat. Hist. Soc. Spec. Publ. 10.

Morse, D. H. 1968. A quantitative study of foraging male and female spruce-woods warblers. Ecology 49:779–784.

Orians, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor 68:321–337.

Robins, J. D. 1971. Differential niche utilization in a grassland sparrow. Ecology 52:1065–1070.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the Great Tit (*Parus major*). J. Anim. Ecol. 39:619–668.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. Freeman, New York, New York.

Wiens, J. A. 1969. An approach to the study of the ecological relationships among grassland birds. Ornithol. Monogr. 8.

DEPT. ZOOLOGY, UNIV. MANITOBA, WINNIPEG, MANITOBA, CANADA. (PRESENT ADDRESS: DEPT. ZOOLOGY, UNIV. TORONTO, TORONTO, ONTARIO M5S 1A1, CANADA.) ACCEPTED 13 NOV. 1979.

WOS ANNUAL MEETING

The annual meeting of The Wilson Ornithological Society will be held in Sackville, New Brunswick, from 4 to 7 June 1981.

NOTICE OF A VOTE TO CHANGE THE BYLAWS

The membership is herewith notified of proposed changes in the Bylaws which will be voted on at the annual business meeting as follow: Article 2, Section 2, second sentence "Nominations and applications for membership shall be made through the Secretary" and last sentence "Nominations presented in the interim between the annual meetings shall be received and confirmed by the Secretary, . . ." the word "Secretary" to be changed to "Treasurer." These changes will bring our Bylaws into conformance with practices and procedural necessity.

Wilson Bull., 92(4), 1980, pp. 466–474

GEOGRAPHIC VARIATION IN THE INSULATIVE QUALITIES OF NESTS OF THE NORTHERN ORIOLE

V. H. Schaefer

There is considerable evidence for the adaptive nature of nesting habits in birds. Horvath (1964) demonstrated intraspecific variation in the nest placement between first and second broods in the Rufous Hummingbird (*Selasphorus rufus*), and related the differences to temperature. Adults of many species shield young from direct sunlight (e.g., Gabrielson 1913, Howell 1942, Davis 1960), dissipate heat through evaporative cooling (Bartholomew 1966), or construct bulkier, "warmer," nests in colder regions (Schaefer 1953, Corley-Smith 1969, Calder 1973). The time spent incubating is also reduced with increasing ambient temperature (see Kendeigh [1952] for a summary of this literature). But, I know of no previous study that has measured interpopulational variation within a species in the insulative qualities of nests under controlled laboratory conditions.

Audubon (1842) noted that nests of the Baltimore Oriole (*Icterus g. galbula*) in Louisiana were more loosely woven than those of orioles nesting farther north. This loose weave presumably facilitated the dissipation of heat from nestling orioles in the warmer clime. His observation, and the hypothesis (Rising 1969, 1970) that a combination of differential heat tolerance and nest-building strategies might ultimately limit the ranges of the eastern "Baltimore" (*Icterus g. galbula*) and western "Bullock's" (*I. g. bullockii*) orioles—now collectively called the Northern Oriole—stimulated me to investigate the interpopulational variation in the nest-building of these birds (Schaefer 1974). I have previously reported (Schaefer 1976) on variation in the placement and structure of nests of these orioles, and herewith report my findings on variation in the relative insulative qualities of the nests.

STUDY AREA AND METHODS

I collected 263 nests from 15 sites in the Great Plains region of the United States, and from 3 sites in Quebec and Ontario (Table 1). In the Great Plains most Northern Orioles from Colorado, New Mexico, western Texas, and extreme western Kansas and Oklahoma are Bullock's, whereas those from eastern Kansas, Nebraska and Oklahoma are Baltimore. In a "hybrid-zone" (Fig. 1) separating these phenotypes the majority of birds are variously intermediate between the 2 types.

Nests were collected in the fall of 1972 and 1973. Only nests from the current nesting season, identified by attachments of recent twig growth, were taken. Data from localities sampled in both years were pooled because no significant differences between the years were found (Schaefer 1974).

TABLE 1

MEAN NEST CUP TEMPERATURES (°C) AND SE FOR INFRARED (IR) AND ULTRAVIOLET (UV) CONDITIONS AFTER 5 AND 15 MIN EXPOSURE[a]

S[b] locality	Pheno-type[c]	N	IR 5 min	IR 15 min	UV 5 min	UV 15 min
			$\bar{x}$ Temp. ± SE	$\bar{x}$ Temp. ± SE	$\bar{x}$ Temp. ± SE	$\bar{x}$ Temp. ± SE
Russell Springs, Ks.[d]	×	5	1.1 ± 0.2	1.6 ± 0.3	0.8 ± 0.1	1.1 ± 0.4
Protection, Ks.[d]	Ba	18	1.1 ± 0.2	0.6 ± 0.4	0.8 ± 0.1	0.6 ± 0.3
Hugoton, Ks.	Bu	7	1.0 ± 0.4	1.6 ± 0.4	0.7 ± 0.2	0.3 ± 0.4
Elm Creek, Neb.[d]	Ba	9	0.9 ± 0.2	−0.2 ± 0.6	0.8 ± 0.1	−0.2 ± 0.3
Meade, Ks.[d]	×	19	0.9 ± 0.1	1.2 ± 0.3	0.6 ± 0.1	0.6 ± 0.2
Sutherland, Neb.[d]	Ba	9	0.9 ± 0.2	0.8 ± 0.7	0.8 ± 0.1	0.9 ± 0.5
Elkhart, Ks.[d]	Bu	11	0.9 ± 0.2	1.2 ± 0.3	0.7 ± 0.1	0.1 ± 0.3
Guthrie, Tex.	Bu	16	0.7 ± 0.1	0.8 ± 0.4	0.5 ± 0.1	−0.1 ± 0.4
Clarendon, Tex.	Bu	25	0.7 ± 0.1	0.7 ± 0.3	0.6 ± 0.1	−0.2 ± 0.2
Utica, Ks.[d]	Ba	5	0.6 ± 0.3	0.7 ± 0.5	0.4 ± 0.2	0.5 ± 0.5
Big Springs, Neb.[d]	×	6	0.4 ± 0.4	−0.2 ± 0.6	0.5 ± 0.2	0.6 ± 0.3
Crook, Colo.	Bu	14	0.4 ± 0.2	0.8 ± 0.4	0.4 ± 0.1	0.0 ± 0.2
Laval, Que.	Ba	6	0.3 ± 0.2	0.1 ± 0.5	0.4 ± 0.2	0.1 ± 0.3
Campbellville, Ont.	Ba	28	0.3 ± 0.1	−0.2 ± 0.3	0.4 ± 0.1	−0.2 ± 0.2
Channing, Tex.	Bu	28	0.3 ± 0.1	0.4 ± 0.3	0.1 ± 0.1	−0.8 ± 0.2
Kenton, Okla.	Bu	23	0.2 ± 0.1	1.3 ± 0.4	0.1 ± 0.1	0.3 ± 0.2
Pickering, Ont.	Ba	13	0.2 ± 0.1	0.1 ± 0.5	0.3 ± 0.1	−0.4 ± 0.3
Weskan, Ks.	Bu	12	0.2 ± 0.2	0.4 ± 0.5	0.2 ± 0.2	−0.8 ± 0.4

[a] Temperatures are expressed as the difference between the experimental and control nests (minus indicates that the experimental nest heated more than the control).

[b] Results of SS-STP analysis for IR 5 min (see text).

[c] Ba = Baltimore Oriole; Bu = Bullock's Oriole; × = hybrid-zone.

[d] Denotes plains Baltimore Oriole or hybrid-zone locality.

The relative insulative qualities of each nest were assessed in a chamber made of plywood (122 × 47 × 76 cm; see Fig. 2), which prevented disturbances in the laboratory from influencing the results. A randomly chosen nest (from Protection, Kansas) was used as a standard. All other nests were tested against it twice, first with a 275 watt General Electric sunlamp (1.5% ultraviolet radiation, 2.7% visible, 95.8% infrared), then with a 250 watt G.E. brooder bulb (0.3% ultraviolet, 4.9% visible, and 94.8% infrared). The 2 tests are referred to as the "UV" and "IR," respectively.

Two different lamps were used because the degree to which nest characteristics (e.g., color, thickness) influence nest temperature depends on the wavelengths of light to which the nest is exposed. The spectra were deliberately chosen to be primarily in the infrared. It seemed that heating of the nest interior would most likely occur from this form of radiant energy. My purpose was to exaggerate the infrared to detect any experimentally determined trends and override large inaccuracies in the procedure which may occur.

I inserted a Philips thermistor (resistance of 1500 ohms at 20°C) through the bottom of each nest and fixed it at 2 cm above the bottom of the nest cup. The thermistors were connected by lamp cord leads to a Wheatstone bridge circuit attached to a Yellow Springs

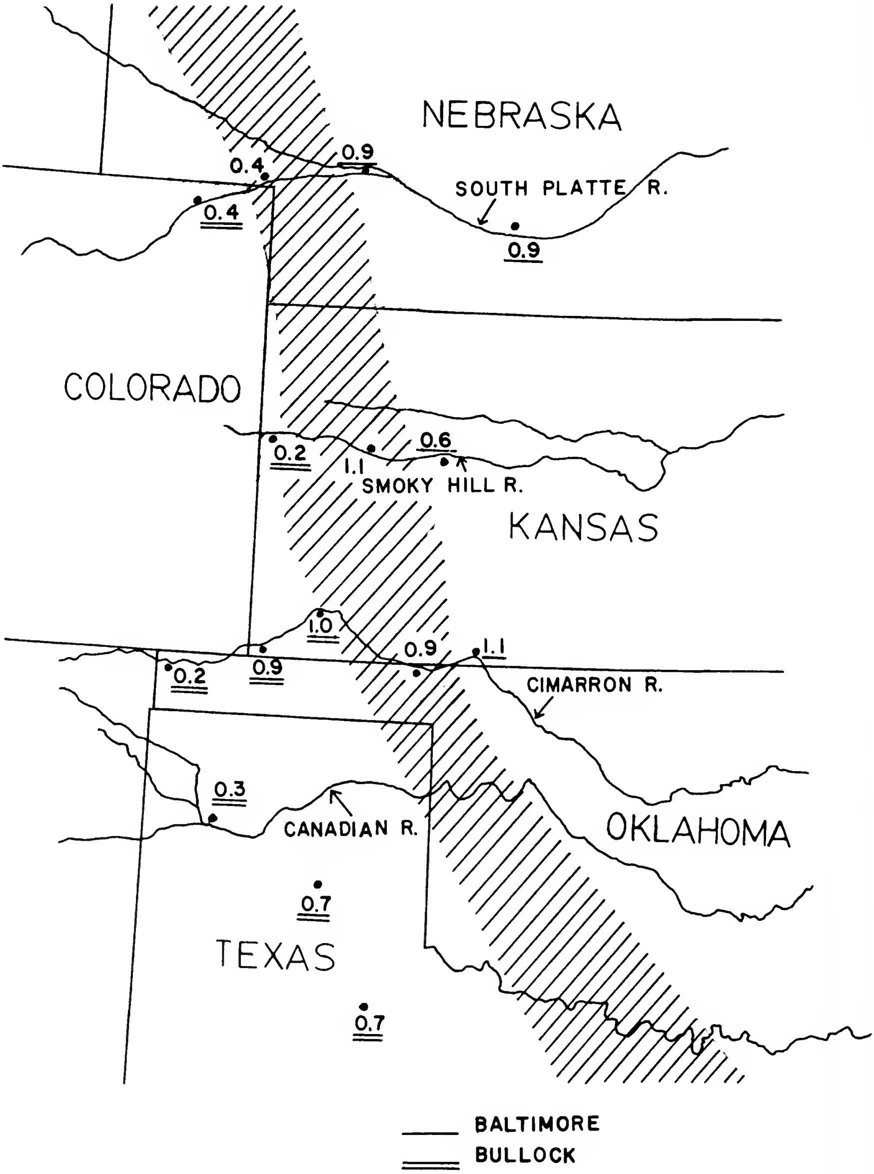


FIG. 1. Map of the central Great Plains showing the sample sites and the experimental values (°C) obtained for the relative insulative qualities of the nests in the IR 5 min experiment. The shaded area approximates the Baltimore-Bullock's oriole hybrid-zone. Localities where the orioles are phenotypically Baltimore are underlined once, Bullock's twice and hybrid-zone not underlined (based on Rising [1970]). Laval, Quebec, and Campbellville and Pickering, Ontario, are not on the map. The experimental values obtained for these localities are 0.3°, 0.3° and 0.2°C, respectively.

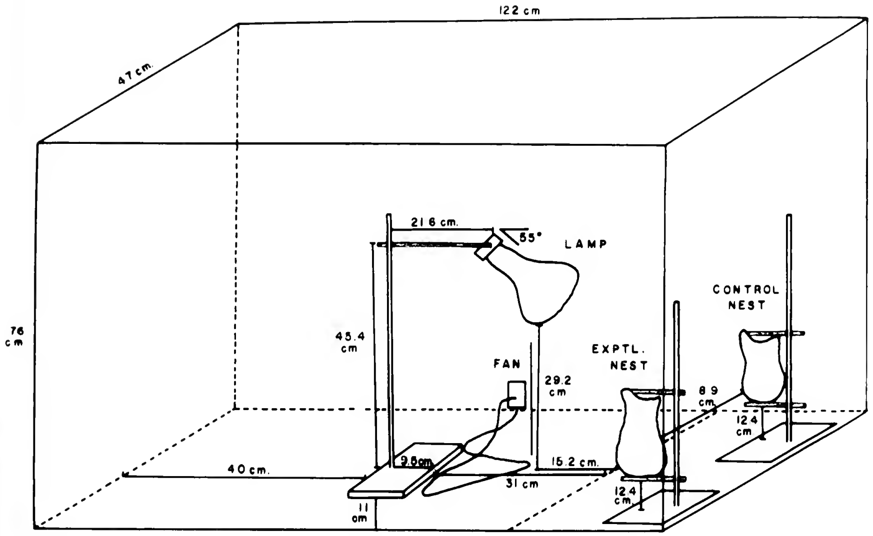


FIG. 2. Schematic diagram of the experimental apparatus used to determine the relative insulative qualities of oriole nests.

Instrument Co. chart recorder. The Wheatstone bridge measured the difference in temperature between the standard and experimental nests.

Temperatures were monitored for 15 min. For the first 5 min a fan within the test chamber provided a turbulent air flow of 6.4–9.6 km/h (measured with a hand-held wind meter). This gave a rough measure of how the nest might be cooled by wind.

Experimental nests were tested in a random order to circumvent possible biases due to changes in experimental conditions between runs. Such biases would mainly originate from the lamps, since intensities and wavelengths of the light emitted depend on usage (Product Manager, Canadian General Electric Co. Ltd., Toronto). Additionally, the standard nest may have been slightly bleached by the lamps, although no visible change in color was noted.

Each nest was placed at a fixed distance from the standard nest, fan and lamp (Fig. 2). The orientation of the experimental nest was standardized by facing the longest attachment closest to the fan and lamp.

RESULTS

Table 1 gives the sample sizes, means and standard errors for the temperature differences between the experimental nests and the standard by locality. The localities are arranged in order of increasing insulation for the IR 5 min condition. The cooler the mean nest temperatures were in relation to the standard nest, the better the nests were insulated from the external experimental source of radiation. Thus, the more negative the number, the more poorly the nests were insulated, and the more positive the value, the better the nests were insulated.

A Model II analysis of variance indicated significant ($P \leqslant 0.05$) differ-

TABLE 2

MEAN NEST CUP TEMPERATURES (°C) FOR INFRARED (IR) AND ULTRAVIOLET (UV) CONDITIONS AFTER 5 AND 15 MIN EXPOSURE FOR THE LOCALITIES (FROM TABLE 1) GROUPED INTO MAJOR TAXA AND REGIONS[a]

Grouping	No. localities	IR 5 min	IR 15 min	UV 5 min	UV 15 min
Canadian Baltimore	3	0.3	0.0	0.4	−0.2
Plains Baltimore	4	0.9	0.5	0.7	0.5
Hybrid-zone	3	0.8	0.9	0.6	0.8
Texas Bullock's	3	0.6	0.6	0.4	−0.4
Other Bullock's	5	0.5	1.1	0.4	0.0
All Bullock's	8	0.6	0.9	0.4	−0.2
All Baltimore	7	0.6	0.3	0.6	0.2

[a] Temperatures are expressed as the difference between the experimental and control nests (minus indicates that the experimental nest heated more than the control).

ences among localities (i.e., data from nests taken at different geographic sites) in the UV 5 min, UV 15 min and IR 5 min conditions. In each case, SS-STP (sum of squares simultaneous test procedure) (Sokal and Rohlf 1969) *a posteriori* tests showed that only 2 or 3 localities at one extreme were excluded from a statistically homogeneous set of localities that included those at the opposite extreme. Some of the data were significantly skewed with heterogeneity of variance so Kruskal-Wallis tests were also used. There was agreement in the results between the parametric and nonparametric methods of analysis.

The localities were also grouped as Baltimore, hybrid-zone, or Bullock's orioles according to the average index values of the birds for the localities given in Rising (1970:328). An average value greater than 24.5 (cf. a maximum of 28) was arbitrarily taken to be Bullock's Oriole, less than 4.7 = Baltimore Oriole and between 4.8 and 24.4 = hybrids. Baltimore Oriole nests were found to be significantly less-well insulated than hybrid-zone and Bullock's Oriole nests in the IR 15 min condition. Hybrid-zone nests were cooler (better insulated) than Bullock's Oriole nests in the UV 5 and 15 min conditions (SS-STP). A map showing the distribution of the experimental values in the Great Plains for IR 5 min is presented in Fig. 1.

Table 2 shows the experimental values for the localities when they are grouped into categories of Canadian Baltimore, plains Baltimore, hybrid-zone, Texas Bullock's and other Bullock's orioles. Notice that the plains Baltimore and hybrid-zone oriole localities have the highest values in each condition except IR 15 min. Also notice that Canadian Baltimore Oriole nests have lower values than plains Baltimore Oriole nests (they heat up more when exposed to external radiation because they are less-well insulated).

TABLE 3

CORRELATION COEFFICIENTS OBTAINED BETWEEN THE RELATIVE INSULATIVE QUALITIES OF NESTS AND MAY AND JUNE WEATHER[a]

	May				June			
Character	IR 5 min	IR 15 min	UV 5 min	UV 15 min	IR 5 min	IR 15 min	UV 5 min	UV 15 min
Total precipitation	0.57*	0.24	0.44	0.31	0.33	−0.25	0.35	0.09
Mean temperature	0.58*	0.59*	0.29	0.16	0.60*	0.62**	0.29	0.20
Minimum daily temperature	0.62**	0.47*	0.38	0.08	0.65**	0.52*	0.41	0.19
Maximum daily temperature	0.34	0.34	0.15	0.13	0.50*	0.48*	0.24	0.18
Highest temperature	0.73**	0.37	0.56*	0.15	0.69**	0.42	0.53*	0.28
Lowest temperature	0.19	0.20	0.06	−0.11	0.41	0.49*	0.24	0.10

[a] *r*, df = 16.

* $P \leq 0.05$.

** $P \leq 0.01$.

Table 3 shows the Pearson product-moment correlation coefficients (r) obtained between the relative insulative qualities of the nests and each of 6 weather variables which may contribute to heat stress in orioles (10-year or more averages based on summaries obtained from the Weather Bureau, U.S. Dept. Commerce and from Environment Canada). Only May and June were considered because they are the months when nest construction and incubation usually occur in orioles.

Nest cup temperatures after 5 min with a turbulent air flow over the nests gave the largest number of significant correlations with both May and June weather. The highest correlation ($r = 0.73$, df = 16) is between the highest temperature for May and the IR 5 min condition, i.e., orioles build well-insulated nests in places with high May temperatures. Nests from localities where the ambient temperatures were higher remained cooler in the experiments.

The IR conditions produced all but one of the significant correlations for each month. Only the highest temperatures for each month were significantly correlated with the UV results. The total precipitation correlated with the relative insulative qualities of the nests for the localities only for the month of May for IR 5 min.

DISCUSSION AND CONCLUSIONS

Kendeigh (1963) found that there was a significant positive correlation between nest and air temperatures in the House Wren (*Troglodytes aedon*). He also found that the temperatures inside nests sometimes exceed air temperatures, especially if the nest was exposed to the sun. Indeed, he mentioned that nest temperatures may be sufficiently higher than optimal incubation temperatures for long enough periods to injure or kill embryos. Even nests shaded throughout most of the day can be exposed to brief periods of damaging sunlight. In areas where ambient temperatures are high any heat perturbations to the nest could be lethal to developing embryos.

Laboratory birds of Baltimore Oriole phenotype seem to be more sensitive to high temperatures than do those of the Bullock's Oriole phenotype (Rising 1969). The hybrid-zone in the Great Plains delimits the western edge of the range of the Baltimore Oriole, a region where it would be exposed to the hottest temperatures it would normally encounter. I earlier determined (Schaefer 1974) that while oriole nest temperatures were significantly correlated with ambient temperatures, they were also significantly lower. However, sometimes nest temperatures exceeded ambient temperatures, and once I recorded a nest temperature of 41°C within a nest *in situ* in Kansas (ambient temperature = 38°C). Thus, Baltimore Orioles may undergo heat stress in the Great Plains and may build better insulated nests. The generally thicker (pers. obs.) nests of Great Plains Baltimore Orioles can prevent the contents from heating up if there is an external source of radiation (as in the case of my experiments) coming from the sun. Most of the trees in the Great Plains are young cottonwoods (*Populus* spp.), which allow the sun to penetrate through the canopy for short periods. In Louisiana, where Audubon (1842) noted that Baltimore Oriole nests were thinner, the orioles may successfully shade their nests but still face a high ambient temperature. In such a region, a thinner nest may be more efficient in keeping the interior cool.

Baltimore Orioles may place their nests on the shaded sides of trees to keep them out of the sun for at least part of the day. However, I (Schaefer 1976) found that in those localities where orioles did seem to place their nests on a particular side of a tree, the relationship seemed to be more with wind (leeward sides were preferred), rather than sunlight. Orioles in the Great Plains may be prevented from nesting on the shaded sides of trees because of strong prevailing winds.

A bulky nest construction helps to keep heat produced by external radiation on the surface of the nest. The heat can then be dissipated by wind (note that the highest correlations obtained between the insulative qualities of nests and locality temperatures occurred when the fan was blowing on the nests [Table 3]). Thus, the interior of a bulky nest may remain cooler than one which is thinner.

The absence of many significant correlations between the UV experimental values and weather for the localities could be due to experimental error. The overall relationships were similar to those of the IR conditions

(Table 2: plains Baltimore Oriole highest, hybrid-zone next, then the Canadian Baltimore and plains Bullock's orioles).

Alternatively, the slightly greater amount of visible radiation in the IR conditions could have exaggerated the differences in the relative insulative qualities of the nests. Natural solar radiation on the earth's surface is 10% UV, 45% visible and 45% IR (Reifsnyder and Lull 1965). Thus, the larger amounts of visible energy in natural solar radiation may make the relative insulative qualities of oriole nests more responsive to nest color. The larger amounts of visible energy in the IR experiments could contribute to explaining why there were more significant correlations with weather with the IR values and fewer for UV. Plains Baltimore Oriole nests are notably lighter than those from Canada. Plains nests may be bleached by the sun more than nests in Canada and may become better insulated against heating as a result.

Total precipitation for the localities correlated significantly only between May and IR 5 min. Possibly, decreased precipitation could contribute to evapotranspiration stress, but the relationship should have been negative and not positive as found. The significance may have been a chance event, or perhaps precipitation is a covariable of locality temperatures which showed a much stronger relationship with the relative insulative qualities of the nests.

SUMMARY

The relative insulative qualities of 263 nests from 18 localities of the Northern Oriole were determined experimentally. Differences in the relative insulative qualities of the nests showed trends of geographic variation. Canadian Baltimore and Bullock's orioles' nests are less resistant to heating by an external source of radiant energy than nests of Baltimore Orioles in the Great Plains and Northern Oriole nests from the Baltimore-Bullock's oriole hybrid-zone. The relative insulative qualities of the nests were significantly correlated with local temperatures.

ACKNOWLEDGMENTS

I thank Dr. J. D. Rising for his supervision and encouragement during the study. Dr. N. Verbeek and F. W. Schueler gave helpful comments and M. Gates provided statistical advice. This project was financed by a National Research Council grant no. 5999 to Dr. Rising. All nests used in the study are currently at the Royal Ontario Museum, Toronto, Canada.

LITERATURE CITED

Audubon, J. J. 1842. The birds of America. Dover Edition, 1967. Vol. 4. Dover Publications Inc., New York, New York.

Bartholomew, G. A. 1966. The role of behavior in the temperature regulation of the Masked Booby. Condor 68:523–535.

Calder, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. Ecology 54:127–134.

CORLEY-SMITH, G. H. 1969. A high altitude hummingbird on the volcano Cotopaxi. Ibis 111:11–32.

DAVIS, J. 1960. Nesting behavior of the Rufous-sided Towhee in coastal California. Condor 62:434–456.

GABRIELSON, I. N. 1913. Nest life of the Catbird. Wilson Bull. 25:166–187.

HORVATH, O. 1964. Seasonal differences in Rufous Hummingbird nest height and their relation to nest climate. Ecology 45:235–241.

HOWELL, J. C. 1942. Notes on the nesting habits of the Robin. Am. Midl. Nat. 28:529–604.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 12.

———. 1963. Thermodynamics of incubation in the House Wren, *Troglodytes aedon*. Pp. 884–904 *in* Proc. XXIII Int. Ornithol. Congr.

REIFSNYDER, W. E. AND H. W. LULL. 1965. Radiant energy in relation to forests. U.S. Dept. Agric., Forest Services, Tech. Bull. No. 1344.

RISING, J. D. 1969. A comparison of metabolism and evaporative water loss of Baltimore and Bullock's orioles. Comp. Biochem. Physiol. 31:915–925.

———. 1970. Morphological variation and evolution in some North American orioles. Syst. Zool. 19:315–351.

SCHAEFER, E. 1953. Contribution to the life history of the Swallow-tanager. Auk 70:403–460.

SCHAEFER, V. H. 1974. Geographic variation in the placement and structure of the nests of three taxa of North American orioles. M.Sc. thesis, Univ. Toronto, Toronto, Ontario.

———. 1976. Geographic variation in the placement and structure of oriole nests. Condor 78:443–448.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco, California.

DEPT. BIOLOGICAL SCIENCES, SIMON FRASER UNIV., BURNABY, BRITISH COLUMBIA V5A 1S6. (PRESENT ADDRESS: DEPT. BIOLOGY, DOUGLAS COLL., P.O. BOX 2503, NEW WESTMINSTER, BRITISH COLUMBIA V3L 5B2 CANADA.)

Wilson Bull., 92(4), 1980, pp. 475–488

FALL MIGRATION OF SAW-WHET OWLS AT PRINCE EDWARD POINT, ONTARIO

R. D. Weir, F. Cooke, M. H. Edwards and R. B. Stewart

The Saw-whet Owl (*Aegolius acadicus*) is a permanent resident in woodlands across extreme southern Canada from Vancouver Island, British Columbia to Cape Breton, Nova Scotia. In Ontario and Quebec, this species occurs to 50°N (Godfrey 1966). Bent (1938) thought movements of saw-whets were too irregular to be true migration, whereas Taverner and Swales (1911) considered the Saw-whet Owl to be migratory. More recent data substantiate this claim. Spring movements have been described in the Toronto, Ontario, area (Catling 1971) and at Whitefish Point, Michigan (Kelley and Roberts 1971a, b). Fall migration has been reviewed by Woods (1972). Mueller and Berger (1967) reported Saw-whet Owls to be regular fall migrants in Wisconsin.

Holroyd and Woods (1975), analysing banding records and recoveries for 1955–1969, showed an annual autumnal movement from Canada by saw-whets that followed Ohio and Mississippi rivers and the Atlantic Coast. Systematic studies of autumn migration in Ontario have not been reported in the literature even though 48% of the 4802 Saw-whet Owls banded in North America during 1955–1969 were banded there (Holroyd and Woods 1975). We do not know how many of these were in autumn migration.

Here we document the movements of Saw-whet Owls through Prince Edward Point in fall, the sex and age profiles of the birds in the flights, and the relationship between these movements and weather parameters.

STUDY AREA AND METHODS

Data were gathered on 190 ha surrounding the lighthouse at Prince Edward Point (43°57′N, 76°54′W), on the eastern tip of the Long Point Peninsula on the north shore of Lake Ontario 40 km southwest of Kingston (Fig. 1). The area is well known for heavy passerine migrations (Weir 1972a, b) and autumnal raptor flights (Goodwin 1974). Much of the Point cleared earlier for farming now comprises extensive ungrazed grassland with scattered red cedar (*Juniperus virginianus*) and small deciduous bushes. Remaining woodland consists mainly of deciduous trees and white cedar (*Thuja occidentalis*).

There were 3 major mist net areas: (1) area A (cedar woods)—used all 4 years of study; (2) area B at the extreme tip of the Point—used 1976 and 1978; and (3) area C (Point Traverse)—used 1977 and 1978. Nets (up to 120 m in length) were placed perpendicular to the main axis of the woods in laneways cut through the bushy openings between wooded areas, in natural clearings, in woods and in open areas at the edge of woods. Nets were 2.5–3.5 m high. Mesh sizes were either 30 mm or 36 mm, and most were tethered. Nets were usually opened at dusk and closed at dawn. During inclement weather nets were closed. Nets were

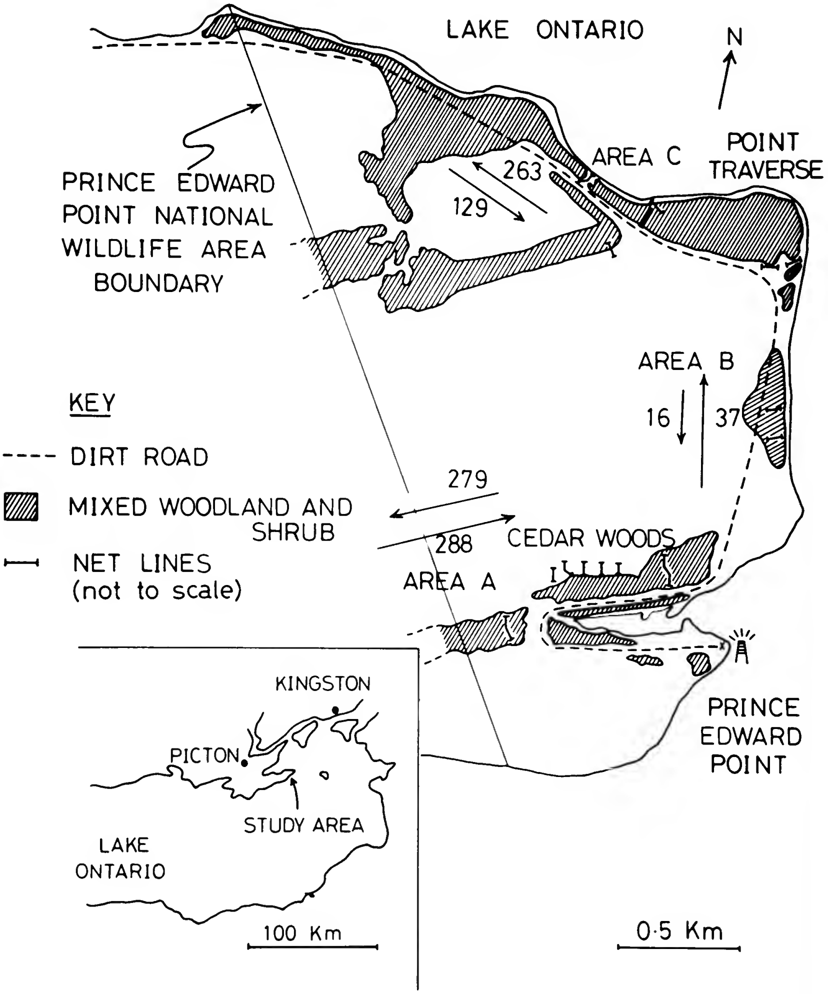


FIG. 1. Saw-whet Owl migration study area at Prince Edward Point, Ontario.

set every night between 18 Sept. to 6 Nov., 23 Sept. to 6 Nov. and 24 Sept. to 4 Nov. in 1976, 1977 and 1978, respectively. In 1975, nets were set on 10 nights between 27 Sept. to 9 Nov.

Data were collected by a number of banders, often with help from several volunteers. Nets were checked at intervals of 1–2 h. Captured owls were removed, placed in numbered cloth bags and taken to the observatory for processing. The side of the numbered net the owl flew into was recorded. Birds were weighed and examined for plumage and molt details. Both wings (chord) were measured on each bird.

Weather conditions and wind velocity were recorded at regular intervals throughout the night. These data were supplemented by records from the Atmospheric Environment Service

TABLE 1

COMPARISON OF AUTUMN SAW-WHET OWL CATCHES AT PRINCE EDWARD POINT

	1975	1976	1977	1978
HY owls/index[1]	—	95/4.7	389/7.9	123/2.4
PHY owls/index	—	94/4.7	163/3.3	180/3.6
Total owls/index	83/36.5	190/9.4	552/11.2	303/6.0
Average net area (m^2)	227	592	1175	1265
Nights with >100 m^2 net area	10	34	42	40

[1] Owls per 1000 m^2 of net per night.

for 3 nearby sites: (1) Main Duck Island, 19 km off shore to the east; (2) Trenton, 60 km WNW; and (3) Kingston, 40 km NE.

Owls were aged by relative color of primary and secondary flight feathers. Presence of both dark (unworn) and paler (worn) flight feathers indicated the partial postbreeding remex molt typical of a post hatching year (PHY) bird. Birds with flight feathers of uniform coloration without wear denoted hatching year (HY) individuals. Birds that showed pale uniform coloration in flight feathers accompanied by worn tips were also assigned as PHY. One bird initially identified as PHY in 1977 had all dark feathers when recaptured in 1978, suggesting that some at least of the PHY birds have a complete postbreeding molt when caught. Thus our classification of birds as either HY or PHY was not error-free.

Although many owls were in various stages of body molt, none showed any sign of molting remiges or rectrices, other than the occasional asymmetrical sheathed feather which probably reflects replacement of a lost feather. The presence of dark and light feathers in the remiges suggests an interrupted wing molt.

Saw-whet Owls show reversed sexual dimorphism; the average female has longer wings and weighs more than males (Earhart and Johnson 1970). There is overlap in both wing length and body weight of the sexes. Birds with wings 135–140 mm were classified as sex unknown (U). Because of overlap in wing length, we used the criteria males ≤ 134 mm and females ≥ 141 mm to assign sex (modified from Wood 1969, Sheppard and Klimkiewicz 1976, North American Bird Banding Techniques 1977).

To analyse age and sex dependent differences in migration times, birds classified as HY♂, HY♀, PHY♂ and PHY♀ were examined. In each year when these categories were identified, the season was divided into 3 time periods—early, middle and late—such that approximately equal numbers of owls were assigned to each period.

RESULTS

Table 1 shows the number of owls caught and the amount of netting conducted 1975–1978. The index used is that described by Mueller and Berger (1967). Since the banding in 1975 was exploratory, intermittent and concentrated on peak migration dates, the migration index for that year is not comparable with those of the other 3 years. In 1975, no attempt was made to age or sex the birds. During 1976–1978, the number of adult owls, corrected for intensity of netting, remained relatively constant (PHY in-

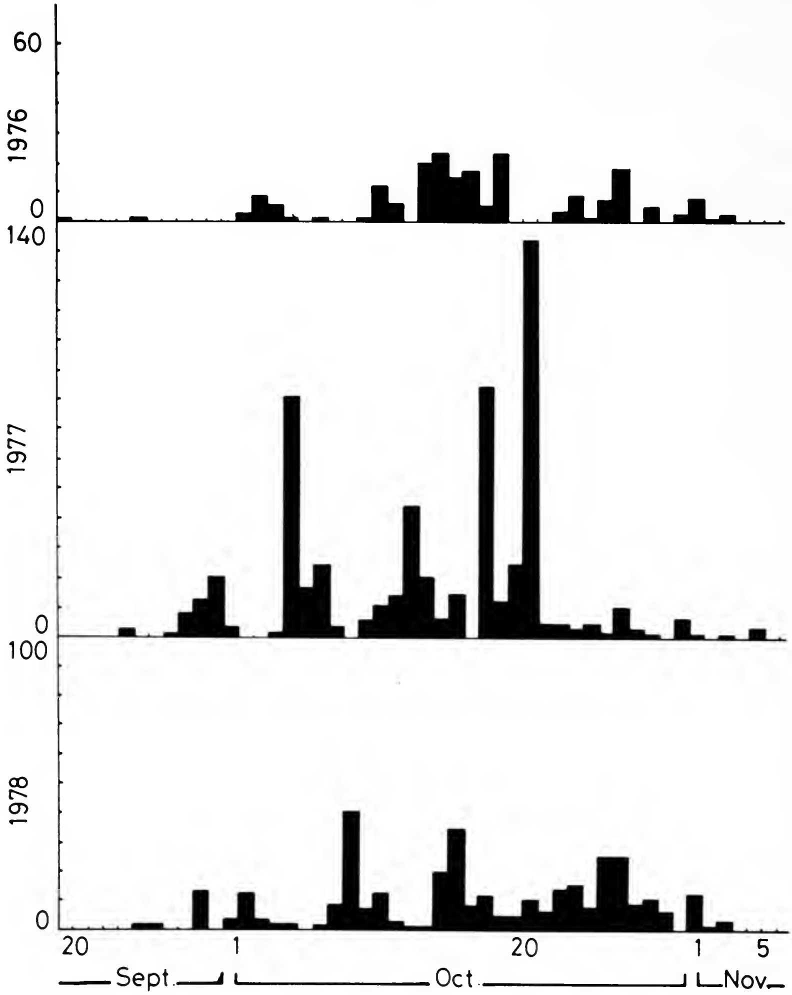


FIG. 2. Nightly Saw-whet Owl banding totals at Prince Edward Point, 1976–1978.

dex: 3.3–4.7), whereas there was considerable fluctuation in the relative numbers of hatch year birds (HY index: 2.4–7.9). Of the annual fluctuation in owl totals, 84–100% are accounted for by the fluctuation of HY birds.

Seasonal patterns of capture are shown in Fig. 2. Most owls were caught in October with a peak in mid-month. Numbers caught fluctuated daily. By about the end of the third week of October 75% of the owls were caught; 50% of all captures were during the second and third weeks of October.

TABLE 2
SEX AND AGE DISTRIBUTION OF SAW-WHET OWLS, 1976–78

Year	HY♂	HY♀	PHY♂	PHY♀	HY U	PHY U	U U	Total
1976	46	16	36	30	35	26	1	190
1977	187	84	62	49	118	52	0	552
1978	54	23	55	57	46	68	0	303

Sex and age distribution.—Table 2 shows the relative distribution of all the age and sex classes 1976–1978. In each of these years, respectively, the ratios HY♂ to HY♀ were 2.9, 2.2, 2.4 and PHY♂ to PHY♀ were 1.3, 1.3 and 1.0. Since sex could not be assigned in 32.6%, 30.8% and 37.6%, of the birds, respectively, making definitive statements on sex ratios was difficult. For owls of known sex, there is a significant departure in all 3 years from the distribution expected, assuming that all ages and sex classes move through in a similar seasonal pattern (Table 3). In 1976 and 1978, females migrated significantly earlier in the season than males ($\chi^2_2 = 9.55$, $P < 0.010$ and $\chi^2_2 = 19.19$, $P < 0.001$, respectively) while in 1977 the difference was not significant ($\chi^2_2 = 2.99$, $P < 0.10$). In 1977, the year of high numbers of HY birds, the young birds moved through significantly earlier than the older birds ($\chi^2_2 = 30.24$, $P < 0.001$) and the young females preceded the young males ($\chi^2_2 = 6.71$, $P < 0.05$). In 1976, no significant difference in timing was observed between HY and PHY ($\chi^2_2 = 0.31$, $P < 0.90$), but HY females preceded HY males ($\chi^2_2 = 10.77$, $P < 0.005$). In 1978, HY birds migrated later than PHY ($\chi^2_2 = 10.83$, $P < 0.005$), the reverse of the situation in 1977.

Local distribution.—Patterns of movement and directions of flight could not be observed directly in most cases. Although a netted owl could have flown in from anywhere across 180°, we have some insight into predominant flight directions in the 3 major net areas by recording the side of the net into which the owl had flown. In areas A and C, the nets were aligned in a north-south direction, thus intercepting predominantly east-west movement, while in area B, predominantly north-south movement was intercepted. In area A, there was no predominant flight direction in any of the 3 years (Table 4). In area B, 70% of 53 owls were caught flying north. In area C, 67% of 392 were caught flying west. The predominant flight directions are shown in Fig. 1.

Weather.—Analyses of daily synoptic weather maps for the autumns of 1976 and 1977 (Ludlum 1976, 1977) showed that almost always when 10 or more birds were caught, the Prince Edward Point area experienced a high pressure system pushing out a low towards the northeast. The relative

TABLE 3

SEASONAL MOVEMENT OF OWLS, CLASSIFIED IN TERMS OF AGE AND SEX

		Time of season					
		Early[1]		Mid		Late	
Year	Age/sex	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
1976	HY ♀	10	5.1	4	5.3	2	5.6
	HY ♂	9	14.7	17	15.1	20	16.2
	PHY ♀	12	9.6	9	9.8	9	10.6
	PHY ♂	10	11.5	12	11.8	14	12.7
		$\chi_6^2 = 11.92, P < 0.05$					
1977	HY ♀	42	28.4	31	31.4	11	24.2
	HY ♂	70	63.2	68	70.0	49	53.9
	PHY ♀	7	16.6	22	18.3	20	14.1
	PHY ♂	10	20.9	22	23.2	30	17.9
		$\chi_6^2 = 37.74, P < 0.001$					
1978	HY ♀	6	7.3	9	7.3	8	8.3
	HY ♂	8	16.9	18	16.9	27	19.2
	PHY ♀	31	18.2	18	18.2	8	20.6
	PHY ♂	15	17.6	15	17.6	25	19.9
		$\chi_6^2 = 27.35, P < 0.001$					

[1] See Methods.

positions of the centers of the 2 pressure cells varied, but in every case their combined circulatory effect was to produce NW winds and clear skies after the passage of a cold front. The movement of owls was assessed in relation to wind direction and speed, and cloud cover over the Point.

For the initial analysis, observations were placed in either 1 of 4 wind directions (NE, SE, SW, NW), or calm, and the night was divided into 3 time periods (18:00–22:00, 22:00–02:00 and 02:00–06:00). In each time period, the number of captures and the total hours when wind was blowing in that direction while the nets were open were tabulated as a function of wind direction. The results of the data for 1976, 1977 and 1978 are similar; 1977 data are illustrated (Table 5). Trapping success was linked with wind direction and most owls were caught when winds were blowing from the north-west quadrat. When wind direction was further subdivided, it was found that most owls were caught during WNW winds (Fig. 3). Fewest owls were caught when the winds blew from NE through S. None was caught during the 3% of the time when the wind speed exceeded 25 km/h.

Significantly fewer owls were caught during the first 4 h of the night than during the later periods (Table 5; $\chi^2_1 = 21.04$, $P < 0.001$ from col-

TABLE 4

DIRECTIONS OF FLIGHT OF OWLS CAUGHT IN 3 AREAS, 1976–1978

	Predominant flight direction	Year 1976	1977	1978	Total
Area A	East	75	125	88	288
	West	82	131	66	279
Area B	North	9	—[1]	28[2]	37[2]
	South	3	—	13	16
Area C	East	—[1]	93	36	129
	West	—	192[2]	71[2]	263[2]

[1] No nets.
[2] $P < 0.05$.

umns 2 and 3). However, this was the time when nets were being opened, and thus could influence the results. Wind directions were distributed equally among the 3 time periods and no bias is introduced because of different wind directions at different times of the night.

The number of Saw-whet Owls netted as a function of cloud cover was computed. In each year, 1976–1978, the results are similar; significantly more owls were caught in the <20% cloud category. Following the procedure adopted for wind analysis, the cloud data from 1977 are illustrated in Table 6.

Recaptures.—Among the owls caught at the Point, 25, 134 and 52 were recaptured there within the same season in 1976, 1977 and 1978, respectively and include 0, 20 and 5 birds recaptured a second time. The time

TABLE 5

NUMBER OF OWLS CAPTURED AS A FUNCTION OF WIND DIRECTION AND TIME OF NIGHT, 1977

Wind direction	No. of Owls Time 18-22	22-02	02-06	Total	No. of h 18-22	22-02	02-06	Total
Calm	6	22	37	65	7.5	21	9	37.5
NE	14	19	30	63	31	54	61	146
SE	1	0	0	1	17	29	25	71
SW	6	29	100	135	15.5	33.5	34	83
NW	44	158	86	288	15	30.5	38	83.5
Total	71	228	253	552	86	169	167	421
Owls/h	0.8	1.4	1.5	1.3				

$\chi_4^2 = 479.5$, $P < 0.001$.

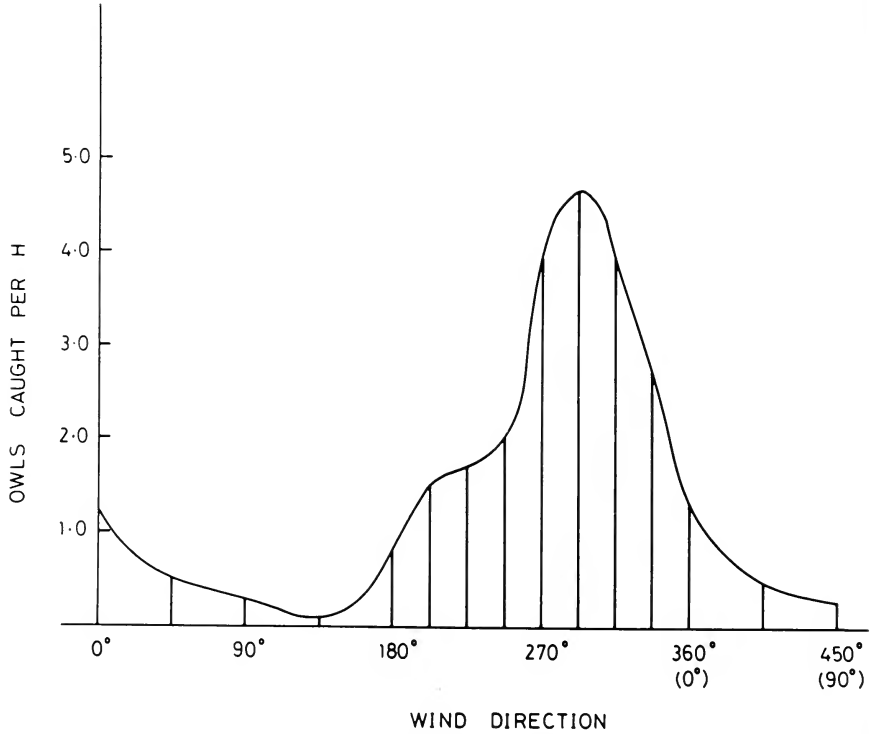


FIG. 3. Predominant wind direction when owls were caught.

between initial capture and recapture, including second recaptures, is shown in Fig. 4. The percentages of the different age and sex categories among recaptured birds is not significantly different from that of the total banded sample ($\chi^2_3 = 4.11$, $P < 0.20$).

Recaptured owls showed weight changes between capture and recap-

TABLE 6

NUMBER OF OWLS CAPTURED AS A FUNCTION OF CLOUD COVER, 1977

	Percent cloud cover			
	<20%	30–90%	>90%	Totals
Owls caught	436	42	74	552
Owls expected	243	67	251	552

$\chi_1^2 = 308.5$, $P < 0.001$.

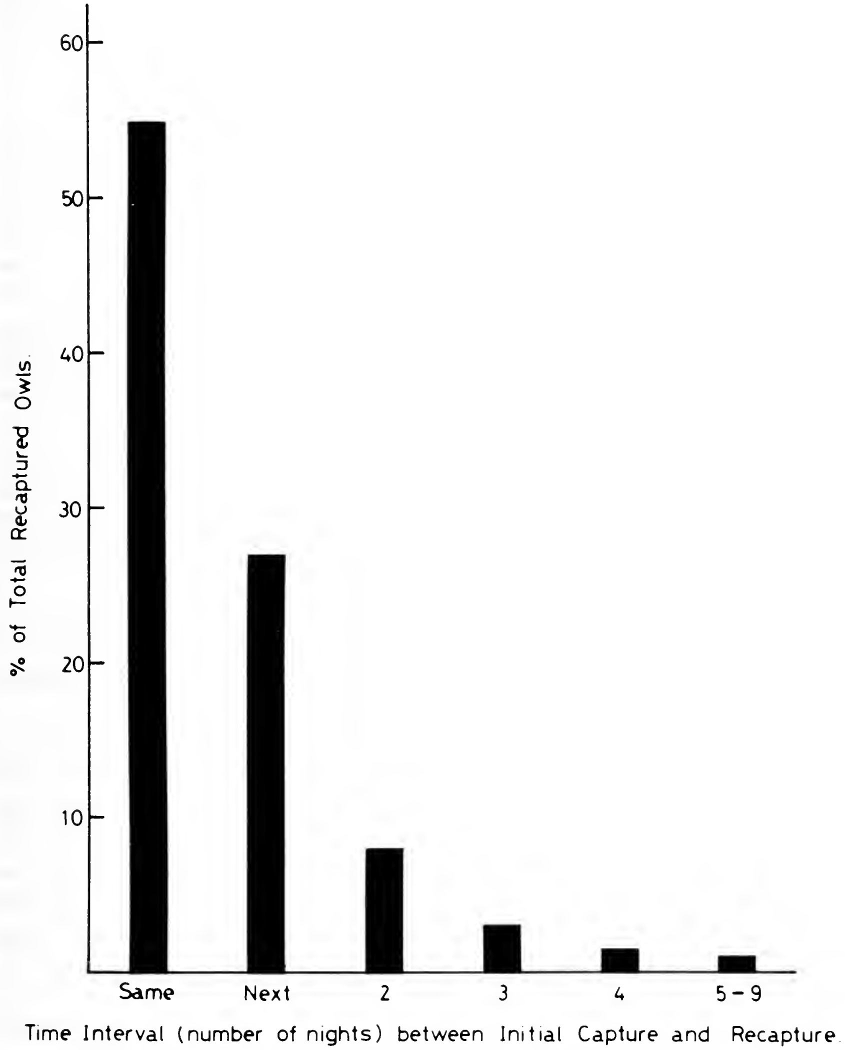


FIG. 4. Number of nights between capture and recapture of owls.

ture. Some 63% lost weight, 29% gained and 8% showed no change. Among birds recaptured within 30 h of the original captures, (i.e., on the same or succeeding night), 73 had lost weight. There was a strong positive correlation between weight loss and number of hours between capture and recapture ($R = 0.611$, $P < 0.001$) for those birds which had lost weight, approximately 0.3 g/h. Birds caught more than 30 h later showed a less consistent pattern, but this is expected since these birds are more likely to have eaten in the intervening time.

DISCUSSION AND CONCLUSIONS

Evidence of migration of owl species is difficult to obtain but we have gained some insight into what is happening with the Saw-whet Owl. This study supports the thesis that saw-whet's migration is regular in large numbers and is not irruptive as is the Goshawk (*Accipiter gentilis*) (Bent 1937, Mueller et al. 1977) or Great-gray Owl (*Strix nebulosa*) (Vickery and Yunick 1979). The autumn arrival times and quartile dates of the Saw-whet Owl at Prince Edward Point show annual consistency not characteristic of irruptive species. In addition, the numbers of saw-whets netted in autumn 1978 do not parallel numbers of those owl species that irrupted into eastern Ontario in winters 1978–1979 (Bell et al. 1979).

The year-to-year variation in saw-whet numbers after correcting for netting effort seems to result from variations in the numbers of HY birds, possibly reflecting variation in annual reproductive success north of Lake Ontario. This may account for the so-called invasional characteristic of the species (Bent 1938).

Timing of migration in terms of age when combining sexes appears to be random. There was no significant difference in 1976, HY preceded PHY in 1977 (the year of large numbers of HY birds) and HY followed PHY in 1978. Mueller and Berger (1967) noted no consistent difference between the time HY and PHY birds migrate. However, the data suggest that cues which lead to migration affect the sexes differentially. In 1976 and 1978, females (HY and PHY as separate or combined) migrated significantly earlier than males (HY and PHY separate or combined); in 1977 HY females preceded HY males. On no occasion did males precede females. If the larger heavier females are more vulnerable to a diminishing food supply than males, they may leave the breeding areas earlier. There is no indication from recaptures that 1 age class migrates more slowly than the other, nor that the 2 sexes differ in the length of time which they remain at the Point. The cause of differential sex migration is unknown.

There is a strong correlation of NW winds and clear skies with high catches of owls. In this respect, saw-whets are similar to nocturnal passerines (Bennett 1952, Lack 1960) and diurnal birds of prey (Bagg 1971).

Since the majority of migrating owls cannot be seen, their movements must be inferred indirectly from the patterns of local movement. Their migration direction is southwards in autumn and several concentration points exist along the north shores of Lake Erie and Lake Ontario (Holroyd and Woods 1975). Woodford (1959) showed a general SW displacement in autumn from Toronto. It seems that saw-whets, as they move southwards during October, are concentrated by the lower Great Lakes and their response to the eastern Lake Ontario shoreline determines their arrival route to Prince Edward Point. We suggest the 2 most likely routes are either across the water from the N-NE direction of Kingston (Fig. 1), or over land, out along the peninsula from the west. Either route is consistent with NW winds.

If the owls move from the NE by following the Lake Ontario shoreline, then NW winds may displace the birds laterally, thereby forcing them away from their preferred route and out over the water. Wind drifted migrants are common on the Atlantic Coast (Baird and Nisbet 1960, ref. therein). However, the sheer number of owls and capture sites suggest that the majority arrive at the Point via the land route, are swept downwind (eastwards) from the mainland and backtrack westwards when they reach the end of the peninsula. The findings of a predominantly westward flight of owls caught in area C and northward flight in area B are consistent with this hypothesis. There is 1 problem raised by it, however. Why do we not find an excess of birds flying east into the nets of area A? Perhaps the randomness of the catch here is caused by owls pausing to hunt and feed. It is possible that nets located closer to the shore would intercept more birds flying east.

Additional information reinforces our view that most of the owls arrive at and escape from the Point via the land route. Water barriers affect the movement of diurnal migrants and they respond by following well-marked topographical features (e.g., Cape May or Nantucket) (Baird and Nisbet 1960, Richardson 1972). In the Netherlands, the Chaffinch (*Fringilla coelebs*) shifts its flight path over the land and away from the sea (Van Dobben 1953). Ulfstrand (1960) notes Scandinavian studies show that along coastlines, where NW winds come in at an angle of 90° in relation to the primary SW direction of migration, the diurnal migrants are forced over the coastline at new angles, a fact of great importance for their reactions.

The Black-capped Chickadee (*Parus atricapillus*) in its southward diurnal movement responds to the Great Lakes by flying along the shorelines and following them to places where short water crossings or land bridges permit onward movement in their preferred direction (Bagg 1969). Topography induces different directions of movement in different parts of the same shoreline. In the Toronto area, chickadees fly west following the north shore of Lake Ontario whereas in the eastern section of Lake Ontario, they fly eastwards along the north shore out along the peninsula leading to Prince Edward Point (Bagg 1969).

Our own observations at the Point over the past 10 years show that hawks and Blue Jays (*Cyanocitta cristata*) also follow the shoreline out to Prince Edward Point. The numbers are greatest on W-NW winds and upon reaching the tip of the peninsula, they spiral upwards and backtrack westwards against the wind. This tendency is well known in low flying birds which follow lines of diversion into the wind (Lack and Williamson 1959, Baird and Nisbet 1960, Lack 1963). Such birds seem to be in retromigration, returning to their preferred direction even though flying against the wind expends extra energy (Nisbet 1957, Lack 1959).

No studies known to us mention owls so we can only speculate that they behave as several species of hawks which normally avoid water crossings, but will cross water in certain geographical locations (Wood 1933, Goodwin 1979). We do not know whether any number of saw-whets cross Lake Ontario from Prince Edward Point. We have not carried out netting on the small islands located several km offshore. Perhaps some owls use the islands as stepping stones into New York State. Saw-whets have appeared occasionally aboard lake steamers (Taverner and Swales 1911; Perkins 1964, 1965) and in migration disasters over Lake Huron (Saunders 1907, Goodwin 1970).

A comparison of owl numbers at Prince Edward Point with those reported at Cedar Grove, Wisconsin (Mueller and Berger 1967) shows considerably higher indices at the Point (9.4, 11.2 and 6.0 vs 1.14, 2.79 and 2.54). These differences probably reflect Prince Edward Point's location on the north shore of a major body of water which impedes southerly migration.

SUMMARY

The migration of Saw-whet Owls during autumns of 1975 through 1978 was discussed. During that time 1128 birds were captured. Yearly fluctuation in the number of owls caught is largely accounted for by the fluctuations in number of hatch year birds. The highly significant correlation of NW winds and clear skies with owl catches suggests that these conditions stimulate migration in the Prince Edward Point area. In 1977, juvenile birds of both sexes migrated significantly earlier in the fall than adults, whereas in 1976 and 1978, female birds of both age categories migrated earlier in the season than males.

ACKNOWLEDGMENTS

We are grateful to those dedicated members of the Kingston Field Naturalists and students of Queen's University who made possible the processing of the large numbers of owls. In particular, the help of licensed banders—K. F. Abraham, M. M. Boyd, V. Collins, J. C. Davies, M. J. B. Evans, M. Goossens, R. F. Healey, H. R. Quilliam, B. Rattray and L. Shorrock is appreciated. We thank Mr. C. S. Hirschey for permission to carry out this work on his private land at Prince Edward Point in 1976 and 1977, and the Canadian Wildlife Service in 1978. We also thank Dr. W. E. Godfrey and Mr. R. Poulin at the National Museum of Canada, Ottawa, and Drs. J. C. Barlow and R. D. James at the Royal Ontario Museum, Toronto, for permission to examine the Saw-whet Owls in the ROM's collection. We acknowledge helpful discussions with Mr. P. Buckholtz, Mr. H. Ginn and several of the licensed banders. We are most grateful to H. R. Quilliam and M. Goossens for their considerable assistance in the preparation of several of the tables. The work was done under banding permits and raptors licenses issued by the Canadian Wildlife Service and the Ministry of Natural Resources of Ontario, respectively.

LITERATURE CITED

BAGG, A. M. 1969. The changing seasons. Audubon Field Notes 23:4–12.

———. 1971. The changing seasons. Am. Birds 25:16–23.

BAIRD, J. AND I. C. T. NISBET. 1960. Migration and drift. Auk 77:119–149.

BELL, G. P., F. J. S. PHELAN AND R. C. P. WYPKEMA. 1979. The owl invasion of Amherst Island, Ontario, January–April 1979. Am. Birds 33:245–246.

BENNETT, H. R. 1952. Fall migration of birds at Chicago. Wilson Bull. 64:197–220.

BENT, A. C. 1937. Life histories of North American birds of prey. Pt. I, U.S. Natl. Mus. Bull. 167.

———. 1938. Life histories of North American birds of prey. Pt. II, U.S. Natl. Mus. Bull. 170.

CATLING, P. M. 1971. Spring migration of Saw-whet Owls at Toronto, Ontario. Bird-Banding 42:110–114.

EARHART, C. M. AND N. K. JOHNSON. 1970. Size dimorphism and food habits of North American owls. Condor 72:251–264.

GODFREY, W. E. 1966. The birds of Canada. Natl. Mus. Canada Bull. 203.

GOODWIN, C. E. 1970. Ontario-Western New York. Audubon Field Notes 24:38–42.

———. 1974. Ontario-Western New York. Am. Birds 28:44–48.

———. 1979. Ontario region. Am. Birds 33:171–174.

HOLROYD, G. E. AND J. G. WOODS. 1975. Migration of the Saw-whet Owl in eastern North America. Bird-Banding 46:101–105.

KELLEY, A. H. AND J. O. L. ROBERTS. 1971a. Spring migration of owls at Whitefish Point. Jack-Pine Warbler 49:65–70.

——— AND ———. 1971b. Spring migration at Whitefish Point, Michigan, 1966–1970. Ont. Bird Banding 7:1–29.

LACK, D. 1959. Migration across the North Sea studied by radar. Pt. 1. Survey through the year. Ibis 101:209–234.

———. 1960. Weather and migration. Auk 77:171–209.

———. 1963. Migration across the southern North Sea studied by radar. Pt. 5. Movements in August, winter and spring and conclusion. Ibis 105:461–492.

——— AND K. WILLIAMSON. 1959. Bird migration terms. Ibis 101:255–256.

LUDLUM, D. M. (ED.). 1976. Daily weather maps: September and October 1976. Weatherwise 29:302–361.

———. 1977. Daily weather maps: September and October 1977. Weatherwise 30:254–261.

MUELLER, H. C. AND D. D. BERGER. 1967. Observations on migrating Saw-whet Owls. Bird-Banding 38:120–125.

———, ——— AND G. ALLEZ. 1977. The periodic invasions of Goshawks. Auk 94:652–663.

NISBET, I. C. T. 1957. Passerine migration in south Scandinavia in the autumn of 1954. Ibis 99:228–268.

NORTH AMERICAN BIRD BANDING TECHNIQUES. 1977. Vol. 2, Pt. 6. Ageing and sexing. Can. Wildl. Serv. and U.S. Fish and Wildl. Serv.

PERKINS, J. P. 1964. 17 flyways over the Great Lakes. Pt. I. Audubon 66:294–299.

———. 1965. 17 flyways over the Great Lakes. Pt. II. Audubon 67:42–45.

RICHARDSON, W. J. 1972. Autumn migration and weather in eastern Canada. Am. Birds 26:10–17.

SAUNDERS, W. E. 1907. A migration disaster in western Ontario. Auk 24:108–110.

SHEPPARD, J. M. AND M. K. KLIMKIEWICZ. 1976. An update to Wood's bird bander's guide. N. Am. Bird Bander 1:25–27.

TAVERNER, P. A. AND B. SWALES. 1911. Notes on the migration of the Saw-whet Owl. Auk 28:329–334.

ULFSTRAND, S. 1960. Some aspects on the directing and releasing influence of wind conditions on visible bird migration. Pp. 730–736 *in* Proc. XII Int. Ornithol. Congr.

VAN DOBBEN, W. H. 1953. Migration in the Netherlands. Ibis 95:212–234.

VICKERY, P. D. AND R. P. YUNICK. 1979. The 1978–1979 Great Gray Owl incursion across northeastern North America. Am. Birds 33:242–244.

WEIR, R. D. 1972a. Spring migration at Prince Edward Point, Ontario (1971). Can. Field-Nat. 86:3–16.

———. 1972b. Spring migration at Prince Edward Point, Ontario (1972). Ont. Field-Biol. 26: 20–34.

WOOD, M. 1969. A bird bander's guide to determination of age and sex of selected species. Coll. Agric., Pennsylvania State Univ., State College, Pennsylvania.

WOOD, N. A. 1933. Birds of Keweenaw Point, Michigan. Pap. Michigan Acad. Sci., Arts, Letters 17:713–733.

WOODFORD, J. 1959. Returns and recoveries of Saw-whet Owls banded at Toronto, Ontario. Ont. Field-Biol. 13:19–33.

WOODS, J. G. 1972. An introduction to the literature on the Saw-whet Owl. Ont. Bird Banding 8:8–23.

DEPT. CHEMISTRY AND CHEMICAL ENGINEERING, ROYAL MILITARY COLL. KINGSTON, ONTARIO, CANADA (RDW); DEPT. BIOLOGY, QUEEN'S UNIV., KINGSTON, ONTARIO (FC); DEPT. PHYSICS, ROYAL MILITARY COLL., KINGSTON, ONTARIO (MHE); AND DEPT. MICROBIOLOGY, QUEEN'S UNIV., KINGSTON, ONTARIO (RBS). ACCEPTED 17 MAR. 1980.

RESEARCH GRANTS

The Eastern Bird Banding Association and the Western Bird Banding Association are each offering a research grant of $250 in aid of research using bird banding techniques or bird banding data. Applicants should submit a resume of his or her ornithological or banding background, the project plan and budget to the joint selection committee chairman: Robert C. Leberman, Powdermill Nature Reserve, Star Route South, Rector, Pennsylvania 15677. No formal application forms are available, and the amount requested should not exceed $250. The deadline for receipt of applications is 15 March 1981.

Wilson Bull., 92(4), 1980, pp. 489–496

DIRECTIONS AND TIMING OF GREAT BLUE HERON FORAGING FLIGHTS FROM A CALIFORNIA COLONY: IMPLICATIONS FOR SOCIAL FACILITATION OF FOOD FINDING

Helen M. Pratt

Patterns of foraging trips of several species of colonially nesting birds have been examined recently for evidence that colonies serve as "information centres" to assist the members in finding food (Krebs 1974, Hoogland and Sherman 1976, Snapp 1976, Custer and Osborn 1978, Erwin 1978). According to this hypothesis colonial nesting is advantageous for species depending on food that is unevenly distributed and concentrated in areas of temporary abundance. Individuals who have difficulty finding food are able to follow their more successful neighbors to good feeding sites, thus reducing searching time and enhancing feeding success (Ward and Zahavi 1973).

Krebs (1974) found that Great Blue Herons (*Ardea herodias*) in a colony near Vancouver, British Columbia, tended to depart for intertidal feeding grounds in groups and birds from neighboring nests were likely to feed in the same areas on the same days. He suggested that less successful herons may have followed more successful individuals from the colony to areas of prey concentration. Although the statistical analysis of heron departures suggests that herons may follow each other on foraging trips, tracking individual birds as they leave the nest provides a more direct test of this hypothesis.

This paper presents data on timing and directions of departures taken by breeding herons as they flew to feeding grounds from nests in a central California heronry. The results are analyzed for evidence of following and for information about the degree of colony dependence on the adjacent estuary for food.

METHODS

The heronry was located in a narrow canyon at Audubon Canyon Ranch about 5.8 km north of Stinson Beach, Marin Co., California. The herons nested approximately 24–30 m from the ground in the tops of coast redwoods (*Sequoia sempervirens*) that grew in the bottom and up the north facing slope of the canyon. Bolinas Lagoon, a shallow 570-ha estuary opening onto the Pacific Ocean, lies at the mouth of the canyon to the west (Fig. 1). Behind the heronry to the east a steep ridge of mountains separates the shore from populated areas adjoining the northern stretches of San Francisco Bay.

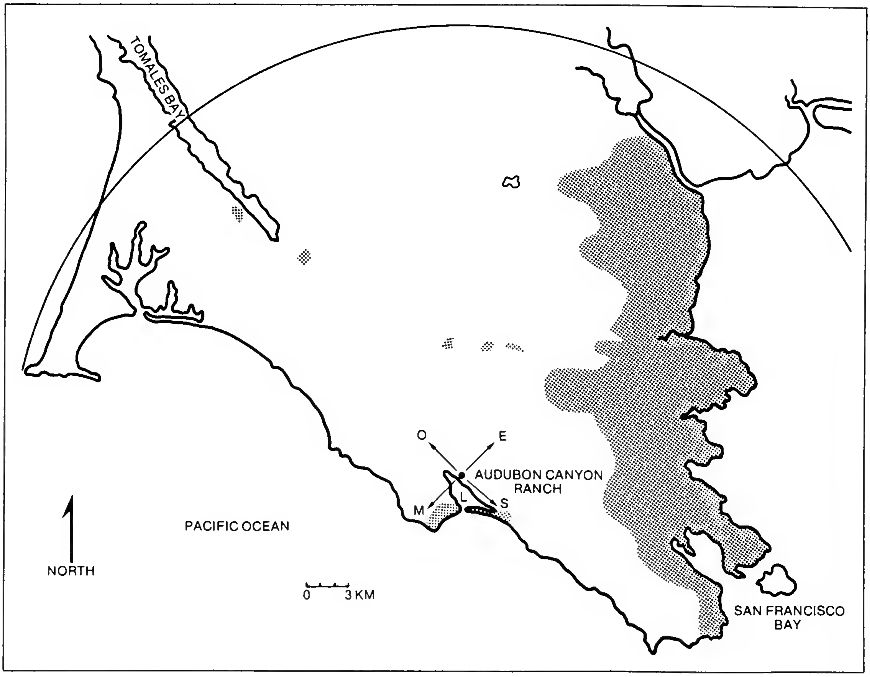


FIG. 1. Map of Marin County showing the location of the heronry at Audubon Canyon Ranch with directions taken by departing herons: L = lagoon, S = south, E = east, O = Olema Valley, M = Bolinas Mesa. Shading indicates populated areas. The arc encompasses the area within 30 km from the heronry.

The herons were observed from an overlook on the south facing slope of the canyon above the level of most nests and about 90–180 m from them. Due to the distance and/or habituation of the herons to humans at the overlook, observers caused no detectable disturbance in heron behavior.

I identified nests by plotting and numbering them on a panorama of the heronry. A team of observers tracked herons as they flew from the colony. Two persons stationed at the nest overlook recorded the time a heron flew, the nest number when possible, and in a few cases where plumage differences enabled differentiation of members of the pair, they noted which individual left. Other observers stationed on a hill overlooking the lagoon at a spot about 275 m from the nest overlook and within view of it recorded the time the heron was sighted, its direction and, for those landing in the lagoon, its destination on a map divided into quadrats of 387 m^2. Except for the first 2 sessions when it was necessary to use arm signals, the teams communicated with each other by portable CB transceivers. All observations were taken with 7× binoculars and 20× spotting scopes.

The teams tracked herons once weekly from 14 April through 2 June 1976, and from 22 March through 24 May 1977, on 16 different days. Observations from 12 May 1976, are not included in this analysis because, due to unusually hot weather, some herons on leaving the nests went directly to a drinking spot rather than hunting for prey (Pratt 1977). This behavior

TABLE 1

NUMBER OF HERON DEPARTURES IN THE OBSERVED DIRECTIONS

	1976	1977	Total	Percent
Lagoon	20	14	34	45
Olema Valley	8	7	15	20
South	8	5	13	17
Bolinas Mesa	4	4	8	10
East	2	4	6	8
Total	42	34	76	100

is considered atypical since we did not see herons going out to drink on other days. We tracked herons in the morning on 7 days between approximately 09:30 and 12:00 for a total of 11 h 30 min; afternoon observations included here were made between 13:30 and 18:00 on 8 days for a total of 14 h 55 min.

Breeding pairs numbered 40 in 1976 and 41 in 1977. Most herons were either incubating eggs or attending chicks fewer than 4 weeks old at the time of tracking.

RESULTS

Departure directions.—We tracked 76 foraging herons for the 2 years combined (Table 1). I identified the nests of 57 departing herons; 19 others left from perches in trees. I distinguished individuals from their mates by differences in crown plumage on 12 departures.

The herons flew in 5 clearly distinguishable directions (Fig. 1). The relative frequency of directions taken was essentially the same in both years (Table 1). Bolinas Lagoon was the most frequent destination (45% of departures). A flight path northwest above the Olema Valley was second in frequency (20%). All but 1 of the herons taking this route flew until out of sight. The 1 bird that was the exception to this flight pattern landed in a pasture near the north end of the lagoon. The herons that flew south (17%) followed the western edge of the coastal hills; 5 (7%) veered east before being lost to view. Those flying over Bolinas Mesa (10%) either continued northwest up the coast or landed in pastures on the mesa. Those flying east (8%) circled above the heronry many times, for up to 11 min, gaining altitude until they flew over the ridge that rises to a height of 460 m behind the heronry.

We tracked only 1 individually identified heron more than once. On 3 different days this bird flew directly to a channel bordering the road on the east side of the lagoon. This bird did not join groups of feeding herons even when they were present. Of the remaining herons that went to the lagoon, 11 landed near other herons.

Intervals between departures.—If the herons at Audubon Canyon Ranch

TABLE 2
NUMBER OF DEPARTURES AT DIFFERENT INTERVALS

Intervals (min)	No. of departures
1–4	15
5–8	13
9–12	9
13–16	8
17–20	3
21–24	5
25–28	1
29–32	1
>32	7

followed each other to feeding grounds, directions taken on successive departures would be the same and intervals between departures would be short. Since most herons either landed in the lagoon or flew out of sight within 4 min of departure, I grouped departures into 4-min intervals to analyze for evidence of following (Table 2). Only 3 of the 15 herons that left within 4 min of another went in the same direction as the preceding bird, all going to the lagoon. One landed near the leading bird and displaced it. The others landed in different areas from the preceding heron. Thus during the time of these observations breeding herons showed no tendency to follow each other on leaving the colony.

Timing of departures.—Herons that were incubating or attending small chicks usually left promptly when relieved. In 53 instances of nest relief, 40 (75%) of the relieved herons left within 5 min or less. A bout of twig presentations followed nest relief at 5 of the 13 nests where the heron lingered. Of 23 arrivals at nests with chicks old enough to be left unattended except for feeding, 7 (30%) left at once. The others remained perched on branches preening or resting often for the duration of observations.

Relation of departure directions to tide.—The data in this study do not show that the direction of departing herons differed with the tides (Table 3). About the same number of birds went to the lagoon on ebbing as on flowing tides and frequency of departures in the other directions showed no tide related trends.

DISCUSSION

The timing of departures and directions taken by the herons leaving the colony at Audubon Canyon Ranch indicated that they were behaving independently rather than following other birds. The hypothesis that follow-

TABLE 3
DIRECTIONS OF DEPARTING HERONS ACCORDING TO TIDE

	Ebbing	Flowing	Slack
Lagoon	15	17	2
Olema Valley	5	6	4
South	5	5	3
Bolinas Mesa	4	2	2
East	4	2	0
Time observed	12 h 10 min	10 h 50 min	3 h 25 min

ing is advantageous assumes that successful individuals lead others to locations of previously discovered food abundance (Ward and Zahavi 1973). This strategy would be effective where food resources are temporarily abundant but spatially confined, e.g., in ponds subject to seasonally diminishing water levels as described by Kushlan (1976). There is a difficulty, however, in applying this hypothesis to Great Blue Herons using estuarine feeding grounds where prey concentrations can change both spatially and temporally relatively quickly. During incubation and for the first 3–4 weeks of the nestling period Great Blue Heron parents usually remain at the nest until relieved by the mate (Pratt 1970). Thus, departure for the feeding grounds at this stage in the breeding cycle is determined primarily by nest relief. Nest relief usually occurs only once or twice during the daylight hours and attentive spans are long. During incubation, spans of 12 h or more are common. I have observed, after hatching, spans of 4–9 h (Pratt 1970, unpubl.) and some could be longer. Since herons at continuously attended nests remain there for several hours after arrival, prey concentrations exploited on 1 foraging trip could disperse or move before the next trip; feeding grounds accessible at low or medium tides could become inundated. Under these circumstances the quickest way to find food might be to search for and join other feeding herons. Krebs (1974) demonstrated that herons are attracted to others on the feeding grounds with the result that aggregations build up where food is plentiful through local enhancement. An alternative might be to fly directly to familiar feeding grounds known to be accessible most, if not all, of the time.

The limited data presented here suggest that the Audubon Canyon Ranch herons selected foraging spots in 2 ways. Some landed near others in the lagoon, apparently attracted by conspecifics. They were perhaps exemplifying the process of build up of feeding aggregations through local enhancement, similar to those reported by Krebs (1974). Heron feeding aggregations have also been reported by Palmer (1962), Kushlan (1976), Willard (1977) and Bayer (1978). The direct, purposeful flight of those flying in other directions and the observation of the heron that went to the same general area in the lagoon on 3 different days suggest that other individuals went directly to favorite feeding areas. Herons have been reported to return to the same feeding sites repeatedly (Owen 1955), to feed solitarily (Bovino and Burtt 1979), and under some circumstances to defend feeding territories (Palmer 1962, Hedeen 1967, Krebs 1974, Bayer 1978).

A heron was seen catching pocket gophers (*Thomomys bottae*) on several days during the breeding season of 1978 in a field about 0.5 km from the heronry (J. Church, pers. comm.). Only 1 bird was present in the field at a time, but it was not identified and impossible to determine whether the same individual returned repeatedly.

Promptness of departure for the feeding grounds was related to the stage in the nesting cycle. Herons incubating or attending small chicks tended to leave at once, whereas herons from nests with older, unattended young were more likely to linger in the heronry. Delayed departure could be interpreted as indicating that lingering herons were waiting to follow more successful birds to feeding grounds as speculated by Krebs (1974:110). On the other hand it might indicate low motivation to search for food. Birds from continuously attended nests were limited in available foraging time and would likely be under pressure to leave for feeding grounds immediately on relief. Herons from nests with unattended young had more time for hunting and after a successful foraging trip might be inclined to postpone departure after feeding the chicks.

Custer and Osborn (1978) found that herons from a North Carolina colony flew farther to feeding grounds during high tide. In this study, departure directions did not change with changing tides (Table 3). However, the data are limited, and since on tracking days the highest tides were at night, feeding areas were accessible in the lagoon at all observations. More observations, particularly at tidal extremes, might show that tides affected heron destinations in the lagoon and possibly departure directions. Further studies of heron foraging flights, especially under different ecological conditions, i.e., inland sites near lakes and rivers where water levels change relatively slowly, and at different times in the breeding cycle are needed to resolve the question of whether herons sometimes follow each other to feeding grounds.

Though these observations did not show that breeding adults followed others, a study of heron flights at other stages of the breeding cycle might produce different results. Perhaps during the pre-incubation period when nest attendance is less critical, herons find good feeding spots by following other birds. Or, if prey became unusually scarce or difficult to find, herons might resort to following neighbors on foraging flights. Late in the nesting cycle flying young might tend to follow adults or each other. For a period varying from 1–3 weeks before reaching independence, young herons leave the nest for part of the day, but return to be fed by their parents (Pratt 1970). I have no data on the timing or directions of their flights but it seems possible that they might leave immediately after other herons and follow them from the colony.

Although the resources of the adjacent estuary were important to the colony, the feeding range of the herons at Audubon Canyon Ranch apparently encompassed a much wider area. None of the birds was marked and the destinations of those not landing in the lagoon is unknown, but the majority flew to other feeding grounds, perhaps at some distance. Some observers believe that Great Blue Herons may fly distances up to 80 km from nesting colonies to feeding grounds (Court 1908, Reinecke 1910, Miller 1943). Data on foraging flights at colonies with mixed species of herons and ibises suggest that long distance feeding flights are common in the Ciconiiformes (Dusi et al. 1971, Custer and Osborn 1978). Great Blue Herons fly about 40 km/h (Palmer 1962). Potential feeding grounds at the edges of Tomales Bay and San Francisco Bay, as well as in pastures and farm ponds, lie within 45 min flight of the colony in all directions taken by the herons (Fig. 1).

SUMMARY

Directions and timing of foraging flights of adult Great Blue Herons did not indicate that they followed each other from the colony to feeding grounds. Some herons apparently went directly to predetermined feeding areas, while others joined aggregations in the adjacent estuary. Herons on less than half of the departures went to the estuary. The majority appeared to be flying to other more distant feeding grounds. Herons incubating or attending small young left promptly, whereas herons at nests with older, unattended young tended to linger in the colony.

ACKNOWLEDGMENTS

The following people helped track herons: James Browning, Karen Schwartz, John Kipping, Kathy Kipping, Kirsten Williams, Kit Lee and Audubon Canyon Ranch Research Associates. Gary Page, David Clark, Tom Custer, David DeSante and Erwin Klass read earlier drafts of the manuscript and made helpful comments. I thank them all. This is contribution number 196 of the Point Reyes Bird Obsrvatory.

LITERATURE CITED

Bayer, R. D. 1978. Aspects of an Oregon estuarine Great Blue Heron population. Pp. 213–217 *in* Wading birds (A. Sprunt, J. Ogden and S. Winkler, eds.). Natl. Audubon Soc. Res. Rept. 7.

Bovino, R. R. and E. H. Burtt, Jr. 1979. Weather-dependent foraging of Great Blue Herons (*Ardea herodias*). Auk 96:628–630.

Court, J. 1908. Treganza Blue Heron. Auk 25:291–296.

CUSTER, T. W. AND R. G. OSBORN. 1978. Feeding habitat use by colonially-breeding herons, egrets, and ibises in North Carolina. Auk 95:733–743.

DUSI, J. L., R. T. DUSI, D. L. BATEMAN, C. A. MCDONALD, J. J. STUART AND J. F. DISMUKES. 1971. Ecological impacts of wading birds on the aquatic environment. Water Resour. Res. Inst., Bull. No. 5.

ERWIN, R. M. 1978. Coloniality in terns: the role of social feeding. Condor 80:211–215.

HEDEEN, S. 1967. Feeding behavior of the Great Blue Heron in Itasca State Park, Minnesota. Loon 39:116–120.

HOOGLAND, J. L. AND P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecol. Monogr. 46:33–58.

KREBS, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour 51:99–134.

KUSHLAN, J. A. 1976. Wading bird predation in a seasonally fluctuating pond. Auk 93:464–476.

MILLER, R. F. 1943. The Great Blue Heron. The breeding birds of the Philadelphia region (Pt. II). Cassinia 33:1–23.

OWEN, D. F. 1955. The food of the heron *Ardea cinerea* in the breeding season. Ibis 97:276–295.

PALMER, R. S., (ED.) 1962. Handbook of North American birds, Vol. I. Yale Univ. Press, New Haven, Connecticut.

PRATT, H. M. 1970. Breeding biology of Great Blue Herons and Common Egrets in central California. Condor 72:407–416.

———. 1977. Great Blue Herons interrupt nest-guarding to drink. Condor 79:501–502.

REINECKE, O. 1910. The Great Blue Heron. Oologist 27:15–17.

SNAPP, B. D. 1976. Colonial breeding in the Barn Swallow (*Hirundo rustica*) and its adaptive significance. Condor 78:471–480.

WARD, P. AND A. ZAHAVI. 1973. The importance of certain assemblages of birds as "information centres" for food finding. Ibis 115:517–534.

WILLARD, D. E. 1977. The feeding ecology and behavior of five species of herons in southeastern New Jersey. Condor 79:462–470.

POINT REYES BIRD OBSERVATORY, 4990 SHORELINE HIGHWAY, STINSON BEACH, CALIFORNIA 94970. ACCEPTED 30 OCT. 1979.

Wilson Bull., 92(4), 1980, pp. 497–505

CHOICE OF NEST BOXES BY COMMON GOLDENEYES IN ONTARIO

Harry G. Lumsden, R. E. Page and M. Gauthier

Nest boxes were hung on trees for Common Goldeneyes (*Bucephala clangula*) in Scandinavia over 240 years ago (Linnaeus *in* Phillips 1925, Lloyd 1854) to provide a ready source of eggs for human consumption. The use of boxes to increase stocks is more recent and has been practiced in Europe as well as North America.

Few data exist in North America on the size of natural cavities chosen by goldeneyes. Sixteen cavities found in New Brunswick (Prince 1968) had an average inside diameter of 20.6 ± 4.1 cm, a depth of 46.2 ± 19.6 cm, and the average size of the entrance hole was 22.4 ± 16.3 cm long × 11.4 ± 3.6 cm wide. Ten of these 16 cavities were open at the top like a chimney. Siren (1951) tested hollow pine logs in Finland with a variety of dimensions and recommended specific measurements. Palmer (1976) also made recommendations. These are summarized in Table 1 with the measurements of nest boxes used by 5 other investigators in their studies of nesting goldeneyes. The purpose of this paper is to describe the results of selection experiments in which goldeneyes were presented with boxes with a variety of features.

MATERIALS AND METHODS

The work was started in 1974 and continues on 3 study areas in Ontario: Elk Lake (47°44′N, 80°20′W); the Englehart River including Robillard, Kinogami and Kushog lakes, known collectively as Long Lake, near the village of Charlton (47°48′N, 79°59′W); and on the Mattagami and Muskego rivers west and south of Smooth Rock Falls (49°17′N, 81°38′W).

We used nest boxes made from 1.27 cm sheeting grade plywood, with a relatively rough surface. The internal measurements were 21 × 24 cm × 45 cm high at the back, with a roof that sloped downward to 42.5 cm at the front. The bottom of the entrance hole was varied in 1 experiment, but in others was 33 cm from the floor; it was cut into a removable inspection plate held in place on the front of the box by 2 turn buttons. The outside of the boxes was stained and all exposed plywood edges and knots were treated with clear marine varnish. Boxes were mounted in sets of 2 or 3, on 2 horizontal supports nailed about 3 m from the ground to trees on the lake shore or river bank. Where 3 boxes were used the center one was aligned with the tree trunk; branches and shrubs were trimmed so that entrances were unobstructed and visible from the water. The boxes were visited at intervals averaging about 4 days (1–10 days), beginning as soon as ice melt permitted in late April or early May and continuing well into June.

The first test compared the response of goldeneyes on Elk Lake to dark vs light interiors of the boxes. There were 73–75 sets available annually for 6 years. We hypothesized that a searching female would respond to the dark entrance of a cavity and that, when given a choice, the bird would choose the hole that appeared darkest. Two boxes were mounted side by side, 60 cm apart, one of each pair was painted black inside, the other was clean, unstained plywood. All exteriors were stained light brown. Entrance holes were oval, measuring 10.5 cm wide × 8 cm high.

For the second selection test, compass bearings taken at right angles to the horizontal axis of the sets of boxes on Elk and Long lakes were recorded and grouped for analysis. The Elk Lake boxes and 100–105 sets on Long Lake were available annually for 6 years for this analysis.

The third test compared the choice by goldeneyes on Long Lake and the Mattagami and Muskego rivers among sets of 3 boxes with large (13 cm wide × 10 cm high), medium (10.5 × 8 cm) or small (7.5 × 6 cm) oval entrance holes. Box interiors were painted black. The smaller Hooded Merganser (*Mergus cucullatus*) nests in this area as well as the goldeneye and may compete for nesting cavities. It was hypothesized that the 2 species would divide the available cavities on the basis of size of entrance hole. The smallest entrances were large enough to admit Hooded Mergansers, but too small for goldeneyes. The positions of the 3 types of boxes in each set, and the order of placement of the sets around the shore, were systematically varied according to a Latin Square. Sets were spaced 0.6–1.2 km apart. The number of sets of boxes on the Mattagami and Muskego rivers varied from 64–46 because many box trees were cut by beaver (*Castor canadensis*) or were knocked down by ice at breakup. For 2 years, 103 and 105 sets of boxes on Long Lake were used in this test.

The variation in the depth of boxes (22–41 cm) used in previous studies (Table 1) and the frequency with which goldeneyes used relatively shallow, rotted-out Common Flicker (*Colaptes auratus*) holes in Ontario, suggested that material can be saved if goldeneyes accepted shallow boxes as readily as deep ones.

The fourth test compared choices by goldeneyes of shallow boxes, 18 cm from the floor to the bottom of the entrance hole; medium-depth boxes 25.5 cm deep and deep boxes, 33 cm deep. All were fitted with large entrance holes, 13 × 10 cm. One hundred and 101 sets of boxes on Long Lake were used for this test in 1975 and 1976. Their depth was adjusted with the use of wooden inserts that provided false bottoms.

The fifth test was the influence of the tree species on box selection. We selected trees for boxes primarily for their proximity to the shore and their relative immunity from cutting by beaver. We therefore favored black ash (*Fraxinus nigra*) and balsam poplar (*Populus balsamifera*), over trembling aspen (*P. tremuloides*) and white birch (*Betula papyrifera*). Conifers were seldom chosen since they were small or sparsely distributed near water, or were situated in dense cover. Other factors affecting our selection of trees for boxes included spacing along the shore, access by boat and size and visibility from open water. A total of 174 sets of boxes over a 5 year period were used in this test.

Choice by a goldeneye was defined as the laying of 1 or more eggs in a box, even though the female may subsequently desert. In all tests the results involve multiple use of some of the boxes in different years, in some cases by the same female. To ensure independence of data for statistical analysis, boxes were scored only as used or not used, and the number of uses per box was ignored.

RESULTS

Goldeneyes generally selected black instead of unstained interiors (Table 2), based on data excluding multiple use of the same box. Including multiple uses, there were 39 choices of black and 13 of unstained boxes.

There was no evidence for selection of nest boxes facing 8 sectors of the compass (Table 3). Nor was there selection for southerly (90° through S to 270°), or northerly facing boxes ($\chi^2 = 0.061$, df = 1, $P > 0.05$).

TABLE 1
SUMMARY OF DIMENSIONS AND MATERIALS USED FOR GOLDENEYE NEST BOXES

Source	Cavity		Entrance hole			
	Floor area	Total depth	Size	Height above floor	Height of box above ground	Construction material
Siren (1951) recommendation	19–22 cm diameter	—	10–11.5 cm	35 cm	3–4 m	hollow pine logs
Palmer (1976) recommendation	23 × 23 cm	60 cm	10.5 × 8 cm	—	—	—
Gibbs (1961)	25.4 × 25.4 cm	61 cm	8.9 cm diameter	—	—	rough lumber
Johnson (1967)	30.5 × 30.5 cm	61 cm	12.7 × 10.2 cm or 11.4 × 8.9 cm ellipse	—	—	wood
Johnson (1967)	30.5 cm diameter	76.2 cm	—	—	—	metal drums
Rever and Miller (1973)	15.2 × 19.0 cm	61 cm	12.7 cm diameter	39.4 cm	2.4–3.7 m	spruce boards
Corbould (1969)	17.8 × 22.9 cm	43.2 cm	11.4 × 8.9 cm	22.9 cm	—	lumber
Irving Benson (pers. comm.)	21.6 cm diameter	—	11.4 × 12.7 cm	21.6 cm	—	hollow cedar logs

TABLE 2

CHOICE OF NEST BOXES BY GOLDENEYES IN SETS WITH 1 BLACK AND 1 UNSTAINED INTERIOR OF WHICH 1 OR BOTH BOXES IN EACH SET WERE USED

	Number of boxes	
	Used	Unused
Black interior	23[a]	2
Unstained interior	7	18
Cochrane Q = 36.15, df = 1, $P < 0.001$		

[a] Both boxes in some sets were used simultaneously by different females.

Both species of ducks showed a strong preference for large entrance holes. Goldeneyes used boxes with large holes in 32 cases, medium in 3 and were unable to squeeze through the small entrances. Hooded Mergansers chose the large in 9 cases, the medium in 4, and the small entrances in none. Table 4 summarizes the data after multiple use of single boxes has been eliminated.

In all cases goldeneyes selected deep boxes ahead of the medium and shallow. In total, 12 different boxes were used 16 times, but no medium or shallow boxes were used (Cochrane Q test = 24, df = 2, $P < 0.001$). Alignment of a box with the trunk of a tree in the center of a set of 3 did not influence selection on Long Lake and the Mattagami and Muskego rivers. Goldeneyes used the right, center and left boxes 17 times each. In the fifth test there is no evidence that the species of tree on which the set of boxes was mounted influenced the goldeneyes in their choice (Table 5).

DISCUSSION

Our data demonstrate that the colors of the interiors of nest boxes can influence the degree of use by target species. Such preferences have been tested experimentally in only a few species. Blagosklonov (1970) showed

TABLE 3

ACCEPTANCE OF NEST BOXES BY GOLDENEYES FACING 8 SECTORS OF THE COMPASS ON ELK AND LONG LAKES

	N-NE	NE-E	E-SE	SE-S	S-SW	SW-W	W-NW	NW-N
Available	17	32	13	7	18	50	26	11
Used	6	12	6	2	5	19	11	6

$\chi^2 = 1.28$, df = 7, $P > 0.05$, using the correction for continuity of Siegel (1956)

TABLE 4

CHOICE BY GOLDENEYES AND HOODED MERGANSERS OF BOXES WITH LARGE, MEDIUM AND SMALL ENTRANCE HOLES

Species	Entrance size	Number used	Number unused
Goldeneyes			
	large	28[a]	1
	medium	3	26
Cochrane Q = 23.14, df = 1, $P < 0.001$			
Hooded Mergansers			
	large	9[a]	3
	medium	4	8
	small	0	12
Cochrane Q = 10.16, df = 2, $P < 0.01$			

[a] Different females simultaneously used 2 boxes within a set.

that the Pied Flycatcher (*Muscicapa hypoleuca*), in the Moscow region, chose boxes with white or clean interiors more frequently than those with black or dirty interiors. Pitts (1977) also demonstrated that Eastern Bluebirds (*Sialia sialis*) and House Sparrows (*Passer domesticus*) in Tennessee selected boxes with white interiors more frequently than those with black. However, Lumsden (1976) reported that Starlings (*Sturnus vulgaris*) in Ontario, as with the goldeneyes in this study, chose black interiors in preference to unstained plywood interiors.

Light within the box was probably one of the influences affecting these choices. Blagosklonov (1970) reported that reflected light levels in boxes

TABLE 5

SPECIES OF TREE ON WHICH SETS OF BOXES WERE MOUNTED AND THEIR USE BY NESTING GOLDENEYES

Species of tree	Number available	Number used	Percent used
Trembling aspen	13	5	38
Balsam poplar	76	23	30
White birch	28	8	29
Black ash	51	10	20
Conifer	7	1	14
Totals	175	47	—
$\chi^2 = 1.94$, df = 4, $P > 0.05$			

with dirty interiors were much lower than in clean boxes. He concluded that the size of the entrance hole, the depth of the cavity and other factors are of secondary importance and only influence acceptance of a cavity to the extent that they affect light. From this it would appear that some species prefer a higher reflected light level, while others, such as the Starling, desire a darker cavity.

Most cavity nesting birds depend greatly on holes excavated by woodpeckers. A number of studies have shown that woodpeckers often cut the entrance to their cavities facing in a specific direction. Conner (1975) briefly reviewed this phenomenon and showed that different species of woodpeckers respectively orient the entrance to their nests to the southwest, to the southeast and even to the northeast.

The Bufflehead (*Bucephala albeola*) typically uses flicker holes as nest-sites. McLaren (1958), using largely Erskine's data, studied the use by 5 species, including Buffleheads, of flicker holes in British Columbia. These records, re-analyzed here, indicated that flicker nest holes in use by all species faced in a southerly (SE–SW) direction more frequently than to the north (NW–NE) ($Z = 4.37$, $P < 0.001$, binomial test for large samples). However, the Bufflehead's choice was not significantly in favor of southerly facing entrances ($Z = 0.788$, $P > 0.05$). Buffleheads did, however, have a tendency to choose sites which offered a relatively unobstructed flight path to the entrance hole (Erskine 1972).

The direction of rain-winds or the warming effect of sunshine may affect the choice of cavities with specific compass orientation by hole nesting species and also of boxes by goldeneyes. Dement'ev and Gladkov (1967) report that a major cause of nest desertion by goldeneyes at the Rybinsk reservoir in the unusually wet summer of 1951 was soaking of nests by rain. Since nest entrances facing the prevailing rain-winds are more likely to become saturated than those facing away, birds may select against boxes facing rain-winds.

The Atmospheric Environment Service has supplied us with weather records for Earlton airport which lies about 25 km east of the center of the Elk Lake/Long Lake study areas. Hourly records of wind direction when rain was falling were compiled for 1957–1976 for May and June, the months of most laying and almost all incubation. Only winds of more than 5 mph were included to calculate the percent frequency of rain-winds blowing from 16 points of the compass. The highest frequency of rain-winds (32%) were from NW, NNW and N. From the choices of box orientation (Table 3) there is no evidence that goldeneyes were influenced by the direction of rain-winds.

If sunshine warming goldeneye boxes with a southerly exposure (90° through south to 270°) had any influence, one would expect that northerly facing boxes (270° through north to 90°) would differ in their rate of use from those with a southerly orientation. Since this choice pattern did not prevail, we conclude that goldeneyes were not influenced by this factor. It is, however, possible that either conflicting choice patterns obscured any specific directional orientation that they might have had, or that relatively large birds like the goldeneye and Bufflehead are not influenced to the same extent by these factors as smaller cavity nesting woodpeckers and passerines.

The choice of large entrance holes by goldeneyes was somewhat unexpected. Most of the papers cited in Table 1 recommended or used smaller holes than the large entrances chosen by goldeneyes in this study. However, Prince (1968) showed that the entrances to natural cavities used by goldeneyes averaged 22.4 × 11.4 cm. There were 2 occasions in our study when the inspection plate containing the entrance hole fell off the box, providing an entrance 21.5 × 13.5 cm. This extra large entrance was chosen in both cases in preference to a 10.5 × 8 cm entrance. Bent (1925) mentioned hearing much scrambling and scratching as an incubating goldeneye climbed to a small opening of a natural cavity. Incubating females on our study areas sometimes tried to flush as the field crew grounded their boat on the shore beneath the box tree. Frequently the female would make more than 1 attempt to jump to the entrance, falling back onto the eggs with much flapping and scrambling. Other females seemed to jump to the entrance without difficulty. A large entrance hole probably facilitates escape from a cavity at the approach of a predator.

The Hooded Merganser accepted large entrances 9 times, medium entrances 4 times, but also rejected the small entrances, although they could have had exclusive use of them. This suggested that the goldeneye and Hooded Merganser do not divide the cavity niche in the Long Lake area on the basis of the size of the entrance hole.

Creation of new nest holes each year by the Great Black Woodpecker (*Dryocopus martius*) (Siren 1951) resulted in numerous old cavities being available as goldeneye nest-sites in Finland. In New Brunswick, Prince (1968) reported that only 3 of 46 cavities that he studied were made by Pileated Woodpeckers (*D. pileatus*), the rest being formed as a result of tree rot where limbs had broken off. In addition, most of the cavities were in hardwoods such as silver maple (*Acer saccharinum*), some were in American elm (*Ulmus americana*) and 1 in a butternut (*Juglans cinerea*). Forty-three (93%) were in living trees that could be expected to stand for many years.

Most of the natural cavities available close to the water in the Elk Lake area were in trees with relatively soft wood, such as trembling aspen, balsam poplar, white cedar (*Thuja occidentalis*) and white spruce (*Picea *glauca*), or in harder black ash and white birch. The rectangular entrances of the Pileated Woodpecker were evident in very few cavities. Most holes resulted from initial excavation by flickers and subsequent enlargement by rot. Measurements of such holes are lacking since most were in dead and rotting trees unsafe for climbing. Erskine (1978) estimated that about one-half of all nests in trembling aspen in the dry climate of British Columbia were still useable after 7 years and one-third after 15 years. In the relatively damp climate of northern Ontario dead aspens and birches do not stand for many years. It is likely that flicker cavities do not rot to a great depth before the tree falls. Natural cavities available to goldeneyes likely would be serviceable for relatively few years and would tend to be shallower than those in living hardwoods or those made by Pileated Woodpeckers.

The goldeneyes on Long Lake did not indicate adaptation to shallow cavities in their choices, however. Although Prince (1968) showed that the range of depth of natural cavities chosen by goldeneyes ranged from 15–76 cm (average 46.2 cm), we found that goldeneyes at Long Lake favored boxes 33 cm deep. Perhaps still deeper boxes would be preferred.

SUMMARY

Choices among boxes offering a variety of features were recorded for goldeneyes in a series of controlled experiments in northern Ontario. Goldeneyes preferred boxes with black interiors, large entrance holes (13 × 10 cm) and a depth of at least 33 cm. Compass orientation, alignment with a tree trunk and species of tree on which the boxes were situated were not factors in selection.

ACKNOWLEDGMENTS

We are grateful to the following assistants who helped check the nest boxes: G. Bain, J. Knowles, F. Close, R. Stitt, N. Quinn and A. Corbould. We also thank D. Fraser and E. Addison who read the manuscript, A. Erskine and E. Bolen who gave many useful criticisms and D. Fraser who suggested the statistical procedures. P. Tessier and his staff provided much help during the fieldwork. This paper is Ontario Ministry of Natural Resources, Wildlife Research Section Contribution No. 79-4.

LITERATURE CITED

Bent, A. C. 1925. Life histories of North American wildfowl. U.S. Natl. Mus. Bull. 130.

Blagosklonov, K. N. 1970. On the importance of illumination in the nests of birds nesting in tree hollows. Biulletin Moskovskogo obshchestva ispitatelei prisody. Otdel biologichesku 75:45–47. Translation by J. Holowacz.

Conner, R. N. 1975. Orientation of entrances to woodpecker nest cavities. Auk 94:371–374.

Corbould, E. A. 1969. Utilization of artificial nest structures by Common Goldeneyes and Hooded Mergansers. Unpubl. Rept., Ontario Ministry of Natural Resources Files.

Dement'ev, G. P. and N. A. Gladkov. 1967. Birds of the Soviet Union, Vol. 4. Publ. for

Smithsonian Inst. and N.S.F. Washington, D.C. by Israel Prog. for Sci. Transl. (Jerusalem).

Erskine, A. J. 1972. Buffleheads. Can. Wildl. Serv. Monogr. No. 4, Dept. Environment.

———. 1978. Durability of tree holes used by Buffleheads. Can. Field-Nat. 92:94–95.

Gibbs, R. M. 1961. Breeding ecology of the Common Goldeneye (*Bucephala clangula americana*) in Maine. Ms. thesis, Univ. Maine, Orono, Maine.

Johnson, L. L. 1967. The Common Goldeneye duck and the role of nesting boxes in its management in north-central Minnesota. Minn. Acad. Sci. 34:110–113.

Lloyd, L. 1854. Scandinavian adventures. Vol. II. London, England.

Lumsden, H. G. 1976. Choice of nest boxes by Starlings. Wilson Bull. 88:665–666.

McLaren, W. D. 1958. A preliminary study of nest-site competition in a group of hole-nesting birds. M.Sc. thesis, Univ. British Columbia, Vancouver, British Columbia.

Palmer, R. S. (ed.). 1976. Handbook of North American birds, Vol. III. Yale Univ. Press, New Haven, Connecticut.

Phillips, J. C. 1925. A natural history of the ducks, Vol. III. Houghton Mifflin Co., Riverside Press, Cambridge, Massachusetts.

Pitts, D. T. 1977. Do Eastern Bluebirds and House Sparrows prefer nest boxes with white or black interiors? Bird-Banding 48:75–76.

Prince, H. H. 1968. Nest sites used by Wood Ducks and Common Goldeneyes in New Brunswick. J. Wildl. Manage. 32:489–500.

Rever, M. and R. S. Miller. 1973. Common Goldeneyes and the Emma Lake nest boxes. Blue Jay 31:27–30.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York.

Siren, M. 1951. Increasing the goldeneye population with nest boxes. Suomen Riista 6:83–100, 176, 189–190.

ONTARIO MINISTRY OF NATURAL RESOURCES, WILDLIFE RESEARCH SECTION, WILDLIFE BRANCH, P.O. BOX 50, MAPLE, ONTARIO L0J 1E0 CANADA. ACCEPTED 25 FEB. 1980.

COLOR PLATE

The color plate Frontispiece of the Guayaquil Woodpecker (*Campohilus* [*Phloeceastes*] *gayaquilensis*) has been made possible by an endowment established by Dr. George M. Sutton.

GENERAL NOTES

Wilson Bull., 92(4), 1980, pp. 506–508

First description of the nest, eggs and nestling of the Guayaquil Woodpecker (*Campephilus* [*Phloeoceastes*] *gayaquilensis*).—On 29 May 1978, with J. William Eley, Enrique Ortiz, Bernard Peyton and our Peruvian guides, Daniel Cruz Quispe and Bernabé Florez Cobos, I discovered an active nest of the Guayaquil Woodpecker (*Campephilus* [*Phloeoceastes*] *gayaquilensis*). Although the species occurs from SW Colombia to NW Peru (Meyer de Schauensee, The Species of Birds of South America and their Distribution, Livingston, Narberth, Pennsylvania, 1966:227), my notes apparently provide the first description of the nest, eggs and nestling of this woodpecker.

The nest-site was in the valley of the Quebrada de Pavas (5°39′30″S, 79°45′15″W; elev. 355 m) in the western foothills of the Andes, 36 km N of the town of Olmos and 12 km NE of the small village of Boca Chica, Department of Lambayeque, Peru. The mountains and valley in the vicinity of the nest (Fig. 1) were covered with virgin dry tropical forest. Macedo Ruiz (Boletin de Lima 1:5–11, 1979) lists the common trees and shrubs of these forests.

At 10:30, as I walked along a trail that ascends the valley, a Guayaquil Woodpecker (sex unknown) flushed from a living tree containing its nest. Sr. Ortiz and our guides identified this tree as a frejolillo or huayruro. The Peruvian name "frejolillo" is sometimes used to refer to trees in at least 2 genera in different families: *Capparis*: Capparidaceae (Mapa Ecologico del Peru: guia explicativa. Oficina Nacional de Evaluacion de Recursos Naturales, Lima, 1976) and *Erythrina*: Fabaceae (Macedo Ruiz 1979). In Soukup (Vocabulario de los Nombres Vulgares de la Flora Peruana, Colegio Salesiano, Lima, 1970), huayruro refers to *Erythrina*; and although "frejolillo" does not appear, the name "frijol del arbol," refers also to *Erythrina*.

The nest cavity was in the main trunk about 6 m above the ground. Its irregularly shaped entrance was large enough (about 75 × 100 mm) to admit my hand, and it was about 30 cm deep. I could not reach the cavity's bottom or its contents, but using a mirror, I saw 1 egg and 1 newly-hatched young. The shell of the hatched egg was still in the nest. The eggs were white and immaculate—typical large woodpecker eggs. The nestling was making weak chirping sounds. Its eyes were closed, and it appeared naked; however, in the dim light of the cavity, sparse down probably would not have been obvious. It had a conspicuous eggtooth.

I visited this nest again at 13:50. After approaching within 6–8 m of the female at the cavity entrance, I made several color transparencies (Frontispiece). I never saw more than 1 adult at this site.

Casual reference to the nesting of this species has been made at least twice in the literature. Goodfellow (Ibis 44:207–233, 1902) stated, "A pair of these woodpeckers bred in October [1898] in the trunk of a tall dead tree standing in the clearing near our hut." This was near Santo Domingo de los Colorados, Pinchincha, Ecuador. Leck (Auk 96:353–363, 1979) said the species, ". . . was found nesting in 1977 . . . ," also in Ecuador, in an area 47 km S of Santo Domingo de los Colorados along the Rio Palenque. Leck (pers. comm.) wrote, "I don't have the details . . . the nesting record was passed on to me without any specifics."

The closest relative of *C. gayaquilensis* is the widely distributed Crimson-crested Woodpecker (*C. melanoleucos*). Peters (Check-list of Birds of the World, Vol. 6, Harvard Univ. Press, Cambridge, Massachusetts, 1948) regarded *C. gayaquilensis* as a subspecies of *C. melanoleucos*, but Meyer de Schauensee (1966) maintained them separate on the basis of strikingly different plumage patterns.

FIG. 1. Nest-site of the Guayaquil Woodpecker in dry tropical forest, NW Peru.

Regarding the nesting of *C. melanoleucos* in Surinam, Haverschmidt (Birds of Surinam, Oliver and Boyd, Edinburgh and London, United Kingdom, 1968) stated, "[it] makes a hole with an oval entrance in dead trees . . . ." Kilham (Wilson Bull. 84:28–47, 1972) implied that on his study area in the humid forests of Panama, *C. melanoleucos* nests only in dead trees, and concluded, "most pairs had difficulty finding suitable nest stubs . . . [and] in some cases failed to nest." Three nests of another close relative, the Pale-billed Woodpecker (*C. guatemalensis*), found by Skutch (Pacific Coast Avifauna, No. 35, 1969) in Costa Rica were all in dead trunks that stood in clearings in the forest. As Short (Wilson Bull. 91:16–28, 1979) has pointed out, the advantages of nesting in an isolated tree may be sufficient to cause a woodpecker to depart from its typical nesting site. Our information on this point is likely to be biased, however, since we can find nests in clearings more easily. Short (1979) reasoned that cavities in live trees generally reduce losses to competitors and predators. Perhaps in a dry tropical forest with fewer predators and competitors, Guayaquil Woodpeckers can afford to take the extra time required to excavate a cavity in a living tree. In these relatively "safer" forests, however, there should be less pressure to nest in living trees. Possibly excavating a cavity in a hard dead tree in a dry forest, where decomposition is slow, is more difficult than excavating in some living trees. The irregularly shaped entrance of the Lambayeque nest cavity suggests that it may have been an enlargement of an existing hole, perhaps a further inducement to excavate in a living tree. Since the only other reported nest of the Guayaquil Woodpecker was in a dead tree in a clearing, which nest site, if either, is typical remains unknown.

This pair of woodpeckers presumably began their nesting in early May at the end of the rainy season. *Campephilus melanoleucos* and *C. guatemalensis* follow this same pattern in Panama (Kilham 1972) and Costa Rica (Skutch 1969), respectively.

Acknowledgments.—I am grateful to Babette M. Odom, John S. McIlhenny, Edmund W.

Mudge, H. Irving Schweppe and Laura R. Schweppe for their financial support of the LSUMZ Peruvian expeditions, and to our colleagues of the Dirección General Forestal y de Fauna of the Ministerio de Agricultura in Lima for granting the necessary permits for fieldwork. The knowledge and hospitality of Srs. Manuel A. Plenge and Gustavo del Solar greatly facilitated my studies of Peruvian birds. I thank E. Eisenmann, J. A. Jackson, J. P. O'Neill, K. C. Parkes, J. V. Remsen and L. L. Short for their comments and suggestions during the preparation of this note. A grant from the Chapman Memorial Fund enabled me to study the nests and eggs of neotropical birds at the American Museum of Natural History in 1979.—MORRIS D. WILLIAMS, *Museum of Zoology, Louisiana State Univ., Baton Rouge, Louisiana 70893.* *Accepted 5 Aug. 1980.*

Wilson Bull., 92(4), 1980, pp. 508–509

The nest and territoriality of a female Tyrian Metaltail.—There are no previous records of nesting of the Tyrian Metaltail (*Metallura tyrianthina*), or any other species in this genus. A female Tyrian Metaltail was discovered building a nest on 19 July 1978, in a small cave at 2400 m on the slopes of Cerro Fonté, Vereda de Ferralarada, Municípío de Choachi, Cundinamarca, Colombia (4°32′N, 73°51′W). The small cave measured 1.2 m deep by 2.4 m wide by 1.8 m high and the pendent nest was attached to plant rootlets and moss near the back wall at a height of 1.3 m. Because we had to leave the area on 25 July neither a completed nest nor contents were seen. The nest, collected before departure, consisted of a mass of moss with pieces of fern and plant fibre and measured 14 × 7.5 × 7.5 cm; at the top was a small nest chamber partially covered by a domed roof of moss. The nest cup lacked lining material.

A total of 9.5 h on 5 days was spent watching in the territory of the nesting female metaltail. Building occurred between 07:25–09:54 on 3 days, when material, mostly moss, was collected nearby, so close that often the female went in with it every 30 sec, entering through the open mouth of the cave and slipping out at the side through overhanging vegetation. On 21 July, the last day building was observed, all material brought was added to the roof. The female also engaged in frequent nest shaping on this day, entering the nest cup and pressing down with her tail as she faced inwards, with her breast and neck as she faced outwards, pausing to adjust the material of the roof above her.

The feeding territory of this female consisted of a triangle of woodland measuring 20 × 25 × 24 m, 1 side being a rocky boundary with the cave. This rocky face extended 46 m and was covered with a 1–7 m wide strip of shrubby vegetation, ending in a group of young eucalyptus (*Eucalyptus* sp.) trees, 1 of which was in flower. All this wooded and shrubby area was included in the female's territory; it was surrounded by rough pasture with scattered trees.

The main nectar resource in the territory on 17 July, when the female's territorial activities were first noted, consisted of a number of *Palicourea angustifolia* (Rubiaceae) shrubs with a total of 59 flowering spikes, 8–10 blooms per spike. The female defended this resource from other metaltails, including a male, and from a female Mountain Velvetbreast (*Lafresnaya lafresnayi*). The female metaltail also fed within the territory on 2 vines of *Manettia coccocypseloides* (Rubiaceae), flowering eucalyptus, and some shrubs of *Palicourea* cf *anacardifolia* with only a few blooms still in flower.

Within the territory the female metaltail uttered a *chack* call between feeding probes. She occasionally sang in flight and when perched, particularly in the morning between dawn and

08:00. The song, which lasted 2 sec, I transcribed as *whit-ser see see see see see*; at times the last 4 notes were delivered in a crescendo. Male metaltails were not heard singing this song, but 2 other females were heard to sing it, which suggests that it may be characteristic of females.

Large rocks and rocky outcrops, clothed in moss when in woodland, were a feature of the slopes of Cerro Fonté between 2400–2500 m. Many similar nest-sites were therefore available for metaltails, which were among the most abundant hummingbird species in the area. It seems probable that during the breeding season the availability of such rocky nest-sites affects the local distribution of this species.

Nests situated in caves or rocky overhangs occur in 3 other hummingbird genera, the hillstars *Oreotrochilus* (Dorst, Oiseau R.F.O. 32:95–126, 1962), the comets *Sappho* (Contino, Hornero 11:265–270, 1975) and the lancebills *Doryfera* (Snow and Gochfeld, Bull. Br. Ornithol. Club 97:121–125, 1977). The amelioration of temperature extremes at high altitudes enjoyed by *Oreotrochilus* roosting and nesting at these sites is well documented (Carpenter, Univ. Calif. Publ. Zool. 106:1–74, 1976). In addition, nesting success is unusually high, probably because of the protection provided from predators. Night temperatures at Cerro Fonté fell to 5°C under a veranda, and at times there were chilling misty rains, so safety and protection from the elements have probably influenced the evolution of the metaltail's choice of nest-site.

Female territoriality over nest-site and adjacent feeding area is normal in the Andean Hillstar (*Oreotrochilus estella*), for whom nest-sites are scarce and probably limit local breeding populations (Carpenter 1976). Female Anna Hummingbirds (*Calypte anna*) also defend nest-site and nearby nectar resources, but apparently choose the nest-site after a suitable nectar source has been found (Stiles, Univ. Calif. Publ. Zool. 97:1–109, 1971). Further study will probably prove the relatively scarce nest-site to be the more critical factor in the choice of territory by female metaltails.

I acknowledge with thanks financial assistance from the Frank M. Chapman Memorial Fund of the American Museum of Natural History—BARBARA K. SNOW, *Old Forge, Wingrave, Aylesbury, Buckinghamshire, England.* *Accepted 7 Aug. 1979.*

Wilson Bull., 92(4), 1980, pp. 509–511

Male escorting and protecting females at the nest cavity in Mountain Bluebirds.—The Mountain Bluebird (*Sialia currucoides*) is a monogamous, hole-nesting species with parental care almost evenly divided between males and females (Power, Condor 68:351–371, 1966; Power, The Mountain Bluebird, Ph.D. thesis, Univ. Michigan, 1974). In 9 breeding seasons of observation in Cascade County, Montana, between 1961 and 1977, I found that males generally were present when their mates entered or left their nests during the period from pair formation through the brooding of young chicks. During 1976 and 1977, I counted the number of times the male was present when the female arrived or departed at 17 nests in the nest-building through brooding stages. Closed circuit television was used to observe the interiors of 6 of these nests.

A total of 342 arrivals (N = 176) and departures (N = 166) were observed. On 329 (96%) occasions (168 arrivals, 161 departures), the location and behavior of the male was determined. The male was in view of the female on 265 (81%) occasions, i.e., on 138 (82%) arrivals and 127 (79%) departures. Because males frequently were not near their nests at other times and females usually did not enter or leave their nests in the absence of males, I find it appropriate to refer to the presence of males at these times as "male escorting."

Males also escorted females in more active ways than by merely being present. From early pair formation through laying, males often encouraged females to enter the nest cavity by giving a display similar to the nest demonstration display of the congeneric Eastern Bluebird (*S. sialis*) described by Krieg (N.Y. State Mus. Sci. Serv. Bull. 415, 1971). This display was sometimes given as late as the incubation stage, albeit rarely. On 69 (50%) occasions when the male was present at the nest, the female entered the nest only after the male first had gone to the nest box (N = 28), or encouraged her by displays (singing, calling and wing-flicking; N = 31), or mate-feeding (N = 10). Similarly, on 81 (64%) occasions when the male was present, the female came off the nest after the male returned from a period of absence (N = 4), or signalled her by displays (N = 46), coming to the nest entrance (N = 13), or offering a mate-feeding (N = 18). On 4 occasions, when a female frightened by a vehicle refused to return to her nest to incubate, her mate unsuccessfully attempted to induce her to return by carrying nesting material to the entrance (N = 3) or to the female herself (N = 1).

The importance of the male in encouraging the female to return to the nest was shown dramatically at a nest box (numbered 41a) in 1976. This nest box was attached to a booth, allowing observation of its interior. Since I did not acquire closed circuit television until the following year, I observed this nest by sitting in the booth and watching it through a single lens reflex camera (55 mm). Although I was as quiet as possible, my occasional movements, the noise of writing notes and my eye showing through the reflex lens all made the female very nervous and she frequently left the nest. On 2 occasions the male seemingly induced the female to re-enter the nest by going there himself and uttering soft, screechy noises not heard at other times. The male appeared to be even more frightened of me than the female when inside the nest box.

Male escorting probably evolved partly to reduce males' risk of cuckoldry because escorting informs males of females' whereabouts during and beyond the time when surreptitious insemination of their mates could occur (Power and Doner, Am. Nat., in press). However, Pinkowski (Auk 95:606–607, 1978) found in Eastern Bluebirds that male escorting reduces female hesitancy in entering the nest. Females could be expected to be less hesitant if escorting reduced the probability of their own predation.

Predation at or near the nest is a real threat for female Mountain Bluebirds. At least 4 of about 91 females nesting in 1975 and 1976 were killed. Due to frequent nest censuses and color wing-tagging it was possible to estimate mortality and population size through identification of distant and flocked individuals, as well as those on or near their nests. At least 3 of these 4 females were apparently killed by hawks, judging from feathers strewn around the nest-sites. The contents of these 4 females' nests were not disturbed, but those of another 3 females were eaten or removed by a red squirrel (*Tamiasciurus hudsonicus*), by a deer mouse (*Peromyscus maniculatus*) and by an unknown agent, respectively. The female survived in the deer mouse case and perhaps in all 3, although 2 females whose nests were destroyed were never seen again. Parallel to these observations, I have twice seen male Mountain Bluebirds chasing least chipmunks (*Eutamias minimus*) away from the vicinity of their nests, and frequently have seen Cooper's Hawks (*Accipiter cooperii*), American Kestrels (*Falco sparverius*) and Merlins (*Falco columbarius*) hunting over the study area.

Male escorting should reduce the threat of predation on females. Furthermore, inspection of cavities by males before females enter should reduce the threat of ambush to females by predators (mammals?) hiding in nests. Finally, signalling females to emerge and giving alarm notes when predators are near should reduce the threat of ambush to females from hawks waiting outside nest cavities.

Despite the apparent value of these services, females still incurred most of the predation risks of nesting, as shown by the absence of known male deaths during the time when at least 4 females were killed. It is noteworthy that males performed the risky task of inspecting nest cavities significantly less often than the non-risky task of indicating that it is safe for females to emerge from their nests ($\chi^2 = 49.9$, df = 1, $P < 0.001$). By reducing the risk of predation on their mates, males probably increase their own chances of reproductive success by protecting the lives of their future or actual offspring.

I thank C. G. P. Doner, P. C. Hanson and G. B. Van Vliet for help in fieldwork, and the National Science Foundation for partly supporting my research through grants BNS76-08840 and BNS77-09299.—HARRY W. POWER, *Dept. Biology, Livingston Coll., Rutgers Univ., New Brunswick, New Jersey 08903.* *Accepted 19 Sept. 1979.*

Wilson Bull., 92(4), 1980, p. 511

Solitary Vireo nest used by a Western Flycatcher.—In northern Napa County (2.7 km SSW Aetna Springs), California, we discovered a Western Flycatcher (*Empidonax difficilis*) using the nest of a Solitary Vireo (*Vireo solitarius*). The nest was first observed 8 May 1977, when it contained 4 vireo eggs and 1 Brown-headed Cowbird (*Molothrus ater*) egg. When we approached, a vireo flew from the nest, and, with another vireo, presumably its mate, scolded us as we examined the contents. On 14 May, a vireo was brooding 4 nestlings and 1 unhatched cowbird egg. We did not observe the nest again until 4 June when 2 Western Flycatcher eggs were found in it. The identity of the eggs was confirmed on 5 June when we found a Western Flycatcher on the nest, which contained 3 flycatcher eggs, of which one had probably been laid that morning. The nest had not been modified from its condition at the time of the vireo nesting. We watched the bird for several minutes from within 6 m after it had flown from the nest. Because we had been observing several flycatcher nests in the area, our identification of the bird as a Western Flycatcher was immediate. In addition, the eggs had the brownish spotting typical of a Western Flycatcher rather than the blackish or dark gray spotting of a Solitary Vireo. We returned to the nest 18 June hoping to photograph nestlings and the brooding adult flycatcher; however, we found the nest deserted.

The nest was located at the end of a branch of a toyon (*Heteromeles arbutifolia*) shrub within a dense stand of Douglas-fir (*Pseudotsuga menziesii*). The nest was a well-formed cup suspended 1.5 m above ground. The few surrounding toyon leaves did not conceal the nest. The nest-site was typical of local Solitary Vireos, but atypical of the Western Flycatcher. Local flycatcher nests were invariably placed on solid structures (often man-made), usually resting against a solid vertical wall, with some kind of "roofing" directly above them.

The poorly concealed, abandoned nest of a Solitary Vireo would probably be an easily found egg receptacle of appropriate size (both species weigh 12–14 g) for a flycatcher whose nest had been destroyed. In our study area, young vireos fledged by 4 June at all 8 of the nests that we observed in 1977. Flycatchers were incubating eggs until at least mid-June. Thus, late-nesting or re-nesting flycatchers could use vireo nests without confronting the vireos. Once the first egg was laid psychological attachment to that nest-site would probably develop and the remainder of the nesting cycle would therefore be completed in the "adopted" nest. To our knowledge, this is the first report of a Western Flycatcher laying its eggs in the nest of another species.

We thank the Biological Field Studies Association for allowing us access to the study area and Dr. N. K. Johnson for providing us with the weights of the birds and his comments on the manuscript. Dr. J. C. Barlow also reviewed the manuscript.—GEOFFREY A. HAMMERSON AND BETH P. LAPIN, *Dept. Biological Science, California State Univ., Hayward, California 94542.* (Present address GAH: *Dept. Environmental, Population and Organismic Biology, Univ. Colorado, Boulder, Colorado 80309.)* *Accepted 30 July 1979.*

Wilson Bull., 92(4), 1980, pp. 512–513

Bilateral wing display in the Sage Thrasher.—A particular bilateral wing display termed wing-flashing has been the subject of many notes in this journal particularly involving the Mockingbird (*Mimus polyglottus*) (see Horwich, Wilson Bull. 77:264–281, 1965). However, other Mimidae have also been observed exhibiting similar behavior (Hailman, Wilson Bull. 72:346–357, 1960) wherein both wings are simultaneously lifted high above the back for a short period. Some confusion probably exists between wing-flashing and other bilateral wing movements. True wing-flashing is described as wing extension interrupted by 1–5 "hitches" or pauses and followed by rapid wing closure (Whitaker, Wilson Bull. 69:361–363, 1957; Hailman 1960). Perhaps due to the problem of definition the origin and function of wing-flashing have been disputed. The display has been associated with foraging (Hailman 1960), "uneasiness" and landing after flight (Horwich 1965) and agonistic displays (Selander and Hunter, Wilson Bull. 72:341–345, 1960).

Sage Thrashers (*Oreoscoptes montanus*) use a bilateral wing display throughout the early and middle stages of the breeding season in south-central Idaho. The wings are not raised in "hitches" but the display may be homologous with wing-flashing. Although I have never worked with marked birds, I believe it was only the male that displayed. A typical display sequence was as follows. The male performed an undulating circular flight over a part of his territory while continuously vocalizing, landed on a perch with wings extended high over his back and repeatedly raised and lowered his wings while singing from the perch. In some cases, the display was of low intensity with only partial raising and lowering of the wings. Thus, the display seemed to vary with motivation. In most cases, a displaying bird was some distance from other displaying birds. However, I have seen up to 4 birds perched within 3 m of each other, all displaying. It seems clear that the bilateral wing display in the Sage Thrasher is primarily a territorial display.

Horwich (1965), Hailman (1960) and Selander and Hunter (1960) have evidence of wing-flashing in young mimids that suggests the basic movement is innate. This behavior was observed early in development and decreased with experience so that the display was given more "appropriately" in adults. Horwich (1965) found that 69% of wing-flashes in young Mockingbirds were associated with escape tendencies, ambivalence and "uneasiness" towards strange objects. Selander and Hunter (1960) found that adult Mockingbirds wing-flashed at owls and in territorial encounters with conspecifics. Several authors report mimids wing-flashing at snakes (see Horwich 1965).

In all of these instances and in some of my observations there are elements of approach-avoidance. Selander and Hunter felt that wing-flashing was a ritualized flight intention display. However, Horwich (1965), myself and others have observed an association between bilateral wing displays and landing after flight. Horwich believed that balancing was the primary basis for the movement in fledglings. So there may be 2 separate primitive functions, flight and balancing, with similar motor patterns leading to the original display. In Sage Thrashers, the display may thus be most precisely considered as a ritualized balancing movement.

In Mockingbirds, the wing-flash has apparently undergone strong secondary evolution to accompany foraging, as Hailman (1960) believed that to be the primary function of the movement in adults of that species. In Sage Thrashers, the bilateral wing display has evolved to serve primarily as a visual display; I have never seen it used by foraging thrashers. The selective pressure for such a display is understandable given the thrasher's uniform low habitat where the display can be seen for more than 200 m. The bilateral wing display also complements the striking flight display of the species. Observations of bilateral wing displays and their functions in other mimids should provide further insight into understanding these displays and, more generally, into why the Mimidae apparently have a propensity for this use of the wings.

These observations were made while conducting research supported by the Frank M. Chapman Memorial Fund of the American Museum of Natural History and the Society of Sigma Xi.—TERRELL D. G. RICH, *Dept. Biology, Idaho State Univ., Pocatello, Idaho 83209.* (Present address: *P.O. Box 204, 518 S. Alta, Shoshone, Idaho 83352.)* *Accepted 3 Aug. 1979.*

Wilson Bull., 92(4), 1980, pp. 513–519

A comparison of avian foraging at flowering trees in Panama and New Guinea.—Mixed-species foraging aggregations at fruiting and flowering trees are striking features of the humid tropics, where in some instances, 10–15 species of birds, from 5 or more families, may share the same, temporarily super-abundant resource (Moynihan, Smithson. Misc. Coll. 143:1–140, 1962; Land, Wilson Bull. 75:199–200, 1963; Diamond and Terborgh, Wilson Bull. 79:273–282, 1967; Terborgh and Diamond, Wilson Bull. 82:29–52, 1970). Birds visiting flowering trees consume nectar, pollen and insects. Though it is often difficult for the field observer to discern which item is being taken by which species (Snow and Snow, Auk 88:291–322, 1971), the tree represents a locus of high abundance for all 3 resources, and the result is aggregations of invertebrate and vertebrate foragers.

In this note I discuss observations made at a single flowering tree in Panama in January 1978, and compare these with data of a similar nature that I gathered in Papua New Guinea in 1975–1976. My short-term observations in Panama cannot be generalized for the Neotropics or even for Panama in all seasons; but the data, limited as they are, indicate potentially significant differences among foraging by Neotropical honeycreepers and New Guinea honeyeaters and lories. In treating these data, I ask 2 questions: (1) to what extent is there some sort of flocking organization, as opposed to unstructured aggregation, at flowering trees; and (2) does the pattern of resource-use in Panama differ from that in New Guinea?

Methods.—I watched a single flowering tree in relatively undisturbed mature second-growth forest along the Pipeline Road, Canal Zone, Panama. The tree was a 27-m high *Luehea seemanii* (Tiliaceae), surrounded by an uneven canopy varying in height from 22–33 m. During the period of observation, 12–15 January 1978, the *Luehea* was festooned with small, whitish, pedicellate blossoms. There were no other flowering trees in the immediate vicinity. Observations were made from a 28-m aluminum tower that stood about 30 m from the tree and afforded an unimpeded view of the entire crown of the *Luehea.* I censused all birds visiting the tree every 15 min, for a period of 5 min. Each 5-min census is considered an "instantaneous snapshot" of avian use of the tree. I also noted all instances of intra- and interspecific aggression. At no point were more than 16 birds in the tree at once; I had no difficulty watching and taking notes simultaneously. All identifications were made using 8.5 × 44 Swift binoculars, with the aid of Ridgely's Guide to Panamanian Birds (Princeton Univ. Press, Princeton, New Jersey, 1976).

My observations in New Guinea were made sporadically from April 1975 through June 1976. I observed at several localities on New Guinea proper (Wau, 1100 m, June–July 1975; Goroka, 1500 m, September 1975; Mt. Missim, 1050, 1400 and 1750 m, December, January and March 1975–1976; and Bulldog Road, 2600 m, on 10 occasions during 1975–76). I also watched on New Ireland in February 1976 and on Goodenough Island in April 1976. Nearly 100 different flowering trees were watched during the period, from sea level to 3000 m. Because the observations were incidental and not the focus of my main research, I did not

TABLE 1

OBSERVATIONS OF BIRDS FORAGING AT FLOWERING *LUEHEA*, 12–15 JANUARY 1978

Date	12 Jan.			13 Jan.										14 Jan.										15 Jan.								
Time	10:45	11:00	17:30	07:15	09:15	09:30	09:45	10:00	10:15	10:30	10:45	11:00	11:15	07:45	08:00	08:15	08:30	08:45	09:00	09:15	09:30	09:45	10:00	09:00	09:15	09:30	09:45	10:00	10:15	15:15	15:30	
Species																																
Shining Honeycreeper (*Cyanerpes lucidus*)					3	3	1		3			3			3	6	4	5	1	5	2	4	7	5	4	4		1	2			66
Red-legged Honeycreeper (*C. cyaneus*)					3	5	4	1							4	2	3	3	4	3	1	6	6	3	4							52
Blue Dacnis (*Dacnis cayana*)					3	2	2		1							3	2	3		4	2	2	2	2	2	2						32
Green Honeycreeper (*Chlorophanes spiza*)					2	1	2	2	2				1					1	2	1	2	1	1	2	1	2	1	2	2			28
White-necked Jacobin (*Florisuga mellivora*)	1						1	1									1				1				1							6
Summer Tanager (*Piranga rubra*)	1	1							1			1	1						1													6
Tennessee Warbler (*Vermivora peregrina*)								1							1	1					1			1								5
Unidentified hummingbird (Trochilidae)									1		1		1		1							1			1	1						7
Other visitors[a]				1		1																1								1		4
Total individuals/census	2	1	0	1	11	12	10	5	8	0	1	4	3	0	9	12	10	12	8	13	9	15	16	13	13	9	1	3	4	1	0	206

[a] Four species each visited only once: a wood warbler (13 Jan., 07:15), *Euphonia* (13 Jan., 09:30), a *Lophornis* hummingbird (14 Jan., 10:00) and a Great Crested Flycatcher (*Myiarchus crinitus*) (15 Jan., 15:15).

TABLE 2

DETERMINATION OF THE STATISTICS OF CONSOCIATIVE FLOCKING BY HONEYCREEPERS AT A FLOWERING TREE

	No. observation periods = 27	
Species	No. times observed	Probability of occurrence
Shining Honeycreeper	19	0.70
Red-legged Honeycreeper	15	0.56
Blue Dacnis	14	0.52

	No. species present	1 species	2 species	3 species
Prob. of chance co–occurrence:	$(1 - P_1)(1 - P_2)(1 - P_3)$	$P_1(1 - P_2)(1 - P_3) +$ $P_2(1 - P_1)(1 - P_3) +$ $P_3(1 - P_2)(1 - P_1)$	$P_1P_2(1 - P_3) +$ $P_1P_3(1 - P_2) +$ $P_2P_3(1 - P_1)$	$P_1P_2P_3$
Expected:	1.71	8.02	11.76	5.5
Observed:	7	4	4	12

$\chi_3^2 = 31.18$, $P < 0.001$

Chlorophanes flock association

Number of periods of observation when at least 1 honeycreeper was present in the tree = 22. *Chlorophanes* was present on 18 occasions; $P_4 = 18/22 = 0.82$. All 4 honeycreepers will co-occur by chance at a frequency of $P_{123} \times P_4$, where $P_{123} = 0.55$; on 55% of my 22 observations I saw all 3 "flockers." By chance, then, all 4 honeycreepers should co-occur at a frequency of $0.55 \times 0.82 = 0.45$.

	All together	All not together
Expected:	$0.45 \times 22 = 9.92$	$0.56 \times 22 = 12.32$
Observed:	10	12

$\chi_1^2 = .0226$, $P > 0.70$

collect normalized and systematic data as I did in Panama. Instead, I monitored relative inter-individual aggression and species-abundance at the different locales.

Panama flowering tree.—During the 31 censuses made at the Panamanian flowering tree (*Luehea*), 12 species of birds were noted, but only 8 were regular visitors (Table 1). Of the 206 observations of individual foragers, 178 (86%) were of honeycreepers (either Blue Dacnis [*Dacnis cayana*], Red-legged [*Cyanerpes cyaneus*], Shining [*C. lucidus*], or Green [*Chlorophanes spiza*]). These 4 species were the key foragers at the flowering tree, coming in pairs and small parties. Other species invariably visited the tree as solitary foragers, represented by a single regular individual that visited each day for a period of time (Table 1).

Snow and Snow (1971) discussed the ecology and morphology of the 4 honeycreepers that were the dominant foragers during my observations (for biometric data and a comparative photograph of the birds, refer to that paper). Of these 4 species, the *Dacnis* and 2 *Cyanerpes* seemed to come and go from the tree as a heterospecific flock. *Chlorophanes* was often in the tree with the other 3, but neither associated, nor came and went with the "flock."

To determine if the 3 honeycreepers acted as a coordinated flock (see Table 1), I tested whether their presence together in the tree or mutual absence from the tree deviated from a random association produced by their respective temporal distributions at the tree (Table 2). Censuses in which I saw no birds at the tree were excluded from the test, so that the birds would not appear more gregarious than they really were. The average probability for presence of each species in the tree at any random census was computed by dividing total number of censuses with the species present by absolute total number of censuses with any birds in any tree. From these probabilities, the expected frequency of co-occurrence, if the birds were acting independently, was computed and compared with observed frequencies. Table 2 shows that *D. cayana*, *C. cyaneus* and *C. lucidus* were forming a non-random consociation at the feeding tree. The fourth species, *Chlorophanes spiza*, segregated from this flock (Table 2).

My observations on inter-individual aggression further confirmed the census results. The 3 flocking species showed very little inter-individual aggression—I recorded no interspecific aggression and only 1 case of intraspecific aggression. When a small flock of 5–10 birds entered the tree, the birds foraged in clumps rather than spreading out for maximum spacing of individuals. In some cases, 3–4 birds would forage within the same m^3 of vegetation.

In contrast, *Chlorophanes* showed entirely different dispersion and interspecific behavior. This species chased the other honeycreepers on a number of occasions, and never foraged near the others. Rather, a pair of these birds (male and female) defended an apparent feeding territory in a discrete portion of the tree. I saw no other conspecifics enter the tree, and the other honeycreepers seemed to forage away from the "territory" established by the pair of *Chlorophanes*. The pair of *Chlorophanes* was rather sedentary, and while the flocking birds arrived and departed frequently, the *Chlorophanes* remained in their territory for long periods. During all 4 days of observation the pair remained in the same restricted area of the flowering *Luehea*.

New Guinea flowering trees.—Birds that fed in flowering trees in New Guinea were dominated by honeyeaters (Meliphagidae) and lories (Psittacidae). In addition, flycatchers (Muscicapidae), warblers (Acanthizidae), drongos (Dicruridae), birds of paradise (Paradisaeaidae), sunbirds (Nectariniidae) and white-eyes (Zosteropidae) often fed in flowering trees. Table 3 shows assemblages from 3 diverse localities in Papua New Guinea. These 3 samples vary in composition, although their behavior was similar.

The 3 visitors to the cocoanut palm (*Cocos nucifera*) comprise the simplest feeding group. The interactions that took place among these birds typify all New Guinea observations. The brush-tongued lories (in this case *Charmosyna placentis*) visited the tree in monospecific flocks of 3–4 birds. The sunbird and honeyeater visited solitarily. All intra- or interspecific actions between individuals were aggressive—supplanting, threatening and even chasing. There was no evidence of heterospecific flocking nor any form of inter-individual cooperation.

Among all New Guinea feedings assemblages that I have observed, only lories, white-eyes and the warbler, *Acanthiza murina*, form flocks that feed in flowering trees. All are monospecific. Even in these cases there is inter-individual aggression among flock members.

Honeyeaters usually dominated in a flowering tree, whatever the elevation or locale. Although honeyeaters feed in multispecies aggregations, they are invariably solitary and aggressive. In no instance have I observed organized heterospecific flocks visit New Guinea trees to feed on flowers.

My brief observations at the tree in Panama indicated a quiet, even orderly, aspect of group feeding. My New Guinea experiences involved avian assemblages that were veritable riots of inter-individual aggression. In general, the organizing factor among the New Guinea birds seemed to be dominance hierarchy, based on size and aggressiveness. The larger species were usually more successful; thus, they occupied the favored feeding spots with minimum harrassment. But, even under the best of circumstances, the dominant species in a tree spent most of the time supplanting and chasing conspecifics and smaller heterospecifics. This is documented by Terborgh and Diamond (1970) and Ripley (Am. Nat. 93:127–132, 1959).

TABLE 3
REGULAR AVIAN VISITORS TO 3 FLOWERING TREES IN PAPUA NEW GUINEA

Cocoanut Palm (*Cocos nucifera*)
(Coastal scrub, New Ireland Province, 7–8 February 1976)

Species	Abundance[a]	N[b]	$\bar{x}$ weight[b]	SD[b]
Yellow-fronted Blue-eared Lory (*Charmosyna placentis*)	3–4	9	35.5	±4.3
Black Sunbird (*Nectarinia sericea*)	1–2	1	9.7	—
Red Myzomela (*Myzomela cruentata*)	1–2	3	9	±0

Rhus taitensis (Anacardiaceae)
(Mid-montane second-growth forest, Morbe Province, July 1975)

Species	Abundance	N	$\bar{x}$ weight	SD
Rainbow Lory (*Trichoglossus haematodus*)	5–10	4[c]	113.1	±10.6
Spangled Drongo (*Dicrurus hottentotus*)	1	3	78.8	±2.3
Long-billed Honeyeater (*Melilestes megarhynchus*)	1	10	46.6	±1.7
Mt. Red-headed Myzomela (*Myzomela adolphinae*)	3–4	2[c]	7.1	±1.3
White-marked Honeyeater (*Meliphaga albonotata*)	1–2	14	30.7	±2.3
Tawny-breasted Honeyeater (*Meliphaga flaviventer*)	2–3	12	47.3	±4.2
Marbled Honeyeater (*Pycnopygius cinereus*)	2–3	7	48.8	±3.9
Cinnamon-breasted Wattlebird (*Melidectes torquatus*)	4–7	7	52.4	±3.6
Black-fronted White-eye (*Zosterops atrifrons*)	10–25	11	11.5	±0.7

Xanthomyrtus papuanus (Myrtaceae)
(Upper montane primary forest, Morobe Province, October 1975)

Species	Abundance	N	$\bar{x}$ weight	SD
Fairy Lory (*Charmosyna papou*)	2	1[c]	119	—
Plum-faced Mountain Lory (*Oreopsittacus arfaki*)	5–10	2	22.4	±0.1

TABLE 3
CONTINUED

Xanthomyrtus papuanus (Myrtaceae)
(Upper montane primary forest, Morobe Province, October 1975) (continued)

Species	Abundance	N	$\bar{x}$ weight	SD
Orange-billed Mt. Lory (*Neopsittacus pullicauda*)	4–6	3	35.7	±2.4
DeVis Tree Warbler (*Acanthiza murina*)	3–5	1[c]	9	—
Black and Red Honeyeater (*Myzomela rosenbergii*)	3–6	15	11	±2.5
Black-throated Honeyeater (*Meliphaga subfrenata*)	1–2	4	33.75	±2.4
Brown-backed Streaked Honeyeater (*Ptiloprora guisei*)	2–3	10	24.2	±1.7
Belford's Melidectes (*Melidectes belfordi*)	1–2	4[c]	82	±6.4
Sooty Honeyeater (*Melidectes fuscus*)	1	1[c]	44	—

[a] Abundance indicates average number of individuals observed in the tree simultaneously during active periods of foraging.
[b] Data are from Diamond (Nuttall Ornithol. Club, Cambridge, Massachusetts, 1972).
[c] Beehler field data, taken 1975.

Discussion.—During my studies, Panamanian honeycreepers foraged in a fashion different from the honeyeaters and other New Guinea visitors to flowering trees. My Panamanian data, limited to observations at 1 tree and in 1 season, cannot show that this difference is apparent year-round, or even from tree to tree. Moynihan (1962) mentions aggression among the species of honeycreeper that I discuss, but his observations are vague, not necessarily related to activities at flowering trees and often discussed out of context of foraging activities. (He was more concerned with the ontogeny of flock development and behavioral hierarchies without relation to the energetics and ecology of the situation.) In periods of high forager abundance, levels of aggression in feeding trees seem to be increased (Leck, Condor 74:54–60, 1970). Carpenter and MacMillen (Science 194:639–641, 1976) show that in Hawaii, the Iiwi (*Vestiaria coccinea*) is territorial in a flowering tree when the nectar resource is rich enough for defense to be justified, but not so rich that it would be a waste of time to try to monopolize it.

In Panama, the 3 flocking honeycreepers came and went as a group, while *Chlorophanes* did not. Diets may give an indication of why this foraging difference may exist. The 3 flocking species spent much of their time taking primarily nectar (Snow and Snow 1971), which can be quickly depleted during the day. The nectivorous birds must compete with bees and other insects; thus, it pays them to work efficiently to maximize caloric intake. By feeding as an organized group, the flock of honeycreepers can systematically "crop" the nectar resource in the manner of Cody's finch flocks in the Mojave Desert (Cody, Theoret. Pop. Biol. 2:142–158, 1971). This might explain why the honeycreeper flocks congregated in 1 section of the tree when they foraged. *Chlorophanes*, on the other hand, spends less time nectar-feeding (Snow and Snow 1971) and more time taking arthropods that visit flowers. It may pay *Chlo-*

rophanes to stake out a space in the tree and systematically to feed on foraging insects. The arthropods are probably a rapidly renewing resource that is difficult to harvest, but which pays a relatively high nutritional reward. Renewal may be so rapid as to be "instantaneous"—making the resource temporally stable, quite unlike the rapidly depleted and slowly renewing nectar resource. The sedentary and aggressive characteristics of *Chlorophanes* may reflect the most economical foraging strategy.

I can only speculate as to why my limited Panamanian observations are so radically different from those I made in New Guinea. The birds that regularly visit flowering trees in New Guinea are more diverse and include many birds that are much larger than the honeycreepers. The Panamanian species all resemble the *Myzomela* honeyeaters—a small specialized subset of the diverse New Guinea assemblage. The majority of flower-visitors in New Guinea are only opportunistically nectivorous; most spent their time gleaning insects from the flowers and foliage (pers. obs., unpubl. data, Terborgh and Diamond 1970). Probably the level of insectivory makes cohabitation in the tree more difficult (as with *Chlorophanes*). The result in New Guinea is higher levels of aggression. The 2 specialized New Guinean groups, the lories and *Myzomela* honeyeaters, have probably been unable to form cooperative alliances (as in Panama) because of the effect of continual interference from aggressive and solitary species that share the feeding trees.

Acknowledgments.—Support for fieldwork in New Guinea was provided by the Thomas J. Watson Foundation, Smithsonian Institution and Sigma Xi. The government of Papua New Guinea kindly gave permission to study in the country. Princeton University provided support for the trip to Panama. I thank John Terborgh for guidance in the field, and Jared Diamond and James Karr for criticism of an earlier draft of this note.—BRUCE BEEHLER, *Dept. Biology, Princeton Univ., Princeton, New Jersey 08544. Accepted 2 Jan. 1979.*

Wilson Bull., 92(4), 1980, pp. 519–523

Foraging by Yellow-bellied Sapsuckers in central Illinois during spring migration.—Yellow-bellied Sapsuckers (*Sphyrapicus varius*) breed throughout the coniferous and deciduous forests of the northeastern United States and Canada, and overwinter primarily in the southeastern U.S. (Howell, Auk 70:118–126, 1953). They regularly pass through the deciduous forests of central Illinois during spring and fall. In this note, I report on observations made on the foraging of these birds during the springs of 1974 and 1975.

My first 2 study areas were located in Hart Memorial Woods along the Sangamon River near Mahomet, Champaign Co., Illinois. The woods contained 2 distinct areas—a relatively dry upland (9.6 ha) and a wetter flood plain (3.4 ha). My third study site, called Briarwood (6.2 ha), was an open, pastured woodlot. A detailed analysis of vegetation composition and vertical structure for all 3 areas is presented in Williams (Ph.D. thesis, Univ. Illinois, Champaign, Illinois, 1977). Root et al. (Trans. Ill. State Acad. Sci. 64:27–37, 1971) provide a description of seedlings and saplings.

Hart upland, containing 565.3 trees/ha, was dominated by white (*Quercus alba*), black (*Q. velutina*) and red (*Q. rubra*) oaks. The floodplain area (239.9 trees/ha) was dominated by silver maple (*Acer saccharinum*). Briarwood, with the fewest trees (24.2/ha), contained mostly bur oak (*Q. macrocarpa*), shagbark hickory (*Carya ovata*) and white oak.

I examined the foraging of Yellow-bellied Sapsuckers by quantifying: (1) activity of the bird; (2) tree species occupied; (3) height of bird in tree; (4) condition of substrate (dead or alive); and (5) limb diameter, at signals given every 10 sec by an electronic metronome (Weins et al., Ecology 51:350–352, 1970). Observations were begun in March and ended in

TABLE 1

THE PERCENT USE BY YELLOW-BELLIED SAPSUCKERS OF TREE SPECIES IN 3 HABITATS IN CENTRAL ILLINOIS DURING SPRING

Tree species	Availability[a]	1974	1975
	Hart upland		
		N = 852	N = 608
Shagbark hickory	†	16.2	67.9
Mockernut hickory (*Carya tomentosa*)	†	54.5	17.3
Bitternut hickory (*C. cordiformis*)	0.02	12.1	3.1
Red, black oak	0.57	6.8	2.4
White oak	0.35	8.1	6.6
Other	0.04	3.2	3.7
	Hart lowland		
		N = 326	N = 372
Bitternut hickory	0.02	26.4	64.2
Maple	0.26	33.4	18.5
Black walnut	0.03	23.0	4.6
Cottonwood (*Populus deltoides*)	†	8.6	4.0
Other	0.67	8.6	8.7
	Briarwood		
		N = 585	
Shagbark hickory	0.14	92.7	—
Mockernut hickory	†	1.1	—
White oak	0.03	3.1	—
Other	0.43	3.1	—

[a] Availability index values are the proportion of the total basal area/ha for each species; Chi-square values for comparisons between trees available and trees occupied = 1095.6 (df = 5), 907.3 (df = 5) for 1974 and 1975 in Hart upland, respectively; in the lowland, values equal 288.1 (df = 4) for 1974 and 396.8 (df = 4) for 1975; in Briarwood for 1974, Chi-square = 668.5 (df = 3); $P < 0.005$ in all cases.

† Values less than 0.01.

mid-May for both years. I visited each study area at least every other day when Yellow-bellied Sapsuckers were present. After an individual was located, I timed the bird up to 5 min and then searched for a new bird. This method reduced my sample size somewhat, but it also reduced bias by including observations from as many different birds as possible.

The number of individuals observed during the course of this study is difficult to estimate. Assuming that birds left after spending only 1 day in an area, I timed 37 and 50 different birds in 1974 and 1975, respectively. Comparisons of data were tested for significance ($P <$ 0.05) by Chi-square contingency analysis. Percentages of sugar in sap were transformed using the arcsine transformation and tested for overall significance with ANOVA. Means were compared using the Newman-Keuls test (Zar, Biostatistical Analysis, Prentice-Hall, Englewood Cliffs, New Jersey, 1974).

During migration Yellow-bellied Sapsuckers foraged almost totally on the exudate of trees.

TABLE 2

THE RATE OF FLOW AND PERCENT SUGAR OF EXUDATE FROM TREES IN HART WOODS

Tree species	Flow rate	% sugar $\bar{x}$ (±SE)	N	Significant difference at $P < 0.05$[a]
1. Shagbark hickory	+	10.1 (±0.85)	10	3, 4, 5, 6
2. Bitternut hickory	+	11.1 (±0.87)	10	3, 4, 5, 6
3. Mockernut hickory	+	6.4 (±0.71)	8	2, 4, 5, 6
4. Sycamore	+++	1.3 (±0.16)	3	3, 2, 1
5. Black walnut	+++	1.7 (±0.1)	8	3, 2, 1
6. Hop-hornbeam	+++	1.2 (±0.1)	5	3, 2, 1
7. Maple	+++	2–4[b]	—	—

[a] Numbers refer to trees in the "Tree species" column; mean values that were different from the species on left are given in right hand column.

[b] Maples did not yield sap when drilled 15 April 1979; I suspect they had "run" earlier; data from Marvin (The physiology of maple sap flow. Pp. 95–124 *in* The Physiology of Forest Trees, K. V. Thimann, ed., Ronald Press, New York, New York, 1958).

+ = light flow, ++ = moderate, +++ = heavy.

Pooled data from both years and all 3 areas showed they drilled rows of holes in trees 25% of the time and probed for sap 18% of the time (also see Tate, Auk 90:840–856, 1973).

Yellow-bellied Sapsuckers did not forage randomly, but rather concentrated their foraging on a narrow range of trees (Table 1). Notably, birds preferred hickory trees in all 3 areas. In another study, I reported similar observations (Williams, Am. Midl. Nat. 93:354–367, 1975). Additionally, they selected maple and black walnut (*Juglans nigra*) trees in the lowland. In the spring of 1975 (March–April), I mimicked sapsucker borings in the dominant tree species in Hart Woods at biweekly intervals (N = 5 for each species) and found that some trees exuded large volumes of sap, especially maples, black walnuts, sycamores (*Plantanus occidentalis*) and hop-hornbeams (*Ostrya virginiana*). Hickory trees consistently yielded only small volumes of exudate and oaks, ashes (*Fraxinus* sp.), elms (*Ulmus* sp.) and hackberries (*Celtis occidentalis*) exuded no sap at all. Unfortunately, I did not test for sugar concentration at this time. If sap wells in hickories do not produce as much sap as do holes in some other trees, then why do Yellow-bellied Sapsuckers forage more often on them? I hypothesized that the caloric reward in hickory sap is higher, making it a preferred food. To test this idea, I returned to Hart Woods on 15 April 1979, drilled holes (3 mm wide × 10 mm deep) in the limbs and trunks of all tree species in the woods, and measured the exudate with a hand refractometer. I qualitatively estimated the flow rate of those trees that yielded sap from borings made not only on 15 April 1979, but also during the spring of 1975. From this analysis, the exudate from hickory trees contained more sugar than did other species that yielded sap (Table 2, $F_{5,38} = 63.0$, $P < 0.001$), but flowed less. These data support the hypothesis.

The flow of sap from wounds in trees is a complex process influenced by the species of tree, weather, season and time of day (Zimmermann, The Formation of Wood in Forest Trees, Academic Press, New York, New York, 1964). Some tree species develop a positive pressure in their xylem vessels in early spring and, when punctured, yield large volumes of relatively dilute xylem sap (2–4% sugar), while other species exude relatively concentrated sap (10–20% sugar) from phloem cells in small amounts (Zimmermann, pers. comm.; Milburn

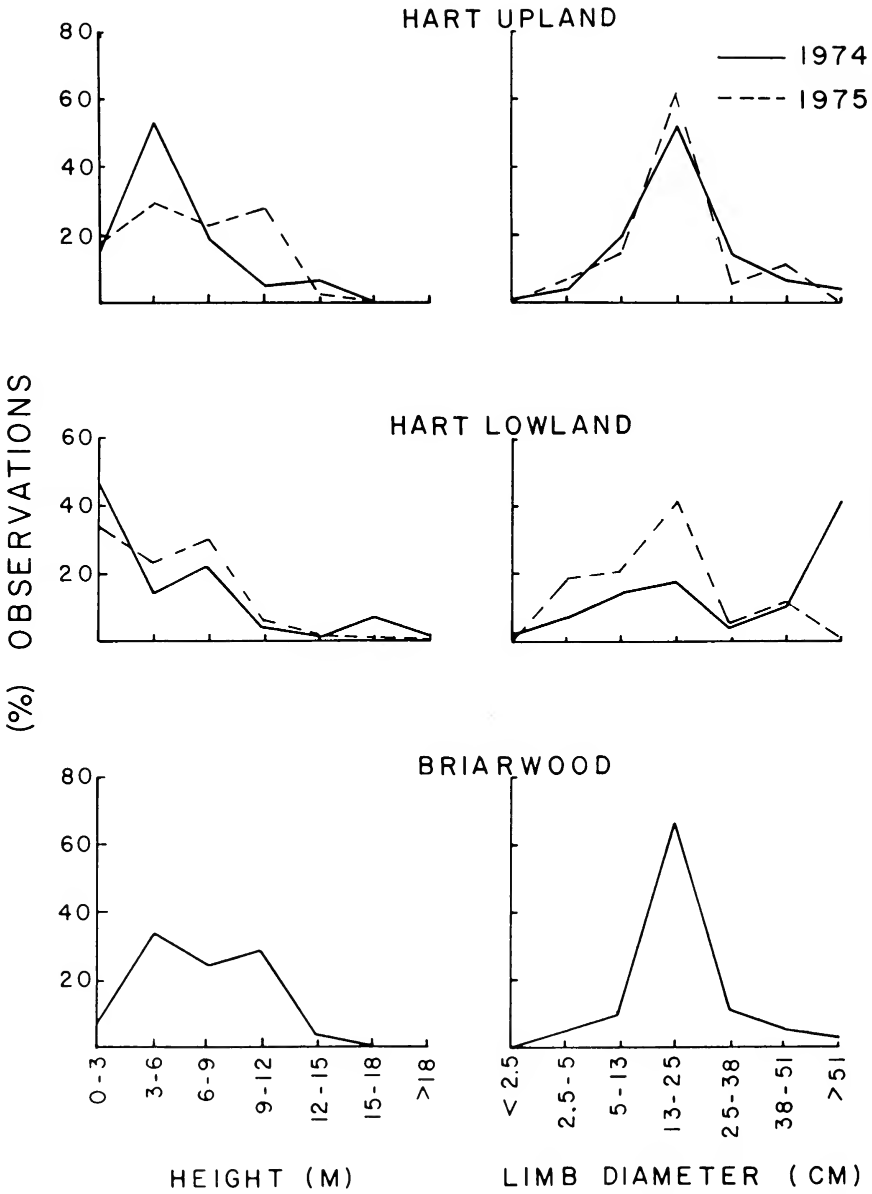


FIG. 1. Percent observations for height categories and limb sizes used by the Yellow-bellied Sapsucker during spring migration.

and Zimmermann, Principes, J. Palm. Soc. 18:67–68, 1974). The higher concentrations of sugars in hickory sap may indicate that sieve tubes of the phloem are, at least in part, the source; whereas the dilute sap of maples, black walnuts, sycamores and hop-hornbeams probably comes principally from xylem vessels. From borings made in trees (maples, elms, hackberries and red oaks) used by Yellow-bellied Sapsuckers in spring in Michigan, Tate (1973) found the sugar concentration of the sap to average about 3%. Kilham (Auk 81:520–527, 1964) reported that birches (*Betula* spp.) are the main sources of sap for Yellow-bellied Sapsuckers in summer in central New Hampshire, and found that phloem exudate from yellow birch (*B. lutea*) contained about 19% sugar.

Yellow-bellied Sapsuckers preferentially used the lower and middle height categories in all 3 study areas (Fig. 1). Moreover, they most often exploited living limbs in the 13–25 cm range in all 3 areas, but also used trunks of trees in the lowland. Larger limbs at lower heights may yield more sap per unit time for the birds.

Apparently Yellow-bellied Sapsuckers forage on hickory trees during spring migration because the exudate is relatively high in sugars. Why they forage in the middle and lower portions of the canopy on larger limbs needs further study, but at least for hickory trees, the phloem may be thicker in this region and thus the flow rates of exudate possibly higher.—JOSEPH B. WILLIAMS, *Dept. Natural Science, Pepperdine Univ., Malibu, California 90265.* (Present address: *Dept. Biology, Joseph Leidy Laboratory of Biology G7, Univ. Pennsylvania, Philadelphia, Pennsylvania 19104.*) *Accepted 16 Oct. 1979.*

Wilson Bull., 92(4), 1980, pp. 523–524

Mallards capture and eat American toads.—For more than 2 years I have kept Mallards (*Anas platyrhynchos*) in cages at the edge of a pond in the deer enclosure at the Field Station for the Study of Animal Behavior, Duke University, Durham, North Carolina. In addition to the caged ducks, 7 females and 3 males released in summer 1978 remained on the pond, and they spent much of their time near the cages.

As my son, Karl, and I approached the pond at 10:45 on 1 April 1979, we heard a chorus of the common American toad (*Bufo americanus*). The sky was clear and the temperature an unseasonally warm 25°C. We could see 30 or 40 toads in the shallow water near the duck cages, but when we approached for closer examination, the toads moved out from land. No duck showed any interest in the toads at the time.

The chorus continued, and we noticed that the larger toads were floating in the water with their legs outstretched. They retained this position and remained immobile as we approached; they were still too far from land to catch without a net.

At 11:30 Karl observed a female Mallard catch a large toad in the water. Immediately a male Mallard tried to take it from her, and there was a tug-of-war over the prey. The female maneuvered the immobilized toad into position in her mouth, the toad's legs dangling from the sides of her bill and after several attempts succeeded in swallowing it head first. The activity excited 4 other female ducks and another male; there were 7 ducks stalking, catching and swallowing toads. Male Mallards relied more on stealing toads from females than on capturing their own. A toad captured from behind was immobilized by being beaten on the surface of the water, after which it was manipulated in the mouth until it could be swallowed head first. Swallowing required considerable effort because of the large size of the toads; it usually took place in the water, but 1 male Mallard carried a toad onto land and swallowed it there. In 15 min the ducks caught and consumed at least 12 toads. They abruptly stopped feeding on toads and moved out toward the center of the pond at about 11:45.

Meanwhile, the chorus was reduced in volume, and many toads were in amplexus very close to land where the shallow water was filled with strings of toad eggs. Some pairs would move away when gently prodded with a stick, but others would not move. We had no difficulty picking up a pair of toads in amplexus.

McAtee (U.S. Dept. Agric. Bull. No. 720, 1918) found that 90.53% of the stomach contents of wild Mallards is vegetable matter; the remains of frogs were found in 19 of 1578 Mallard stomachs examined. The Black Duck (*Anas rubripes*) consumes more animal food than the Mallard, about 25%, mostly molluscs (McAtee 1918), and may eat small toads (Bent, Life Histories of North American Waterfowl, Pt. 1. U.S. Natl. Mus. Bull. 126, 1923).

Our observations are most remarkable since large toads are generally avoided by predators (Lutz, *in* Venomous Animals and Their Venoms, Vol. II, W. Bucherl and E. Buckley, eds., Academic Press, New York, New York, 1971). They secrete anti-predator venoms, bufotenine and 5-OH tryptamine (Low, *in* Evolution in the Genus *Bufo*, W. F. Blair, ed., Univ. Texas Press, Austin, Texas, 1972), through orifices over the parotid glands (Chen and Chen, J. Pharm. Exper. Therap. 47:281–293, 1933). The Mallards captured and swallowed the large toads with avidity. We saw no evidence that the toads were distasteful or irritating to the ducks, nor did we observe any regurgitation of toads that had been swallowed.

These observations were made while I was conducting research supported by the National Science Foundation, Grant PCM79-00582.—NANCY S. MUELLER, *Dept. Biology, North Carolina Central Univ., Durham, North Carolina 27707.* *Accepted 20 Aug. 1979.*

Wilson Bull., 92(4), 1980, p. 524

Dipper swallowed by trout.—On 24 June 1976, we caught a Dolly Varden trout (*Salvelinus malma*) in Big Creek, a stream adjacent to the University of Idaho's Taylor Ranch Field Station. The stomach of the fish contained a Dipper (*Cinclus mexicanus*). Predation by fish on Dippers has, to our knowledge, never been reported. The predacious Dolly Varden eats fish (Roos, Trans. Am. Fisheries Soc. 88:253–260, 1959), small mammals and birds (Dymond, The Trout and Other Game Fishes of British Columbia, Can. Dept. Fisheries, Ottawa, Ontario, 1932). Since Dippers feed on fry (Bent, U.S. Natl. Mus. Bull. 195:103, 1948), they would be in frequent contact with predatory fish.—CHARLES L. ELLIOTT AND STEVE PECK, *Coll. Forestry, Wildlife and Range Sciences, Univ. Idaho, Moscow, Idaho 83843.* (Present addresses: CLE *Dept. Botany and Range, Brigham Young Univ., Provo, Utah 84602 and* SP *240 Parkview Dr., Burlington, Wisconsin 53105.)* *Accepted 24 Sept. 1979.*

Wilson Bull., 92(4), 1980, pp. 524–526

Team-hunting and food sharing in Parasitic Jaegers.—Parasitic Jaegers (*Stercorarius parasiticus*) breed regularly in arctic Alaska (Bailey, Colorado Mus. Nat. Hist. Popular Ser. No. 8, 1948; Pitelka, Arctic and Alpine Res. 6:161–184, 1974). They take a wide variety of animals as prey, but during the breeding season specialize either on birds, or birds and small mammals (Maher, Pac. Coast Avif. 37, 1974). At other breeding locales Parasitic Jaegers are known to rely heavily on kleptoparasitism of seabirds (Arnason and Grant, Ibis 120:38–54, 1978).

Parasitic Jaegers regularly team-hunt in pairs or small groups. Team-hunting occurs as: (1) three or more jaegers hunting near one another, but acting singly (group hunting), or (2) two birds hunting cooperatively by assisting each other. Both group and cooperative hunting are known from the breeding grounds (Anderson, *in* Bent, U.S. Natl. Mus. Bull. 113, 1913; Gabrielson and Lincoln, Birds of Alaska, Wildl. Manage. Inst., Washington, D.C., 1959; Parmelee et al., Natl. Mus. of Canada Bull. 222, 1967; Maher 1974; Eisenhauer and Paniyak, Auk 94:389–390, 1977; Arnason and Grant 1978; Martin and Barry, Can. Field-Nat. 92:45–50, 1978), but the extent to which the jaegers depend on these techniques and the conditions under which they are exhibited are unknown.

During the summers of 1977, 1978 and 1979 I observed Parasitic Jaegers foraging daily over tundra at Prudhoe Bay and Franklin Bluffs, Alaska (70°15′N, 148°20′W). The jaegers often hunted in pairs, notably towards the end of summer after the hatching of resident shorebirds and passerines. Typically, 1 bird would fly a few meters above the tundra and the other about 10 m above and slightly behind. Group hunting involving 3–5 birds was most commonly observed during spring and fall migration, but occasionally also during mid-summer.

I saw 3 instances of cooperative hunting attacks and 1 group hunting attack at close range. The first observation, on 1 August 1977, involved 2 dark-phase jaegers and an immature female Pectoral Sandpiper (*Calidris melanotos*). When first seen, the jaegers were chasing the sandpiper in level flight. The jaegers pursued the sandpiper to a gravel road where it took refuge in the grass. The leading jaeger forced the sandpiper up, and after a quick series of alternate stoops by both jaegers, 1 caught the sandpiper in its bill, just above the grass. The jaeger carried the flapping sandpiper about 20 m, landed on the tundra and then placed the prey under its feet. The jaeger killed the victim by stabbing with its beak at the head and thorax region; both jaegers then plucked the sandpiper. Two min later, the first jaeger (the captor) picked up the sandpiper in its bill and allowed the second jaeger to tear bits of meat from the prey. After a few bites, the jaegers reversed roles and the first jaeger fed while the second jaeger held the sandpiper. After another 4 min and 2 more reversals, the jaegers had effectively divided up the catch.

The second and third instances, on 11 August 1977 and 7 August 1979, respectively, both involved chases of Lapland Longspurs (*Calcarius lapponicus*). In each case the longspur sought refuge near a gravel road and did not flush from the grass despite rapid stoops by both jaegers, who soon gave up the chase.

The group hunting attack was seen on 3 August 1978. Three jaegers were seen flying together about 15 m high when a Semipalmated Sandpiper (*C. pusilla*) flushed beneath them. All 3 jaegers took chase but 1 quickly turned back. The remaining 2 jaegers dove to the level of the sandpiper and chased it in level flight. The jaegers were 2 m apart and positioned above and below the sandpiper. After approximately 250 m the lower jaeger caught up to the sandpiper and grabbed it in its bill as the sandpiper tried to dodge right. This jaeger carried the bird 200 m and then landed. The second jaeger followed the first and then veered off and flew away. During this chase there was no cooperation between the 2 jaegers; the successful jaeger was the first to catch up with the fleeing sandpiper.

The dates of my observations on cooperative hunting were after the hatching of eggs for nesting Parasitic Jaegers (Maher 1974). At least one of the pairs of jaegers observed is known to have been nesting and I suspect it of the others. Maher (1974) found that nesting jaegers frequently left the nest-site together after the eggs hatched and that both adults were absent for about 50% of the time, presumably hunting together.

Because nesting jaegers are intraspecifically territorial (Maher 1974) it is unlikely that non-mated pairs would hunt cooperatively and share food. However, in group hunting, in which each jaeger takes advantage of the group but acts independently with respect to the prey, migrating and unmated jaegers may tolerate each other's presence. Also, in coastal areas where group hunting significantly increases the success of Parasitic Jaegers engaging in kleptoparasitism (Arnason and Grant 1978) mated birds may leave their nesting territory to hunt in groups with other jaegers.

Several other workers have made observations on cooperative and group hunting in Parasitic Jaegers resembling those above. During the 3 summers of my work I received reports of no fewer than 15 instances of the hunting procedure from 3 different areas in Alaska. Cooperative hunting may be an important contribution to the success of Parasitic Jaegers in hunting birds. The Long-tailed (*S. longicaudus*) and Pomarine (*S. pomarinus*) jaegers prey much less on birds than does the Parasitic Jaeger (Maher 1974) and no reference could be found describing cooperative hunting in either of the former species. Sharing of food, however, has been recorded in all 3 species (Andersson, Ornis Scand. 2:35–54, 1971; Martin and Barry 1978; Pitelka, unpubl. data). This behavior may facilitate pair bond maintenance and the tearing of prey into small pieces which would make swallowing easier (Andersson 1971).

These observations were made during work undertaken for the Los Alamos Scientific Laboratory under D.O.E. contract W-7405-ENG-36. W. C. Hanson, B. Kessel, W. J. Maher, J. P. Myers, F. A. Pitelka, M. A. Pruett and C. M. White made helpful comments on an earlier draft of this note.—STEPHEN G. PRUETT-JONES, *Museum of Vertebrate Zoology, 2593 LSB, Univ. California, Berkeley, California 94720.* *Accepted 1 Sept. 1979.*

Wilson Bull., 92(4), 1980, pp. 526–527

Incubating Wood Duck and Hooded Merganser hens killed by black rat snakes.—Wood Duck (*Aix sponsa*) nest boxes (N = 78) were erected 2–8 m above high water level in seasonally fluctuating river swamp ecosystems on the Department of Energy's Savannah River Plant, a 81,000-ha area occupying portions of Aiken, Allendale and Barnwell counties, South Carolina. Protection from predators was provided by 42 cm wide wraparound shields placed 0.5 m below the nests boxes. Nest boxes were inspected bi-weekly during the nesting seasons of 1973, 1974 and 1975 and monthly during the nesting seasons of 1976 and 1977.

The black rat snake (*Elaphe obsoleta*), an excellent swimmer, readily circumvented predator shields and was the only known nest predator during the 5 years of observation. This species destroyed 24 of 76 nests (32%) initiated from 1973–1975. Noteworthy is evidence that nesting Wood Duck and Hooded Merganser (*Mergus cucullatus*) hens may also be killed during rat snake nest depredations. The following 4 incidents were observed: (1) On 26 March 1974, I found a 162 cm long rat snake which had eaten 10 of 12 eggs in a nest box with a dead female Wood Duck. The Wood Duck's neck was twisted, possibly broken. (2) On 3 April 1975, I found a large black rat snake which had consumed several eggs in a nest box with a dead female Wood Duck. Again the Wood Duck's neck was twisted. (3) On 17 April 1975, I found a dead female Wood Duck with a twisted neck in a nest box. No snake or eggs were present. (4) On 15 April 1977, I found a large rat snake which had consumed several eggs in a nest box containing a dead female Hooded Merganser. The carcass was so decomposed that condition of the neck could not be determined.

These data suggest that large rat snakes occasionally kill incubating Wood Duck and Hooded Merganser hens. I believe the deaths to be the result of circumstance rather than active defense by the hen or pursuit by the snake. Wood Duck nest boxes have 1 hole which serves as entrance and exit. After the snake has partially entered the nest box, the hen may attempt to leave the box through the hole occupied by the snake. The rat snake may react to this apparent attack by striking and coiling its body around the bird (with the coils ultimately ending up around the hen's neck). The hen's death is possibly caused by her attempts to escape.

Other investigators have reported deaths of incubating Wood Duck hens in conjunction with nest predation, primarily by raccoons (*Procyon lotor*) (Grice and Rogers, Massachusetts Div. Fish and Game, Fed. Aid Proj. W-19-R, 1965; Cunningham, Southeast Assoc. Game and Fish Comm. 22:145–155, 1968; Beshears, Alabama Dept. Conserv. and Nat. Resour., Fed. Aid Proj. W-35, Job I-F, 1974). Only 1 instance of a black rat snake killing an incubating Wood Duck hen was found in the literature (Hester and Dermid, The World of the Wood Duck, J. P. Lippincott Co., Philadelphia, Pennsylvania, 1973).

The 3 Wood Duck deaths attributed to black rat snakes in my study (1973–1975) represented 4% of all Wood Duck nests initiated (N = 76) on the study area. The death of an incubating hen has a greater potential impact on the population than the loss of a clutch or the loss of individual hatchlings because that hen can make no further contribution to the population. Black rat snake predation on incubating Wood Duck and Hooded Merganser hens and nests could have a significant impact on the reproductive success of populations using natural cavities in southeastern river swamp ecosystems.

This study was supported under contract EY-76-C-09-0819 between the United States Department of Energy and the University of Georgia. This is technical contribution No. 1668, South Carolina Agricultural Experiment Station, Clemson University, Clemson, South Carolina.—T. T. FENDLEY, *Dept. Entomology; Fisheries and Wildlife, Clemson Univ., Clemson, South Carolina 29631.* *Accepted 1 Sept. 1979.*

Wilson Bull., 92(4), 1980, p. 527

Sandhill Cranes nesting in Illinois.—On 24 May 1979 at 13:30, I flushed a pair of Sandhill Cranes (*Grus canadensis*) from a plowed field at Deer Lake, Antioch Township, Lake Co., Illinois. One bird flew a short distance away; the other walked towards me and stopped within 6 m of me. Both cranes were calling. The pair were brown, except for their gray necks and wing coverts. Two downy chicks accompanying the closer bird scurried away.

Deer Lake is a private hunt club consisting of 404 ha of open water, deciduous woods and marsh. The field in which the cranes were found was adjacent to an extensive cattail (*Typha* spp.) marsh. The owner of the property has noted the presence of a pair of cranes during the last 3 summers, but saw no signs of nesting (W. Brook, pers. comm.). Several Sandhill Cranes have also summered at Chain of Lakes State Park about 13 km southwest of Deer Lake, but again no actual evidence of nesting has been observed (D. Johnson, pers. comm.).

Although Sandhill Cranes were formerly common breeders in Illinois, my observations indicate the first definite nesting in the state since 1872. At that time a nest was found in Champaign County (Bohlen, An Annotated Checklist of the Birds of Illinois, Illinois State Museum, Springfield, Illinois, 1978:46).—JOEL GREENBERG, *922 Sumac Lane, Mt. Prospect, Illinois 60056.* *Accepted 7 Aug. 1979.*

Wilson Bull., 92(4), 1980, pp. 527–529

A Mallard × Mottled Duck hybrid.—Hybrids between Mallards (*Anas p. platyrhynchos*) and other species of *Anas*, are frequently found in the wild (Cockrum, Wilson Bull. 64:140–159, 1952; Gray, Bird Hybrids, A Checklist with Bibliography, Commonwealth Agricultural Bureau, Bucks, England, 1958; Johnsgard, Am. Midl. Nat. 77:51–63, 1967). However, reports of crosses between a Mallard and Mottled Duck (*A. fulvigula maculosa*) are rare.

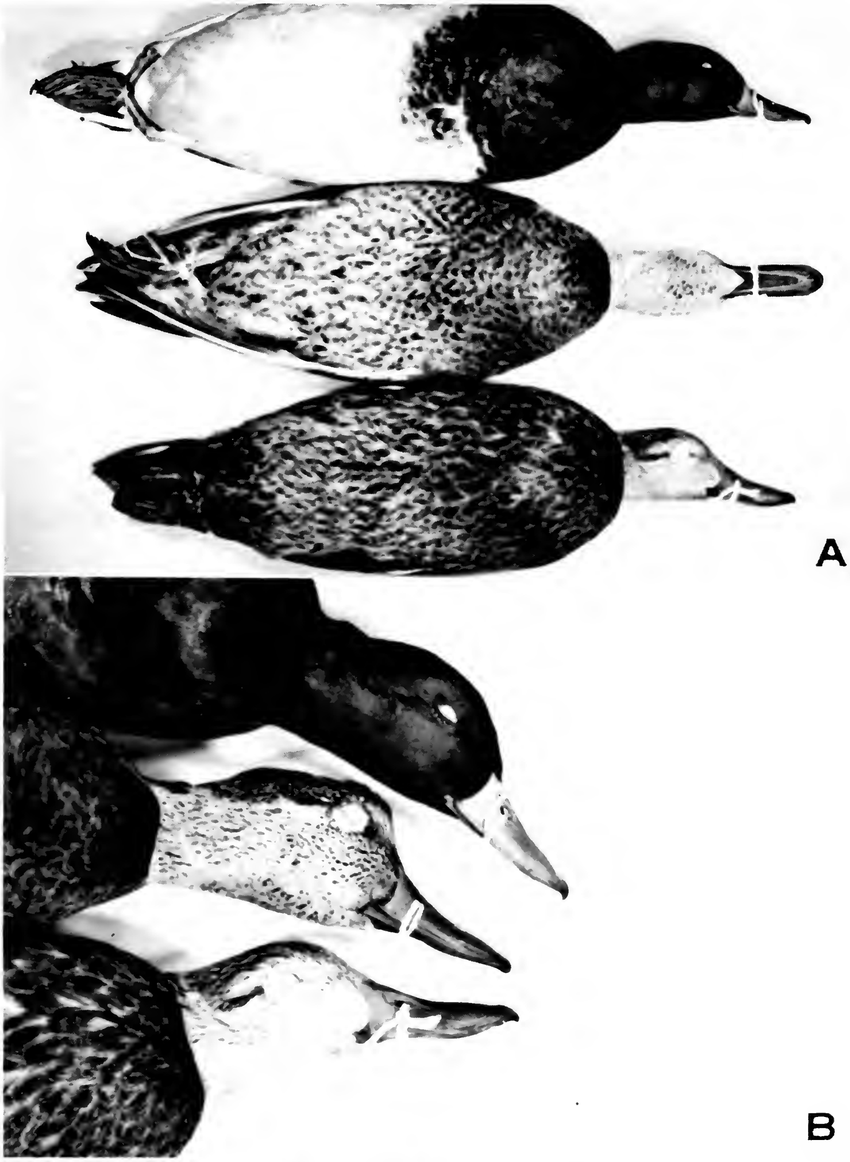


FIG. 1. A. Comparison of Mallard (WM #1286) (top), Mallard × Mottled Duck hybrid (CCSU #123) (center), and Mottled Duck (WM #1315) (bottom). B. Comparison of heads.

A. V. Fitzgerald took a male duck at Tule Lake, Nueces Co., Texas, during the 1975–1976 waterfowl hunting season, which had traits of both a Mallard and a Mottled Duck. Tule Lake is a natural lake located in the southwest wind-tidal flat of the Nueces River flood plain.

Hubbard (The Biological and Taxonomic Status of the Mexican Duck, New Mexico Dept. Game and Fish Bull. 16, 1977) examined 4 Colorado specimens reported as Mexican Ducks (*A. diazi*) and believed these specimens to be Mallard × Mottled Duck hybrids. Out of 383 pairs of Mottled Ducks in Louisiana, Weeks (Breeding Behavior of Mottled Ducks in Louisiana, M.Sc. thesis, Louisiana State Univ., Baton Rouge, Louisiana, 1969) observed 2 pairs of Mottled Duck males mated with Mallard females and 2 pairs of Mallard males mated with Mottled Duck females. Phillips (Genetics 6:366–383, 1921) crossed a female Mallard and a male Mottled Duck and reported the plumage variations in the resulting birds. The F^2 generation of this cross varied from pure Mallard-like to nearly pure Mottled Duck types. The plumage of the hybrid in my report is intermediate to plumage variations described by Phillips.

After preparation of the hybrid specimen, the bill color changed from a yellow-olive to a dark olive. This color change was also noted in other Mottled Duck specimens prepared for the Corpus Christi State University specimen collection. The prominent plumage features that distinguish the hybrid from a Mottled Duck are iridescent green behind the eye, numerous vermiculated feathers, a chestnut-tinted chest, recurved black-tipped tail feathers, and a subdued white bar on the anterior of the speculum (Fig. 1).

The prepared specimens were measured as described in Palmer (ed., Handbook of North American Birds, Vol. I, Yale Univ. Press, New Haven, Connecticut, 1962). The tail, exposed culmen, middle toe and tarsus measurements are within the range of both species. Measurements so broadly overlap that a comparison would provide no information about size differences. The hybrid wing (chord), 290 mm, is in the range of the Mallard, 271–297 mm, ($\bar{x}$ = 282.2), which is reported to be larger than that of Mottled Ducks, 245–267 mm ($\bar{x}$ = 256.8) (Oberholser, Bird Life of Texas, Vol. 1, Univ. Texas Press, Austin, Texas, 1974).

In regions of known or suspected sympatry, hunters' kills should be checked for Mallard × Mottled Duck hybrids so that the status of hybridization can be monitored because it potentially threatens the existence of the Mottled Duck as a distinct species. In northeastern North America, Black Ducks (*A. rubripes*) hybridize with Mallards (Heusmann, Wildl. Soc. Bull. 2:171–177, 1974), thus similarly threatening the specific status of *A. rubripes*.

I express my appreciation to Gene W. Blacklock for preparation of the hybrid specimen and editorial assistance, and to Brian R. Chapman for his editorial assistance and use of the Corpus Christi State University facilities.—DAVID A. NELSON, *Dept. Biology, Corpus Christi State Univ., Corpus Christi, Texas 78411.* *Accepted 18 Sept. 1979.*

ORNITHOLOGICAL LITERATURE

Wilson Bull., 92(4), 1980, pp. 530–539

Birds of the Great Plains: Breeding Species and their Distribution. By Paul A. Johnsgard. Univ. Nebraska Press, Lincoln, Nebraska, 1979:539 pp., 30 color photographs with captions, 5 black-and-white photographs with captions, 330 range maps, 8 numbered text figs., numerous line drawings, 6 tables. $25.00.—Prior to the publication of this book there existed no summary of the distribution and breeding biology of the birds of the Great Plains. This was a deficiency regretted by many biologists and biogeographers, for the Great Plains contains the most extensive grasslands in North America, and is a region of faunal transition, where north meets south, and east meets west (it is said that more bird species reach a limit to their distribution in Kansas than in any of the other United States).

The Great Plains is neither a sharply defined nor easily delimited region. Johnsgard states that it extends from the vicinity of Great Bear Lake in the Northwest Territories of Canada south to the Pecos River and Balcones Escarpment in Texas, and from the Central Lowlands in the Mississippi and Ohio river drainages west to the eastern slope of the Rocky Mountains. He writes that after contemplating a book about this entire region he felt constrained to deal with a more restricted area; he chose one that corresponds more or less to what is called the "central plains"—extending from the 49th parallel (the U.S.–Canadian border) south to southern Oklahoma and thd 34th parallel (in Texas and eastern New Mexico), and lying essentially between the 95th and 104th meridians. He selected this region because its ornithology is rather uniformly well known, and because it includes "as many of the essentially grassland dominated states as feasible (p. xix)."

However, the common conception is that the Great Plains is the extensive, fairly level region of semiarid grassland extending from central Saskatchewan southward to central Texas (Webb, The Great Plains, Grosset and Dunlap, New York, New York, 1932)—a region more properly called the central "prairies." If some restriction were required, I would have preferred that Johnsgard had chosen the prairies, a biotically defined region that conforms to the popular conception of the "Great Plains."

The introduction is a series of useful and clearly written essays on the topography, climate, vegetation and avian zoogeography of the central plains region—the region covered by the book. It is perhaps only here that it is imperative that the reader remember that this is not a book about the prairies, for the included region contains not only a major portion of the prairie grasslands, but also boreal forests (northwestern Minnesota, Black Hills), southern floodplain hickory-oak-pine forests (eastern Oklahoma) and pinyon-juniper scrub (northeastern New Mexico and western Oklahoma). In the faunal analysis of the "Great Plains" the effect of including birds that breed only in these habitats is striking. For example, of the 37 northern woodland species listed in Table 1 (p. xl–xli), most are restricted in their breeding to the Black Hills and northwestern Minnesota; perhaps one (the American Woodcock [*Philohela minor*]) might qualify as a prairie species. Table 6 (p. xlv) summarizes the zoogeographic data; Johnsgard calculated that no fewer than 17% of the plains birds are of northern origin. Were we to exclude the species characteristic only of boreal forests (e.g., Spruce Grouse [*Dendragapus canadensis*]; Gray Jay [*Perisoreus canadensis*]; Red Crossbill [*Loxia curvirostra*]), however, the proportion is more like 2%! Similarly, the "eastern woodland element" is inflated by the inclusion of eastern Oklahoman birds (Red-cockaded Woodpecker [*Dendrocopos borealis*]; Fish Crow [*Corvus ossifragus*]; Brown-headed Nuthatch [*Sitta pusilla*]), etc. The total effect of these inclusions is to underestimate the significance of the "endemic" element in the prairies. A breakdown of the species associated with grasslands is given in Table 3 (p. xliii). The reader can calculate that of these, 42% are endemic; this is to be compared to the figure of 5% for the entire avifauna given in Table 6. I have no quarrel with Johnsgard's analysis; he chose a region and described it. But because the region is a quiltwork of different habitats, the result is of limited ecological meaning.

Following the introduction there are accounts of the distribution and breeding biology of 330 species that have been known to breed in Johnsgard's area. It is these accounts that make the book of value. Each is a carefully compiled summary of a species' biology, with special reference given to information from the central plains region, and contains information on nest placement, clutch-size, time of breeding, etc. The information is accurate, succinctly presented and (when possible) broken down by local area. Thus, we learn that the American Redstart (*Setophaga ruticilla*) nests from late May to late July in North Dakota, and from May to June in Kansas; that Red-winged Blackbird (*Agelaius phoeniceus*) clutches average 3.6 eggs in North Dakota, and 3.4 in Oklahoma.

The maps that accompany each account are clear; the "usual" breeding ranges are shaded, and dashed lines enclose peripheral or sporadically used areas; isolated dots show local breeding sites. There is, in the text, an accompanying statement of the range with limited citations to the literature about some extralimital records. It was a massive job to put these maps together, and I have not studied them all critically. There are a few minor errors or inconsistencies in the Kansas ranges—the region that I know best. For example, the Ash-throated Flycatcher (*Myiarchus cinerascens*) is found regularly along the Cimarron River in southwestern Kansas; the reproductive condition of specimens indicates that they breed there. This is one of the few places where this species is sympatric with the similar Great-crested Flycatcher (*M. crinitus*), and it would have been nice to note their cooccurrence there. There is a good breeding record of the Poor-will (*Phalaenoptilus nuttallii*) in Cowley County (Bull. Kans. Ornithol. Soc. 26:17–19, 1975). The Eastern Bluebird (*Sialia sialis*) breeds regularly throughout western Kansas, as does the Warbling Vireo (*Vireo gilvus*), etc. But these "oversights" are minor; in some cases interpretations are involved (to my knowledge there are no actual nesting records of the flycatcher, bluebird, or vireo outside the shaded areas on the maps); no two people would draw the maps precisely the same way.

Birds of the Great Plains was written for "a rather broad, nontechnical audience," and it has been assembled with enough precision and care that it will be widely appreciated in the central plains region. It is a handsome book with many pleasant illustrations. It does not contain new information, but it is a useful compilation; there are enough citations to original sources that serious students will value it both as an overview and as a point from which thorough local work can be initiated. A similar book written about the entire plains region, or about an ecologically defined portion of the plains, would have been of more interest to biogeographers, but even they will find much in this volume of interest.—JAMES D. RISING.

ELEONORA'S FALCON: ADAPTATION TO PREY AND HABITAT IN A SOCIAL RAPTOR. By Hartmut Walter, illus. by Noel L. Diaz. University of Chicago Press, Chicago, Illinois, 1979:410 pp., 36 black-and-white plates with caption figs., 59 numbered text figs., 28 tables including 4 appendices. $35.00.—The Eleonora's Falcon (*Falco eleonorae*) is similar in length to a Peregrine (*F. peregrinus*) with extremely long wings and tail, but with a much slighter build. Adults show an almost 3:1 ratio of 2 color phases; the more common with throat, cheeks and belly of cream-color to buffy, and the least common with a dark brown to slate-black plumage. Its reproductive life separates Eleonora's Falcon from the mainstream of the raptor world. Not only does it breed colonially, as do few other *Falco* species, but it breeds in late summer and early fall (eggs laid mid-July to early August). From 1965 to 1977 Hartmut Walter visited some islands of southern Europe and northern Africa where approximately 12,000 falcons occur in some 148 breeding colonies. He mainly studied a western colony (Moroccan Mogador), and another in the eastern range, Greek Paximada. In this book, Walter presents what he has learned of the natural history of this species and compares his findings with those in the literature.

The reproductive habit that makes this species so interesting is adaptation to an abundant food source, the estimated 5 billion migrant birds that cross from Europe into Africa and beyond every fall. About 15 species make up 90% of the diet for this falcon, with shrikes (*Lanius* spp.), Whitethroats (*Sylvia communis*) and other Old World warblers (*Phylloscopus* spp.) comprising the bulk. Walter calculates that Eleonora's Falcons use 0.02–0.04% of the total migrants for food. Migrants are caught over open waters of the Atlantic and Mediterranean just as the autumn breeding Sooty Falcon (*F. concolor*) catches migrants over the sands of Libya.

At Paximada, the falcons rise to a given altitude and "float" into the wind in almost uniform distribution, forming a 3-dimensional "net" that must be run by migrating birds. Once prey is sighted, several falcons converge in competitive, yet frequently successful, pursuit. On Mogador, where migrants approach almost at sea level, low altitude searching flights are used more often.

The author presents interesting ideas relating to the dependence of this falcon upon the migrational pulse of its prey species, most of which are nocturnal fliers. Eleonora's Falcon colonies are placed to intercept these migrants. The combination of strategic location and migration routes of individual prey species allow concentrated hunting by the Paximada colony only during the morning, whereas the Mogador falcons hunt almost all day. Food availability may be a major factor influencing the existence of a larger clutch, and therefore accounting for the greater number of young fledged per pair at Mogador during the study. The greater density of nesting pairs at this location may be influenced by both food supply and the more complex structure of the substrate, which allows increased visual privacy from neighbors. Stressing the migrational food supply, Walter suggests Eleonora's Falcon could not have existed in the Mediterranean basin 18,000 years ago, when glaciation would have decreased bird migration to half the present volume. He postulates further that both absence of appropriately placed islands and differences in migration routes for North American birds account for the lack of a raptorial counterpart of Eleonora's Falcon in the Carribean area.

A colonial raptor is an ideal subject for sociobiological studies and this pioneer effort has revealed a number of problems for further analysis. At Paximada clutches range from 1–4 eggs, and hatching is correlated with the arrival of migrant prey; adults eat insects until this time. Walter determined that laying of large clutches begins before that of smaller clutches, but could not determine whether larger clutches were produced by older, dominant birds. One might ask if large clutches in a colony are associated with central nest-sites, most elevated sites, or the position of a pair in dominance hierarchy. Because raptors frequently pirate prey from each other, a colonial bird exposing prey in its feet would be susceptible to piracy. The author includes a few such observations with a short discussion. Again it would be useful to know if certain individuals specialize in piracy and if low ranked males are more often pirated. Prey plucking, which other raptors may complete away from the nest, in this species is almost always done at the nest. Also, the female rarely takes aerial food transfers from her mate as do other falcons. Both behaviors presumably result from the pressure of piracy by other members of the colony. The sedentary behavior of the young following nest departure is unusual in the genus. Perhaps this is due to the territoriality of adult neighbors. One wonders how the flight and pursuit skills so essential to this aerial predator are perfected.

Eleonora's Falcons leave the colonies in October and early November. Although their migration routes are not known, they winter in Madagascar and the Mascarene Islands, where they mingle with wintering Sooty Falcons and hawk insects above the forest canopy. From late March to early May they begin returning to their breeding grounds and eat both insects and the avian migrants that have started returning north. Insects comprise the mainstay of the diet until breeding begins again.

In his discussion of dispersion, territoriality and sociability, Walter compares raptors to illustrate a social spectrum ranging from solitary to extremely sociable. He includes the Prairie Falcon (*Falco mexicanus*) in a group of falcons not in regular contact with other breeding pairs, and which he "guesses" will never show a significant overlap of home ranges between neighbors. This is contradicted by the dense population (some 150–200 pairs) that nest along less than 100 miles of the Snake River. The author also considers the selection pressures responsible for reversed sexual dimorphism in raptors. He suggests that functional retention of both ovaries in birds of prey makes females more vulnerable to egg breakage (by struggling prey). A larger body size would allow more protection against this hazard. Those raptors showing the greatest disparity in size between sexes are those that undertake the most daring chases. In turn large female body size would afford the greatest protection for eggs. Considering that nearly all male raptors feed the female during courtship, pre-egg-laying and egg-laying phases of reproduction the above size hypothesis would seem without foundation.

This work contains a few statements that could mislead the reader, due to a lack of comparison with other species, or by the isolated context in which an observation was made. For example, Walter ascribes bowing primarily to the male and repeatedly interprets it as an appeasement behavior toward the female (pp. 208, 211, 251 and elsewhere). Bowing in most falcon species is exhibited by both sexes in a much wider context, ranging from courtship to sheer aggression. Elsewhere (p. 242), the author describes males perching above rival males in "an upright posture with wings slightly spread and bill half-open." No doubt such a posture was used in this context, but again, such displays are common for both sexes, (including half-grown nestlings of all *Falco*, indeed, of many Falconiformes in general) as the most severe agonistic expression toward another raptor or other threatening object, followed by either attack on foot or retreat. In places, Walter has a tendency toward anthropomorphism that is somewhat aggravating, at least to this reader.

Despite the above, as well as the absence of a list of tables and figures, the greatest faults of the book lie in the sometimes too lengthy presentations and the occasional redundancy. Each subject is covered for each colony, as opposed to reducing the material for the entire topic into a single, but meaningful comparison. Choosing to discuss each colony results in a longer and more expensively produced text and considering the tedious nature of some subjects, it is more difficult for the reader to follow. Occasionally the author seemingly collected more data than he could make complete use of but decided to present in raw form anyway. However, the book is of considerable interest and is a valuable contribution to the literature of the Falconidae. It will probably be too detailed for the casual reader but is certainly intriguing for the serious biologist and a welcome resource for raptor or colonial bird enthusiasts.—STEVE K. SHERROD.

PENGUINS. By Roger Tory Peterson. Houghton Mifflin Co., Boston, Massachusetts, 1979:238 pp., 4 photographic essays, 137 line drawings. $25.00.—The word "penguin" triggers a series of images of Antarctica and the "comical, adorable, and handsomely attired"

Adelie Penguins (*Pygoscelis adeliae*). However, there are 17 species of penguins, and most are found, not in Antarctica, but in the sub-Antarctic.

This book is a pictorial essay of all penguin species and their associates, not an in-depth academic work. The photographs are stunning. Adelie Penguins cascading off an ice lip, a female Galapagos Penguin (*Spheniscus mendiculus*) standing next to her mate yawning, Chinstrap Penguins (*Pygoscelis antarctica*) negotiating the surf and a Gray-headed Albatross (*Diomedea chrysostoma*) on its final landing approach are, to my eye, some of the best. Many of the color photographs capture penguins sharply and clearly in magnificent settings. Two photos, one of an Emperor Penguin (*Aptenodytes fosteri*), another of a group of Royal Penguins (*Eudyptes schlegeli*) with elephant seals (*Mirounga*) are of lesser quality; one of rusting boilers would have been better left out. The other photos draw the reader back again and again: they are too rich to absorb in one sitting. The line drawings are excellent, and illustrate well a variety of penguin poses and behaviors.

The specialist will be frustrated by the lack of references, but many original observations are presented. For example, Peterson has seen both melanistic and albinistic chicks and adult penguins. He gives graphic descriptions of Giant Fulmars (*Macronectes giganteus*) and leopard seals (*Hydrurga leptonyx*) eating penguins. It is noted that a rockhopper (*Eudyptes crestatus*) was paired with an Erect-crested Penguin (*Eudyptes sclateri*) on Macquarie Island, and that an introduction of several King Penguins (*Aptenodytes patagonica*) on an island in Norway was unsuccessful. All are useful bits of intriguing information that make the book worth reading.

Although not given in great detail, salient natural history features of many species are discussed. Penguins show a variety of reproductive traits: Emperor and King penguins, the largest species, lay 1 egg; the other species lay 2. King Penguins may raise 2 young every 3 years, but Jackass Penguins (*Spheniscus demersus*) can raise 4 in 1 year. Some species, like the Royal Penguin, nest in dense colonies, but others, like the Galapagos Penguins, nest solitarily or in small aggregations.

The history of discovery and exploitation of penguins, from the human-aided demise of the Great Auk (*Pinguinus impennis*) (not a penguin, of course) to the boiling down of 400,000 Falkland Island penguins in 1857, is well told, as is the present-day conservation story. However, careful editing could have eliminated much redundancy in the text, e.g., Peterson notes three times that a reduction in whales is correlated with an increase in penguins. Much of the information presented in the text can also be gleaned by reading the picture captions; this benefits the browsing-only reader.

The information presented is generally correct, but two speculative conclusions are unfounded and probably erroneous. Peterson puzzles about the lack of penguins in the Arctic and discusses their Northern Hemisphere ecological equivalents—the auks (Alcidae). He suggests that predators like foxes and wolves, and steep cliffs, might preclude flightless birds in the North, but also points out that the Great Auk bred safely on a few rather flat islands where flight was unnecessary. Otters and foxes do appear to be more important predators of seabirds in the Northern Hemisphere than in the Southern, but they alone cannot account for the lack of flightless Northern Hemisphere species. The distribution of aboriginal people in Arctic waters and their reliance on the sea and islands for food may be an equally important selective factor favoring flight and cliff nesting.

Second, Peterson believes that because penguins are flightless, the Equatorial countercurrent would have prevented them from going deep into the Northern Hemisphere. Swimming against currents is problematic, but warm tropical waters also lack suitable food. Penguins are confined to relatively productive waters where upwelling is common, so I believe that the scarcity of food in tropical waters is a more important barrier to their spread northward. When penguins do get into the Northern Hemisphere (in the Galapagos) they are dependent on the rich waters of the Cromwell Current.

It would have been preferable to have less discussion of taxonomy and population size, as both topics are fraught with problems. The casual estimates of seabird numbers given are a grave disservice; these "guess-timates" are prone to be quoted and misused to document changes in population size.

This book provides an entertaining and informative text about penguins, their ecological equivalents and their associates, despite redundancy, lack of references and undocumented assertions. It goes well beyond being merely a magnificent pictorial essay about fascinating groups of birds. Specialists will find the book enjoyable leisure reading, and amateurs a good survey into the lives of the penguins of the world.—P. DEE BOERSMA.

RESEARCH IS A PASSION WITH ME: THE AUTOBIOGRAPHY OF MARGARET MORSE NICE. Doris Huestis Speirs (ed.). Consolidated Amethyst Communications, Inc., 60 Barbados Blvd., Unit 6, Scarborough, Ont. M1J 1K9, Canada, xii + 324 pp. $12.95 ($9.95, soft cover).—This lovely book is an illuminating account of the decades-long education and development of a great ornithologist. Konrad Lorenz has contributed a brief foreword and an appendix describing his debt to Dr. Nice, C. O. Whitman and Wallace Craig. The introduction and second appendix describe the Margaret Nice Ornithological Club and its important role in serving as co-publisher of this book. There is an 18-page bibliography, a helpful 29-page index and a 2-page geneological chart. Scattered throughout the text and concluding pages are 11 superb photographs of the author and/or her family.

There are 32 chapters in the book. Adorned with charming sketches used as chapter heads and tails (which are taken from the author's published work) each chapter begins with descriptions of Dr. Nice's childhood in Amherst. They continue with her college years at Mount Holyoke, her graduate work at Clark University and the awakening to her vocation—the study of nature, especially birds. Six chapters cover her faunal studies in Oklahoma and another eight her work on the Song Sparrow. Others involve her trips to Europe, the tragedy of her young friend, Joost ter Pelkwijk, her happy work on precoccial birds and her great review of incubation periods throughout the ages.

In general, Dr. Nice plays down her family life and sticks somewhat impersonally to her experiences as an ornithologist. Nearly every AOU and Wilson Society meeting that she attended is mentioned, usually with references to the papers that interested her. To her, the International Ornithological Congresses were greatly attractive affairs. Like most scientists, she enjoyed meeting colleagues, although I think she was, to the very end, a rather shy person. Her comments in this book about her colleagues are, however, quite constrained—even when they were close friends or much admired. "Chicago is," she wrote me in 1950, "rather disappointing when it comes to people who are studying birds." This, and her isolation from a university community may have made scientific meetings of so much interest to her. Her autobiography does mention many of Dr. Nice's honors, but not her honorary membership in 12 ornithological and conservation societies. Was she proud of these? I think so; but she was also a very modest person.

This book tells a lot, but not everything, about Margaret Nice. Nothing is mentioned about her irritation on being referred to as "a housewife." "I am not a housewife," she once said in my presence. "I am a trained zoologist!" Nor is anything said about the dreariness of her environs in Chicago. As one who lived in Chicago for a year as her near-neighbor, I appreciate how much her later years had to involve summer escape trips to the Delta Waterfowl Research Station, library work and writing in order to overcome an urban environment of House Sparrows (*Passer domesticus*) and Starlings (*Sturnus vulgaris*). Her last 25 years were indeed a triumph of the spirit.

Reading this book should be an incentive to the young. The text does reveal the extraordinary combination of enthusiastic but patient field worker that Dr. Nice always was, as well as the fantastic scholar that in the end she became. Her psychological ups and downs when writing "SS II" (p. 238) echo the feelings of most persons who have ever attempted to write a monograph (including a Ph.D. thesis). It was Darwin who wrote: "Oh if one only could but observe!" Dr. Nice undoubtedly felt the same; her fortitude in publishing her results compels admiration. I think the same can be said of this interesting volume.—JOSEPH J. HICKEY.

HANDBOOK OF THE BIRDS OF INDIA AND PAKISTAN. Vol. 1, 2nd ed. By Sálim Ali and S. Dillon Ripley. Oxford University Press, London (England) and New York (New York), 1978:382 pp., 23 plates (19 color), numerous drawings and maps. $29.95.—The standard reference work on the birds of India and adjacent regions was published in 10 volumes between 1968 and 1975. This new edition of Vol. 1 has been extensively revised and expanded, and we may hope that the intention is to continue this revision through the entire series. After brief introductory accounts of the history of ornithology in the region, the organization of the work and the zoogeography of the area are reviewed. The bulk of the text is devoted to detailed species accounts and keys for the orders Gaviiformes, Podicipediformes, Procellariiformes, Pelecaniformes, Ciconiiformes, Anseriformes and Falconiformes. One might wish for a better quality paper for such an important reference work, but the price is very reasonable considering the amount of information and the number of color plates provided.—ROBERT J. RAIKOW.

INDIAN HILL BIRDS. By Sálim Ali, illus. by G. M. Henry. Oxford University Press, New York, New York, 1980 (1949):188 pp., 72 plates (64 color). $24.95.—This is an unrevised reprint of a book first published in 1949 and out of print since 1974. The only modification is a new preface indicating changes in geographical names. It is intended as a field guide to the birds of the Indian hills, and covers 300 species, of which 117 are illustrated. The species accounts include field characters, distribution and habits.—R.J.R.

ISLAND ECOLOGY. By M. L. Gorman. Chapman & Hall, London, England; distributed in U.S.A. by Halsted Press of John Wiley and Sons, Inc., New York, New York, 1979:79 pp., 38 black-and-white figs., 7 tables, paper cover. $4.95.—From Darwin and Wallace to MacArthur and Wilson, island ecology has played an important role in the development of theories of evolutionary ecology. This concise and clearly written little book will serve as an admirable introduction to the subject for students and others not familiar with recent developments. The approach is analytical rather than merely descriptive. Phenomena are examined through a choice of carefully selected examples taken mostly from recent literature, questions are posed, and the merits of suggested solutions are examined. Most of the book concerns oceanic islands, including problems of colonization, numbers of species, competition and dangers of island life. Continental habitat islands are also considered, and the book ends with an enlightening discussion of how the principles of island ecology may help in the design of nature reserves. Although various groups of organisms are discussed, one is struck by the disproportionate role that studies on birds have played in the development of theories of island ecology.—ROBERT J. RAIKOW.

REPRODUCTIVE PERFORMANCE OF THE EASTERN BROWN PELICAN, PELECANUS OCCIDENTALIS. By Ralph W. Schreiber. Contrib. Sci. Nat. Hist. Mus. L. A. County, 317:1–43, 1979. Price not given.—Data on clutch-size, hatching success and fledging success from 8 breeding seasons, with a discussion of human disturbance bias.—R.J.R.

A BUNDLE OF FEATHERS. By S. Dillon Ripley (ed.). Oxford University Press, London, England, 1979:241 pp. $16.95.—This is a *Festschrift* dedicated to the gifted Indian ornithologist Sálim Ali on the occasion of his 75th birthday on 12 November 1971. Although most of the manuscripts for the 21 chapters were submitted during 1972, and the book contains a publication date of 1978, the actual date of publication is 1 November 1979. Dr. Ali does not move so slowly, and he visited the United States on his 80th birthday to attend the fourth Triennial meeting of the International Wildlife Fund. Earlier that year he had been awarded the J. Paul Getty Prize of the World Wildlife Fund for his world leadership in the field of conservation, at which time he was doing fieldwork in India.

The 21 chapters attest to the breadth of Sálim Ali's interests and talents. They deal with life history and field biology, zoogeography and systematics, and migration and biomedicine. Examples of the chapters are "The food of *Collocalia* swiftlets" (Tom Harrison), "Physiological adaptations in the Rosy Pastor" (J. C. George), "The voice of the Indian Hill Myna" (Brian Bartram), "The Asian Honeyguides" (Herbert Friedmann), "Problems resulting from the discontinuous distribution of *Muscicapa latirostris*" (Erwin and Vesta Stresemann), "Two tropical forests and their birds" (H. Elliott McClure) and "The role of birds in the natural foci of tick-borne arboviruses in western Siberia" (G. Netsky, G. Malkov and I. Bogdanov). In his tribute, Yoshimaro Yamashina speaks of Sálim Ali's "warm cordialness" and his "agreeable presence," traits that anyone who has had the pleasure of meeting him will recognize with warm personal memories. The book is a fitting tribute to Sálim Ali and a valuable addition to ornithological literature as well.—ANDREW J. BERGER.

THE NESTING SEASON: THE BIRD PHOTOGRAPHS OF FREDERICK KENT TRUSLOW. Commentary by Helen G. Cruickshank. Viking Press, New York, New York, 1979:136 pp., 75 color, 29 black-and-white photos. $25.00.—Looking at the illustrations in this book is rather like revisiting old friends. Many are superb photographs, both esthetically and scientifically, originally published in National Geographic, Audubon, National Wildlife and other magazines. It is good to have them available in more permanent form.

In this posthumous book, Truslow's photographs are accompanied by a 45-page "Commentary" by long-time friend Helen Cruickshank, who also prepared the captions for the color plates. The text is a summary of avian breeding biology with a strong conservation flavor, and is written in a popular style. As is so often the case in this type of writing, there are generalities and/or stylistic mannerisms that result in inaccuracies, e.g., the statement that after the breeding season "The fiery red of the male scarlet tanager fades [sic] and its back becomes green and its underparts yellow" (p. 54); molt is not mentioned until the following paragraph. Mrs. Cruickshank also seems to have worked largely from her personal experience, Truslow's field notes and secondary sourcebooks, and thus missed a number of recent discoveries that would have enhanced and improved the book. Surely the phenomenon of cooperative breeding deserved ample discussion in a text of this length? Nor would an author well acquainted with the recent literature have made statements such as the one in the caption on Spotted Sandpipers (*Actitis macularia*) (p. 96) that the female remains close by the nest during incubation and later helps to feed the young. It is now known that this species is polyandrous, and the female remains only with the last male she has courted. I also noticed 2 identification errors in the photographs: the "Sooty Terns" on p. 29 are Noddy Terns, and the nestling "Rough-legged Hawks" on pp. 118–119 are Ferruginous.

The color printing is good, although some of the photographs were reproduced better (if smaller) when they originally appeared in magazines. A few present their subjects much larger than life-size, which is annoying to some readers, but a delight to others. I would have preferred to see some not so enlarged as to cut the bird in half by extending it across 2 pages. The book also includes a Foreword by O. S. Pettingill, Jr., an Afterword by Mrs. Truslow, a peculiarly located (pp. 59–61) list of "Latin" names of the birds (with no page references), and photographic notes on the color plates, but no index.

In a $25.00 book, it is too bad that the publishers did not reduce the length of the generally unremarkable text (which is accompanied by curiously unrelated black-and-white photographs) and substitute more of Truslow's fine color work—which is, after all, the subject of the book, yet takes up only about half of the pages.—MARY H. CLENCH.

OTHER EDENS: THE SKETCHBOOK OF AN ARTIST NATURALIST. By John Henry Dick. Devin-Adair, Old Greenwich, Connecticut, 1980:273 pp., maps, numerous black-and-white illus. $19.95.—Other Edens briefly outlines some of the adventures and encounters of the author during his travels to various parts of the world in search of wildlife. Among the places visited are Africa, India, New Guinea, the Arctic in Alaska and Greenland, Texas, the Falkland Islands and Antarctica, and the American tropics in Costa Rica, Guatemala, Peru and the Galapagos.

The initial chapters are about big game hunting expeditions and the author's gradual conversion to a naturalist/photographer. The latter chapters are mainly of a more appealing nature and reflect a concern for the world's rapidly dwindling wildlife resources.

While the accounts are often as concerned with the logistics of travel as with the wildlife seen, the reading is never boring. Scattered throughout are numerous black-and-white sketches by this talented artist, of birds, mammals, reptiles and landscapes, adding considerably to enjoyment of the book.—ROSS D. JAMES.

THE BIRDER'S FIELD NOTEBOOK. By Susan Roney Drennan (ed.). Doubleday & Co., Inc., Garden City, New York, 1979: approx. 80 pp. $4.95.

THE NORTH AMERICAN BIRDER'S LIBRARY LIFELIST. By Susan Roney Drennan (ed.). Doubleday & Co., Inc., Garden City, New York, 1979:630 pp. $24.95.—These are not books except in their physical form, but record-keeping aids for birders. The first is a pocket-sized, soft-covered field notebook in which the observer will find places provided for recording the field characteristics of birds, and notes on the date, time and place of observations, along with weather information and other data. The second is a hefty hard-cover volume to be kept at home, in which 30 years of field observations can be recorded, rather like noting births, deaths and weddings in the family Bible. Over 800 species are covered in a standard format, with places to record dates, places, habitats, etc., along with a small space for comments. The utility of these volumes is questionable. One would be limited by the space and format provided. I would think that most birders who are interested in keeping detailed or long-term records of their observations would do better to improvise their own systems, and to take advantage of the flexibility offered by ring binders. Cost is another consideration; it seems like a lot of money to pay for books that you write yourself.—R.J.R.

A GUIDE TO BIRD-WATCHING IN EUROPE. By James Ferguson-Lees, Quentin Hockliffe and Ko Zweeres (eds.). The Bodley Head, Ltd., London, England. Available in the U.S.A. from Chatto, Bodley Head & Jonathan Cape, Salem, New Hampshire. 336 pp., numerous line drawings and maps. $6.95 (paper), $10.95 (cloth).—This guide to finding and seeing birds in Europe contains 25 chapters, each covering a particular country or region, and written by an observer experienced in the area. The ornithological societies, publications, and research efforts (especially banding) are briefly introduced for each country. The main text includes discussions of topography, habitats, and specific information on what kinds of birds are found in particular areas. The book closes with a 36 page table summarizing the status of each of 432 species in each country.—R.J.R.

A GUIDE TO HAWK WATCHING IN NORTH AMERICA. By Donald S. Heintzelman. Pennsylvania State University Press, University Park (Pennsylvania) & London, (England), 1979: 284 pp. $6.95 (paper), $12.95 (cloth).—Brief species accounts of North American hawks, helpful hints on hawk watching, and a compilation of hawk migration lookouts in the United States and Canada. Illustrated by black-and-white drawings and photographs of numerous species at rest and in flight.—R.J.R.

INDEX TO VOLUME 92, 1980

By Nancy J. Flood, Gary R. Bortolotti and David J. Brooks

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. Common names are as they appeared in the volume. Reference is made to books reviewed, reviewers and announcements as they appeared in the volume.

This issue of *The Wilson Bulletin* was published on 26 February 1981.

THE WILSON BULLETIN

Editor JON C. BARLOW
Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Assistant Editor MARGARET L. MAY

Senior Editorial Assistants GARY BORTOLOTTI
NANCY FLOOD

Editorial Assistants KEITH L. BILDSTEIN
DOROTHY M. RICHARDSON
C. DAVISON ANKNEY
RICHARD R. SNELL
JAMES D. RISING

Review Editor ROBERT RAIKOW
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor WILLIAM A. LUNK
865 North Wagner Road
Ann Arbor, MI 48103

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "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 (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss 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.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

MEMBERSHIP INQUIRIES

Membership inquiries should be sent to Dr. Robert C. Whitmore, Division of Forestry, West Virginia University, Morgantown, West Virginia 26506.

CONTENTS

GENERAL NOTES