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THE WILSON ORNITHOLOGICAL SOCIETY ANNOUNCES

PAUL A. STEWART AWARDS

The Paul A. Stewart Fund for Ornithological Research has been established by donations from Paul A. Stewart. Income from this endowment will be awarded annually to support research in ornithology, especially studies of bird movements based on banding and analyses of recoveries and returns and investigations pertaining to economic ornithology. Several Stewart Awards in the amount of $200 each will be available each year. Stewart Awards will be equally available to students, amateurs, and professionals.

LOUIS AGASSIZ FUERTES AND MARGARET MORSE NICE AWARDS

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is 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 contributions 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 are applicable 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 and facilities generally available at the colleges. High school students are eligible. In some years 2 Fuertes Awards of $200 each have been made, in some years, one. One Nice Award is made annually in the amount of $200.

Persons interested in those awards may write to **Clait E. Braun, Wildlife Research Center, P.O. Box 2287, Fort Collins, Colorado 80522.** Completed applications must be received by **1 March 1979.** Final decisions will be made by the Council of The Wilson Ornithological Society at the annual meeting of the Society, 12–15 April 1979.

INDIVIDUAL AUDITORY RECOGNITION IN THE LEAST TERN (*STERNA ALBIFRONS*)

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ABSTRACT.—Playback experiments performed in a colony of Least Terns near Fort Macon, North Carolina, demonstrated that adults can distinguish the call of their mate from that of a stranger. Sonagram analysis of the "Purrit-tit-tit" call, the most common vocalization used when an adult approaches its mate, revealed that both temporal and spectral characteristics of the first note of the call varied significantly among individuals, whereas all measured features of the second note were not significantly different for different birds. Presumably the first note is used to convey an individual's identity, while the second note indicates a tendency to approach the mate and perform certain courtship behaviors. *Received 17 January 1978, accepted 26 March 1978.*

IN his review of individual auditory recognition in birds, Beer (1970a) stated that the best evidence for the existence of vocal recognition comes either from colonial species, for which the omnidirectional properties of sound far exceed those of visual signals in a crowded colony, or from species that inhabit thick vegetation, as foliage obstructs vision but does not greatly hinder sound transmission. This study examines vocal recognition between mates in the Least Tern (*Sterna albifrons*), a colonially-nesting larid.

Individual recognition by voice has been hypothesized for several species of colonial birds and documented for a few. Most investigations deal with auditory communication between members of a mated pair or between parent birds and their young. According to Beer, investigators have used three approaches in the study of vocal recognition in birds: field observation, sound analysis, and playback experiments. Field observation has provided circumstantial evidence for the existence of auditory recognition between mates in several colonial species (e.g. *Sterna hirundo,* Tinbergen 1931 and Palmer 1941; *Larus argentatus,* Tinbergen 1953) and between parents and offspring (e.g. *S. fuscata,* Watson and Lashley 1915; *L. argentatus,* Goethe 1937; *S. sandvicensis,* Hutchinson et al. 1968). However, some method of experimentation is usually necessary to eliminate the possibility that a bird is actually responding to visual rather than auditory stimuli, as in most cases colonial birds can see as well as hear one another (Beer 1970a).

Several investigators have performed experiments to test the ability of parent birds to recognize their own chicks. Although individual recognition of chicks has been demonstrated for several species of colonial nesters (e.g. *Anous stolidus* and *S. fuscata,* Lashley 1913; *S. bergii,* Davies and Carrick 1962; *S. maxima,* Buckley and Buckley 1972), such experiments usually do not reveal the relative importance of visual and auditory modalities for such recognition. However, Miller and Emlen's (1974) study of the effect of altering a chick's voice and appearance on the recognition of young by their parents in the Ring-billed Gull (*Larus delawarensis*) revealed that vocally impaired chicks 12 to 20 days old were accepted whereas visually altered chicks were not. In some species, at least, visual rather than auditory stimuli are important for the development of chick recognition.

Experiments involving the recognition of parents' voices by chicks have met with somewhat more success due to the ease with which chicks can be manipulated.

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Controlled playback experiments, performed under both natural and laboratory conditions, demonstrate that in most cases chicks of colonial species clearly distinguish between the voice of a parent and the voice of a strange adult (*Uria aalge,* Tschanz 1968; *L. atricilla,* Beer 1969, 1970b; *S. hirundo,* Stevenson et. al. 1970). White (1971) reported that chicks of the Gannet (*Sula bassana*) seem to have the ability to recognize the voice of a parent in a playback test, but do not always do so. Presumably in this species there is no particular advantage for vocal recognition between parents and young since, unlike the species listed above, Gannet chicks are not mobile and remain on the nest until fledging.

Investigators have also studied the ability of adult birds to discriminate the call of the mate from that of other adults in the colony. Hutchinson et. al. (1968) recorded "fish calls" from 40 adult Sandwich Terns (*S. sandvicensis*) and analyzed various temporal and spectral parameters of sonagrams of these calls. They concluded that the general "patterning" of the call was always characteristic for each individual. However, they were unable to perform playback experiments to test whether the adults did, in fact, use such characteristics to identify their mates by voice. They were also unable to record more than one sequence of vocalizations from each individual. Intra-individual variation is probably greater among calls from different sequences than among calls in the same sequence (see below). In a more conclusive investigation, playbacks showed that adult Gannets recognize vocalizations of their mates (White 1971). Sonagram analysis of landing calls of individual Gannets suggested that recognition resulted from individually consistent temporal changes in amplitude (White and White 1970).

To demonstrate individual auditory recognition, playback experiments must show that test birds respond selectively to vocalizations from different individuals. Analysis of physical characteristics of the vocalization should reveal one or more sources of interindividual variation. Using this procedure, I investigated auditory recognition between mates in Least Terns. On numerous occasions, I observed that an individual sitting quietly on its nest would suddenly stand and call repeatedly just as its mate, vocalizing loudly, approached the territory. Vocalizations of other individuals were always ignored. Least Terns are colonial nesters that form stable pair bonds for at least one, and possibly several, breeding seasons. Both the male and female participate in incubating the eggs and raising the young. During the incubation period, members of a pair alternate incubation duties approximately every hour (Moseley 1976). On some occasions, particularly during the first few days of incubation, nest relief ceremonies involve a brief period of visual and vocal displays between mates near the nest. However, after about a week of incubation, members of a pair become very efficient at switching places, to the extent that an incubating bird leaves the nest and flies out of the colony, vocalizing repeatedly, at what seems to be the instant it hears the voice of its mate. Auditory signals appeared to be the primary mode of communication in such interactions.

I therefore performed a series of playback experiments designed to test the ability of adult Least Terns to recognize the call of their mates. I have previously identified 10 discrete vocalizations of adult Least Terns (Moseley 1976). The vocalization that is typically associated with approach to the nest and courtship behavior between mates, and the call that occurred most frequently in playback sequences, was the "Purrit-tit-tit," named by Schönert (1961). This vocalization is a 4- or 5-syllabled call approximately 0.5 s in duration, with the dominant frequency of most syllables between 4–5 kHz (Fig. 1). It was nearly impossible to establish by ear which physical

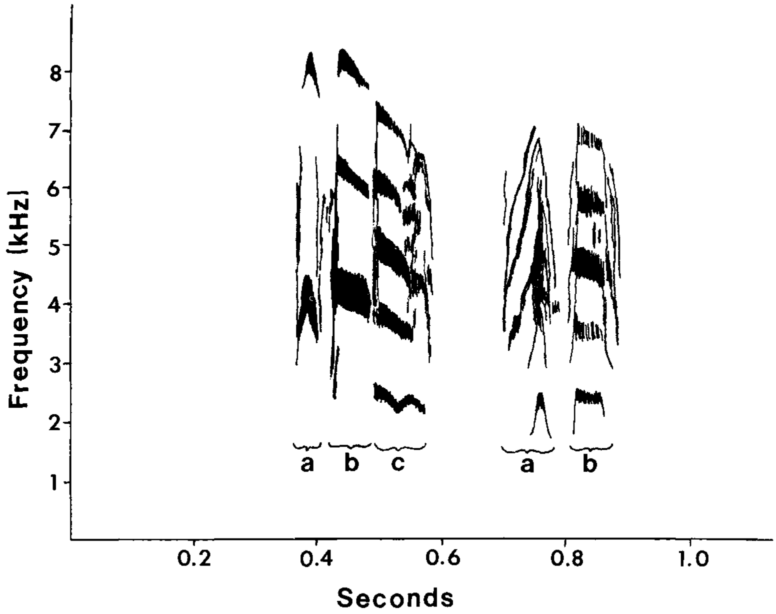

Fig. 1. Representative "Purrit-tit-tit" vocalization, divided into its component segments.

features of the vocalizations differed among various birds. I therefore performed a quantitative analysis to determine which features of the "Purrit-tit-tit" varied sufficiently among birds to permit voice discrimination.

PLAYBACK EXPERIMENTS

METHODS

This study was part of a general investigation of Least Tern behavior and communication conducted in a nesting colony on the north side of Bogue Banks, approximately 1 km northwest of Fort Macon, Carteret County, North Carolina. The center of the colony lies about 200 m inland from Bogue Sound. Between 45 and 50 pairs of Least Terns nested on a former dredge spoil area in May 1975. During my visits to the colony, I observed the terns from a burlap-covered blind, similar to the one described by Robins (1972). Least Terns were unaffected by the presence of the blind and resumed apparently normal behavior within 5 min after I entered the blind.

In order to identify individual birds, I devised a method for color-marking nesting terns with dye from a bottle placed at the nest and activated from within the blind (Moseley and Mueller 1975). The method was easy to repeat if the dye began to fade.

For the playback experiments, I first recorded sequences of vocalizations from 14 marked birds as they approached their nests, either for a courtship feeding or a nest relief. These sequences averaged 25 s in duration (SD = 12, N = 23) and consisted of one or more of the vocalization types in the Least Tern's repertoire. Occasionally, calls of both members of a pair occurred in a sequence. Recordings were made with a Uher 4000 Report I-C tape recorder and a Dan Gibson Electronic Parabolic Microphone. The most complete sequence from each pair was later incorporated into a test tape for use in the playback experiment.

A test tape consisted of a sequence of vocalizations recorded from the terns at a particular nest, a 30-s interval of silence, a sequence of vocalizations from another pair of birds from the same colony, and a final 30-s interval of silence. I scored the responses of a test bird during the playback and the following 30-s interval according to the following scale of response intensity, based on numerous hours of observing the responses of incubating terns to the approach of their mate or a strange tern: 0—no response to playback sequence; 1—flies over territory, calling "Purrit," and returns to nest; 2—rises from nest, looks upward and calls "Purrit" and "Purrit-tit-tit"; 3—remains at nest and "Chatters" continuously; 4—approaches to within 15 cm of speaker while "Chattering"; 5—flies off nest and out of colony, calling "Peedee." Category 0 describes the typical response of an incubating tern to the approach of a stranger. Categories 1 and 2 describe responses that occur occasionally at the approach of a stranger but more often at the approach of the mate. Categories 3, 4, and 5 include responses and specific vocalizations associated only with the approach of the mate, in order of increasing intensity of response. The order of presentation of calls was randomized during the experimental series. Since most courtship feedings and nest relief ceremonies are accomplished in 15 s or less, I felt that, using the above procedure, I would observe all important responses to the playback and yet keep the test situation similar to a natural interaction.

Prior to each playback experiment, I placed a Magitran speaker (33 × 41 cm, frequency range 40–20,000 Hz) 2 m from a nest on the ground in an upright position aimed at the nest. A 15 m cord attached the speaker to the Uher tape recorder in a nearby blind. Volume of the playback tape was adjusted to a level that, to my ear, was similar to the volume of calls given by a tern approaching its nest. As all test birds had nests within 17 m of the blind, I could easily observe all behaviors and vocal responses to a test tape.

RESULTS

The test tapes consisted of a variety of vocalization types. Because many sequences contained voices of both mates at a nest, it was necessary to determine the response of a bird to a recording of its own voice to eliminate the possibility that a test bird responded to its own calls rather than those of its mate in a playback experiment. Fortunately I recorded three sequences containing the voice of only one individual. These recordings were obtained as a tern approached its nest when its mate was absent, a situation that arose rarely, and therefore provided only three usable sequences for this test. Following the procedure described above, I broadcast to each bird a recording of its own call and that of a stranger. In all cases, the test birds completely ignored both the recording of their own voice and the call of the strange tern. Thus, although the sample size is small, I conclude that a Least Tern does not respond to a recording of its own voice.

Figure 2 summarizes the results of playback experiments conducted during May of 1975. Least Terns responded significantly more ($P < 0.005$) to playbacks of calls of their mates than to calls of other individuals in the colony. Thirteen out of 14 test birds exhibited no response to the playback of vocalizations of a strange tern. However, each sequence of calls of a test bird's mate elicited a response, usually of the type typically observed when an incubating tern is approached by its mate. Because responses of test birds were scored on an ordinal scale, I used the non-parametric Wilcoxon Matched-Pairs Signed-Ranks test to compare responses of each individual to the two playback situations (Siegel 1956). This technique has been used effectively in previous studies of individual recognition (Emlen 1971).

SONAGRAM ANALYSIS OF INDIVIDUAL VARIATION

METHODS

After completing the playback experiments, I prepared sonagrams of all recordings containing "Purrit-tit-tit" calls attributable to birds of known identity, most of which had been subjects in the playback experiments. Vocalizations were analyzed on a Kay Elemetrics 7029A Sonagraph, using both the wide (300 Hz) and narrow (45 Hz) bandwidth filters and the 80–8000 frequency setting. I then measured 10 temporal and 5 spectral characteristics of 45 "Purrit-tit-tit" calls of 10 individuals. To measure temporal and spectral parameters, I used an overlay of 0.1-in ruled tracing paper, calibrated to the frequency and

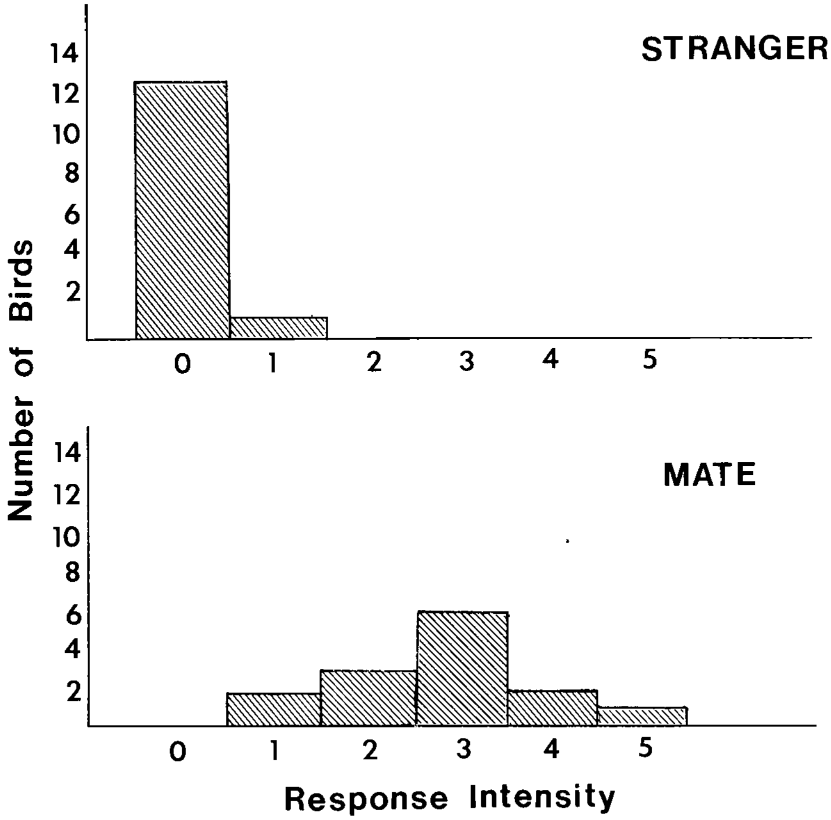

Fig. 2. Responses of test birds to playback experiments. The top histogram illustrates the responses of 14 test birds to a recording of calls by a strange tern; the lower figure illustrates the responses of these birds to a recording of calls by their mates. Significance by the Wilcoxon Matched-Pairs Signed-Ranks Test: $P < 0.005$.

time scales of the sonagraph. I measured the duration of notes and syllables to within 2 ms and dominant frequency of syllables to the nearest 50 Hz. Standard deviations of all parameters consistently exceeded any error that might have resulted from measurements at this level of precision.

To analyze the data, I selected the F statistic, defined as $F = s_1^2/s_2^2$ where s_1^2 equals the variance of sample 1 and s_2^2 equals the variance of sample 2 (Hays 1973). For each parameter, I compared the variance of a sample of calls from 9 different birds (s_1^2) with the variance of a sample of 9 calls by the same individual on different occasions (s_2^2). If the ratio was greater than the tabled value of F for the appropriate degrees of freedom, I concluded that the calls of different birds vary significantly more with respect to the parameter than calls by the same bird.

RESULTS

Figure 1 illustrates a typical "Purrit-tit-tit" vocalization, divided into its component segments (notes, syllables, inter-note and inter-syllable intervals). "Purrit-tit-tits" of different individuals varied considerably in structure (Fig. 3). One method of analyzing physical characteristics of vocalizations for individual differences is to compare calls given by one bird with vocalizations given by several other birds. Presumably if 10 calls by the same bird show significantly less variability with

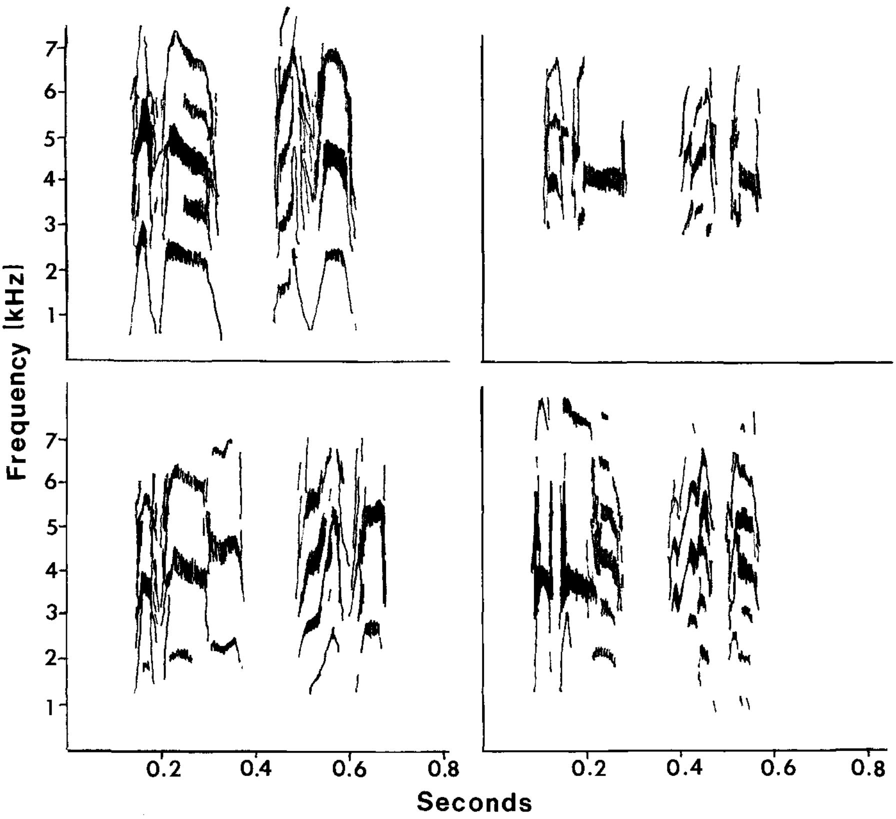

Fig. 3. "Purrit-tit-tit" vocalizations of four different individuals.

respect to a certain parameter than 10 calls each from a different bird, individuals should be able to identify each other by voice alone. A group of calls in the same sequence by the same individual is, however, an inadequate sample with which to compare vocalizations of different individuals. For example, five repeated "Purrit-tit-tit" calls by one bird on the same occasion are likely to show less variability than "Purrit-tit-tits" by the same bird on five different occasions. Slight changes in relative strengths of tendencies associated with delivery of the calls at different times, differences in transmission of the signal, and the physical condition of the bird could contribute to increased variability in different sequences. If only calls from the same sequence are used, it is possible that statistical analysis could indicate sufficient variability among individuals to allow for individual recognition where, in fact, none exists. To be conservative in this analysis, I selected only calls by marked birds for which I had recordings on two or more occasions separated by at least 30 min.

Table 1 presents the results of statistical analysis of temporal and spectral features of this vocalization. The duration and dominant frequency of all components of the "Purrit" note are significantly more variable for calls by different birds than for calls by the same individual ($P < 0.05$). However, the duration and frequency of the components of the second note are not significantly different among birds. Selected F-values are given in the last row of Table 1.

TABLE 1. F-results: individual variation among temporal and spectral characteristics of the "Purrit-tit-tit" vocalization of Least Terns.

Note	Segment	Temporal characteristics[a]	Spectral characteristics[a]	Actual F-values[b]
"Purrit"	Syllable a	+	+	24.4 (3.6)
	Syllable b	+	+	10.3 (3.4)
	Syllable c	+	+	9.8 (3.4)
	Total "Purrit"	+	*	10.2 (3.4)
"Tit-tit"	Syllable a	–	–	3.1 (3.7)
	Syllable b	–	–	3.2 (3.5)
	Interval between a & b	–	*	2.4 (3.5)
	Total "Tit-tit"	–	*	3.3 (3.5)
	Inter-note interval	+	*	43.6 (3.4)
	Total "Purrit-tit-tit"	+	*	10.0 (3.4)

[a] + = significant ($P < 0.05$); – = not significant; * = not applicable to spectral analysis.

[b] F-value for vocalizations from one individual compared with vocalizations from nine other birds. Number in parentheses is tabled value of F ($P < 0.05$) for appropriate degrees of freedom. Where actual value exceeds tabled value of F, the vocalizations of nine different birds are significantly more variable than calls given by the same individual.

DISCUSSION

My results indicate that, for each parameter tested, sufficient variability exists in the temporal and spectral features of the "Purrit" note to permit discrimination by voice. It is possible that only one or two features of the note are actually necessary for individual recognition. To establish which feature or combination of features is most important, one must artificially alter the calls on tape and conduct additional playback experiments. This work is presently in progress with the Least Tern.

The "tit-tit" note is remarkably consistent among all birds. Whereas the "Purrit" note is frequently used alone, the "tit-tit" note rarely occurs alone in a sequence. Presumably the "Purrit" and "tit-tit" convey different messages. The contexts in which the "Purrit" note occurs alone indicate that the major message conveyed by this vocalization is identification of the signaler. A Least Tern typically calls repeated "Purrits" as it leaves the colony (following a "Peedee" series, Moseley 1976), or when feeding alone or in small groups. In addition, a tern on its nest occasionally calls "Purrit" in answer to the "Purrit-tit-tits" of its approaching mate. In aerial courtship, the tern without the fish (the presumed female) also uses the "Purrit" (Moseley 1976). In each context, the adaptive value of a vocalization that conveys a bird's identity is clear. The use of the "Purrit" by the presumed female in aerial courtship aids in familiarizing the male with her voice. Later in the breeding cycle, when nest reliefs occur frequently, repeated "Purrits" by an incubating bird in answer to its mate could help the arriving bird locate its nest in the midst of a uniform colony and thus permit rapid incubation shifts. The use of this vocalization by foraging birds could serve to orient others from the colony to a plentiful source of food. The value of vocalization that conveys identity in this context, however, is not clear, and it may be that the "Purrit" is used by feeding birds simply because it is the most appropriate vocalization in the species' repertoire for communicating a bird's presence without implying any erroneous information about its motivational state.

The complete "Purrit-tit-tit" vocalization is highly associated with two social contexts: when approaching the mate, or when carrying a fish either during aerial courtship displays or prior to a courtship feeding (Moseley 1976). A Least Tern calling "Purrit-tit-tit" is therefore conveying at least two discrete messages. It identifies itself with the "Purrit" note, and, with the "tit-tit" note, indicates a tendency to approach the mate and perform certain non-agonistic behaviors, such as courtship feeding or assuming incubation of the eggs. The "tit-tit" note, because of its structural consistency, conveys an easily recognizable message of intent to approach without aggression. Because it is always accompanied by the "Purrit," no structural variability in the "tit-tit" is required for individual recognition to occur.

The ability to communicate auditorily both identity and a tendency to behave sexually with a mate or potential mate is an advantage in a crowded colony of morphologically similar birds. During early courtship, each member of a pair learns to recognize its mate by voice and probably by sight so that efficient trading of incubation duties can occur later. After the first week of incubation, members of a pair rely heavily upon auditory communication during nest reliefs. An incubating bird simply flies off its nest when it hears the "Purrit-tit-tits" of its approaching mate, and the nest relief is accomplished rapidly with little or no visual communication between birds. The frequent use of the "Purrit-tit-tit" during early courtship also helps to insure that strangers do not later interfere with or participate in incubation activities at the wrong nest. It is not uncommon for a strange bird with a fish to land or attempt to land near an incubating bird (Moseley 1976). On such occasions, the intruder is often driven off before it lands. Apparently the occupant of the nest recognizes a strange "Purrit-tit-tit" call before it visually recognizes the intruder, and reacts aggressively to prevent the stranger's continued approach.

For a colonially-nesting species of morphologically similar birds, the ability to identify individuals by auditory signals probably permits recognition at greater distances than visual signals would allow. When a tern approaches its mate on a nest, the subsequent interaction occurs very rapidly. The use of auditory signals is therefore an expedient strategy for enabling rapid localization of an individual in a crowded colony.

ACKNOWLEDGMENTS

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A symposium on **The Integrated Study of Bird Populations** will be held at Wageningen, the Netherlands, from 17–21 September 1979 on the occasion of the 25th anniversary of The Institute for Ecological Research of the Royal Netherlands Academy of Arts and Sciences. Invited speakers will address bird populations in relation to food supplies and territorial behavior, optimal foraging strategies, energetics of free-living birds, and Red Grouse and Great Tit population dynamics, and facilities will be available for display of posters on related subjects. Further information may be obtained from **I.A.C., Postbus 88, 6700 AB Wageningen, The Netherlands.**

The second **International Congress of Systematic and Evolutionary Biology** will be held at the University of British Columbia, Vancouver, Canada on 17–24 July 1980. A number of symposia will be offered, and sessions for contributed papers will also be organized. Those interested in receiving an information circular in the spring of 1979 should write to **Dr. G. G. E. Scudder, Department of Zoology, University of British Columbia, 2075 Wesbrook Mall, Vancouver, B.C. V6T 1W5 Canada.**

JUVENILE DISPERSAL AND DEVELOPMENT OF SITE-FIDELITY IN THE BLACK-CAPPED CHICKADEE

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ABSTRACT.—Dispersal of young was studied in a non-migratory population of the Black-capped Chickadee (*Parus atricapillus*) in southeastern Wisconsin. Eighty-eight chickadees were color-banded as nestlings. After fledging, the birds remained with their parents on or near the parental territory for about 3 weeks. In late June or early July family breakup occurred suddenly, with the young moving rapidly away. Most of the birds disappeared completely from the area; 6 were later discovered in the breeding population at distances of 0.4 to ca. 11 km, with a median dispersal distance of 1.1 km. This movement appeared to be an innate dispersal mechanism. In contrast, among 103 chickadees first trapped in July and early August as independent juveniles and later found on their breeding territories, the median distance from point where banded to territory was 204 m (maximum = 1,160 m). As distances up to 2.4 km could have been detected in our study area, we conclude that by late July and August chickadees have virtually finished dispersing and are developing site tenacity in the places where they will subsequently breed. Whether dispersal also occurs in spring was investigated using the monthly patterns of arrivals and disappearances from winter feeders. Adults and summer-banded juveniles inhabiting the parts of the study area nearest the feeders arrived for the first time at the feeders in November and December, but birds from more remote areas continued to arrive through the winter and spring. In previously unbanded juveniles there was an increase in arrivals in March and April. On the basis of an analysis of loss rates by sex and age, we conclude that only about 5% of yearling males and 9% of yearling females undertake some dispersal or spacing movements in spring. Thus, in the Black-capped Chickadee the main dispersal mechanism is an innate, rapid, fairly long-distance movement of the juvenile, taking place in summer just after family breakup. A small fraction of the yearling population undertakes some dispersal movement in the winter or spring. *Received 20 February 1978, accepted 7 September 1978.*

IN ecology dispersal is defined as the movement of an organism from site of birth to site of breeding (Howard 1960, Johnston 1961). Many species have evolved specific behavioral adaptations that insure that dispersal movements will take place at a certain time in the ontogeny of the individual. Additional movement may be forced on individuals of any age by environmental influences such as availability of, or competition for, resources. Howard (1960) refers to these modes of dispersal as innate and environmental, respectively, while Johnston (1961) and Berndt and Sternberg (1968) use dispersal for the former and spacing for the latter. Murray (1967) questioned the existence of innate dispersal in vertebrates and formulated a model in which the dispersal distances observed in nature could be explained solely on the spacing type of movement, "dependent only on the relative dominance of individuals in procuring a breeding site."

While the importance of dispersal in such processes as ecological succession, colonization of islands, and speciation has long been recognized, the intrapopulational aspects have been relatively neglected. Gadgil (1971: 253) states: "Dispersal is one of the most important and among the least understood factors of population biology." Many currently active areas of ecological study require thorough elucidation of dispersal mechanisms on an individual basis for full understanding of the phenomena

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under investigation. For example, the origin, development, and areal extent of song dialects in birds must depend heavily on the precise mode of dispersal in the species—how far and in what directions young birds move from their hatching sites, and at what age in reference to the age of song imprinting or song development. Likewise, many of the ideas concerning the evolution of altruistic behavior rest on certain assumptions regarding dispersal. It is of interest to know, for each species, by what mechanism dispersal is accomplished.

The present investigation of dispersal in the Black-capped Chickadee (*Parus atricapillus*) was part of an intensive study of the population dynamics of this species. The specific questions we tried to answer were: (1) do young chickadees drift slowly and haphazardly away from their birth place or parents (spacing movements), or is there a more directed or predictable movement suggestive of an innate dispersal adaptation?; (2) how far on the average do they move?; and (3) do the movements occur throughout the prereproductive parts of the birds' lives or are they restricted to more specific times?

The Study Area and the Chickadee Population

The study was conducted at the University of Wisconsin–Milwaukee (UWM) Field Station, Ozaukee County, Wisconsin, at the edge of the Milwaukee metropolitan area. The Field Station lies in a morainal area of rather rough topography with substantial areas of natural vegetation. The dominating feature is Cedarburg Bog, about 800 ha in size. This has complex patterns of successional vegetation including several bog lakes, sedge marshes, bog shrub zones, large areas of bog conifer forest, and some swamp hardwood forest near the periphery. Several islands in the bog basin support upland forest, while a large interior portion is occupied by string bog, a coniferous forest-edge type of habitat found in many Canadian bogs but unusual this far south (Grittinger 1970). Surrounding the bog are many smaller bogs and swamp forests, extensive patches of upland hardwood forest, old fields in various stages of succession, and cultivated fields. Most of the interior of Cedarburg Bog is a designated Wisconsin State Scientific Area, as are parts of the UWM Field Station located on the west side of the bog.

Figure 1 depicts all the regularly utilized chickadee habitat in the Cedarburg Bog and Field Station region. The blank areas (fields, pastures, marshes) contain hedge rows, patches of trees or shrubs and the like that provide corridors for chickadee movement. There are few substantial barriers to chickadee dispersal. The chickadee population work has been conducted mainly within a 440-ha area referred to hereafter as the basic study area. The boundaries and configuration of this area were established after several years of observation of the movements of color-banded chickadees visiting the Field Station winter feeders (Fig. 1). Few of the color-banded birds range beyond the boundaries of the basic area either in winter or in the breeding season. Likewise, there are few unbanded birds breeding within the basic study area.

The basic study area contains three "intensive study areas" (Fig. 1): a 26-ha gridded plot in upland forest (but including some peripheral wetland forests), an 18-ha gridded plot in bog conifer forest, and a 16-ha ungridded area in string bog where locations could be accurately determined by natural landmarks. In or near these plots seven winter feeders were located. These were in operation from 15 November to 30 April each year. There are also many privately operated winter bird feeders around Cedarburg Bog; those that are known to us are shown in Fig. 1. Most chickadee flocks in this area are within range of winter bird feeders.

The Black-capped Chickadee is the only parid occurring in this area. Most chickadees in the basic study area are color-banded during their first winter of life and study of these birds over 10 yr has shown the population to be stable and non-migratory. We cannot exclude the possibility of an occasional bird migrating, but such birds must certainly form a negligible fraction of the population. Since 1970 breeding season populations within the basic study area have varied from 201 to 284 individuals, including non-territorial birds. There is a regular pattern in population size, high one year and low the next, although there were two low years in succession in 1973 and 1974. Although there are some slight density-dependent effects on reproduction they are not enough to offset the differences in breeding density; thus in years of higher breeding density the overall number of juveniles becoming independent is also higher than in the years of low breeding density. There is a strong inverse relationship between the density of juveniles in

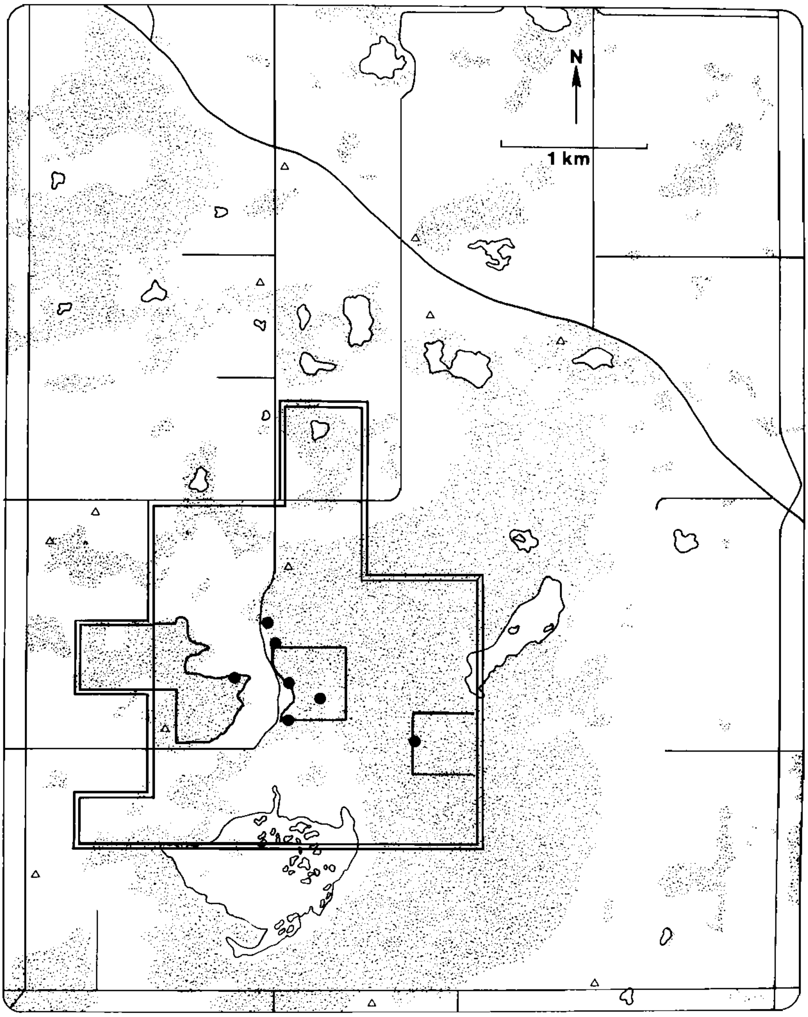

Fig. 1. Cedarburg Bog area showing all suitable chickadee habitat (stippled). Double boundaries enclose the basic study area. Single boundaries enclose the intensive study plots: from left, upland deciduous forest, bog coniferous forest, string bog. ● = UWM winter feeders. △ = privately-owned feeders.

July and August and the number of juveniles banded at that time that are recovered in the study area in winter. For reasons explained beyond we believe that this represents differences in survival rather than dispersal. Since 1970 winter populations have varied between 238 and 324, depending largely on the survival of juveniles. Details of the population dynamics will be reported elsewhere.

METHODS

Movements of birds color-banded as nestlings.—In 1970, 1971, and 1972 a total of 88 nestlings were banded from 19 nests in the intensive study areas. All of these were natural nests and most were 3–16 m above ground. Considerable effort was involved in climbing to the nests (often with the aid of a forester's swing), cutting into the nest cavity, extracting and banding the nestlings, and replacing them in the cavity after repairing it with wire and tape. Each family was given a distinctive color code. All of the banded families successfully fledged with one possible exception, a low nest with 5 nestlings that may have suffered predation, although the evidence was equivocal.

After the birds fledged in late June or early July, the color-banded families were followed and studied until the time of family breakup. Meyer continued to search for the young birds in the intensive study areas throughout July and August. Meanwhile in July and early August of each year we were systematically netting independent juveniles throughout the basic study area (see below), and we especially watched for the birds color-banded as nestlings.

In the winters following banding of the nestlings, the intensive study areas and our winter feeders were under close surveillance for these birds. In addition, Meyer conducted extensive special searches not only throughout the basic study area but through all chickadee habitat within 3 km of the banding areas, i.e. essentially all of the chickadee habitat shown in Fig. 1. Notices were placed in local newspapers asking for notification of the occurrence of color-banded birds at private feeders.

In each breeding season, a total count census of all chickadees in the basic study area was conducted, and those birds banded as nestlings that survived and entered the breeding population were then detected. The locations of such birds were plotted on large scale maps so that straight line distances from hatching site to wintering or breeding location could be measured. For precise determination of the breeding location the nest-site was used where known; however in the majority of cases the center of the pair's activity during the population's main period of incubation (8 May–5 June) had to be used. Stefanski (1967) showed that during incubation chickadees restrict their movements to small areas near the nest site.

Movements of birds banded as independent juveniles in summer.—Between 1 July and 20 August each year since 1969 we have trapped samples of independent juvenile chickadees from all parts of the basic study area except near the periphery, using portable mist nets into which birds were lured by playback of tape-recorded songs or calls. It should be stressed that in our summer trapping we caught only a fraction (perhaps 25–50%) of the juvenile chickadees present in the area.

Birds banded as independent juveniles were retrapped at the winter feeders and individually color-banded and then detected during the annual breeding season censuses, as described above. Straight line distances were measured between the sites where captured in July or August and the places where located the next breeding season.

Movements in the fall, winter and spring.—A general bird-netting operation in the intensive study areas in the fall of each year provided much information on the locations and movements of both juvenile and adult birds. In winter and early spring the feeders were under observation at least 1 day a week and usually more frequently. Detailed records were kept of the locations, dates, and times of occurrence of color-banded birds at the feeders.

Age and sex determination.—Because this population has been color-banded since 1967 the ages of most birds in the population since 1970 have been accurately known. Birds first trapped after early November could not be aged by the standard methods of plumage features or skull ossification. However, as the study area was initially set up to encompass the flock ranges of all birds likely to visit the winter feeders, and as most adults in the area at the beginning of each winter are already banded, we believe that a high proportion, perhaps 90%, of the unbanded birds trapped in winter and spring are first-year birds.

Sex was determined provisionally at the time of first capture by wing chord measurements and later verified by behavioral characteristics during the breeding season.

RESULTS

Onset of post-fledging dispersal.—Observations of six families in the upland woods showed that after the young fledged the families stayed together for about 20 days (Holleback 1974). Generally they remained within or close to the parents' original territories, but occasionally families were seen up to 300 m outside the parent's nearest observed boundary. Family dissolution was abrupt, i.e. on one day the parents and young were observed together, while on the next only the parents could be located. Again, a few exceptions were noted, when parents were seen still feeding and caring for some of their offspring while others were seen in distant places. We had 19 observations of at least 12 different color-banded juveniles from the 6 families in the 3 weeks following attainment of independence. These varied from 180 to 760 m from their nest sites, and from 50 to 590 m from the nearest locations where they had been seen with their parents. However these birds were not subsequently seen

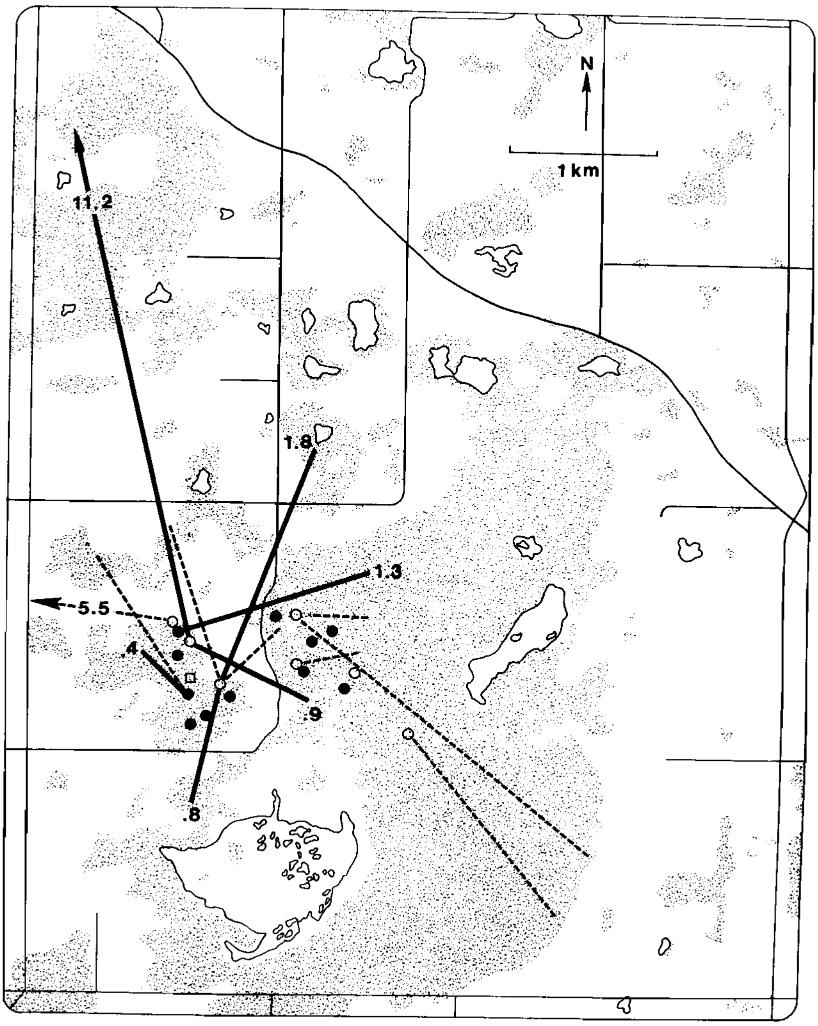

Fig. 2. Dispersal of chickadees banded as nestlings. □ = 1970 nest; ○ = 1971; ● = 1972. Broken lines connect birthplace and winter location. Solid lines connect birthplace and breeding location. Numbers at ends of solid lines are distances in km. All birds found breeding were also located in winter but their winter locations are not shown.

in these same places and were evidently in transit at the times of observation. Most of the 88 birds banded as nestlings disappeared completely from the intensive study area immediately after family breakup.

Only a few attempts were made to track individual juvenile birds during this period and these were usually unsuccessful. On 3 July 1976 Weise followed one unbanded independent juvenile at a distance without disturbing it. In about 30 min, flitting from tree to tree and pausing now and then for foraging, it moved 500 m in a generally southerly direction, passing unaccosted through three adult territories. It was then approached by two other juveniles, and there was a brief chase and some dominance or aggressive calls. The bird under observation then moved 200 m farther south at which point it was lost to view while still continuing in the same direction. We believe this exemplifies the sort of movement involved.

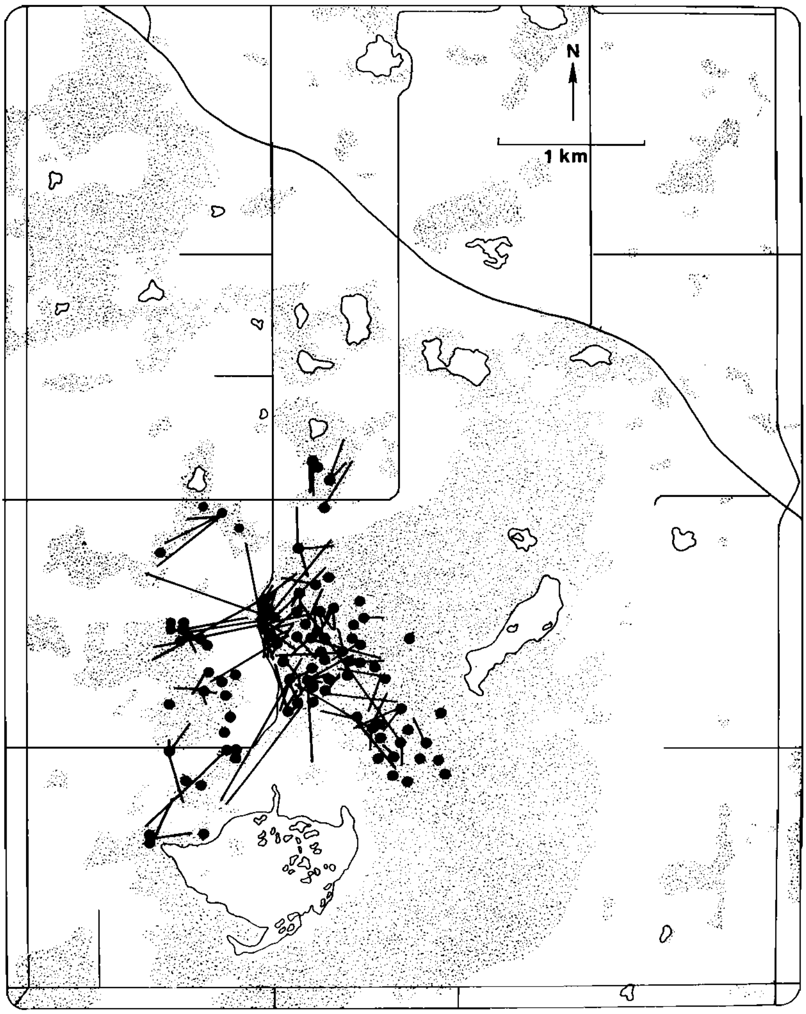

Fig. 3. Movements from place where individuals were banded as independent juveniles in July–August to their breeding sites in subsequent years. Composite of 6 yr. ● = point where juvenile chickadees were banded (regardless of whether any were subsequently found breeding).

During the winters of 1971–72 and 1972–73 Meyer, in his searches of the entire vicinity around the Field Station, located 12 of the 88 birds banded as nestlings (Fig. 2). Straight line distances from hatching point to winter locations varied from 0.5 to 2.4 km. In addition, one bird was reported and verified at a winter feeder 11.2 km from its birthplace, and another was killed by a cat at a residence 5.5 km away. The directions taken by the birds appeared to be random. The median distance for the 14 birds was 0.8 km.

Since daily foraging ranges of chickadees in winter may exceed 1 km, these winter records shed little light on the crucial question of distance from birth place to breeding place. In the routine breeding season censuses in the basic study area, five of the birds banded as nestlings were located as breeding birds. In addition the bird at the distant (11.2 km) feeder was observed there in subsequent winters and can

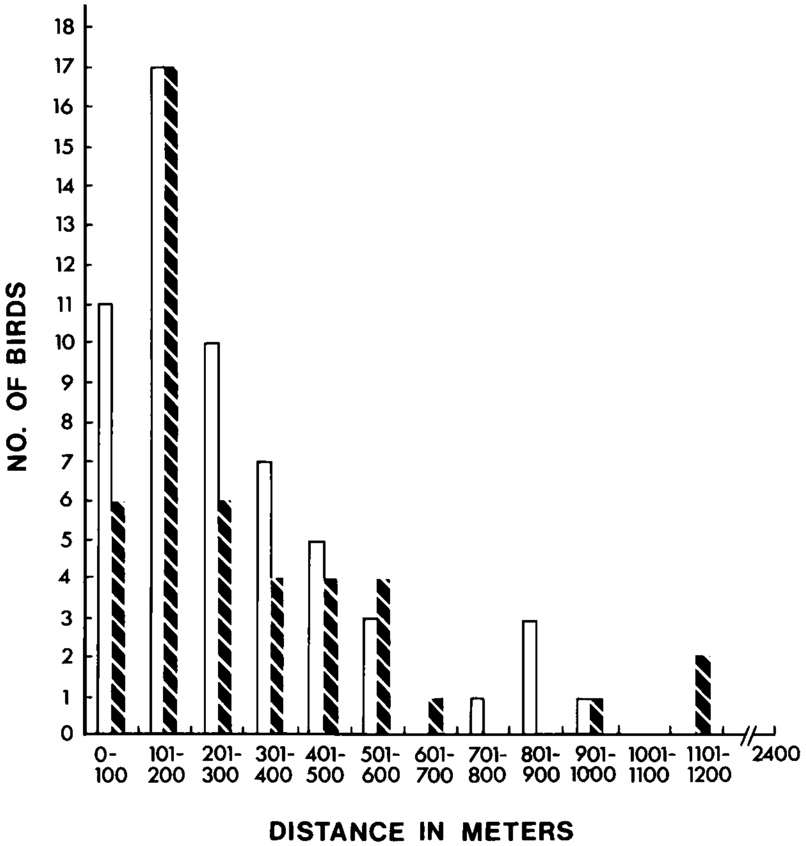

Fig. 4. Distances from point where individuals were banded as independent juveniles in July–August to their breeding sites in subsequent years. Composite of 6 yr. Open bars = males, N = 58, median = 211 m; solid bars = females, N = 45, median = 198 m.

be presumed to have nested within a km or so of that site. Thus, the distances from birth places to breeding sites for six birds were: 0.4, 0.8, 0.9, 1.3, 1.8 and ca. 11 km, with a median of 1.1 km. This median is probably a minimum estimate since, while we know for certain that there were no others of these birds within our study area, it is quite likely that there were a few undetected survivors that bred outside the study area at distances greater than 1 or 2 km.

Eleven of the 14 winter records and 4 of the 6 breeding records were of nestlings banded in 1971. This we attribute to the difference in survival rate in juveniles in low versus high density years. In 1972, the number of juveniles becoming independent was about one-third higher than in 1971, with consequent higher mortality and fewer birds entering the wintering or breeding population of the next year. We cannot determine from our data whether these differences in juvenile density have effects on the speed or distance of dispersal as well as on survival.

Most of the winter records and all of the six breeding records were of birds originating in the upland forest habitat. Of 40 birds from nests in bog forest or string bog, only 4 (10%) were subsequently recorded in winter or the next breeding season, compared with 10 of 48 (21%) from upland forest nests. On the other hand, in birds

TABLE 1. Distance from point where chickadees were banded as independent juveniles in July–August to their breeding territories in the subsequent year. The comparison is with a Poisson distribution.

	Distance (m)										
	1–100	101–200	201–300	301–400	401–500	501–600	601–700	701–800	801–900	901–1000	over 1000
Observed	17	34	16	11	9	7	1	1	3	2	2
Expected	2	13	24	26	19	11	5	2		1	

banded as independent juveniles in July or August (after the initial dispersal period, see below), 35% of those settling in bog forest survived to winter, compared with 37% of those settling in upland forest (data from 6 yr). This suggests that bog forest birds suffered greater mortality than upland forest birds while still in the family group stage, but from what cause we do not know.

Cessation of dispersal and development of site-attachment.—From 1969 to 1975, 481 chickadees were banded in July and early August as independent juveniles and 185 of these were recovered at the winter feeders and given individual color codes. Ninety-seven were located on their breeding territories in the first year after banding. Six others were non-territorial the first breeding season after banding, but restricted their activities to small areas in which they had territories in subsequent years. Figure 3 shows for this sample of 103 birds the straight lines from the points where initially banded as independent juveniles to the territories or nest sites in the next breeding seasons. The main point to observe is that these distances are very much shorter than those in Fig. 2. A frequency diagram of these distances (Fig. 4) shows that the longest distance we recorded was 1,160 m, although we could have detected distances up to 2,400 m. The median distance was 211 m for males, 198 m for females, 204 m for sexes combined. The small sex differences were not statistically significant ($\chi^2 = 0.124$, $P > 0.50$, Median test, Siegel, 1956). Ninety percent of the birds had territories within 600 m of the point where banded. This distribution was compared with a Poisson distribution, following the procedures of Kluijver (1951) and Johnston (1956). Appropriate adjustments were made for differences in the areas of the concentric rings around the points of banding and also for the proportion of suitable habitat in each ring. The observed distribution departs significantly from the Poisson ($\chi^2 = 100.8$, $P < 0.005$), with much higher values than expected in the shorter distance classes and somewhat higher (but not significant) values in the longest classes (Table 1).

We also examined the possibility that birds trapped early in July might still be dispersing while those trapped later in the summer were not. In this population,

TABLE 2. Effect of the date when trapped on the distance between the place where individuals were trapped as independent juveniles and their breeding territories in the subsequent year.

	Distance (m)											
Period of trapping	1–100	101–200	201–300	301–400	401–500	501–600	601–700	701–800	801–900	901–1000	over 1000	Median
July 1–20	3	8	5	2	0	1	0	1	0	0	1	195
July 21–31	6	9	6	6	3	2	1	0	0	0	0	195
August 1–20	8	17	5	3	6	4	0	0	3	2	1	198

families begin to break up and independent juveniles become noticeable about the first of July each year. By 15 July nearly all families have dissolved. Thus, during much of July there must be many juveniles moving relatively rapidly and for long distances as described in the previous section, and one could hypothesize that distances from banding site to subsequent breeding territory would be longer at that time than later. We split the sample (sexes combined) into three time periods: 1–20 July, 21–31 July, and 1–20 August (Table 2). The median distances were nearly identical.

A possible explanation for the lack of a date-distance relationship lies in our method of trapping, which we believe contained a bias in favor of the more mature juveniles who had developed sufficient social behavior and aggressiveness to respond to playback of songs or calls. In fact we found it difficult to trap any juveniles at all in early July. Using total hours spent in the field as a measure of trapping effort, our success rate in trapping juvenile chickadees was: 1–10 July, 0.09 birds/h; 11–20 July, 0.59; 21–31 July, 1.09; and 1–20 August, 1.43. Thus we believe that the birds trapped in early or mid-July were those that had hatched and become independent earliest and had by that time reached the requisite state of maturity, while later-hatched birds were still dispersing and not responding to our song playbacks. Some confirmation of this was obtained in 1977, an exceptionally early breeding year, when independent juveniles were first noted on 18 June. In the 1–10 July period we had a success rate of 0.98 birds/h, far higher than usual.

Still another question concerned possible differences between the summers of high density and low density juvenile populations. Birds trapped in 1970, 1972, and 1975, the high density years, were compared with those trapped in 1971, 1973, and 1974. The numbers in this case were disparate, 40 in the former group, 63 in the latter, due to the differences in survival rates mentioned previously. For the low density years the median distance from banding point to the next year's territory was 194 m, while for the high density years it was 217 m, but the difference was not significant ($\chi^2 = .554$, $P > 0.05$). In the low density sample 7 birds (11.1%) moved over 500 m, compared with 9 birds (22.5%) in the high density sample. Again, however, the difference was not significant ($t_s = 1.640$, $P = .10$; test for equality of percentages, Sokal and Rohlf 1969).

Movements in winter and spring.—In our study, movements of chickadees in winter or spring should have been detectable as (1) an influx of unbanded birds at the feeders, (2) a permanent disappearance in the spring of birds that had been present at the feeders in winter, or (3) the presence in the breeding population of a substantial number of unbanded birds.

The last alternative was not the case. Although there were some unbanded birds breeding each year near the periphery of the basic study area, there were very few in the central parts. Therefore we assume that any birds entering the central portions of the area between 15 November and 30 April found their way to the feeders and were trapped and color-banded.

Figure 5 shows the monthly patterns of arrival of new birds at the feeders. Only birds of known sex were included (about 85% of the total). Since many birds lived more than 1 yr the number of records of adult arrivals is larger than the number of individual chickadees. The month-to-month patterns of arrival were similar for adult birds and birds banded as juveniles in July and August. Most of these birds along with their unbanded (juvenile) flockmates found the feeders and started using

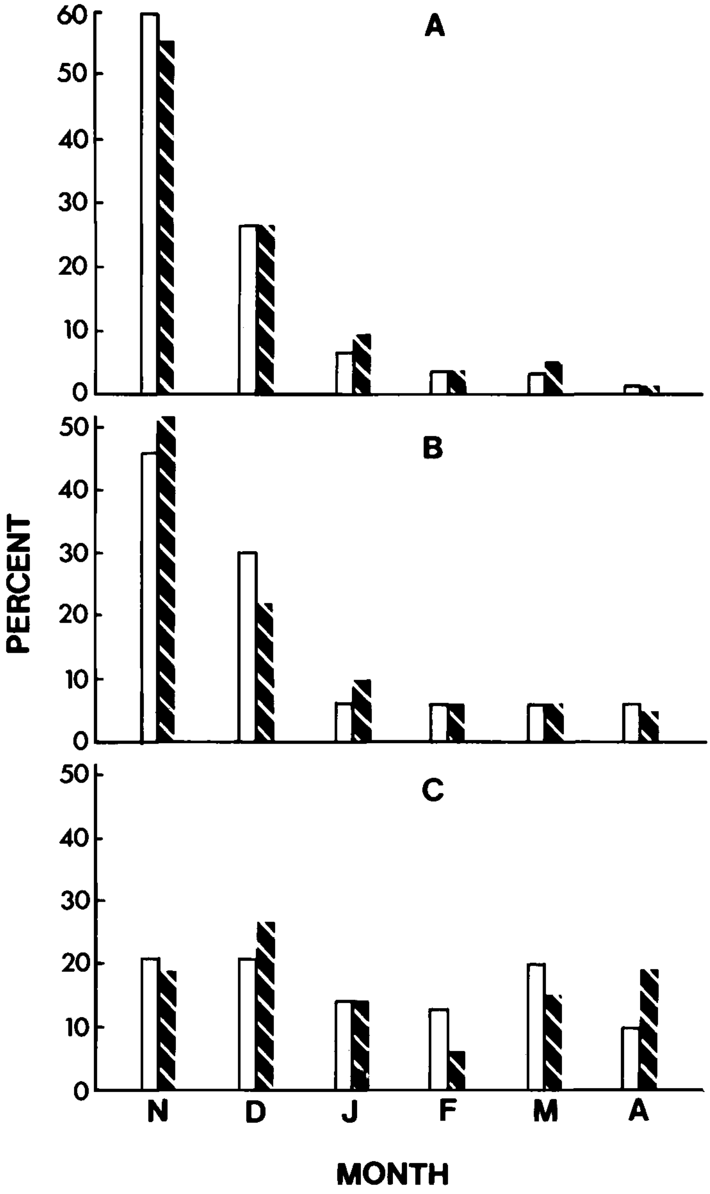

Fig. 5. Month of first arrival of chickadees at UWM winter feeders, expressed as percentage of total for each class and sex. Composite of 6 yr. Sexes as in Fig. 4. A = adults banded in previous years, N = 330 males, 285 females. B = independent juveniles banded in July–August, N = 97 males, 88 females. C = previously unbanded birds (believed to be 90% juveniles), N = 182 males, 223 females.

them shortly after they were set out in mid-November. December arrivals were mostly flocks from near the periphery of the basic study area, and small numbers of such birds continued to arrive throughout the winter. In several cases we could verify that March or April arrivals were flocks that had spent the winter in parts of Cedarburg Bog remote from the feeders. Typically such a flock consisted of 1 or

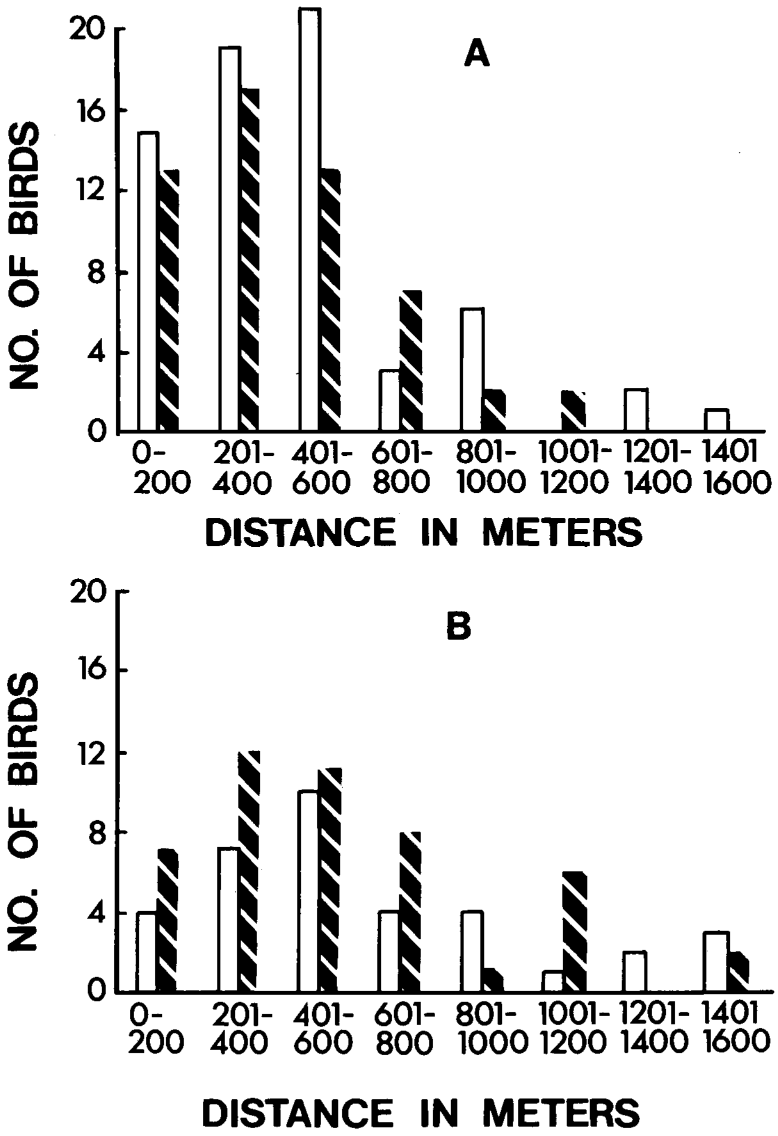

Fig. 6. Distance from winter feeder to territory, comparing previously unbanded chickadees arriving at feeders in early winter with those arriving in spring. Composite of 6 yr. Sexes as in Fig. 4. A = birds arriving 15 November–31 December; males, N = 66, median = 380 m; females, N = 54, median = 366 m. B = birds arriving 15 March–30 April; males, N = 35, median = 531 m; females, N = 46, median = 473 m.

2 color-banded adults accompanied by 3–6 unbanded flockmates. Birds banded as juveniles the previous summer were seldom present in these flocks because we avoided trapping for juveniles in areas near or beyond the boundaries of the basic study area. In short, the continued arrival in late winter and spring of known adults and some unbanded birds was the result of expansion of the daily foraging range, rather than dispersal in the proper sense. Such birds returned to their remote sources for breeding.

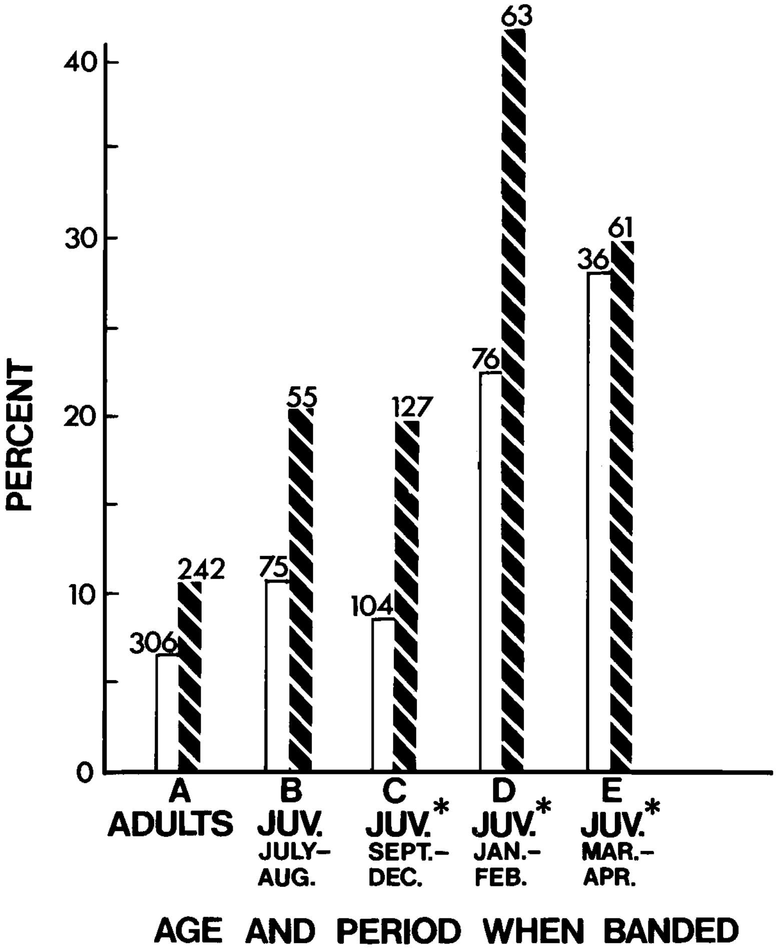

Fig. 7. Losses of chickadees from study area in spring, expressed as percentage of numbers present at feeders in 15 March–30 April period. Composite of 6 yr. Sexes as in Fig. 4. Numbers above bars indicate N in each class. * = birds first trapped after early November that could not be aged. We believe 90% are juveniles (see text).

Nevertheless, the monthly pattern of arrival of previously unbanded birds (Fig. 5C) was sufficiently different from that of adults and summer-banded juveniles to suggest that other factors might be involved. The main difference was that in March there was an increase in the arrivals of unbanded birds of both sexes, in April a further increase in females, but a decline in males. One possible explanation would be that these were birds from remote flocks that were simply expanding their daily foraging ranges, as described above. If so their breeding territories should have been located near the borders of the basic study area, long distances from the feeders. To test this we measured the distance from winter feeders to breeding territory for unbanded birds first arriving at the feeders in March and April as compared with those from flocks from the central part of the basic study area, which arrived at the feeders in November and December (Fig. 6). Of 78 males and 101 females that arrived in November and December, 66 and 54, respectively, were later found on territory. For the March–April group 55 males and 76 females were recorded, and 36 and 46, respectively, were found on territory. Males arriving at the feeders in spring did have territories significantly farther from the winter feeders than did those arriving in early winter, the medians being 531 m and 380 m respectively (χ^2 = 5.25, P = 0.05). In the females, the difference was similar in magnitude, 473 m vs 366 m, but was not significant (χ^2 = 2.53, P = 0.20). In both sexes there were larger than expected numbers of the spring arrivals settling to breed within short distances of the feeders, where they almost certainly were not present in the fall or early winter.

If there was immigration into the study area in March and April it stands to reason that there would be a corresponding emigration. Figure 7 shows the losses of birds from the basic study area in the 15 March–30 April period. These were birds that were never recorded again after having been present at the feeders during that period of a particular year. Assuming that the adult male loss rate of 7% is entirely due to mortality and that the mortality of young birds had by this time of year become identical to that of adults, we can subtract the adult loss rate from the total percentage loss and attribute the rest to emigration movements. Thus, for juvenile males that were known to be in the central part of the study area in summer, fall, or early winter (Fig. 7, B and C) only about 3–5% of the birds dispersed in the spring. In those previously unbanded males (believed to be nearly all juveniles) arriving in mid-winter about 16% moved away permanently at the beginning of the breeding season, as did 21% of those arriving in early spring.

The adult female loss rate was 11%. Assuming this to be mortality and subtracting as above, we conclude that about 9% of the juvenile females present before mid-winter dispersed in the spring. For those arriving in mid-winter about 29% moved away, and for spring arrivals about 18%.

DISCUSSION AND CONCLUSIONS

We infer from these data the following picture of Black-capped Chickadee dispersal. After fledging the young remain with their parents for about 3 weeks, moving around within or near the parental territory. Territorial defense by adults is diminishing at this time. As soon as the family group dissolves the young begin relatively rapid and long-distance movements away from their birthplaces. They do not merely drift gradually from their parents' territory to adjacent territories, but exhibit a positive behavior pattern involving movements of longer distance than would be necessary simply for feeding or escaping the aggressiveness of other birds. This is not to imply that the movements are continuous or straight-line flights, or that some birds may not end up near their places of origin. This dispersal phase persists for only a few weeks and carries the birds a median distance of 1.1 km; a small proportion of the movements may exceed several km.

By mid- or late July this dispersal movement is diminishing and the birds are developing site attachments in their new locations. We believe that little dispersal occurs in late summer or fall, despite the fact that a large number (296 of 481) of the birds banded in July and August were not recovered in winter or thereafter. We believe this loss was due mainly to mortality. Our argument is that if the summer to winter loss were due to dispersal, with birds moving about the area searching for suitable places to settle, the emigration would be offset by immigration of unbanded juveniles, as our study area is surrounded by extensive areas of chickadee habitat.

Thus in the years when the juvenile density in summer was high, and the observed recovery rate in winter was low, there should have been large numbers of immigrating unbanded juveniles trapped in our fall netting operation. In years when the summer density was low and recovery rate in winter high, there should have been lower numbers trapped in fall. Instead, the opposite was observed. There was a direct relationship between recovery rate and the number of unbanded birds trapped in fall. Our second argument against continued dispersal in the fall is based on Fig. 4. Since we could have detected movements up to 2,400 m we hypothesized that if much dispersal occurred after the July–August banding period we should have distances broadly distributed over the full range of the graph. Instead, they were strongly concentrated at the short end of the range.

Probably the cessation of the dispersal movement is related in some way to the maturation of social behavior and aggressiveness, which leads the juveniles in late July and August to join adults in localized areas and form small flocks that will persist until spring. Our observations, including retrap records of summer-banded juveniles and sight records of color-banded adults, indicate that the range of movement of each flock is quite restricted at this time (late summer). Later in the fall and early winter the flocks expand their ranges considerably. While this brings birds to areas where they have not been seen before, e.g. residential areas or bird feeders, it is not true dispersal, as the birds will return to breed within the range occupied by the flock in late summer.

A fraction of the first-year birds, especially females, undertake some permanent movements in the winter or spring away from the places where they were found in late summer. The questions are: how large is the fraction, and what causes them to move? Analysis of the permanent disappearances of birds from the feeders in March and April suggests that about 5% of the males and 9% of the females in the first-year population undertake spring movements. Presumably the winter and spring influxes and losses at our feeders represent the movements of this fraction of the large reservoir of yearling chickadees in the Cedarburg Bog area. Whether these are entirely spacing movements or are due to some birds failing to develop site tenacity cannot be answered.

This interpretation of the spring dispersal is somethat at variance with those of others who have studied this species. Butts (1931), Bowdish (1938), and Odum (1942) suggested or implied that substantial movements of chickadees occur in spring at the time of territorial establishment. Smith (1967) reported that many (32–49%) of the birds that wintered in her study area disappeared within a 2-week period in spring, concommitant with the appearance of large numbers of unbanded birds (none of which remained in the area to breed, however). Glase (1973) also reported a "general" movement at this time, during which 47.5% of the wintering birds disappeared. In our study we did not find such high loss rates even among the yearlings. Our data indicate that while there are certainly movements in the spring, only a small proportion of the yearling population is involved.

In other respects, our data are consistent with those of others. Median dispersal distances (hatching site to breeding site) reported for a variety of small song birds are: Great Tit (*Parus major*) 500 m (Kluijver 1951), Blue Tit (*Parus caeruleus*) 700 m (Berndt and Sternberg 1968), European Nuthatch (*Sitta europaea*) 900 m (Berndt and Sternberg 1968), Pied Flycatcher (*Ficedula hypoleuca*) 1,000 m (Berndt and Sternberg 1968), Song Sparrow (*Melospiza melodia*) 285 m in Ohio and 185 m in a

California salt marsh population (Johnston 1956). English and Belgian populations of the Great Tit have dispersal distances similar to those reported by Kluijver (Perrins 1965, Dhondt and Hublé 1968). Other investigators (Butts 1931, Odum 1941, Kluijver 1961, Glase 1973) have banded nestling Black-capped Chickadees. Aside from one of Butts' birds which may have bred about 2 km away, in all these studies it was simply reported that none of the birds was found later as a breeding bird in the study areas, implying relatively long dispersal distances consistent with the 1.1 km median distance reported here.

Goodbody (1952) found an explosive dispersal in the Great Tit beginning within a couple of weeks after fledging and peaking within a short time. This is similar to what we observed in the chickadee, although he concluded that "thereafter birds continue to move outwards from their birthplaces." Johnston (1956) also found a similar limited period of movement in salt marsh Song Sparrows, reporting that these movements ceased and the birds developed site attachments by late summer. Dhondt (1971) suggested that site attachment might develop before autumn in Belgian Great Tits. We believe our data concerning juveniles trapped in summer provide further evidence for the development of site attachment at that time, although homing experiments would be required to prove this conclusively. We concur with Brewer and Harrison (1975) that site (or habitat) selection probably takes place in late summer in many species, since the ultimate factors affecting breeding success (food supply, vegetative cover, etc.) would be more readily discernible then than they would be in the spring at the time of territory establishment.

One question that arises from these findings is whether the summer dispersal movement of juvenile chickadees is an innate dispersal mechanism or an environmentally forced spacing movement. We believe the evidence favors the former. First, at the time of family breakup the adults are no longer rigorously defending their territories and do not attack juveniles unless the latter approach very closely. Second, while aggression between parents and young is at least partly responsible for the dissolution of the family (Holleback 1974), the young would need to move only a short distance—a few tens of meters, perhaps—to escape. Third, if competition for food, foraging sites, or other resources were a driving factor in the dispersal it is likely that short distance movements and a diffuse dispersion pattern would result, rather than the observed long distance movements culminating in flock formation. Such competition might have some influence on the total distances traveled and on where the dispersal terminated, without being the driving or initiating force. Finally, since young are dispersing in all directions, those emigrating from a particular area are replaced by immigrants from another, with little net change in numbers. Little is gained in terms of reduction of competition. Since we cannot discern any external causes we hypothesize that in the chickadee this dispersal behavior is an evolved, innately-programmed adaptation.

The evolution of such an adaptation need not be based on group selection, as suggested by Howard (1960). The chickadee is a highly social species in which survival is enhanced by supposedly altruistic behavior, such as antipredator warning calls. Trivers (1971), in listing the situations favoring the selection of altruistic behavior, suggests the case in which the dispersal rate is low during all or a significant portion of the lifetime, so that the individual interacts repeatedly with the same neighbors. This idea can be turned around to state that it would be advantageous for an individual of a species with altruistic behavior to have its dispersal confined to a brief period as early in its life as possible, so that it spends most of its life among familiar neighbors or flock members. Likewise, the advantages of late summer habitat and site selection alluded to above should also favor the evolution of a brief, early dispersal mechanism.

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BREEDING CYCLE AND BEHAVIOR OF THE SEMIPALMATED SANDPIPER AT BARROW, ALASKA

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ABSTRACT.—Pair formation of *Calidris pusilla* near Barrow, Alaska occurs 3–6 days after the territory is established. The pair is then engaged in nest scraping displays during 2–3 days, in which 10–12 scrapes are made by the male and examined by the female. Eventually 2–3 scrapes are lined by the female, and in one of these the first egg is laid 4–6 days after pairing. During the egg-laying period further lining is performed by the female and partial incubation takes place by both sexes. Continuous incubation commences 8 h prior to laying of the 4th egg. Male and female alternate in incubation: in the first 2 days a turn lasts 3–5 h, and the duration gradually increases up to 13–14 h during the 2nd week. Long incubation turns reduce the number of approaches to the nest and may therefore reduce the chances of it being discovered by predators. The incubating bird is intermittently engaged in egg-rolling and in camouflaging the nest by bending adjacent grass blades over its back, and is constantly alert. The off-duty bird may feed 2–3 km away from the nest. The eggs hatch after 20 days of incubation, all within 1 day. Females desert the family 2–8 days after hatching: they desert late if hatching is early, and early if hatching is late in the season. After female departure the family moves from the nesting territory, typically in a high-centered polygonal area, to establish a home range as far as 2–3 km away, often in a low-centered polygonal area. During the first 6–8 days after hatching, the male prepares each evening a scrape for night brooding. After fledging, the male and young join wandering flocks. *Received 24 January 1978, accepted 11 October, 1978.*

THE four common breeding calidridine species of Barrow, Alaska, *Calidris alpina, C. pusilla, C. melanotos,* and *C. bairdii,* constitute a significant component of the tundra ecosystem, feeding on arthropods and being preyed upon by birds and mammals. They also function as a link between the terrestrial and aquatic trophic webs. The breeding biology of *C. alpina* and *C. melanotos* at Barrow was studied by Holmes (1966) and Pitelka (1959), respectively, but the other two species remained relatively unknown.

The Semipalmated Sandpiper (*C. pusilla*) the smallest and often the commonest of the four species, has a Nearctic breeding distribution (Pitelka et al. 1974) and winters in southern United States and in Central and South America (McNeil 1969, Ashmole 1970, Baker and Baker 1973). The time-energy budget of this species was studied at Barrow in 1973 (Ashkenazie and Safriel 1979), and the bioenergetic implications are to be incorporated in an integrated synthesis of the structure and function of the tundra ecosystem at Barrow (see Brown and West 1970). A knowledge of the breeding cycle and the behavioral repertoire of this sandpiper, as well as of the phenology of the population during 1973, is essential for evaluating the significance of its time-energy budget. This paper describes the reproductive cycle as observed during 1973, and supplements the description with some additional observations made by Safriel during several previous years.

STUDY AREA AND METHODS

The tundra at Barrow (72°21′N 156°40′W) is a plain with an intricate network of rivers, streams, lakes, and ponds covering about 50–75% of the surface (Hussey and Michelson 1966). The remaining

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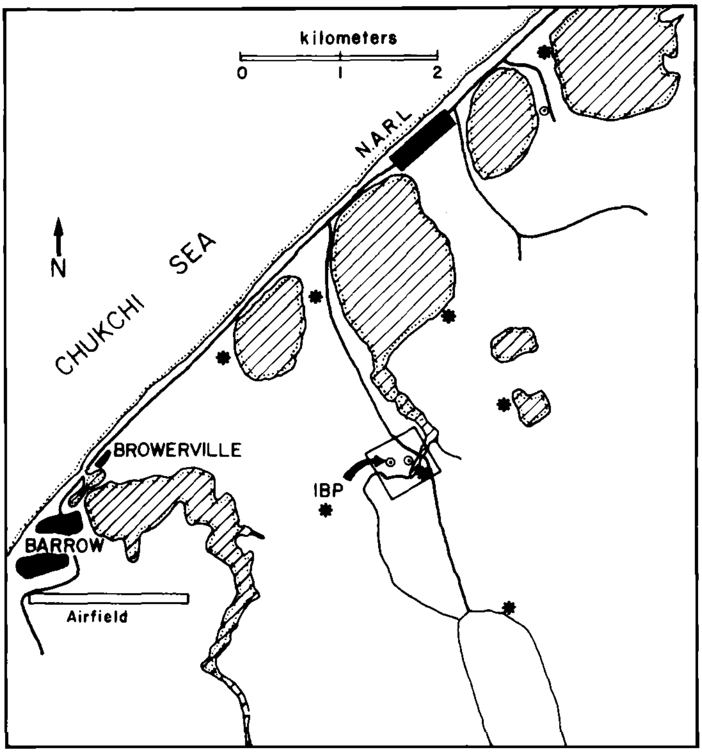

Fig. 1. The study area. ⊙—site of nest whose owners were under detailed surveillance; *—site of a territory whose owners were under less detailed surveillance; IBP—International Biological Program Intensive Site.

landscape is made up of several habitats arranged in a mosaic of polygon centers, rims, and troughs. The daylight is continuous between 10 May and 2 August. Based on records of 46 successive years (1921–1967), daily mean temperatures above freezing prevail as of 11 June (MacLean and Pitelka 1971) by which time thaw is normally well underway. Thawing starts on polygon tops and eventually all troughs, ponds, and lakes become snow- and ice-free. The mean annual precipitation during the 46 years was 118 mm, the wettest months being July and August (Brown 1968).

Our study was conducted from 1 June, when only a small portion of the population was present, to 4 August 1973, by which time most birds left our study areas. Compared with the 46-year record, the average daily air temperatures in 1973 were below normal during the study period, except for a few warm days at the beginning of June and at the end of July.

Observations on color-banded individuals were recorded on a portable cassette tape-recorder during continual watches of the birds through a 20× telescope or 8 × 30 binoculars. In 1973, 20 different birds were followed, of which 3 pairs were under close surveillance (Fig. 1), and altogether 500 h of observations were recorded (Ashkenazie and Safriel 1979). Incubating birds were followed using time-lapse photography (Minolta Autopack 8D6 super-8 movie camera equipped with an intervalometer-P time-lapse device). Additional observations of the same population were made during the 1968–1972 breeding seasons (Safriel 1971).

RESULTS

Arrival.—The birds arrived in two distinct waves: the first at the end of May and the beginning of June, the second during the second half of June. Consequently, there were two laying peaks in the 1973 season, around 10–11 June, and 20–22 June. The first clutch was started on 3 June, the last one on 29 June. There is some variation in arrival time between years, which is weather dependent (Holmes 1966, Safriel in prep., Schamel pers. comm.). First arrivals usually appeared during late May, when about 90% of the area is snow-covered, but a significant arrival of breeding birds during mid- and late June was less common.

It is not known how long the birds spend on their way, what their strategy of fuelling is, and in what physical state they arrive at Barrow. A flow of northbound *C. pusilla* has been detected in New Jersey between 10 May and 7 June, with an average peak around 20 May (Urner and Storer 1949); further north, in Anaktuvak, Alaska, the detected passage lasted only 9 days (Irving 1972).

The birds arrived at Barrow in flocks of 5–10 individuals of unknown sex. In *C. alpina,* males arrive first and females later, and only when thaw is late do the birds arrive mated (Holmes 1966). Nearly simultaneous with the arrival of the first *C. pusilla* flocks, banded males were observed on established territories, and in these territories females were not seen for some time.

The territorial male prior to pair formation.—Males established territories right after their arrival and the process was probably accelerated when males returned to their last year's territory; there is some evidence that *C. pusilla* are site-tenacious when their previous breedings in that site were successful (Norton, Ailes, and Curatolo MS, Safriel 1971). The male spent most of the time within the boundaries of his territory, and his activities were frequently interrupted by territorial display flights or by agressive encounters with other males. These activities intensified as the number of established territories increased. Pair formation occurred 3–6 days after the territory was established, when a female alighting in the territory was accepted. We observed two cases of females alighting in territories of unmated males. In one case the female had fed in the territory for a short time while being observed by the male, and later it was chased off by him. In the second case the female was accepted. Thus, females seem to be attracted to territories, but once there they may be selected by the males.

Pre-laying period of the pair.—Four to 6 days elapsed between pair formation and laying of the first egg. During that period the frequency of territorial display flights was reduced, and such flights occurred mainly during fixed hours of the day or when small flocks flew over the territory. Rarely the female joined the male in chasing off flocks.

The female determined the greater part of the activity pattern of the male, through choosing their common feeding and resting sites and times. Whatever the female did, she was followed by the male, who performed the same activity, but interrupted it by chases and spells of alertness, elicited by other males or by predators.

One or 2 days after pair formation the birds started to engage in nest site presentation or nest scraping display, known also to occur in several variations among other calidridine species (Holmes and Pitelka 1964, Bengston 1970, Holmes 1973, Pitelka et al. 1974). In *C. pusilla* we found performance of this display restricted to 2–3 days. The following description of the display is based on observations of one pair. The male selected sites with dense cover of grass where a scrape was formed by pressing the grass with the breast while rotating the body. The female stood nearby and watched. When the scrape was prepared, the male perched on its edges and attained a posture in which it leaned forward, with the wings bearing upon the edges of the scrape, and extended its neck forward. The female approached the male from behind, and entered the cup by pressing itself under the male's belly. She examined the cup for a few seconds, made a complete turn within the cup while it was being thatched by the male, and then emerged from the point of penetration. The male then rose from the cup edges, stepped away to stand by the scrape, and started preening. After a while the male lured the female to another site, where another scrape was formed and the same ritual repeated. Having prepared 10–12 scrapes, the male ceased to make new ones, but led the female to scrapes previously prepared for her examination. By that time the female tended to spend more time checking 2–3 particular scrapes. At that stage the male seemed impatient to wait for the female until she emerged from the scrapes she examined, and ran between scrapes without waiting for the female to follow. The female too, started checking scrapes at her own initiative, unaccompanied by the male. She might check any scrape in the area, not necessarily those made by her mate, and on one occasion a female was observed checking a scrape prepared by a neighboring *C. bairdii.* Those 2–3 scrapes favored by the female were lined by her with lichens and grass shoots. This lining activity was performed ritually, through the "sideway building" display (Tinbergen 1959, Holmes and Pitelka 1964, Harrison 1967), in which the female sat within the cup, picked lining items from the vicinity of the cup and threw them backwards over her back. The picked items slid down from both sides of the bird's back and settled on the cup's surface. At the stage that lining was being constantly added to the favored scrapes, copulations occurred.

The pair during egg-laying period.—The egg-laying period lasted 4 days, with one egg laid per day. We obtained observations on four pairs. An actual laying of a first egg was observed once. This female was still checking two different scrapes 1 h before laying occurred, but then started persistently to visit just one of them, lining it with vegetation at each visit. The visits were then prolonged, the last one taking 20 min, at the end of which a faint vocalization was heard from the nest and slight movement inside the cup was detected. At that point the male, who during that time had been standing near the nest, approached the cup very slowly. The female then emerged and both flew off. The cup contained a warm, pale-pink egg. Within an hour the egg cooled off and attained the strong violet pigmentation typical of this species.

We also observed females several times during the moment of laying of successive eggs, which occurred in the mornings, evenings or at night. Because the period between two successive layings is shorter than 24 h (Norton 1973), every egg within a single clutch is laid at a different time of the day.

When the first egg was laid, the cup was only sparsely lined and the bottom was moist. After the second egg was laid the amount of lining increased and the cup was dry. The lining thickened throughout the laying period, being continually added to by the female when performing the "sideway building" display. Partial incubation occurred before the clutch was complete. In 1973 incubation started on the first day of laying with incubation spells of 10–15 min totalling to about 2 h per day, performed mainly by the male. The duration of incubation during the laying period increased with time, and altogether eggs were incubated by the male 14% of the total period, whereas females incubated for 4% of the time. The female incubated just before or after an egg was laid, the male incubating during short spells several times throughout the day. Continuous incubation commenced about 8 h prior to the laying of the fourth egg. By this time incubation was shared between male and female, and the shifts occurred every 3 h. Compared with other calidridine species breeding at Barrow (Norton 1972, 1973), incubation prior to clutch completion is most extensive in *C. pusilla.*

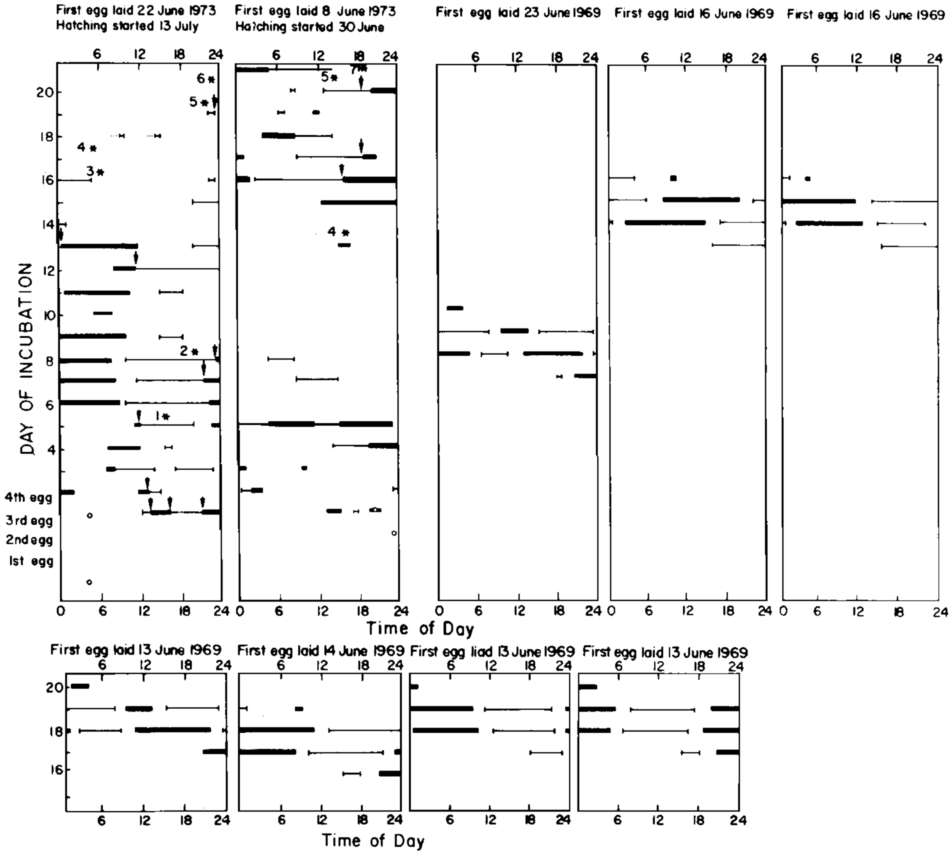

Fig. 2. Incubation schedule in nine nests of *Calidris pusilla* near Barrow. The two nests in 1973 were under continuous surveillance by us and/or by a time-lapse movie camera. The seven 1969 nests were checked every 2 h during 4 successive days. In all nests birds were individually marked. Thick lines, female incubated; thin lines, male incubated; dotted lines, nest observed, but found unincubated; arrows, a shift was actually observed; circles, an egg-laying was actually observed. Key to asterisks: 1* hail storm; 2* female arrived but chased off by male; 3* hail and snow storm; 4* snow storm; 5* eggs chipping; 6* hatchlings preyed upon; 7* first egg hatches; 8* last egg hatches; 9* hatchlings leave the nest.

Other pronounced activities during the egg-laying period were an intensive feeding by the female and protection of the female and nest from predators by the male. The male was aggressive and even chased the female in precopulatory postures, though copulations in that period were not observed.

The pair during incubation period.—The eggs were continually incubated by both male and female throughout the 20 days from the laying of the fourth egg until hatching (Fig. 2). The male and the female alternated in their incubation duties and in the first 2 days each turn lasted 3–5 h. The duration of an incubation turn gradually increased; it lasted 8 h in the fifth and sixth day, and attained a maximum of 13–14 h of continuous incubation per bird during the second week. This duration remained unchanged until about 2 days before hatching.

In *Larus argentatus* the timing of the incubation shift is determined by the bird that is off duty, either male or female (Drent 1970). In *C. pusilla,* however, we

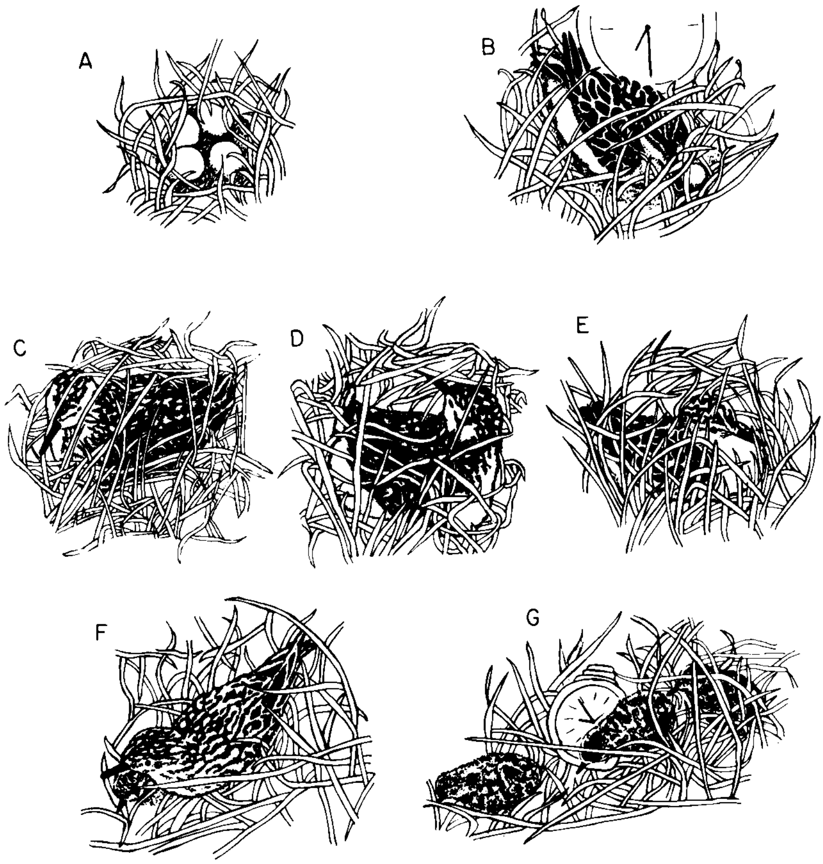

Fig. 3. Behavior of *C. pusilla* at nest (drawn from "8 mm super" film). A. Unattended nest. Note that leaf blades are not fully bent over the cup; B. Arranging the eggs before starting to incubate; C. and D. Bending the blades over the head and back, for camouflage. Note the blades in the bird's bill; E. Alertness while incubating. Note the complete "roof" of blades over the bird; F. Trying to prevent a chick from leaving the cup (while others are still being brooded); G. The moment of nest-desertion. The parent with one chick is leading (not in picture) while the fourth chich is still in cup.

observed four cases in which the female approached the nest earlier than the expected shift and was chased off by the incubating male, later to return on schedule. In two of these cases the female returned 3 h earlier than the scheduled time, on the 5th and on the 8th day of incubation. In all these cases the females involved were recorded first only in the 1973 season and not in the previous years, and hence they were presumably in their first breeding (Safriel 1971) and therefore relatively inexperienced. Also, most of these cases occurred when the weather was bad and when there probably was a temporary food shortage. We do not know why supposedly inexperienced females rather than males sometimes had difficulties in timing their return to incubation duty. It is possible that in *C. pusilla* the feeling of satiation serves as a stimulus for this return. Since males do not lose much weight during the incubation period (Ashkenazie and Safriel 1979), we suggest that by the end of each off-duty period they may be fully satiated. Females, however, lose significant weight in that period, so they may never be fully satiated and hence may not benefit from the timing mechanism suggested for males. They probably time their returns using less efficient stimuli, and these may require experience in order to be correctly interpreted. There was one case during a snow storm in which the female deserted a nest in the middle of her incubation turn and never returned. After a few hours the male returned and started incubating the cold eggs. His turn lasted 15 h. He then adopted a schedule in which 3 h of incubation were interrupted by off-duty periods of 40–45 min, during which the unincubated eggs did not cool off but remained relatively warm. The eggs hatched 2 days after the female's desertion, but were preyed upon immediately (Fig. 2, column 1). A desertion of the clutch by the female during a snow storm was observed in another nest, too, but in this case, on the 13th day of incubation, the male chased the female back to the nest.

By no means can the incubation turn be regarded as a period of rest. When entering the cup and before crouching upon the eggs, the eggs were moved, rolled, and turned with the aid of bill and breast (Fig. 3B). This activity was repeated several times during the incubation turn and was often associated with a change in the bird's orientation. Immediately after sitting on the eggs, and several times during its incubation duty (usually after a change in its orientation), the bird camouflaged the cup by bending adjacent grass blades over the nest and interweaving them with its bill, thus creating a "roof" over the cup (Fig. 3C, D). When not turning the eggs or maintaining the "roof," the bird was constantly alert, carefully examining the surroundings by head movements (Fig. 3E). At the presence of a flying predator in the vicinity the bird lowered its head and back in a typical crouching posture.

When flushed from the nest the incubating bird performed a "broken wing" display followed by the "rodent-run" display (e.g. Brown 1962, Bengston 1970): the bird squattered away from the nest with frequent crouches when the body leaned on one side, one wing flapping and the tail fully spread and depressed toward the ground. *C. pusilla* accompanied this display with a typical vocalization.

When the bird was not flushed but quietly slipped away from the nest, it performed a different display at some distance picking up grass shoots and throwing them away with sharp jerks of the head. Similar behavior is known in gulls (Tinbergen 1959, 1965; Harrison 1967).

When off-duty most of the time was devoted to feeding and preening. When the bird on duty was relieved during the first week of incubation, it first flew to a stream or a pond to bathe and preen and then commenced feeding. During the second week it first fed and only later preened and bathed. Birds of two different nests, in their second week of incubation, were observed (on 28 June) flying immediately from the nest in the polygonal area of the territory to flat plains 2–3 km away from the nest, where they were later discovered feeding in mixed flocks of 70–80 birds with *C. melanotos* and *C. alpina*.

The hatching period.—The following account is based on a time-lapse movie taken at one nest. Two days before hatching the incubation schedule changed, the frequency of changeovers becoming greater and somewhat irregular, and the turns lasting less than 14 h. A change in incubation schedule prior to hatching was also noted in *C. alpina, C. melanotos,* and *C. bairdii* (Norton 1973) and in *Larus argentatus* (Drent 1970). This alteration in schedule coincided with the commencement of vocalizations from the eggs that were produced by the embryos' breathing mechanism and became more frequent and stronger as the time of hatching approached. This phenomenon is known in most precocial birds (Gottlieb 1965, 1968; Driver 1967; Gottlieb and Simner 1969; Drent 1970; Orcutt 1974). According to Norton (1973) the alteration coincides with the appearance of holes in the egg shell, 12–48 h prior to hatching, produced by the double egg tooth characteristic of charadriiformes (Jehl 1968) and present in *C. pusilla.* Except for *Arenaria interpres,* in which a female was observed to peck at a hatching egg (Nettleship 1973), it is not known whether parents of *C. pusilla* or other shorebirds assist in the hatching process.

The time from hatching of the first to the last egg was 24 h, but the intervals between hatchings were not identical. The first two chicks to hatch tried to leave the nest a few hours after hatching, but were prevented from doing so by the incubating parent that chased them back to the cup (Fig. 3F). When there were three chicks the parent was unable to manage them all, and the chicks left the cup for feeding tours of a few seconds, then darted back to be brooded by the incubating bird. A few hours after the fourth egg hatched, the nest was deserted (Fig. 3G). In one case a wandering chick lost its way back to the nest; the incubating parent left the cup to brood this chick for a while, then returned to the remaining eggs. In another case the off-duty bird brooded such a chick in the vicinity of the nest.

The pair during young-attending period.—About 16 days elapse between hatching and fledging (Safriel 1971). The following information is based on 10 young-attending families. Females are known to desert the family 2–6 days after hatching (Soikkeli pers. comm., Safriel 1971). We found that in 1973 the timing of female desertion was season-dependent; in two cases of very late breeding, one female deserted on the day of hatching, the other 3 days after hatching. In two other families that bred earlier, the females left on the 6th and 8th days after hatching. One observation suggests that the proximate factor for female desertion is rejection by the male. During the sixth day after hatching (12 July) the female spent most of her time feeding away from the family. From time to time she returned to fly over the territory where male and young were feeding, but was chased off by the male and alighted at some distance. Finally she was chased off for a very long distance; from this final chase only the male returned. We observed this male and the brood for another 10 h, during which the female (banded) was not seen, and she was not recorded on subsequent days in the vicinity of the family or at other visited sites.

There are thus two phases in the young-attending period: in the first both parents tend the young, while in the second it is just the male. In the first phase the family usually stayed within the boundaries of the nesting territory. Usually one parent remained with the young and the other fed, preened, and bathed away from the territory. Although we twice observed females to remain continuously for 2 h with young while the male was away, it seemed that even during the first phase the male tended the young more than the female. In the second phase, after the female left, a pronounced exodus usually took place, the family moving to another locality, sometimes as distant as 2–3 km. There it seemed that in some cases a home range was established in which the young stayed until they fledged and their foraging areas were defended against intrusions of other families (Safriel 1971). In other cases we could not establish whether the family stayed within one area until fledging or if they were on a rather continuous move. Whereas the territory in which the young stayed during the first phase was usually in a high-centered polygonal area, during the second phase the families occupied wet plains, along streams, near big ponds or in low-centered polygonal areas. Sometimes young of different broods fed there together, guarded by their parents. Communication between each parent and its own brood was maintained both vocally and visually.

In the first 4–5 days after hatching the chicks were brooded every 3–7 min, for a period of 3–7 min. Later the frequency of brooding declined, but young were always brooded at night. During the first 6–8 days, each evening the male prepared a shallow scrape for the night brooding. During the first phase the chicks were closely accompanied by a parent and were led to sites probably rich in food for young. All members of the brood then fed together and were brooded together. Later the young tended to disperse and the parent spent more time locating and gathering them, to be brooded solitarily or in pairs rather than all together. Individual variations were detected among members of the same brood in the duration of feeding bouts and brooding frequencies. Young also preened and exercised their wings as of their first day of life. When warned by the parent they crouched in a typical posture.

Males may desert the young just a few days before they fledge (Safriel 1971), but this was not observed in 1973, when males stayed with young on the day of fledging and also for some days later. We also observed flocks in which both young and adults were present. However, in *C. mauri* adults and young form separate flocks (Holmes 1973).

The flocking period.—Around mid-July, when some *C. pusilla* at Barrow still attended young, flocks of this species appeared in the area. Judging from their numbers, most of these birds were not breeders of the Barrow area; Semipalmated Sandpipers as well as other species leave breeding areas in interior Alaska for areas near the coast prior to migratory departure (Myers and Pitelka *in litt.*). Thus, considerable mixing of local populations probably occurred at flocking time, and the birds under our observations undoubtedly joined such flocks.

The size of flocks ranged between 10 and 30 birds, and they were not very coherent; a flock of 11 *C. pusilla* that landed in a pond later split so that only eight birds left the pond in one flock. The flocks were composed of young only, or of adults and young. Because females deserted the family early, it is conceivable that most adults in flocks (especially in late ones) were males. We do not know whether females left solitarily or joined flocks. We also observed mixed flocks of several calidridine species; in one case 5–10 *C. pusilla* were observed in a flock of ca. 100 *C. mauri*.

Individuals in flocks were restless, very sensitive to disturbances, aggressive and vociferous. They frequently changed sites, but preferred pond and river edges. They spent their time feeding, preening, and sleeping. By the end of July no solitary *C. pusilla* were seen near Barrow, and after 4 August no flocks including *C. pusilla* were recorded.

DISCUSSION

The reproductive cycle of *C. pusilla* at Barrow can be schematically summarized by a compartmental flow diagram (Fig. 4). Of all stages in this cycle, incubation deserves special attention. It begins during the laying period, when its timing and duration are crucial. Sandpiper embryos at Barrow are cold-resistant but their cold-sensitivity increases with time (Norton 1972), so eggs should be protected from the outset and hatching success of fertile eggs would be maximal if each of the eggs were constantly incubated from its day of laying. Because the eggs are not laid simultaneously, however, full incubation during the laying period would result in asynchronous hatching, which is highly detrimental to nidifugous young (Soikkeli 1967; Vince 1966a, 1966b, 1968; Norton 1972). Indeed, Norton (1972) found that most

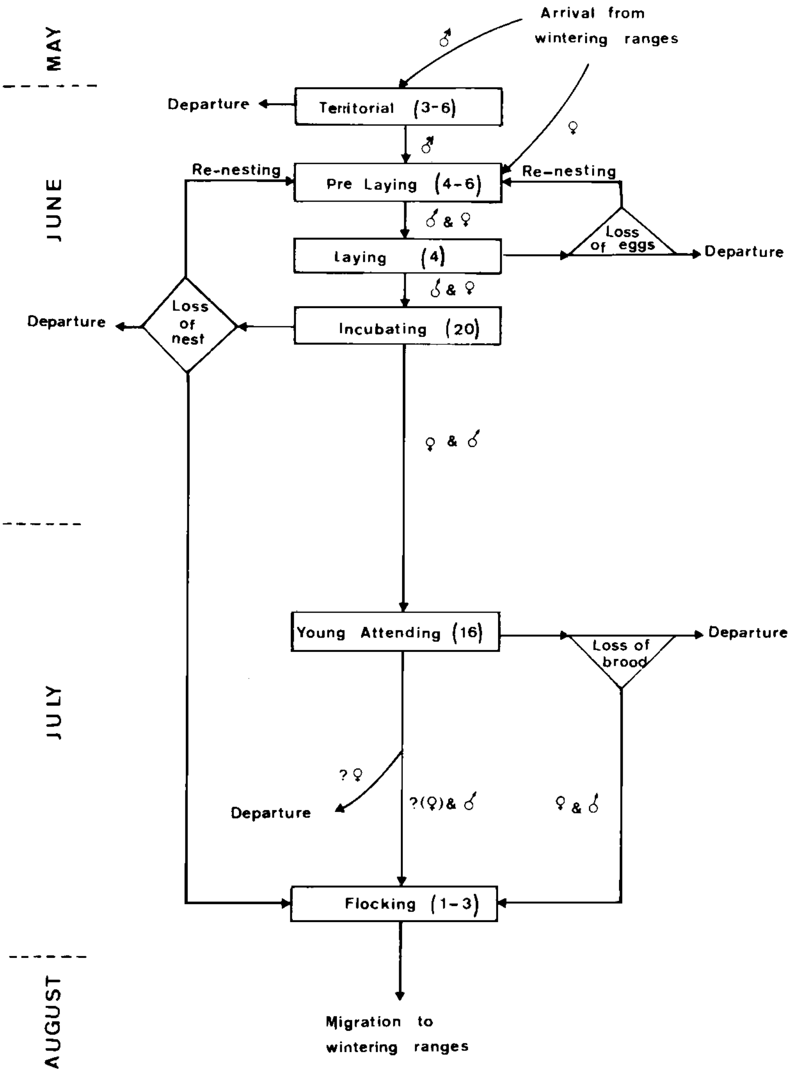

Fig. 4. The phenology of *Calidris pusilla* at Barrow. Rectangles represent reproductive stages, the figures in parentheses stand for the duration of these stages in days. Arrows describe entries and exits from reproductive stages, triangles and rhombus represent events allowing alternative exits. The distances between reproductive stages is scaled to correspond with the time of year (left) in accordance with the behavior of the greater part of the breeding population at Barrow.

cases of mortality among the young occurred during the first 24 h after hatching. We found that when the hatching period was long, the first young to hatch were weakened by hunger and were often lost to predators when they ventured out of the nest to feed. Being then unattended by their parent, they attracted predators by their movements and calls. The last young to hatch were then also at a disadvantage because they were often hastened to leave the nest when still moist and not yet fully recovered from the hatching effort. Alternatively, the parent might desert them when still wet and unattended in the cup while attempting to lure the first young to hatch back to the nest, or while trying to brood them if they were too far away from the cup. The optimal strategy of incubation during the laying period should thus lead to hatching that is not only maximally successful but is also highly synchronized. In order to achieve this the birds should precisely time incubation spells during the laying period, varying their attentiveness according to the prevailing weather. Because the weather is highly unpredictable, the incubation schedule during the laying period should not be stereotyped, and may also vary between different birds.

The gradual increase in the length of incubation turns with the advancement of the incubation period is also known in *Larus argentatus* (Drent 1970). Long turns reduce the number of changeovers, and hence the time that eggs are exposed. The sensitivity of embryos of *L. argentatus* (Drent 1970) and of *C. pusilla* (Norton 1972) to cold and light increases with age, so increasing the length of incubation turns with the advancement of incubation is likely adaptive (Norton 1972). However, the time during which eggs are exposed when a changeover takes place is very short indeed and may well be insignificant. On the other hand, reducing the number of shifts reduces activity around the nest and decreases the chance that predators may discover the nest while following the relieving bird. As parental investment in the eggs increases with time, an egg loss that occurs late in incubation involves a greater amount of wasted effort than a loss occurring earlier. Also, as incubation progresses the season advances, so that in most cases an early loss of eggs can still be replaced, whereas a late egg loss means a lost breeding season. Thus the increase in length of incubation spells as incubation advances may be advantageous because the stakes are then much higher than earlier. It is probably likewise advantageous to make an effort to reduce the chances of predation when incubation is advanced, even at the cost of severe feeding deficiencies at that time. Indeed, females lose significant weight during incubation (Ashkenazie and Safriel 1979). It therefore seems that 14 h is either the longest on-duty time that a bird can tolerate without feeding, or the consequence of the shortest off-duty time required for replacing feeding deficiencies accumulated during the on-duty period.

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DOES THE WING MOLT CAUSE NUTRITIONAL STRESS IN LESSER SNOW GEESE?

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ABSTRACT.—To test the hypothesis that wing molt causes nutritional stress for geese and ducks, I investigated what effect wing molt has on nutrient reserves of adult Lesser Snow Geese (*Chen caerulescens caerulescens*). The study was done in 1971 and 1972 at the McConnell River (60°50′N, 94°25′W), Northwest Territories, Canada. Body weight, weight of body fat, dry weight of breast and leg muscle, and leg bone weight were used to index reserves. The data showed that these geese rely very little, if at all, on catabolism of body tissue to obtain nutrients for feather growth. Thus, I conclude that the molt does not cause nutritional stress for Lesser Snow Geese. I argue that this is predictable and suggest that it is true of other waterfowl. *Received 24 April 1978, accepted 3 October 1978.*

MOLT is a nutrient-costly process in birds (Payne 1972, King 1974). To meet that nutrient demand, a molting bird can use one or more of these tactics: 1) increase its daily nutrient intake, 2) make a compensatory reduction in other nutrient-demanding functions, or 3) catabolize body tissue.

The timing, duration, and pattern of molt vary greatly among bird species (King 1974: 9) and probably are important determinants of the tactic(s) used by a species. Birds that molt and regrow all flight feathers simultaneously apparently have a higher daily nutrient demand than those that have a sequential molt (King 1974: 37). Studies of energy intake by sequential-molters suggest that they use the first and/or the second of the above tactics (King 1974: 37–38). Canada Geese (*Branta canadensis*) are simultaneous-molters, and according to Hanson (1962) are unable to meet the demands of wing molt by increased food intake. Hanson argued that Canada Geese catabolize pectoral muscle and leg bone to get additional nutrients for wing-feather growth. Hence, he hypothesized (Hanson 1962: 13–14, Hanson and Jones 1976: 191) that molt, especially by females, is the most stressful period in the life cycle of waterfowl. Hanson (1962) did not define stress, but presumably meant *a situation in which a bird's nutrient demands exceed its nutrient ingestion, resulting in catabolism of body tissue*. That is how I define nutritional stress in this paper. But for such a situation to be stressful, in an evolutionary sense, the catabolism must result in a lowered fitness of the bird; Hanson (1962: 14) suggested that "the apparent differential stress of molt may be a primary reason for the preponderance of males in populations of adult waterfowl."

Data are presented here to show that the dynamics of nutrient reserves in molting Lesser Snow Geese (*Chen caerulescens caerulescens*) are somewhat like those of Canada Geese. However, I argue that Hanson's hypothesis does not hold for Lesser Snow Geese and that these geese meet the nutrient demands of the wing molt through their food.

METHODS

Data are from geese collected in 1971 and 1972 at the mouth of the McConnell River (60°50′N, 94°25′W), Northwest Territories, Canada. MacInnes (1962) has described the area. As molt phenology and timing of collection periods were nearly identical in the 2 years (Table 1), the data were combined.

TABLE 1. Molt phenology and collection periods.

	1971	1972
Collected Late Incubation geese	26–27 June	19–26 June
Peak of Hatch	27–29 June	26–28 June
Collected Post Hatch geese	6–13 July	6–13 July
First flightless goose seen	16 July	15 July
Collected Early Molt geese	16–26 July	15–27 July
Collected Late Molt geese	28 July–7 August	1–8 August
First flying goose seen	10 August	12 August
Collected flying geese	10–18 August	15–17 August

Molting geese were collected in two ways: free ranging geese were shot by rifle, and every 20th goose was collected from flocks "rounded-up" during mass-banding drives (see Cooch 1956). Specimens were assigned to the following categories (Table 1): 1) *Early Molt,* geese collected during the first half of the wing molt period; 2) *Late Molt*, geese collected during the last half of the wing-molt period; and 3) *Flying*, post wing-molt geese (shafts of primaries and secondaries not blood-filled). All were collected with a rifle.

Dissection techniques were the same as reported in Ankney (1977a) and Ankney and MacInnes (1978). *Body weight,* i.e. the fresh weight of the goose minus intestinal contents, was used as an overall index of nutrient reserves. *Breast muscle* is the total dry weight of the *pectoralis, supracoracoideus,* and *coracobrachialis* muscles. *Leg muscle* is the dry weight of all muscles having either their origin or insertion on the femur or tibiotarsus. *Protein Reserve Index* (Protein R. I.) is the sum of leg and breast muscle. I present dry weights of muscles because water content, as a percent of total wet weight, is not constant but increases as muscle weight declines (Ankney, unpublished data). Thus, dry weight is a more accurate estimate of the muscle's protein content. *Body fat* is the total wet weight of subcutaneous, mesenteric, and abdominal fat (see Ankney 1974 for techniques). *Leg bone* is the fat-free dry weight of the femur and tibiotarsus. To remove fat, leg bones were broken and given two 24-h washings in 30 ml of chloroform in a shaker bath at 30°C. Change in leg bone weight is used as a crude index of changes in mineral composition. I have included for comparison data from *Late Incubation* geese (last 8 days of incubation) and *Post Hatch* geese (1–2 weeks after hatch) that have been reported elsewhere (Ankney 1977a, Ankney and MacInnes 1978).

I used *t*-tests to test for differences between two means; significance was set at the 5% level.

RESULTS

Lesser Snow Geese did not lose weight during the wing molt (Table 2). Mean body weight of females increased significantly between Late Incubation and Early Molt and that of males remained constant during the entire period.

TABLE 2. Mean (±S.E.) body weights, body fat weights, and leg bone weights (g) of adult Lesser Snow Geese collected before, during, and after the wing molt.[a]

	Late Incubation	*P*[b]	Post Hatch	*P*[b]	Early Molt	*P*[b]	Late Molt	*P*[b]	Flying
Body weight									
Females	1,710 ± 20	***	1,900 ± 30	*	1,985 ± 20	NS	2,010 ± 20	NS	2,060 ± 50
Males	2,250 ± 40	NS	2,250 ± 50	NS	2,250 ± 40	NS	2,285 ± 45	NS	2,285 ± 40
Body fat									
Females	55.8 ± 7.2		—[c]		—[c]		—[c]		—[c]
Males	46.1 ± 6.1		—[c]		—[c]		—[c]		—[c]
Leg bone									
Females	23.7 ± 0.5	***	19.3 ± 0.5	***	22.6 ± 0.6	NS	23.9 ± 0.5	NS	23.7 ± 0.9
Males	25.8 ± 0.7	NS	24.3 ± 0.7	*	26.8 ± 0.8	NS	28.2 ± 0.9	NS	29.4 ± 1.0

[a] Sample sizes are: Late Incubation = 41 females, 22 males; Post Hatch = 35 females, 22 males; Early Molt = 28 females, 18 males; Late Molt = 28 females, 14 males; Flying = 12 females, 6 males.

[b] P = probability that means in adjacent columns are different by chance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS indicates $P > 0.05$.

[c] None of the geese in these categories had a measurable amount of Body Fat; see text.

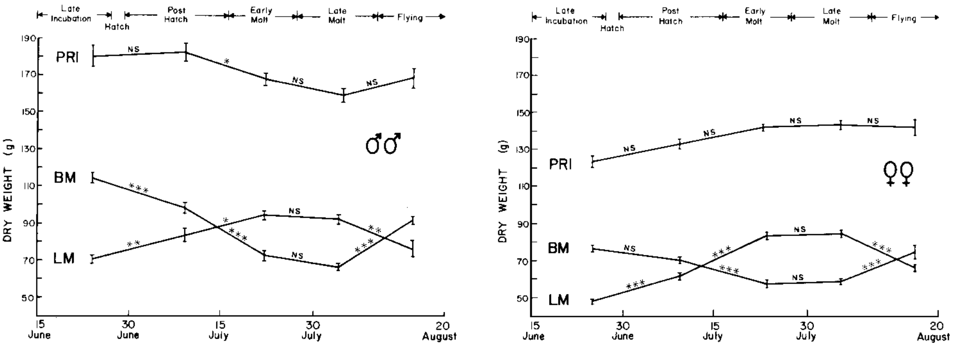

Fig. 1. Changes in dry weights of Leg Muscle (LM), Breast Muscle (BM), and Protein R. I. (PRI) of adult males (left) and females (right). Mean weights (± 1 S.E.) are plotted versus mean collecting date; see Table 1 for ranges of collecting dates. Sample sizes and symbols as in Table 2.

Mean body fat decreased from about 50 g in geese collected during Late Incubation to zero in geese collected during Post Hatch (Table 2). No Early Molt, Late Molt, or Flying geese had a measurable amount of body fat.

Mean leg bone weights of females declined between Late Incubation and Post Hatch but increased between Post Hatch and Early Molt (Table 2). Males showed a similar but less marked pattern. There was no change in mean leg bone weights of either sex during the wing molt.

There were large changes in mean breast and leg muscle weights, of both sexes, before, during, and after the wing molt (Fig. 1). These changes were always at least partially compensatory, i.e. a decrease in one muscle mass was accompanied by an increase in the other. The Protein R. I. of females did not change significantly between successive periods (Fig. 1). But the overall positive change between Late Incubation and Late Molt (124.3 g to 143.6 g) was highly significant ($P < 0.001$). The Protein R. I. of males decreased significantly between Post Hatch and Early Molt (Fig. 1).

DISCUSSION

To interpret these results and to evaluate the hypothesis about the great nutritional stress of molt, it is necessary to review the nutrient-reserve dynamics of nesting Lesser Snow Geese (reported elsewhere: Ankney 1977a, 1977b; Ankney and MacInnes 1978). Males and females arrive at the breeding grounds with large fat and protein reserves. Females rely on these reserves during egg-laying and incubation as they feed little then. Some females, near the end of incubation, starve to death; others desert their nests (to feed). Even females that successfully complete incubation are in poor condition: their mean body weight is 42% lower than that of females arriving at the breeding grounds, their fat reserves have declined by 89%, and their leg and breast muscle have declined by 22% and 40% respectively. Males also use fat and protein reserves during the egg-laying and incubation periods but rely mostly on fat (88% decline); their leg and breast muscles only decline by 8% and 16% respectively. The geese, particularly females, spend much time feeding after the eggs hatch (Harwood 1975). The male of a pair acts as a sentinel for the feeding female and goslings; that is apparently a tactic that enables the female to recover from the stress of breeding.

Females began to recover after hatch as shown by increased body weight and Protein R. I. during Post Hatch and Early Molt (Table 2, Fig. 1). Male body weight did not increase then and Protein R. I. declined slightly. That decline resulted because leg muscle did not increase as much as breast muscle decreased (Fig. 1). But I do not think that the decline indicates nutritional stress in males. I suggest that because leg muscle of males had not declined as much as that of females did during nesting (see above) not as much increase was needed.

Why do these rapid, compensatory changes in leg and breast muscle occur? Hanson (1962: 20–23) noted similar changes in molting Canada Geese and proposed (p. 31) that hypertrophy of leg muscles resulted from extensive use but that atrophy of breast muscle was "an evolutionary adaptation . . . whereby these temporarily inactive muscles can be drawn on for vital constituents thereby maintaining a rapid rate of feather growth." However, Hanson (Hanson and Jones 1976: 192) later realized that hypertrophy of the leg muscle begins before the onset of the flightless condition (as it does in Lesser Snow Geese; Fig. 1). He suggested that "the timing of the onset of the hypertrophy of the leg muscles and their subsequent development must . . . also be explained primarily on an evolutionary basis rather than on a purely functional use-disuse basis." That is not the best explanation for the changes that occur in Lesser Snow Geese. Very soon after the eggs hatch (about 3 weeks before the onset of the wing molt) Lesser Snow Geese families walk to feeding areas, which are up to 50 km away at the McConnell River. There they spend about 20 h per day feeding (Harwood 1975) and often move several km during a day. But I have never seen undisturbed geese fly during that period—they are behaviorally flightless. Thus, not surprisingly, hypertrophy of leg muscle begins before the geese are flightless, and breast muscle, which began to atrophy after the geese arrived to the breeding grounds, continues to do so. The simplest explanation for that is the "use-disuse" hypothesis. Also, note the rapid changes in breast and leg muscle after the geese begin flying (Fig. 1).

There is no indication that Lesser Snow Geese *require* breast muscle protein for the formation of new feather keratin. It may be that some of the amino acids freed by the atrophy of breast muscle are incorporated into feathers; I think it more likely that they are used for the hypertrophy of the leg muscles (as suggested by Hanson and Jones 1976: 192). But the important point is that when the feathers are growing there is no evidence of a net protein deficit. This suggests that the birds are able to meet the protein requirement for feather growth directly from their diet.

That Lesser Snow Geese do not store fat during the wing molt is not evidence of stress but is predictable. They have a highly dependable food source (grasses and sedges, Harwood 1975) and their fall migration is 2 months away. To build and maintain unnecessary fat deposits would be energetically wasteful.

I cannot explain the decrease in mean leg bone weight of males and females that occurred during Post Hatch. Perhaps, as suggested by Hanson and Jones (1976: 192–193), the geese catabolize bone tissue to obtain phosphorus for the rapid hypertrophy of leg muscle. But there were significant increases in mean leg bone weight in both sexes between Post Hatch and Early Molt. This suggests that there was no mineral shortage when the geese were growing new wing feathers. However, as no histochemical analyses of the leg bones were done, I cannot say whether leg bone weights accurately indicate changes in mineral composition. Hopefully, a future investigator will do such analyses and I predict that the results will show that geese (and ducks) do not require body minerals for feather growth.

Hanson's hypothesis about the great nutritional stress of molt for geese and ducks does not apply to Lesser Snow Geese. Hanson apparently based the hypothesis on data that were inadequate. He lacked data from breeding and pre-molt males, and from females during the last half of incubation and the interval between hatch and the wing molt (Hanson 1962: tables 13–16, 20, 21). Therefore any changes in nutrient reserves of the geese that might have occurred during those periods were undetected. Accordingly, the changes that occurred during the wing molt may have been incorrectly evaluated.

Lesser Snow Geese seem able to meet the nutrient demands of wing molt through their diet (tactic 1); the following argument shows why that is predictable even in the absence of data on adult geese. Consider that during the 6 weeks between the end of incubation and the end of wing molt, when adults replace their wing feathers, their goslings: 1) increase in body weight from 90 g to about 1,800 g (Cole and Ankney, unpublished data); 2) grow leg and breast muscles that are nearly adult size (Ankney, unpublished data); 3) grow and ossify a skeleton that is almost adult size (Ankney, unpublished data); and 4) *grow a complete set of body, tail, and wing feathers*. Adults and juveniles have similar diets (Harwood 1975). Thus, it is not surprising that adults can grow wing feathers without catabolizing body tissue. I suggest that other species of waterfowl behave similarly.

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PRACTICAL METHODS OF ESTIMATING VOLUME AND FRESH WEIGHT OF BIRD EGGS

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ABSTRACT.—Bird eggs begin to lose weight as soon as they are laid but their volume and linear dimensions do not change during incubation. The volume of an egg can be estimated within 2% from the relationship: Volume = $0.51 \cdot LB^2$, where L is the length and B is the breadth (maximum diameter). The fresh weight of an egg can be estimated within 2% from the relationship: Weight = $K_W \cdot LB^2$, where K_W is a species-specific constant that can be determined empirically or calculated from published data. *Received 25 April 1978, accepted 28 October 1978.*

IT is frequently useful to know the fresh weight of a bird's egg. One reason is that many aspects of the biology of bird eggs can be predicted from their weight and these predicted values can be used when empirical data are lacking. Alternatively, one way to detect adaptations to unusual situations is by comparing observed values with values predicted for an "average" egg. Some of the parameters that can be predicted from weight are metabolic rate (Rahn et al. 1974), incubation period (Rahn and Ar 1974), water vapor conductance (Ar et al. 1974), the daily rate of water loss (Drent 1970), surface area, density, and shell weight (Paganelli et al. 1974), and the relation of egg weight to adult body weight (Huxley 1923–24, Rahn et al. 1975). Additionally, accurate values of fresh egg weight are required for the calculation of fractional weight loss from the daily rate of water loss (Rahn and Ar 1974) and the estimation of incubation age (Westerkov 1950). However, fresh egg weight can only be determined at the time of laying because the egg immediately begins to lose weight by diffusion of water vapor. This daily loss is proportional to the 0.74 power of egg weight (Drent 1970) and totals about 16% of the initial weight by the end of incubation (Drent 1975). As a consequence, while a great deal of information is available on egg dimensions, there are few reliable reports of fresh egg weight. Fortunately, the linear dimensions of eggs do not change during incubation, and in the present paper I show that they can be used to predict egg volume and fresh egg weight.

Several authors have shown that the volume of a bird egg can be estimated from its linear dimensions (Bergtold 1929, Worth 1940, Westerkov 1950, Stonehouse 1963), and Preston (1974) suggested a more complex approach. In the present paper, I evaluate the accuracy with which volume (V) can be predicted from linear dimensions (L = length, B = breadth or maximum diameter), using the equation:

$$V = K_V \cdot LB^2 \tag{1}$$

A similar relationship exists for initial weight (W), and I evaluate the accuracy with which weight can be estimated from:

$$W = K_W \cdot LB^2 \tag{2}$$

These evaluations show that both volume and fresh weight can be estimated quite accurately from linear dimensions. Volume is most easily estimated with a common

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TABLE 1. Volume coefficients and weight coefficients for eggs of 26 bird species.[a]

Species	(1) N	(2) K_V	(3) COV	(4) W	(5) K_W	(6) COV	(7) K_{WS}	(8) %E
Turdus m. migratorius	12	.504	0.7	6.7	.534	0.9	.537	0.7
Gygis alba rothschildi	15	.520	1.4	21.2	.546	1.6	.551	1.0
Anous tenuirostris	11	.510	1.1	23.7	.531	1.3	.523	−1.5
Fulica americana	3	.499	1.6	26.7	.542	1.7	.547	1.0
Chrysolophus amherstiae	10	.507	1.0	29.5	.548	1.0	.547	−0.2
Syrmaticus s. soemmerringii	10	.503	1.5	31.5	.539	1.4	.544	0.9
Chrysolophus pictus	10	.500	0.9	32.2	.539	0.7	.543	0.8
Phasianus colchicus mongolias	10	.497	1.3	33.8	.546	1.1	.547	0.2
Anous stolidus pileatus	14	.505	1.3	37.5	.534	1.6	.530	−0.8
Amazonetta brasiliensis	7	.514	1.3	37.8	.552	1.3	.554	0.5
Numida m. meleagris	12	.502	1.5	39.0	.565	1.5	.568	0.6
Aix sponsa	3	.518	0.3	43.3	.562	0.5	.571	1.6
Rissa tridactyla pollicaris	9	.498	1.0	51.9	.527	1.0	.537	1.9
Larus heermanni	11	.496	1.1	53.4	.529	1.2	.535	1.1
Sula leucogaster brewsteri	4	.507	1.3	57.8	.540	1.8	.537	−0.5
Lophophorus impejanus	6	.506	1.7	63.7	.546	1.7	.544	−0.4
Phaethon rubricauda	2	.504	1.5	67.7	.544	1.3	.541	−0.5
Anas platyrhynchos	11	.515	1.2	72.4	.560	1.1	.560	0.0
Buteo jamaicensis	2	.510	0.5	74.8	.547	0.3	.551	0.8
Larus occidentalis livens	8	.497	1.5	96.6	.531	1.5	.533	0.4
Pavo muticus	8	.501	1.1	101.2	.552	0.7	.529	−4.2
Pelecanus occidentalis californicus	10	.507	0.8	110.5	.546	1.1	.558	2.1
Anser fabalis	3	.516	0.8	142.6	.567	1.3	.556	−1.8
Dromaius novaehollandiae	8	.507	0.6	631.6	.564	0.6	.566	0.4
Pteroicnemia pennata terapacensis	6	.513	1.2	661.8	.566	1.0	.555	−2.0
Struthio camelus	5	.521	0.5	1692.3	.597	0.4	.595	−0.3

[a] N = sample size; W = weight (g); K_W = observed weight coefficients; COV = coefficient of variation ($100 \times SD/\bar{x}$); K_{WS} = weight coefficient calculated from Schönwetter; %E = percent error [$100 \times (K_{WS} - K_W)/K_W$]; K_V = volume coefficient.

volume coefficient (K_V) that is applicable to eggs of all but a few species in which the eggs are very pointed. Weight must be estimated with a species-specific weight coefficient (K_W) that can easily be determined empirically or derived from values of W, L, and B reported by Schönwetter (1960–77).

METHODS

Initial weight (W), volume (V), length (L), and breadth (B) measurements were obtained on a total of 210 eggs from 26 species. Initial egg weight was estimated from the weight of the egg after filling the air cell with water. The assumptions in this method are that the weight loss of an egg is due exclusively to the loss of water and the volume of the air cell equals the volume of water lost (Drent 1970). More recent experiments have shown that after 18 days of incubation the weight of a chicken egg with its air cell filled with water is within 20 mg of the initial weight of the egg determined within 15 min of laying (Rahn et al. 1976). Egg volumes were determined from the difference between the weight of the egg in air and when suspended in water. Length and breadth were determined to the nearest 0.01 cm with a vernier caliper. The eggs were obtained on various field expeditions and from zoos and commercial sources.

Many of the eggs used to represent a single species were clutchmates and, therefore, do not represent independent samples from the population. As a result, the values of K_V and K_W are not the best possible estimates of the species means. Additionally, since eggs of a single clutch are likely to show less variability than those of the species as a whole, there is probably a tendency to underestimate intraspecific variability. However, we can compare K_V and K_W with respect to the relative amounts of intraspecific and interspecific variability since we are using exactly the same data for the calculation of both constants. Variability is evaluated by calculating the coefficient of variation (= 100·standard deviation/mean).

RESULTS

Observed volume coefficients were calculated from the relationship $K_V = V/LB^2$. The values obtained for the 26 species in this study are presented in column 2 of

Table 1, the coefficients of variation in column 3. The average coefficient of variation is 1.10%. The mean value of K_V for all 26 species is 0.507 ± 0.007 (= SD); the coefficient of variation is 1.44%. Thus, the interspecific variation in K_V is not much greater than the intraspecific variation.

Intuitively, it would seem that K_V should be a function of egg shape since an egg with two rounded ends should have a larger K_V than one with the same length and breadth but one pointed end. To test this, I examined the relationship between shape and K_V with the data of Hoyt (1976), which were based upon a series of eggs selected to represent the full diversity of shape exhibited by bird eggs. These data include the volume, length, breadth, and shape specifiers of 29 eggs. The two shape specifiers are asymmetry (AS) and bicone (BI), as defined by Preston (1968). Bicone quantifies the average roundness of the two ends of the egg, and asymmetry quantifies the difference in the roundness of the two ends of the eggs. A multiple regression of K_V on AS and BI yielded the following relationship:

$$K_V = 0.5228 - (0.1033 \cdot AS) + (0.0740 \cdot BI) \qquad (3)$$
$$(\mathrm{N} = 29;\ \mathrm{r}^2 = 0.757)$$

Weight coefficients were calculated from the relationship $K_W = W/LB^2$. The species means are shown in column 5 of Table 1, the coefficient of variation in column 6. The mean value of the intraspecific coefficients of variation is 1.14, indicating that there is about as much intraspecific variation in K_W as in K_V. The mean value of K_W for the 26 species in this study is 0.548 ± 0.016; the coefficient of variation is 2.83%. Thus, there is about twice as much interspecific variation in K_W as there is in K_V.

Predicted weight coefficients were calculated from the values of W, L, and B given by Schönwetter (1960–77) for the particular species or subspecies (column 7). The mean value of K_W is 0.548 ± 0.016, identical to that derived empirically. Of primary interest is the difference between the measured and predicted value for each species. This is expressed as a percent error and is shown in column 8. The mean absolute error equals 1.0% ± 0.9. Thus, on average, the predicted K_W deviated from the observed species mean by about 1%. In only one case is the error greater than 2.1%.

In more than one-half of the species, the observed values of W, L, or B differ significantly ($P < 0.05$) from the corresponding values published in Schönwetter (1960–77). In fact, more than half the species differ with respect to either two or all three of these parameters. (These differences are, presumably, simply due to sampling errors.) However, the error in predicted K_W is no greater for these samples than it is for those which do not differ with respect to any of the parameters. This is an important observation because it means that, although the absolute dimensions may differ, the relation between W, L, and B for an individual species remains the same.

DISCUSSION

The volume coefficient (K_V) is a function of egg shape (equation 3). However, there seems to be about as much intraspecific variability in the volume coefficient as interspecific variability. This supports the suggestion of several authors that the volume of any avian egg can be estimated from its linear dimensions with reasonable accuracy, using a single value of K_V. Bergtold (1929) and Worth (1940) derived their

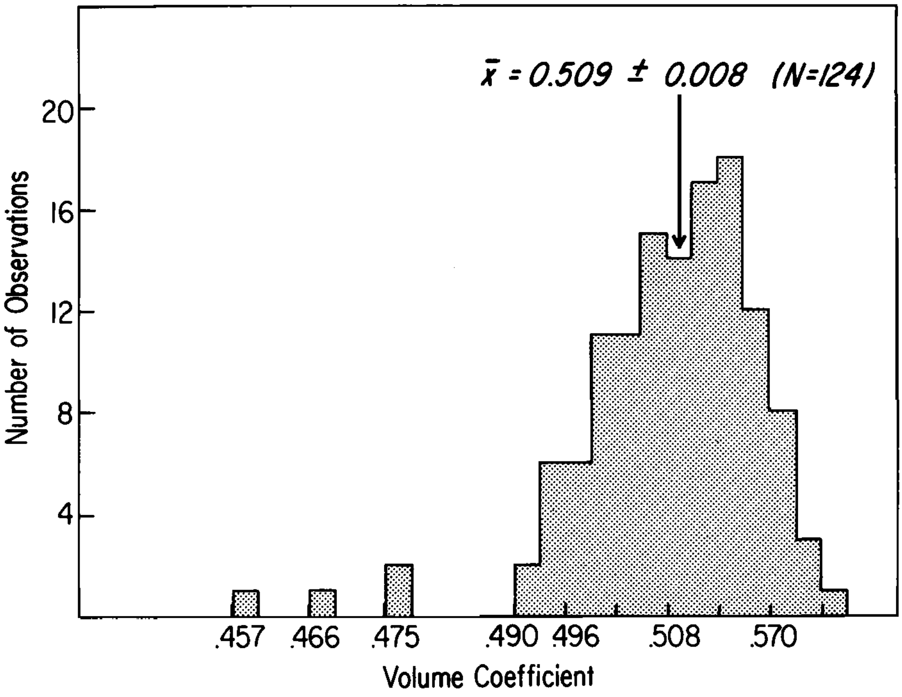

Fig. 1. Frequency histogram of 128 observations of K_V. The mean of K_V is 0.509 ± 0.008 (N = 124). The four low values that were not included in this mean are from very asymmetrical eggs laid by the following species (K_V in parentheses): *Uria aalge* (0.458), *Himantopus mexicanus* (0.467), *Calidris alpina* (0.476), and *Numenius americanus* (0.476). The data are based upon measurements taken from 818 eggs of 115 species. Twenty-six observations are from this study, 29 from Hoyt (1976), 10 from Lofton and Bowman (1978), and 63 (including 60 species and subspecies from the family Anatidae) are unpublished data.

values of K_V by assuming that the volume of an egg is equal to that of an elipsoid of revolution with the same major and minor axes. In this case, K_V = 11/21 (= 0.524). Westerkov (1950) used K_V = 11/21.5 (= 0.512) for pheasant eggs (*Phasianus* sp.), but he did not explain the derivation of this value. Stonehouse (1963) reported a mean K_V of 0.512 for 150 eggs of 10 species of seabirds (no values were reported for individual species) and a mean K_V = 0.512 for 50 Black Swan (*Cygnus atratus*) eggs (Stonehouse 1966). The mean of 124 determinations of K_V on eggs of 115 species of birds (Fig. 1) is 0.509 ± 0.008. Therefore, the volumes of most bird eggs can be determined within 2% from linear dimensions using K_V = 0.51. The major exceptions are very asymmetrical eggs. For these species, it would be best to determine K_V empirically or predict K_V with equation 3 from Preston's shape specifiers.

The weight coefficient (K_W) is a function of both shape and density. The interspecific variability in K_W, therefore, reflects the interspecific variability in both of these parameters. As a consequence, the interspecific variability in K_W is larger than the interspecific variability in K_V and it is probably best to use a species-specific value of K_W for the prediction of fresh weight from linear dimensions. A species-specific value of K_W can be calculated from the data of Schönwetter (1960–77). These values are rarely in error by more than 2%.

The most accurate prediction of fresh egg weight is obtained by refilling the air cell with water. However, this results in the death of the embryo. The second most accurate prediction is obtained by measuring volume (by immersion in water) and multiplying by density. Density can either be determined empirically on a sample of eggs from the population being studied or estimated (Rahn et al. in prep.) from the data of Schönwetter (1960–77). However, the determination of volume by immersion in water might be impractical under some conditions (e.g. field), or undesirable under others (e.g. with near-term embryos). The third most accurate prediction of fresh weight is obtained from K_W and linear dimensions. The weight coefficient (K_W) can either be determined empirically on a sample of eggs from the population being studied, or estimated from the data of Schönwetter (1960–77). All of these methods yield reasonably accurate estimates of fresh egg weight.

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SOCIAL STATUS SIGNALING IN WINTER FLOCKING BIRDS: AN EXAMINATION OF A CURRENT HYPOTHESIS

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ABSTRACT.—S. Rohwer recently has proposed that intraspecific plumage variability in winter flocking birds represents a polymorphism that functions to signal social status. We test several predictions of Rohwer's status signaling hypothesis for Dark-eyed Juncos (*Junco hyemalis*), explore some theoretical implications of our findings for juncos, and discuss the generality of social status signaling. Both darkness of hood and whiteness of tail were positively, although imperfectly, associated with social rank in captive winter flocks of first-year juncos. If plumage differences function as cues to dominance status in this species, our results suggest that their signal value derives primarily from learned associations between plumage attributes and other variables (such as sex or body size) that might influence fighting ability. Ultimate factors possibly responsible for winter plumage variability in juncos, both within and between age/sex classes, appear to be complex; selective pressure for a system of social status advertisement could (but need not) be one of these factors. Findings for some other winter flocking species reveal both similarities to, and differences from, our results for juncos. We suggest that more information on the behavior and ecology of a variety of winter flocking birds is needed before a satisfactory generalized model of social status signaling can be formulated—if such a model is possible. *Received 28 February 1978, accepted 5 September 1978.*

FLOCKING is a widespread phenomenon among birds that winter in temperate regions. Such behavior affords many benefits; for instance, it may facilitate orientation during migration or refuging, aid in the location and efficient exploitation of food, and assist in the detection and mobbing of predators. However, flocking also may impose costs, not the least of which is the promotion of intraspecific competition for essential resources. The cost of such competition may be reduced by social systems, such as social dominance hierarchies, that function to order individual priorities at resources and to regulate the frequency, form, and intensity of aggressive behavior (discussed by Balph 1977a).

Of considerable interest is a hypothesis stating that dominance hierarchies are predetermined by adaptive variation in the appearance of individuals. Rohwer (1975, 1977) observes that wintering birds differ markedly in the degree to which they vary intraspecifically in appearance and indicates that flocking species tend to exhibit polymorphism in plumage coloration or pattern, whereas non-flocking species show monomorphism. He speculates that in flocking species ". . . plumage variability has evolved to signal the approximate social status of each individual" (Rohwer 1975: 594). According to this hypothesis, position in a dominance hierarchy within variably plumaged species is signaled by the "studliness" (Rohwer 1975: 598) of individuals (defined as the degree to which each exhibits black, brightly colored, or contrastingly patterned plumage, particularly of the head or breast). Rohwer predicts such status advertisement to be especially advantageous if individuals change flocks, as it should enable both an incoming bird and established flock members to assess accurately the newcomer's proper social position without engaging in energetically costly fights. From a series of tests using Harris' Sparrows (*Zonotrichia querula*), he concludes that winter plumage variability does serve a status-signaling function in this species. He also indicates, on the basis of qualitative observations of some other winter flocking passerines, including Dark-eyed Juncos (*Junco hyemalis*), that the phenomenon may be a general one. However, Shields' (1977) fine critique points out serious problems in Rohwer's (1975) paper. In the present paper we examine Rohwer's status signaling hypothesis both from an empirical and a theoretical standpoint.

METHODS

An investigation of winter social behavior in Dark-eyed Juncos (Balph 1977a) provided data to test several predictions of the status signaling hypothesis. Thirty-six juncos (*J. h. montanus*) were captured in November 1973 at Logan, Utah and 6 birds placed simultaneously in each of 6 large, outdoor flight pens. Abundant resources were identically distributed in all aviaries. Each "flock" contained two or more members of each sex. All but one of the 36 birds were young of the year. Dominance-subordination relationships among all members of each flock (totaling 90 two-bird relationships) were ascertained from over 2,000 agonistic encounters observed in December at various resources in the flight pens. In addition, early in January 1974, 4 males and 2 females from 2 of the flocks were individually transferred, each for 24 h, to another of the flocks and their social positions determined from over 1,500 recorded encounters.

We ranked junco specimens from the above study relative to one another within groups according to darkness of the hood (i.e. plumage of the head and upper breast), which ranged from black to brownish gray (Fig. 1). An independent observer concurred in our order of plumage ranking. We also ranked birds within each group on the basis of tail pattern (from most to least white, ascertained from notations made when the birds were first captured). The range of plumage variation probably was reduced somewhat in the captive sample by the virtual absence of adults, which are darker-hooded and whiter-tailed on the average than immature juncos (e.g. Miller 1941, Grant and Quay 1970). However, several factors counteracted this effect. First, Balph (1977a) selected for extremes of hood coloration in an attempt to assure representation by both sexes in each captive flock. Second, the population from which the captives were taken appeared to be composed largely of first-year birds (89% of 121 individuals banded in December 1973). Third, plumage variability due to sexual dimorphism (Balph 1975) probably was greater among captives than in wild flocks at Logan, as sex ratios more closely approached unity in the captive flocks (1:1 or 2:1 in favor of males) than in the free-living population (4:1 in favor of males). Finally, the average difference in hood darkness or tail pattern between individuals in the captive flocks probably was greater than in most free-living flocks, as each captive flock contained only 6 birds, whereas wild junco flocks may contain as many as 40 birds (e.g. Fretwell 1969). Plumage variability therefore may have been slightly greater in the captive flocks than in free-living flocks at Logan.

A question remains as to the degree to which our sample was representative of Dark-eyed Junco populations generally. Although all races of this species exhibit some plumage variation both within and between age/sex classes, Miller's (1941) findings indicate that plumage variability is greater in some races than in others and that the degree of variability within a race can differ for different plumage characters. As *J. h. montanus* is one of the more variably plumaged races, associations between plumage and social status (if Rohwer's hypothesis is applicable to juncos) might be exaggerated somewhat. A second problem was that we were unable to test for associations between age, age-related plumage differences, and dominance status, as our sample consisted almost entirely of first-year birds. However, unless age is positively associated with social status independently of plumage characteristics, estimates of correspondence between "signaled" and actual social rank within age classes should not differ from those between first-year birds and adults (except insofar as errors of plumage discrimination might be more frequent within than between age classes). If age predicts social status independently of plumage differences, overall correspondence between the "signaled" and actual social order within a flock should increase as the ratio of first-year birds to adults approaches unity. The age composition of our flocks also prevented us from determining whether or not first-year and older juncos are equally likely to respond appropriately to plumage cues hypothetically signaling social status. If such cues have evolved as social releasers in juncos, we should expect younger birds probably to respond as strongly as older birds. Alternatively, if the cues operate as conditioned reinforcers, correspondence between signaled and actual social position might be greater among older, more experienced birds than among younger individuals; however, we doubt that such a difference would be appreciable, as first-year juncos probably have substantial learning opportunities prior to the formation of winter flocks (see Gabrielson and Jewett 1940: 571), and as selection should favor rapid learning if individuals responding inappropriately are at a survival disadvantage.

We analyzed data from the captive juncos with tests of goodness of fit and contingency table tests of independence. We used the Chi-square statistic to perform these tests except where small (<5) expected values dictated the use of exact Chi-square tests (Radlow and Alf 1975, Agresti and Wackerly 1977). We pooled data only after testing for, and failing to find, heterogeneity at $P \leq 0.05$ (e.g. male-male with female-female relationships for same-sex versus opposite-sex comparisons). Our analysis necessitated breaking a small number of dominance-subordination "ties" (see Balph 1977a); in such cases, we considered the bird winning the majority of observed encounters to be dominant. Within agonistic encounter types, dominant members of junco pairs almost always were winners (>97% of interactions recorded in December and January).

A multivariate paired comparisons analysis to determine the relative contributions of hood darkness, tail pattern, sex, and wing length to social status in juncos would have seemed desirable (see review of experimental designs for paired comparisons data by Davidson and Farquhar 1976). However, our data were not suitable for extant designs, most of which impose rigid constraints upon how data may be obtained (e.g. David 1963: 36–43). An alternative approach was to hold certain variables constant and to study the effects of other variables upon social status. Although in principle the simultaneous effect of several variables upon dominance could be studied using log-linear models for multidimensional contingency tables (Haberman 1974), such models seemed inappropriate for analyzing our data (see Haberman 1974: 144–146 and Bishop et al. 1975: 177). We therefore opted for a series of traditional two-way contingency table analyses.

RESULTS AND DISCUSSION

Plumage variability and social status in juncos.—Dark-eyed Juncos form hierarchically organized, relatively stable flocks during the winter (Sabine 1949, 1955, 1956, 1959; Fretwell 1969) and exhibit considerable plumage variability. In an attempt to determine whether or not plumage differences might serve a status-signaling function in this species, we examined our data for possible associations between darkness of the hood (cited by Rohwer as indicative of "studliness" in juncos) and social status. Darker-hooded members of junco pairs were dominant in 62 (69%) of the 90 two-bird combinations within the resident captive flocks, a result that differed significantly from the null hypothesis of equal dominance ($\chi^2 = 12.84$, df = 1, $P < 0.001$). Hood darkness thus appears to be a predictor of social rank in juncos (at least among first-year birds), although not as strong a predictor as Rohwer (1977: 108) implies for Harris' Sparrows: "Reversals, wherein a studlier bird is dominated by one of lower signaled rank, and disputes over status almost never occur."

Rohwer (1975, 1977) either explicitly or implicitly discounts the importance of such factors as sex, age, body size (as estimated by wing length), and residency status as predictors of social position in several variably plumaged species, including juncos. However, in our captive junco flocks males dominated females significantly more often than the hypothesis of equal dominance would predict (41 of 50 intersexual relationships; $\chi^2 = 20.48$, df = 1, $P < 0.001$) (see also Balph 1977a). In most cases the longer-winged member of a pair was dominant (63 of 81 pairs in which the 2 individuals differed in wing length; $\chi^2 = 25.00$, df = 1, $P < 0.001$). Finally, established flock members were dominant to newly introduced individuals significantly more often than not (25 of 30 relationships; $\chi^2 = 13.33$, df = 1, $P < 0.001$) (see also Balph 1977a). These results agree generally with those of several persons working with free-living flocks of this species (Sabine 1949, 1955, 1959; Fretwell 1969; Ketterson 1974; Ketterson and Nolan 1976). Ketterson's (1974) results additionally indicate that older juncos tend to dominate younger individuals.

Our initial findings demanded further scrutiny, as the factors considered do not vary independently of one another in juncos. Although variability within (and overlap between) age/sex classes often is substantial, males or older birds tend generally to be darker-hooded and longer-winged than females or younger birds (Balph 1975 and references cited therein; Ketterson and Nolan 1976). Rohwer (1977) states that in Harris' Sparrows the plumage "studliness" of individuals reflects social position much more accurately than does sex. We predicted that, if the same is true for juncos, associations between hood shade and social status should be similar for juncos of the same or opposite sex. However, darker-hooded members of junco pairs were dominant in a significantly greater proportion of intersexual than intrasexual relationships (82% of 50, as opposed to 52% of 40; $\chi^2 = 9.02$, df = 1, $P < 0.005$). The figure obtained for intrasexual pairs was very close to 50% chance expectation ($\chi^2 = 0.10$, df = 1, $P > 0.5$). Hood darkness thus appeared to be a poor indicator of social status in our juncos apart from its association with sex.

Rohwer (1975) indicates that plumage "studliness" in Harris' Sparrows is a significantly better predictor of dominance than is body size as estimated by wing length. We reasoned that, if plumage variability functions similarly in juncos, associations between hood darkness and social status should not differ between junco pairs with members of like and unlike wing length. We distinguished between three wing-chord categories in our analysis: short (71–74 mm), medium (75–78 mm), and long (79–82 mm). Darker-hooded members of junco pairs were dominant in 75% of 64 relationships involving birds that differed in wing length, as opposed to 54% of 26 relationships between individuals of similar wing length ($\chi^2 = 3.86$, df = 1, $P < 0.05$). Among birds of similar wing length, the tendency for darker-hooded members of pairs to be dominant did not differ significantly from the 50% expected by chance ($\chi^2 = 0.15$, df = 1, $P > 0.5$). Of 9 relationships involving birds with identical wing measurements, the darker-hooded individual was dominant in 3 cases and the lighter-hooded in 6. Once again, hood shade appeared to be only a weak indicator of social status apart from its association with another variable—in this instance, wing length. Although our sample consisted of first-year birds, whereas Rohwer's (1975) sample contained birds of various ages, the difference should be relatively unimportant in view of Rohwer's (1977) statement that plumage "studliness" is a much more accurate indicator of social status than is age in Harris' Sparrows.

These results led us to ask which, if either, of two related variables—sex or wing length—is a better predictor of dominance status in juncos. The tendency for males to dominate females was no greater when the members of a pair were of different wing length than when they were of similar wing length (exact test, $P > 0.5$). However, the tendency for longer-winged members of pairs to be dominant was significantly greater for intersexual than for intrasexual relationships ($\chi^2 = 4.52$, df = 1, $P < 0.05$). Our results suggest that sex may possibly be a better indicator than wing length of social status in juncos (at least among first-year birds), although Ketterson (1974) suggests the reverse to be the case. Complicating this picture is the finding of Helms et al. (1967) that wing length is positively related to dry fat-free weight in female but not in male juncos.

An additional question was whether or not perceptual errors by individual juncos in assessing the plumage of others could account for social relationships in which the darker-hooded of two birds was subordinate. We predicted that, if such were the case, hood-rank differences between the members of junco pairs should be smaller when darker-hooded birds were subordinate than when they were dominant. An analysis of hood-rank differences revealed a trend in the predicted direction when all pairs were considered together (exact test, $P = 0.05$). However, this trend was no longer evident when intersexual and intrasexual relationships were analyzed

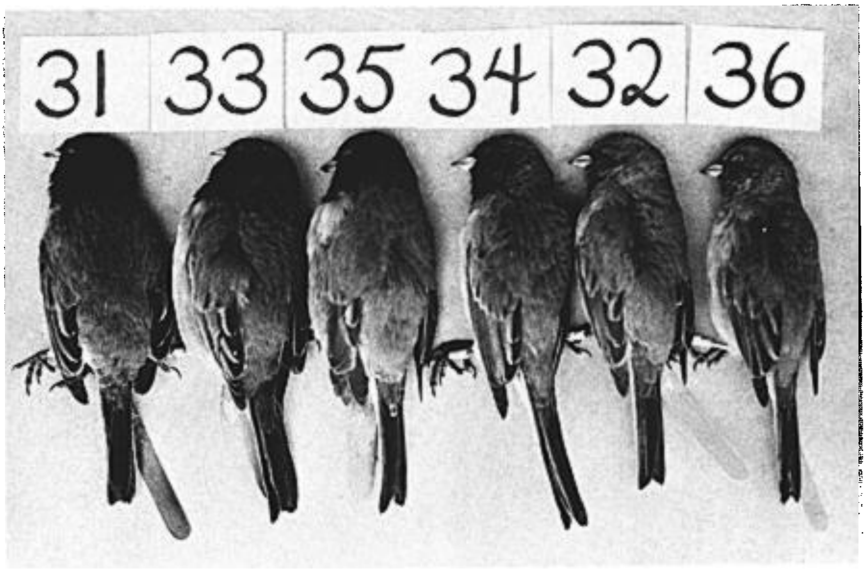

Fig. 1. Variation in darkness of the hood within a representative captive flock of Dark-eyed Juncos. (Numbers symbolize colors of leg tags and bands and are not related to plumage attributes or social status).

separately (exact test, $P > 0.5$ in both cases). The effect observed when all birds were considered together seemed to be due primarily to the disproportionate representation of intersexual relationships (in which females seldom were dominant, whether or not they were close to males in hood coloration) in cells denoting large hood-rank differences. Hence it appeared unlikely that errors of plumage discrimination could account for many of the hood-rank reversals occurring among the captive juncos.

We next examined Rohwer's (1975) proposal that social status signaling permits newcomers to join established flocks and to assume their signaled social positions with little test fighting. We predicted (1) that incoming juncos should assume the social positions predicted by their hoods and (2) that fighting between newcomers and old flock members should be less frequent and intense than if juncos exhibited little or no plumage variability. We tested the first prediction by comparing the "signaled" and actual social positions of newcomers relative to resident flock members in the transfer experiments. Incoming birds were dominant in a significantly smaller proportion of relationships than their hoods predicted they should be (5 of 30, as opposed to 11 of 30 expected; $\chi^2 = 5.17$, df = 1, $P < 0.025$); furthermore, 3 of the 5 cases involved domination of relatively dark-hooded home flock members by a lighter-hooded stranger. Had the strangers remained in the test pen for longer than 24 h, they might have risen in social status as the effect of prior residency waned (Harrington 1973, Rohwer 1977). Three juncos placed in the captive flocks in January 1974 to replace individuals that died (Balph 1977a) did rise slightly in status during the first few weeks following their introduction, although their gains were over birds darker than themselves in two of three instances. These results indicate that resident juncos enjoyed a dominance advantage over introduced birds, particularly at the outset, but that relative darkness of the hood probably was of little importance. We were unable to test the second prediction; nevertheless, agonistic encounters were markedly more frequent and intense between newly introduced juncos and members of a resident flock than among flockmates of long standing (Balph 1977a). Although aggression between newcomers and residents may have been less than if juncos were alike in appearance, the cost of such behavior (as well as the effect of prior residency) still might be sufficient to prevent individuals from joining new flocks readily during the winter. Our results, if applicable to free-living juncos, might partly explain the relative stability of membership often observed in wild junco flocks.

To this point we have considered only one plumage character, hood darkness, as a possible indicator of social status in juncos. Rohwer (1975, 1977) describes "studliness" in juncos solely in terms of this character. However, juncos also vary in several other plumage characters, particularly in tail pattern: the tail is blackish centrally and white peripherally in all birds, but the extent of white relative to dark feathering differs between individuals and tends to be greater in males or older birds than in females or younger birds (Miller 1941, Wood 1951). Tails with much white appear to be more contrastingly patterned (hence more "studly" by Rohwer's criteria) than those with less white. Although white in the tail is largely hidden when juncos are at rest, the pattern is readily visible as the birds move about and thus could be used to signal social status.

An analysis of tail rank in relation to social status showed that whiter-tailed members of junco pairs were dominant in 65 (72%) of all relationships, a result that differed significantly from the null hypothesis of equal dominance ($\chi^2 = 17.78$, df = 1, $P < 0.001$). Whiter-tailed birds were dominant in 74% of intersexual and 70% of intrasexual relationships; this difference was not significant ($\chi^2 = 0.18$, df = 1, $P > 0.5$), suggesting that tail pattern may be associated with social status independently of sex. However, whiter-tailed members of junco pairs were dominant in a significantly greater proportion of relationships between birds differing in wing length (78%) than between birds of similar wing length (58%) ($\chi^2 = 3.85$, df = 1 $P < 0.05$). The figure obtained for pairs of similar wing length was in the predicted direction but did not differ significantly from 50% chance expectation ($\chi^2 = 0.62$, df = 1, $P < 0.5$). Tests for effects of tail-rank distance yielded results roughly comparable to those for hood-rank distance: when all relationships were considered together, whiter-tailed birds possibly were less likely to be dominant when tail ranks were close than when they were farther apart (exact test, $P < 0.3$), but this association disappeared when intersexual and intrasexual relationships were considered separately (exact text, $P > 0.5$ in both cases).

In sum, it appears that tail pattern may be at least as strong a predictor of social status as hood darkness in juncos. This finding seems somewhat surprising, because the hood is located frontally, whereas the tail is not, and because tail pattern is a less stable character through the winter than hood darkness (as rectrices may be lost accidentally and replaced by feathers of the next plumage). If plumage variability in juncos does serve a social status signaling function, the presence of two signal characters might be viewed as an example of signal redundancy functioning to combat confusion in a receiver. Hypothetically, these cues may influence the order of social ranking during hierarchy formation; if they are used after this time, they probably serve to facilitate individual recognition, as winter social relationships (including those in which the duller-plumaged of two birds was dominant) were stable in the captive junco flocks.

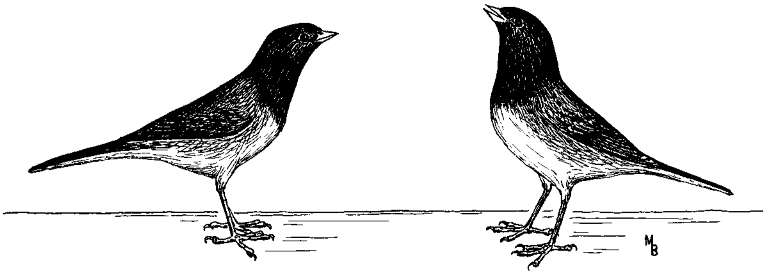

Fig. 2. The junco head dance (drawn from a photograph by M. H. Balph).

Theoretical considerations in juncos.—Our finding that both hood darkness and tail pattern are associated (albeit imperfectly) with social status in wintering Dark-eyed Juncos leads us to explore several questions concerning the evolution and possible communicative significance of these characters. Our first consideration pertains to the direction of the relationship between dominance status and plumage conspicuousness. Although Rohwer (1975) assumes that non-cryptic plumage is associated with high social status in variably plumaged species, the reverse may sometimes be the case, as in the Cassin's Finch (*Carpodacus cassinii*), in which adult males exhibit reddish plumage but are *subordinate* during the winter to females (Samson 1977), which are grayish brown and thus less "studly" by Rohwer's criteria. The form of some winter agonistic displays of juncos (Balph 1977a) might partly explain why visual conspicuousness of the hood or tail is positively associated with social status in this species. The head dance (Fig. 2) is a mutual agonistic display that accentuates the region of contrast between the dark hood and white belly; in addition, one or both participants may fan the tail laterally, exposing its contrasting pattern. The head dance tends to occur when strangers first meet or when a subordinate flock member fails to yield to a dominant at a scarce resource. The tail-up display (Fig. 3) conspicuously exhibits the tail pattern to an adversary and functions as threat. Use by juncos of the hood and the tail in agonistic displays should result in selection favoring enhancement of the display structures through increases in visual contrast. All else being equal, a relatively dark-hooded or white-tailed junco should present a more effective visual stimulus than a duller-plumaged junco during a head dance or tail-up display.

Our next consideration pertains to the location of plumage characters hypothetically used by juncos to signal social status. The placement of the hood is consistent with Rohwer's (1975) prediction that such a character should be situated frontally and ventrally so as to address competitors rather than predators, although the hood also covers the top of the head, which may render dark-hooded juncos more visible to predators against winter backgrounds than light-hooded individuals. More problematical is the white-and-dark pattern expressed on the rectrices, as it is located posteriorly, is hidden from view part of the time, and when exposed can be quite conspicuous from above. If selection for a social status signaling system has played a role in the evolution of the junco tail pattern, we suspect that the location of the signal represents a compromise between this and other (sometimes conflicting) selective pressures. For example, we believe that juncos may use the tail pattern as a cue to flock location—particularly during flight, when white in the tail is flashed most frequently and when the chances for a bird's becoming separated from its flock

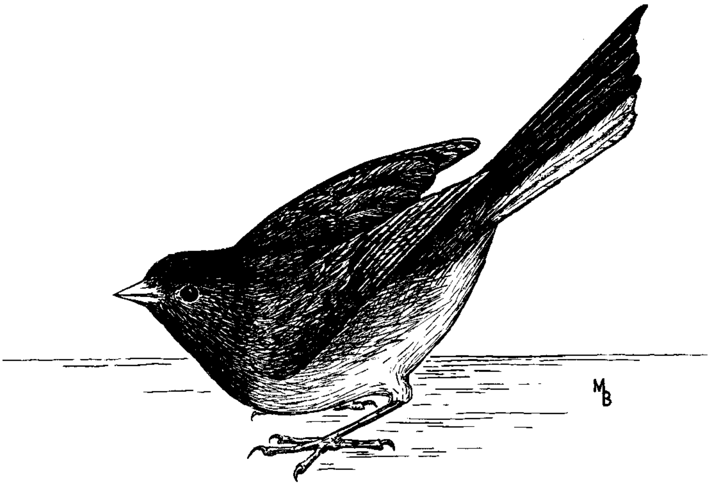

Fig. 3. The junco tail-up display (drawn from a photograph by M. H. Balph).

presumably are greatest. A junco lacking white outer rectrices might be followed less often than others and thus be more likely to become isolated from conspecifics. Although the contrasting pattern of the rectrices may attract the attention of predators, sudden flashes of white accompanied by shifts in flight direction might serve a startle-deception function; hence we think it possible that the tail pattern decreases the susceptibility of juncos to predation.

Our third question concerns the maintenance of plumage variability in wintering junco flocks. An important prerequisite for the development and continuance of a social status signaling system is that individuals of low signaled status be as likely to survive to reproduce as flockmates of higher signaled status lest selection for certain plumage characteristics eliminate winter plumage variability. However, Fretwell's (1969) results, although based upon a small sample size, suggest that subordinate juncos may die or disperse to marginal habitats more frequently than dominants. Perhaps partly in response to this problem, juncos exhibit some geographic segregation of the sexes during the winter, with females wintering farther to the south on the average than males (Ketterson and Nolan 1976). Although differential migration of the sexes might promote the survival of females as a class by lessening intersexual competition (Balph 1975, Ketterson and Nolan 1976), it also may reduce plumage variability within particular junco flocks. We believe, however, that several factors could act to increase intraflock plumage variability.

First, plumage variation within flocks might be promoted if wintering juncos fight more frequently with individuals of similar than dissimilar appearance to themselves. To test this hypothesis, we analyzed data on 992 pecking attacks, flight pursuits, fights, and head dances recorded at various resources in the flight pens during December and for which both participants were known. We used a method of analysis similar to that employed by Rohwer (1975: 601–602) to test the same hypothesis. We weighted expected values to reflect the relative numbers of two-bird combinations of above-average or below-average distance in plumage rank (i.e. >2.33 or <2.33 intervals apart). Agonistic interactions were significantly more common than expected by chance between juncos whose hood ranks or tail ranks were closer together than average ($\chi^2 = 28.10$, df = 1, $P < 0.001$ for hood; $\chi^2 = 5.38$, df = 1, $P < 0.025$ for tail). Our results could reflect heightened aggressiveness between juncos of like appearance, although they also could be produced by differential spacing; for example, Fretwell (1969) and Ketterson (1974) have suggested that low-ranking juncos tend to occupy positions at the periphery of feeding flocks. Ongoing analyses of relationships between social dominance, agonistic behavior, resource use, and spacing in juncos (Balph and Balph in prep.) suggest to us that differential aggression and differential spacing both might be important. To the extent that juncos may be preferentially aggressive toward flockmates of like appearance, it should be advantageous for an individual not to resemble its flockmates closely, as relative dissimilarity could reduce the cost of aggression for that individual. Other considerations being equal, this effect should favor less common plumage characteristics and hence promote intraflock plumage variability. If plumage differences do signal social status in juncos, the cost of agonistic interactions with flockmates of high signaled status possibly could outweigh the advantages of increased social rank for an individual whose advertised status was higher than its underlying abilities warranted, in which case selection might favor correspondence between signaled status and inherent fighting ability.

A second factor that might act to increase intraflock plumage variability could be differential predation. If predators are most likely to take individuals at the periphery of flocks (Hamilton 1971, Vine 1971), and if juncos with black hoods are more conspicuous against winter backgrounds than those with paler hoods, a dark-hooded individual at the periphery of a junco flock should be particularly susceptible to predation. In this case one might expect selection to favor cryptic plumage in peripherally located (i.e. subordinate) juncos.

An additional factor that may increase intraflock plumage variability is suggested by Miller's (1941) finding that juncos exhibit considerable interracial variation in plumage coloration and that more than one race may flock together during the winter in some regions. Characteristics such as wing length, darkness of hood, and whiteness of tail often are not positively associated with one another across races; hence mixing of morphologically dissimilar junco races in some wintering areas could cause confusion as to the meaning of particular plumage cues. Unlike differential aggression or differential predation, which might promote intraflock plumage variability either in the presence or in the absence of a social status signaling system, racial mixing should tend to hinder the development in juncos of a signaling system such as Rohwer proposes.

Our fourth question concerns influences other than those operating in winter flocks that might promote winter plumage variability in juncos. One such factor may be sexual differences in breeding plumage requirements. Because juncos undergo a complete postnuptial but no regular prenuptial molt (Dwight 1900), winter appearances are likely to be affected by summer selective pressures. Male juncos fan the tail laterally during courtship displays (Hostetter 1961, Eaton 1968), and territorial males threaten rivals by raising the breast feathers and alternately elevating and depressing the widely spread tail (Nero 1963). Epigamic or agonistic sexual selection therefore might favor darkness of hood or whiteness of tail in males. Conversely, plumage dullness in females should decrease the likelihood of nest detection by predators (as females apparently perform all incubation and brooding; Greulach 1934, Hostetter 1961) and might facilitate sexual recognition. The potential advantages of cryptic plumage characteristics in the breeding season could outweigh the disadvantages, if any, of such characteristics during the winter for females. A second factor operating during the breeding season to increase plumage variability is hybridization between junco races (Miller 1941), although it exerts an effect only in particular geographic areas. Third, plumage variation within (and overlap between) the sexes conceivably might represent an intermediate stage in the evolution of sexual dimorphism in hood coloration, considered by Miller (1941) to be advanced for the genus. Finally, we think it possible that individual plumage variability in Dark-eyed Juncos is at least partly a byproduct of relatively weak selective pressure for plumage uniformity. For example, variation in the details of hood coloration or tail pattern should not prevent species recognition, as sympatrically breeding emberizines (other than the Gray-headed Junco, *Junco caniceps,* with which *J. hyemalis* interbreeds and may eventually be considered conspecific) do not exhibit the combination of a black or gray hood and white outer rectrices.

Our next consideration pertains to the evolution and hypothetical social significance of individual plumage differences as opposed to sex- or age-related plumage dimorphism. Rohwer emphasizes in general the importance of individual variability and states that, in Harris' Sparrows, "Differences in studliness among individuals much more accurately represent differences in dominance status than do differences in size, or in sex or age class" (Rohwer 1977: 108). Conversely, associations between darkness of hood or whiteness of tail and dominance status in our juncos usually were insignificant within sex or wing-length classes, suggesting that individual plumage variability in this species probably has arisen independently of selective pressure for a social status signaling system. Plumage differences between sex or age classes of juncos might reflect such pressure, although in this case other factors (such as breeding season requirements) also may have played an important role.

We think it unlikely that juncos are strongly predisposed at this stage of their evolution to respond during the winter to plumage cues to sexual dominance status. Relatively dull-plumaged birds were dominant in 18–26% of intersexual relationships among our captives—a much higher proportion than should be expected if plumage cues function as social releasers. We do not know the extent to which age-related plumage variation may be associated with social status in juncos; however, because plumage overlap between ages (like that between the sexes) appears quite extensive, our guess is that such associations may be imperfect and that plumage cues to age-related dominance status are not social releasers. However, plumage differences still might function as conditioned reinforcers. Because male juncos tend to be more aggressive than, and dominant to, females during the winter (Balph 1977a), females may learn to associate male characteristics (such as a dark hood or white tail) with a reduced probability for establishing social dominance. Acquiescence by females should cause males, in turn, to associate female characteristics with an increased likelihood of success. These responses might be generalized to relationships between individuals of like sex but of dissimilar signaled sex; such a secondary effect could be suggested by the weak (for hood darkness) to moderately strong (for tail pattern) positive associations we noted between male-like plumage characteristics and social dominance among members of the same sex in the captive junco flocks. A comparable system of communication might be expected to function between juncos differing in age.

A social status signaling system hypothetically maintained through learned associations might be enhanced in juncos by the form of winter agonistic displays such as the head dance and the tail-up display (Figs. 2 and 3). One could speculate that selection for a status signaling system has produced displays serving expressly to draw attention to variably plumaged structures. However, we do not favor this explanation, as plumage differences apparently are not releasers in wintering juncos, and as the displays themselves denote threat and quite often can be initiated by the duller-plumaged member of a junco pair. We think it likely that the head dance and the tail-up display have evolved under selective pressures primarily or wholly unrelated to social status signaling, but that juncos nevertheless may respond to plumage information provided by conspecifics during the displays.

Although our evidence is indirect, we believe that Dark-eyed Juncos probably are attentive to plumage cues and that a system of social status signaling might operate in winter flocks. However, the roughness of the associations we observed suggests that plumage attributes probably are not the only cues used by juncos to assess their chances for establishing social dominance. This finding perhaps is not surprising, as factors hypothetically influencing plumage variability in this species appear to be complex, and as work by various investigators suggests that many factors (genetic, maturational, and experiential) may be related to social dominance in juncos. We suspect that juncos might benefit from a capacity to form learned associations between a variety of stimuli (morphological, behavioral, and contextual) and probabilities for competing successfully with conspecifics for essential resources during the winter.

Generality of social status signaling.—If social status signaling occurs in Dark-eyed Juncos, it apparently differs in several respects from the model proposed by Rohwer (1975, 1977). As Rohwer developed his ideas primarily from his work on Harris' Sparrows, a comparison of the status signaling system of Harris' Sparrows with that of juncos, as well as an examination of social status advertisement in some other winter flocking species, may reveal something of the general applicability of Rohwer's model.

Harris' Sparrows, like juncos, exhibit considerable plumage variability during the winter. Rohwer notes that the extent of black relative to white (or brown) feathering on the throat, breast, and crown tends to be greatest in adult males and least in first-year females, with substantial variation within, and overlap between, age/sex classes. Winter plumage characteristics are not influenced by requirements of the subsequent breeding season, as Harris' Sparrows, unlike juncos, undergo a regular prenuptial molt (Baumgartner 1968, Jones and Rohwer 1974). However, plumage patterns of the throat and crown apparently are unstable in certain respects through the winter (Baumgartner 1968), which potentially could complicate the relationship between plumage "studliness" and social rank. In addition, although overlap between age classes is extensive for some plumage characters, wintering first-year Harris' Sparrows exhibit a broad, buffy superciliary stripe almost never found in adults (Baumgartner 1968).

Overall correspondence between "signaled" and actual dominance status may be fairly similar for Harris' Sparrows and juncos. Rohwer (1977: 108) notes that ". . . Harris Sparrows somehow achieve a matching of uncanny accuracy between signaled and actual social status." However, his data (Rohwer 1975: 600) indicate that "studlier" (i.e. blacker) Harris' Sparrows won 76% and 70% of 75 and 44 agonistic chases, respectively. Rohwer (1977) later adds that reversals in the first sample were due primarily to the activity of a single bird, although he does not specify the number of individuals involved in encounters that conformed to prediction. Nevertheless, his second result (70%) does agree closely with our results for juncos (69% for hood; 72% for tail). Our figures should be conservative as overall estimates, however, as we studied only one age class of juncos. The results for Harris' Sparrows also may be conservative; Rohwer (1975: 600) notes that avoidance interactions (as opposed to chases) ". . . almost never involve reversals where the studlier loses."

Parallels also might exist between Harris' Sparrows and juncos with respect to sources of correspondence between "signaled" and actual social status. Rohwer (1975, 1977) presents no data to support his conclusion that individual plumage differences among wintering Harris' Sparrows predict social position more accurately than do age or sex differences. More recently, he indicates that plumage "studliness" in this species is a good predictor of dominance status *only* when age and sex classes are pooled (S. Rohwer pers. comm.). Hence the extensive plumage variability occurring within age/sex classes of Harris' Sparrows may remain to be explained, although selection for a status signaling system still might have promoted age- or sex-related plumage differences.

If winter plumage variability in Harris' Sparrows is partly a product of selective pressure for a system of status advertisement, mechanisms for the social control of deception seem as yet unclear. Harris' Sparrows, unlike the juncos we observed, apparently fight most frequently with flockmates of dissimilar rather than similar plumage appearance (Rohwer 1975), which should place individuals of low signaled status at a particular disadvantage during the winter and thereby result in selection for "studly" plumage characteristics. However, pale individuals whose throats and crowns were dyed black experienced a sharp *increase* in attacks by dark flockmates (Rohwer 1977). The results of Rohwer's deception experiments, although suggestive, are nevertheless difficult for us to interpret, as the experiments appear to have lacked stimulus control. For example, flockmates might have perceived a dyed or bleached bird (1) as a changed, but familiar, conspecific; (2) as an unfamiliar conspecific; (3) as a different species; or (4) as a bird exhibiting plumage attributes that were incongruous with other cues (whether visual, vocal, morphological, or behavioral). We therefore do not know to what extent parallels may exist between Harris' Sparrows and juncos with respect to behavioral mechanisms possibly serving to maintain intraflock plumage variability.

In sum, it appears that the social status signaling system of Harris' Sparrows might correspond more closely to what we have hypothesized for Dark-eyed Juncos than to the model proposed by Rohwer. In Harris' Sparrows, as in juncos, associations between plumage attributes and social position appear to be imperfect and may depend primarily upon differences of age or sex. Factors responsible for the origin and maintenance of winter plumage variability probably differ for Harris' Sparrows and juncos but could, we suspect, be complex for both. To date, we believe there is no strong evidence to support Rohwer's (1975: 601) statement that "Apparently, such plumage differences serve exclusively to signal social status . . .," as other (sometimes conflicting) requirements quite probably are important among juncos, and as there seems to be little information available on the form or function of visual displays in Harris' Sparrows.

Winter plumage variability in Dark-eyed Juncos and Harris' Sparrows is largely of a continuous nature. However, some other winter flocking species exhibit a bimodal distribution of plumages. Rohwer (1975: 607) raises the important question: "How does status signaling apply to species . . . exhibiting extreme dichromatism, sexual or otherwise, or non-overlapping age variation?" Our ongoing studies of winter social behavior in the Evening Grosbeak (*Hesperiphona vespertina*), a cardueline finch that shows strong sexual dichromatism, may be relevant to this problem.

Evening Grosbeaks winter in northern Utah in bisexual flocks of medium to very large size. The stability of flock composition and location is considerably less than in Dark-eyed Juncos but possibly varies inversely with the size of a given winter's invasion (Balph and Balph in prep.). We have found that Evening Grosbeaks form stable intrasexual dominance-subordination relationships—based, we believe, upon individual recognition—when winter populations are relatively small, but we suspect that this system tends to break down when flocks are large and unstable. However, a second social system—one that appears to be based upon sexual status advertisement—operates regardless of population size. Male grosbeaks almost always are dominant to females during agonistic encounters (>97% of several thousand recorded interactions). We suspect that the strength of this association may be reinforced by plumage cues to sexual dominance status. Among juncos, by comparison, sexual dimorphism in plumage coloration is incomplete, males are less often dominant to females (82% of relationships in our captive flocks), and conspicuousness of plumage is less strongly associated with actual social position.

Intersexual social status signaling among Evening Grosbeaks might be expected to benefit males to the detriment of females. However, the potential cost to females of lowered social status may be offset by a reduction in intersexual aggression. An analysis of 1,000 1-min samples of agonistic behavior by individual grosbeaks (500 male, 500 female) feeding in flocks at a 0.74 m^2 provisioned platform indicated that grosbeaks were significantly more likely to engage in agonistic encounters with available conspecifics of the same sex than with those of the opposite sex (Balph and Balph in prep.). Females were as likely to fight with other females as males with other males. Differential spacing of the sexes appeared not to be a factor influencing these results, as sex ratios at the feeding platform were similar to those observed in the crowns of trees (Balph and Balph 1976) and as sexual segregation was not evident upon the platform itself. An analysis of the form of 1,500 agonistic encounters revealed a further difference between intra- and intersexual aggression: the tendency for physical contact or for "bree" threat calls to occur during encounters was significantly greater when birds were of like than of unlike sex but did not differ between male-male and female-female interactions (Balph and Balph in prep.). Hence intersexual aggression among wintering Evening Grosbeaks may be reduced not only in frequency, but also in intensity.

Although we do not yet have direct evidence, we strongly suspect that Evening Grosbeaks are attentive to plumage cues to sexual social status. In particular, we believe that the birds may respond to plumage features of the head and perhaps the wings, both of which figure importantly in this species' agonistic displays and which are much more contrastingly patterned in males than in females. Such cues might operate as conditioned reinforcers in grosbeaks, similarly to what we have hypothesized for juncos but with a quantitative difference: because the signals are a more reliable indicator of a bird's ability to win agonistic encounters in grosbeaks than in juncos, grosbeaks should learn to depend more extensively upon them. Alternatively, one or more plumage cues to sexual social status may be social releasers, in which case selection for a predisposition to respond appropriately might have followed (or perhaps accompanied) the evolution of complete sexual dichromatism.

The intersexual social status signaling system that we have hypothesized for Evening Grosbeaks should benefit birds of both plumage types by reducing the cost of intraspecific aggression. Under most conditions, the advantages of such a system may outweigh the disadvantages of subordinacy for females. Only when crowding at a food patch became quite extreme (86 birds/m^2 at a 0.07 m^2 platform) did we find a significant tendency for males to exclude females from positions at the resource (Balph and Balph 1976). A system of intersexual social status advertisement should be particularly advantageous when grosbeak flocks are too large or too unstable in membership to permit individual recognition, as such advertisement could help to control aggression in up to half of all two-bird combinations within a flock.

Factors possibly responsible for the origin and maintenance of winter plumage variability in Evening Grosbeaks may in some respects parallel those hypothesized for Dark-eyed Juncos. In Evening Grosbeaks, as perhaps in juncos, the potential disadvantages of subordinacy among birds of low signaled status may be at least partly neutralized by a reduction of fighting with birds of high signaled status. Evening Grosbeaks, like juncos, exhibit similar breeding and winter plumages and undergo only a slight prenuptial molt, if any (Speirs 1968); hence breeding season requirements may influence winter plumage characteristics. Finally, dominant classes of juncos and (to a much greater degree) Evening Grosbeaks exhibit plumage attributes which, although socially advantageous, may render them more visible than subordinates to predators. Evening Grosbeaks show sexual differences in alarm responses (Balph 1977b) that might function to reduce predation losses and thus promote the continuance of plumage differences signaling social status.

The system of status advertisement we have proposed for Evening Grosbeaks may in some ways resemble those of certain other dichromatic flocking species. For example, Chaffinches (*Fringilla coelebs*), like Evening Grosbeaks, exhibit strong sexual dimorphism and appear to signal sexual social status. Marler (1955a, 1956) found that male Chaffinches were dominant to females in captive winter flocks; however, measurements of individual distance revealed that males were more tolerant of females than of other males. Through a series of experiments, Marler (1955b) demonstrated that the red breast of males is a social releaser evoking aggression. Females dyed to mimic males enjoyed a rise in social status, particularly in relation to other females, but were no longer treated with tolerance by dominant males.

Some other dichromatic species may exhibit quite different systems of social status advertisement. For example, White-throated Sparrows (*Zonotrichia albicollis*) occur in two color morphs that differ both genetically and in aggressiveness. Individuals with white head stripes are more aggressive and socially dominant than those with tan head stripes (Harrington 1973, Ficken et al. 1978). Plumage differences in this species might be expected to signal social status, through learned associations if not through preprogrammed responses. Unlike male Chaffinches or Evening Grosbeaks, white morphs in spring flocks of White-throated Sparrows are equally likely to attack individuals of either morph (Ficken et al. 1978). Plumage dimorphism appears to be maintained through negative assortative mating; white-striped males may monopolize tan-striped females and leave white-striped females to mate with tan-striped males (Lowther and Falls 1968).

In the light of our assessment, we believe that more information on the behavior and ecology of a variety of winter flocking bird species is needed before a satisfactory generalized model of social status signaling can be formulated—if such a model is possible. Comparative investigations are needed at three levels: (1) studies to ascertain whether or not plumage attributes are associated with social status (in those flocking species exhibiting winter plumage variability); (2) experiments to determine whether or not such associations reflect causal relationships, and if so, the extent to which particular visual cues serve as releasers or conditioned reinforcers; and (3) inquiries into factors possibly responsible for the origin and maintenance of various kinds of winter plumage variability. Comparable studies of vocalizations also could prove of value, as social status signaling might occur in more than one modality. Above all, we think it important to recognize the implications for research in this area of Hailman's (1977: 108) observation that the morphology and behavior of animals are shaped by numerous competing selective pressures and that it is therefore inappropriate to search for a single adaptive function for each trait.

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STATUS SIGNALING IN DARK-EYED JUNCOS

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ABSTRACT.—Rohwer (1975, 1977) has proposed that members of certain variably-plumaged avian species may use plumage traits to signal potential dominance status to flockmates. Further, he suggests that plumage variability is maintained because cheaters on the system are detected and persecuted. Data reported herein imply that certain external and noticeable traits of Dark-eyed Juncos (*Junco hyemalis*) are fairly accurate indicators of sex and age class and thus, indirectly, of dominance status. Convergence on signals associated with high status may be prevented by a social system in which dominants are more likely to direct aggressive behavior toward other dominants than toward subordinates. Under such a system, birds whose other traits would lead to subordinate status would suffer a disadvantage if they wore the plumage of dominants. Accurate projection of potential status, whatever that status may be, should prove selectively advantageous. *Received 14 June 1978, accepted 5 September 1978.*

As Rohwer (1975, 1977) has recently noted, some bird species in winter exhibit plumage variability that cannot readily be accounted for by current eco-evolutionary theories such as mimicry, crypsis, or predator/prey-mediated frequency-dependent selection. In these species, certain plumage types seem to be associated with social dominance and other types with subordinance, and he suggests that plumage differences may serve to signal the individual's potential dominance status.

The status-signaling hypothesis produces an apparent paradox: if social dominance is advantageous, then how is plumage variability maintained? Why has not directional selection resulted in monomorphism for the dominant plumage? Rohwer offers two alternative explanations. First, dominant status or correlates thereof may not always be advantageous; traits of subordinates may be favored in some habitats. Secondly, where dominance confers an advantage, convergence on the dominant plumage may be prevented by social regulation of cheating: if subordinate birds were to signal falsely that they were dominant, they would be detected by the true dominants and persecuted.

Consideration of the status-signaling hypothesis will probably be facilitated by separate consideration of the two questions: (1) Does plumage signal potential status? (2) Is plumage variability maintained by social regulation of cheating? Here I describe external cues to potential winter dominance status in the Dark-eyed Junco (*Junco hyemalis*) and offer observations on the maintenance of variability in these cues.

External cues.—Some predictors of dominance in wintering juncos are sex, age, body size as measured by wing length, and arrival date on the wintering grounds as indicated by order of capture (Sabine 1959, Fretwell 1969, Balph 1977, Ketterson 1979, Baker and Fox 1978). Males dominate females, and adults of each sex tend to dominate subadults. Body size is positively correlated with rank, and early arrival confers a dominance advantage. It is not presently possible to determine the mechanisms responsible for the association between these factors and dominance—for example, males may differ physiologically from females in ways that make them more aggressive—but the mechanisms seem irrelevant to the status-signaling hypothesis. The model predicts only that plumage should provide external cues to potential status and that it should be selectively advantageous to heed such cues.

To biologists, juncos provide several external cues to potential status; I shall assume that juncos themselves are at least as able as humans to use those cues. The plumages of the sex and age classes fall into four broadly overlapping categories differing in darkness of color, streaking of the crown, extent of white in the tail, and distribution and number of brown-tipped feathers (Miller 1941, Grant and Quay 1970, Ketterson and Nolan 1976). Additionally, Yunick (1977) has shown that subadult juncos have a grayish-brown iris which changes progressively during their first winter to the red-brown or dark-brown that is characteristic of adults.

Some might argue that the status-signaling hypothesis is interesting only if status is signaled by variability in external cues that are independent of sex and age (Shields 1977), but it seems to me that the value of this hypothesis lies in its potential ability to explain why the sex and age classes (or any other class) should be recognizably different during the nonbreeding season. One purpose of this work is to determine the accuracy with which I can assign juncos to sex and age class on the basis of readily perceivable external cues.

Maintenance of variability.—If external cues signal status, then why does not selection favor convergence toward the dominant signals? It does not seem likely that dominant status in a wintering flock of juncos ever causes a net disadvantage. Fretwell (1969) has shown that dominants banded early in winter are more likely than subordinates to be present in a free-ranging flock at winter's end, and Baker and Fox (1978) have demonstrated higher probability of survival of dominant captive juncos when food is restricted. Yet juncos may reveal their sex and youth, hence subordinate status, by plumage and eye color. If it is physiologically possible for the young to alter eye color by spring, and some do ~~so much soo~~ner, then it is arguable that if it were advantageous to do so, adult signals would be assumed earlier in life. Apparently it is adaptive to retain some juvenile and subordinate traits at least until the first breeding season approaches. Perhaps an individual that is likely to be subordinate in winter gains more by signaling its potentially subordinate status than by mimicking dominant individuals.

What may be the pressure that causes probable subordinates to reveal that fact by their appearance? Rohwer observed disproportionate attack upon initially subordinate Harris' Sparrows (*Zonotrichia querula*) whose appearance he had experimentally altered to make them look like dominants. The altered birds were persecuted by the dominants and began to feed alone or at the periphery of the flock. However, Rohwer's work may be criticized because (1) his samples were small (although his results were statistically significant), and (2) he altered birds already belonging to the flock and presumably known to flockmates as subordinate. Even if the altered birds were not individually recognized after the alteration, they themselves had a history of subordinance and might be expected to withdraw from flockmates whose behavior toward them changed (see Shields 1977 for further comment).

Still, social regulation of cheating seems a viable mechanism worth further consideration. If dominants are more frequently aggressive toward (i.e., "test") individuals that signal potential dominance than toward individuals signaling potential subordinance, and if there is some upper limit on the number (or percentage) of dominants tolerated within a flock (e.g., an evolutionarily stable strategy, Maynard Smith and Price 1973, Maynard Smith and Parker 1976), then it would be disadvantageous to look like a dominant if an individual were unable to withstand the

TABLE 1. Utility of plumage traits and eye coloration to determine sex and age class in wintering Dark-eyed Juncos. Determinations based on plumage alone or on plumage and eye color were compared with determinations made on the basis of a combination of plumage, wing length, skull ossification, and occasional laparotomy.

	Accuracy			
Category	Plumage alone[a]		Plumage and eye color[b]	
Adult male[c]	76%	(n = 37)	87%	(n = 31)
Subadult male	88%	(n = 83)	97%	(n = 33)
Adult female	33%	(n = 12)	100%	(n = 9)
Subadult female	100%	(n = 46)	85%	(n = 27)

[a] Determinations were made October–December 1977 near Bloomington, Indiana (n = 157) and Portage, Ohio (n = 20).
[b] Determinations were made October–November 1978 near Bloomington, Indiana.
[c] Subadults are birds hatched during the preceding breeding season; adults were hatched in any prior breeding season.

testing. Thus another purpose of this paper is to determine whether dominants direct a disproportionate amount of their aggressive behavior toward other dominants.

METHODS

External cues.—Judging by plumage traits alone (Ketterson and Nolan 1976), in the fall and early winter of 1977–1978 I quickly sexed and aged 178 juncos in the hand and then checked these determinations by more deliberate methods believed to be completely accurate (plumage, wing length, skull ossification, and laparotomy in doubtful cases of sex). In the fall of 1978 I repeated this exercise on another 100 juncos, but also considered eye coloration.

Maintenance of variability.—To test whether the social system of juncos could serve to maintain plumage variability, I considered the data of Sabine (1959) on junco dominance hierarchies. For each individual belonging to her most intensively studied flocks (Seattle flock and feeding station flock 1959, Figs. 4 and 1), I first determined the number of birds that each individual dominated. Considering then only each individual's subordinates, I counted the number of aggressive actions an individual directed toward the top half of its array of subordinates and compared that result with the number directed toward the bottom half of the same array. If the number of an individual's subordinates was uneven, then interactions involving the middle bird were divided by two, and half was assigned to each half of the array. This process produced Sabine's observed numbers (see Table 2). To obtain expected numbers of aggressive behaviors toward each half of each individual's subordinates, it was necessary to account for possible rank-associated differences in attendance at Sabine's feeders. To do this, for each array of subordinates I counted all the interactions engaged in by members of the top half, then did the same for members of the bottom half. If, for example, members of the top half of an array were involved in a total of twice as many interactions as were members of the bottom half, this might imply that they were present at the feeder twice as often and thus had twice the opportunity to become the focus of aggression by their top dominant.

Finally, for each individual I found the ratio of aggressive behaviors directed toward the top half of its subordinates (T) to aggressive behaviors directed toward the bottom half (B) and compared observed T:B with expected T:B. The null hypothesis was that observed T:B should exceed expected T:B in only half the cases (see Table 2).

RESULTS AND DISCUSSION

External cues.—Results in Table 1 indicate that on the basis of plumage alone, all subadult females and most adult and subadult males, but few adult females, were recognizable by my quick inspection. Consideration of eye color as well as plumage facilitated recognition of all sex and age classes except subadult females and led to recognition of 91% of the individuals inspected.

Perfect projection of potential dominance status during winter by plumage is not to be expected in juncos. Unlike Rohwer's Harris' Sparrows, juncos undergo a very limited prenuptial molt that involves fewer than all feathers of the head. Therefore,

TABLE 2. Analysis of a junco dominance hierarchy (Sabine 1959, Fig. 4, Seattle flock) to determine whether dominants tend to fight among themselves more often than with subordinates.

	Observed[a]			Expected[b]		
Bird	Top half	Bottom half	Ratio	Top half	Bottom half	Ratio[c]
1	119	68	1.75	2,215.5	1,935.5	1.14
2	128	64	2.00	2,066	1,872	1.10
3	61	43	1.42	2,073.5	1,722.5	1.20
4	127	89	1.43	1,950	1,573	1.24
5	27	17	1.59	1,951	1,479	1.32
6	48	35	1.37	1,901	1,383	**1.37**
7	64.5	38.5	1.68	1,823	1,305	1.40
8	57	12	4.75	1,775	1,227	1.45
9	56.5	33.5	1.69	1,602	1,201	1.33
10	43	27	1.59	1,469	1,175	1.25
11	75.5	49.5	1.53	1,393.5	1,035.5	1.35
12	88	67	1.31	1,309	896	**1.46**
13	58.5	38.5	1.52	1,173.5	825.5	1.42
14	24	16	1.50	1,117	755	1.48
15	73	71	1.03	871	702	**1.24**
16	27	25	1.08	734	649	**1.13**
17	32	30	1.07	644.5	582.5	**1.10**
18	8	9	0.89	659	516	**1.28**
19	24.5	8.5	2.88	412.5	483.5	0.85
20	10	7	1.43	304	451	0.67
21	9	7	1.29	277	372	0.74
22	7	8	0.88	223	293	0.76
23	3.5	2.5	1.40	229	222	1.03
24	10	5	2.00	142	151	0.94

[a] Observed indicates number of displacements directed by a bird toward members of the top and bottom halves of its respective array of subordinates.

[b] Expected is based on availability for displacement as indicated by relative total involvement in aggressive interactions by members of top and bottom halves of each array of subordinates. From the original dominance hierarchy matrix (Sabine 1959), I computed row and column totals for each individual, then summed these for members of the top half of an array and compared the sum to that obtained from the bottom half.

[c] Boldface entries indicate results contrary to prediction, i.e. members of bottom half of array were the objects of displacement more often than indicated by the index of their relative availability for displacement.

even if plumage serves to signal status in winter, it obviously may have other functions in the breeding season and thus be subject to counterselective pressures.

Still, juncos may be able to make finer predictions of potential status than indicated by the data in Table 1. Small but significant differences in size (wing, tail, tarsal and bill length, bill depth) distinguish sex and age classes (Ketterson and Nolan unpublished data) and are associated in a probabilistic manner with status; so juncos may also perceive and utilize this information to evaluate a prospective opponent's likely status.

Further, within each sex and age class, variation is found in both plumage coloration and eye color. Subadult males are the most variable in plumage, ranging from light to charcoal gray and differing markedly in the amount of brown on the back and crown. By early November, 3% of subadults (both sexes) exhibit adult eye coloration; yet by mid-April some are still recognizable by eye color (Yunick 1977, personal observation). Whether this last level of variability is associated with social dominance is not known, but it is a possibility. Black-capped Chickadees (*Parus atricapillus*) hatched early in the breeding season (as judged by degree of skull ossification in early winter) tend to be dominant over members of their year class hatched later (Glase 1973).

The data presented here do not, of course, demonstrate that juncos employ status signaling. What they do indicate is that juncos may be readily assigned to sex and age class and, because sex and age are good predictors of dominance status within a flock, project information that is capable of being used by opponents in evaluating potential status.

Maintenance of variability.—Of the 26 juncos belonging to Sabine's Seattle flock (1959, Fig. 4) only the 24 that dominated at least 2 individuals (i.e., enough to provide a top and bottom half) could be considered (Table 2). Of those, 18 displaced members of the top half of their array of subordinates more often than predicted, and 6 displaced members of the bottom half more often (75%; 95% confidence limits 54.7% to 90.1%). If directing aggression toward another may be considered a kind of "testing," this result may be taken to indicate that dominants test other dominants more often than they test subordinates. However, when the same analysis was performed on the feeding station flock (1959, Fig. 1), the results were ambiguous (data not shown). Only 15 of 25 juncos (60%) displaced members of the top half of their array more often than predicted (95% confidence limits 38.7% to 78.9%). Nevertheless, for both flocks the results clearly differ from those of Rohwer (1977). Whereas he reports that fighting in the Harris' Sparrow is despotic, with dominants focusing a disproportionate number of attacks on the lowest-ranking birds, Sabine's results (as interpreted here) are consistent with the idea that juncos tend to be more aggressive toward stronger rivals.

An obvious criticism of my analysis lies in the method of calculating expected values. The assumption that number of aggressive interactions engaged in can be equated with attendance at a feeder is questionable, as it is well known that subordinates of many species avoid interaction with dominants even when both are present. Still, this tendency to avoid interaction should affect the observed ratio as well as the expected, and may not damage the conclusion. In any case, the analysis is rough and the question of whether dominants tend to be more aggressive toward other dominants should be approached directly. However, other observations of juncos tend to support the conclusion reached on Sabine's data. Ketterson (1979) found male-male interactions to occur more often than expected on the basis of the frequency of males in a flock, and female-female interactions to occur less often.

Infighting among dominants could arise in two ways, only the first of which seems revelant to the hypothesis that such fighting is responsible for the maintenance of variability in external cues to potential status. Dominants might fight more frequently among themselves (1) because dominants recognize stronger rivals by external cues and are more aggressive toward them, or (2) if higher-ranking birds are more persistent in approaching superiors and consequently elicit more attacks by violating individual distance. I cannot add to the discussion of these alternatives at this time.

In summary, juncos vary sufficiently in appearance to justify the prediction that the information thus made available may be used by potential opponents in winter flocks. Convergence toward the complex of dominant signals may be prevented by a net advantage to subordinates in admitting, so to speak, their status. Unwarranted signaling of dominant status may attract the attention of true dominants and result in dissipation of energy, diminished access to resources, or even denial of flock membership for pretenders. While it probably is not advantageous to be subordinate, it may well be advantageous to give the signals of subordinance if that is one's likely status anyway.

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EGG TEMPERATURES OF THE ROCKHOPPER PENGUIN AND SOME OTHER PENGUINS

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ABSTRACT.—Temperatures in penguin eggs were measured by telemetry during undisturbed incubation. During the second half of the incubation period egg temperatures average 29.9–34.4°C in Rockhopper Penguins (*Eudyptes chrysocome*), 35.9–36.2°C in Gentoo Penguins (*Pygoscelis papua*), and 31.9–36.0°C in Jackass Penguins (*Spheniscus demersus*). These temperatures are not markedly lower than those in other birds' eggs. Gentoo and Jackass penguin eggs attain mean temperatures above 30°C within 7 days of incubation but Rockhopper Penguin eggs attain similar high mean temperatures only after 16 days of incubation. Eggs of the Rockhopper Penguin are dimorphic and temperatures in the smaller, first-laid eggs are lower and more variable than in the larger, second-laid eggs. This is attributed to egg size *per se* and to differential positioning of the eggs in relation to the brood patch. *Received 4 April 1978, accepted 28 September 1978.*

PENGUINS spend much of their lives in seawater, a medium with a thermal conductance some 25 times greater than air. Consequently they possess a well insulated integument and other adaptations for reducing loss of body heat to the environment (Stonehouse 1967, Kooyman et al. 1976). Penguins also have lower resting body temperatures than most birds (McNab 1966). This suggests that penguins might have difficulty in maintaining the relatively high temperatures normally associated with successful incubation of avian eggs (Drent 1975). The literature reviewed by Drent (1973, 1975), however, contains very little information on the temperatures of penguin eggs during undisturbed incubation.

During a study of the avifauna of Marion Island in the sub-Antarctic (Williams et al. 1975), we recorded egg temperatures during undisturbed incubation of Gentoo Penguins (*Pygoscelis papua*), Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*). In addition, we recorded egg temperatures in the Jackass Penguin (*Spheniscus demersus*), a species inhabiting cool seas and breeding on arid, hot islands along the coast of southern Africa (Frost et al. 1976). Special attention was given to the Rockhopper Penguin as part of a study aimed at an understanding of the adaptive significance of the species' markedly dimorphic eggs (Gwynn 1953, Warham 1963).

METHODS

We studied penguins during the austral summers 1974/75–1977/78 at Marion Island (46°54′S, 37°45′E), southern Indian Ocean and at Dassen Island (33°25′S, 18°06′E) and Marcus Island (33°03′S, 17°56′E), South Africa. Internal temperatures of the eggs of free-living penguins were measured using procedures described by Drent (1970). A thermistor probe was inserted into the air-space of each egg and sealed into position with epoxy-resin putty. The inner cell membrane was not punctured. The probed egg could be moved freely in the nest. When the temperatures were to be monitored over several days, a wide-spectrum antibiotic was used to sterilize the probe and the area of the egg surrounding it.

Temperatures were recorded at 5-min intervals using a Prelim 170 telethermometer operated from within a blind. The observer was able to enter the blind without being seen by the incubating birds. The thermistor probes were accurate to ±0.2°C when checked regularly against a mercury thermometer. Data from eggs in which embryos did not develop normally, or which were found to have probes that had shifted, were discarded.

Egg temperatures of four species of penguins were monitored for 24-h periods. In addition, eggs of Rockhopper Penguins were monitored twice daily during hour-long spells, each morning from about 0900 (local time) and each night after dark, from about 2100. These Rockhopper Penguin eggs were probed

TABLE 1. Penguin egg temperatures measured by telemetry for 24-h periods or longer.

Species	Egg	Approx. day of incubation	Egg temperature (°C) Mean	Egg temperature (°C) Range	Source
Rockhopper Penguin	Second	5–8	20.8	10.5–36.9	This study
	Second	13–14	14.2	8.4–26.7	This study
	Second	15–18	34.4	29.6–37.9	This study
	Second	28–32	34.2	23.0–37.7	This study
	First	28–32	32.9	22.8–37.9	This study
Macaroni Penguin	First	0[a]	11.7	1.3–33.0	This study
	Second	0–7	23.4	17.2–32.5	This study
Gentoo Penguin	N.D.[b]	0–7	32.0	29.8–33.9	This study
	N.D.	0–7	27.6	16.8–31.8	This study
	N.D.	23–27	35.9	32.3–37.7	This study
	N.D.	23–27	36.2	33.0–37.7	This study
Adélie Penguin	N.D.	N.D.	33.7	29.1–36.8	Ecklund and Charlton 1959
	N.D.	27–28	35.2	30–38	Derksen 1977
Jackass Penguin	First	0[a]	28.9	24.8–33.6	This study
	N.D.	2–5	34.9	31.7–36.9	Frost et al. 1976 and pers. comm.
	N.D.	2–5	34.0	30.2–36.4	Frost et al. 1976 and pers. comm.
	N.D.	13–15	31.9	26.8–36.7	This study
	N.D.	13–15	34.3	29.8–37.6	This study
	N.D.	32–33	36.0	30.0–38.4	This study
	N.D.	34–35	35.8	28.4–38.7	This study

[a] Second egg not yet laid.
[b] Not determined.

and sealed when laid, and remained so until just prior to hatching. Ten eggs were fitted with thermistor probes but embryo development proceeded normally in only four eggs: two first-laid (A) eggs and one second-laid (B) egg in complete clutches, and one B egg in a nest from which the first egg had disappeared at the time the second was laid. Additional data were obtained for a B egg in a complete clutch incubated normally for the first 18 days.

The incubation period is dated from the completion of the clutch. Average incubation periods are: 33–34 days for Rockhopper Penguins (Gwynn 1953, Warham 1963), 35–36 days for Macaroni Penguins (Gwynn 1953, Downes et al. 1959), 35–36 days for Gentoo Penguins (Gwynn 1953), and about 39 days for Jackass Penguins (McLachlan and Liversidge 1978).

The positions of eggs beneath the brood patches of Rockhopper Penguins were recorded at 3 stages of the incubation period by carefully lifting incubating birds off their clutches. This was done at a colony that was otherwise undisturbed by man.

RESULTS

Mean temperatures of incubated eggs of five species of penguins are presented in Table 1. Eggs of Gentoo and Jackass Penguins had mean temperatures of 27.6–32.0°C and 28.9–34.9°C respectively within the first 7 days of incubation. Those of Rockhopper and Macaroni Penguins failed to reach such high temperatures during the first week. Rockhopper Penguin egg temperatures rose markedly above ambient air temperatures only after the second egg had been laid (Fig. 1), and achieved fairly constant temperatures above 30°C only after 16 days of continuous incubation.

Incubation shifts of Rockhopper Penguins (N = 8–12 pairs) at Marion Island are similar to those at Macquarie Island (Warham 1963). Both parents remain at the nest for the first 5 days of the incubation period, with the female usually incubating. The male then leaves for the sea to feed for about 15 days and the female incubates. The male then incubates for about 10 days while the female feeds at sea. The female returns a few days before the chicks hatch.

Among most species of penguins that lay two eggs there is little difference in size

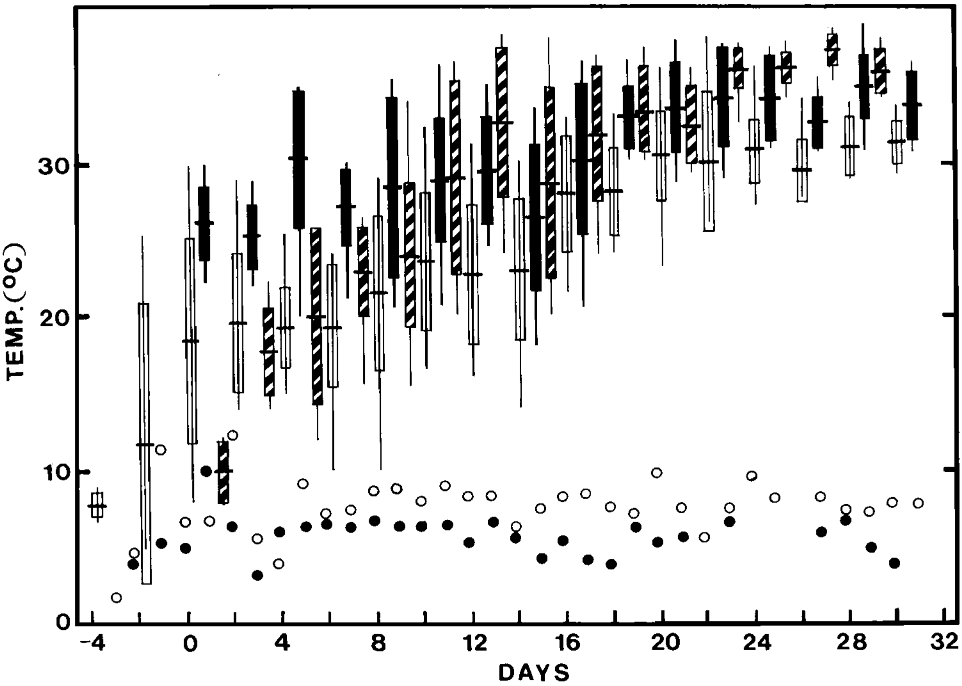

Fig. 1. Internal temperatures of Rockhopper Penguin eggs, including first laid (A) eggs (open boxes) and second laid (B) eggs (black boxes) in complete clutches and a B egg incubated singly (hatched boxes). The mean temperature (horizontal bar), ± one SD (vertical box) and range (vertical line) are given for 2-day intervals. Open and solid circles show the mean shaded air temperature at 20 cm above ground level for daytime and night respectively.

between eggs in a clutch. In the genus *Eudyptes,* however, the first laid (A) egg is significantly smaller than the second laid (B) egg in each clutch (Gwynn 1953, Warham 1963). On average, 4 days elapsed between the laying of the A and B eggs in Rockhopper Penguin clutches at Marion Island (N = 59 clutches). The mean period between laying and hatching of A eggs was 39 days and of B eggs, 34 days. This difference represents an increase of 1 day over the laying interval so that the A egg normally hatches after the B egg at nests where both eggs hatch.

The B eggs in Rockhopper Penguin clutches were maintained at higher and steadier temperatures than the A eggs throughout the incubation period (Fig. 1). The B egg incubated alone initially had a lower temperature than those in completed clutches but this situation was reversed after the tenth day of incubation. After 16 days the mean temperature recorded daily for all A eggs was 29.9°C (range 21.5–38.0°C) and for all B eggs 34.3°C (range 20.4–38.2°C). These results are similar to the means over 24-h periods (Table 1).

Rockhopper Penguin eggs are usually held one in front of the other, or, rarely, laterally placed beneath the elongate brood patch (Table 2). The rear egg contacts the broadest part of the brood patch against which it is pushed by the weight of the bird. The anterior egg makes less contact with the brood patch and, though safe and well covered when the bird is in a prone position, it is often partially exposed when the parent is in a hunched (semi-upright) position (see Warham 1975, Fig. 10.2).

TABLE 2. Positions of Rockhopper Penguin eggs beneath the brood patch in nests containing two eggs.

Week in incubation	Percentage of nests			Number of nests
	First egg anteriorly	Second egg anteriorly	Both eggs laterally	
2	58	37	5	84
3	66	34	0	77
4–5	66	32	2	59

The positioning of Rockhopper Penguin eggs under the brood patch was not random (Table 2). The smaller A egg was usually in the anterior position while the B egg was in the favorable rear position (χ^2 test, $P < 0.05$ for week 2 and $P < 0.01$ for weeks 3–5).

DISCUSSION

Egg temperatures during incubation.—To date, the only published data on temperatures in penguin eggs measured by telemetry, during undisturbed incubation, are those given for the Adélie Penguin (*Pygoscelis adeliae*) (Ecklund and Charlton 1959, Derksen 1977) and the Jackass Penguin (Frost et al. 1976), which are summarized in Table 1. Combining these data with ours, it appears that in four species of penguin the internal egg temperatures during the latter half of the incubation period fall within, or just below, the range of egg temperatures (34–39°C) of 25 species of birds listed by Drent (1973, 1975). This result was not anticipated, since penguins have reduced thermal conductance through the integuments (Kooyman et al. 1976) and their body temperatures at rest are, with those of procellariiform seabirds, some 2°C below the average for species in other avian orders (McNab 1966).

Most birds appear to attain high egg temperatures within a few days of completing laying. Mean egg temperatures of over 30°C were attained during the first 30% of the incubation period in the Herring Gull (*Larus argentatus*) (Drent 1970), the Mallard (*Anas platyrhynchos*) (Caldwell and Cornwell 1975), the Ruddy Duck (*Oxyura jamaicensis*) (Siegfried et al. 1976), the South Polar Skua (*Catharacta maccormicki*) (Spellerberg 1969), the House Wren (*Troglodytes aedon*) (Kendeigh 1963), and in the Gentoo and Jackass Penguins (this study). The delayed maintenance of consistently high egg temperatures in Rockhopper Penguins appears unusual.

An increase in egg temperature during the course of incubation can generally be attributed to increased parental attentiveness, increased heating ability of the brood patch (through increased vascularization and blood flow) or increased heat output by the embryo (Drent 1975). Since parental attentiveness by Rockhopper Penguins approaches 100% once the clutch is complete (Warham 1963), parental inattentiveness seems unlikely to be the cause of the delayed maintenance of high egg temperatures.

In most birds studied to date, the brood patch reaches a definitive temperature by the time the last egg is laid or within a few days therafter (Drent 1975). An exception is the Yellow-eyed Penguin (*Megadyptes antipodes*), in which the brood patch only reached a definitive temperature of 38°C after 36% of the incubation period had passed (15 out of 42 days), with increased vascularization of the brood patch throughout this period (Farner 1958).

Rockhopper Penguin females, which do most of the incubating during the first half of the incubation period, might have a similarly retarded vascularization of the brood patch, although we have no evidence for this to date. The females, having completed ovogenesis and while enduring a fast of 33–45 days (Warham 1963) might not have the energy reserves to afford maximum heat flow to the clutch. The males, however, on their return from the sea to resume incubation duties have replenished energy reserves and can possibly expend more energy in incubation than the females.

Neither Gentoo nor Jackass Penguins endure long fasts during incubation; both species have normal incubation shifts of 1 day (Van Zinderen Bakker 1971, Cooper in press). They can possibly afford greater heat output to the clutch during the first half of incubation than the Rockhopper Penguins. Yellow-eyed Penguins fast for moderately short periods of 1–5 days during incubation (Richdale 1951).

Parental preference within the clutch among Rockhopper Penguins.—The smaller first-laid (A) eggs of Rockhopper Penguins were maintained at lower, more variable temperatures throughout the incubation period than the second-laid (B) eggs. These differences can largely be attributed to size differences *per se* and to parental behavior during incubation.

Small eggs have lower thermal capacities and greater surface area to mass ratios than larger eggs. Under similar conditions small eggs require less heat to be maintained at the same temperature but they would heat and cool faster than larger eggs. This may account for the greater variation and range in temperature of A eggs relative to B eggs of Rockhopper Penguins, but cannot explain the differences between their mean temperatures.

The A and B eggs do not experience similar conditions during incubation. The A eggs occupy the anterior position beneath the brood patch more frequently. Here the brood patch is narrower and the eggs are more exposed to cold air when the parents shift on the nest or adopt the hunched incubation posture. Artificial eggs incubated by Adélie Penguins cooled faster during parental movements when they occupied the anterior position under the brood patch (Derksen 1977).

The relatively less favorable thermal environment experienced by A eggs of Rockhopper Penguins appears to retard embryo growth: although they are laid 4 days before the B eggs and are incubated steadily from at least the same time, A eggs hatch a day or more later than the B eggs. Weinrich and Baker (1978) showed that Adélie Penguin embryonic development was retarded at low temperatures. The A eggs of Rockhopper Penguins might be kept at temperatures low enough to retard embryo growth for appreciable amounts of time, whereas the B eggs seldom were.

Rockhopper Penguins appear to favor the larger B eggs during incubation. Warham (1963) observed that when the parents reposition the eggs following nest relief, the larger B egg was usually tucked under the brood patch first, followed by the A egg. Large eggs generally provide greater stimuli for incubation behavior than small eggs (Tinbergen 1951). Apparently it is advantageous for Rockhopper Penguins to incubate the B egg more diligently than the A egg, since the larger B egg represents a greater investment of energy. Rockhopper Penguins, in common with all eudyptid penguins, have never been known to rear two chicks simultaneously (Warham 1975). In this situation, the B egg, which produces a relatively more robust chick (Gwynn 1953, Warham 1963), is a more valuable investment than the A egg.

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TESTOSTERONE AND DAYLENGTH-DEPENDENT DEVELOPMENT OF COMB SIZE AND BREEDING PLUMAGE OF MALE WILLOW PTARMIGAN (*LAGOPUS LAGOPUS LAGOPUS*)

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ABSTRACT.—Photostimulation of male Willow Ptarmigan resulted in a rapid molt from the white winter plumage to the pigmented plumage of the breeding bird. In castrated ptarmigan the breeding plumage was omitted, resulting in a slow molt from white to pigmented summer (postnuptial) plumage. Feathers were plucked from the head and back of castrated and intact birds kept on short daylength to investigate the effects of testosterone on feather pigmentation. Both castration and testosterone treatment resulted in pigmentation of regenerating feathers, while the untreated, intact birds regenerated white feathers.

Pigmented feathers that regenerated on short daylengths in castrated or testosterone-treated birds were similar to each other, but were not the same as any type of pigmented feather seen in intact or castrated birds exposed to long daylengths. Pigmented feathers that generated in testosterone-treated intact or castrated birds on long daylengths were the same as feathers in breeding males. When compared with control birds, testosterone treatment shortened the interval between photostimulation and the beginning of the molt, while castration markedly lengthened this interval.

Together with the photostimulated development of pigmented breeding plumage in intact males, there was a 100% increase of comb height. Castrates did not show any comb growth, whereas testosterone treatment always resulted in a rapid comb growth, both in intact males on short daylengths and in castrates on short daylengths and on long daylengths.

In the male Willow Ptarmigan, testosterone and perhaps gonadotrophins (LH) affect the pigment producing system. There is a daylength dependent testosterone induction of molt from winter to breeding plumage, and a testosterone-stimulated and a testosterone-dependent comb growth. *Received 15 March 1978, accepted 28 September 1978.*

TOGETHER with a number of arctic and hyperboreal birds and mammals, Willow Ptarmigan (*Lagopus lagopus lagopus*) show a pronounced seasonal dimorphism, displaying a white winter and a pigmented summer plumage. Through the summer there may be several stages, and Johnsen (1929) described as many as four attires in the male and three in the female throughout the year.

Both male and female Willow Ptarmigan show a white *winter plumage,* normally lasting from the end of October to the end of March. The male then begins to molt the white winter feathers and develops a conspicuous pigmented *breeding plumage.* This is characterized by molt and formation of new feathers on the head, upper neck, upper anterior breast and on the back, while the ventral and wing feathers remain. The pigmentation is reddish-brown and black and the feathers are shed in a sequence so that feathers on the back are affected last. This part of the body may attain full coloring at the time when actual mating takes place, or it may not be fully colored at all. The naked wattle or comb over the eye enlarges and appears bright red during this period.

At the end of the breeding period, the male begins to molt into a pigmented *summer plumage.* This may be initiated even before the breeding plumage is completed, and the remaining feathers from the winter and breeding plumage are replaced by bright yellowish and brown feathers with black bars.

In the female, the pigmented plumage starts to develop a little later than in the male, and the feather replacement is not as sequential. The garb is very much like that of the male's summer plumage and is completed at the time of breeding. It is not changed during the periods of egg-laying, incubation, and the first 2–3 weeks of brooding chicks. After brooding, molt starts again, and the female together with the male, who has now more or less completed the summer plumage, gradually change into a pigmented *fall plumage,* consisting of dark brown and black feathers. This stage shows great variations mainly because of the varying number of remaining feathers from the preceding plumages.

The main difference between the sexes, therefore, lies in the breeding plumage of the male, and while the female shows a rather constant feather garb while incubating eggs and rearing young, the male molts continuously from the end of March until the winter plumage is completed at the end of October.

The dramatic change from white to brown in the spring coincides with the annual activation and growth of the gonads. In arctic and subarctic regions, this part of the year is characterized by a rapid and pronounced increase in the daylength. A great number of investigations have described the causal relationship that seems to exist between daylength and gonadal activity in birds (see Farner and Follett 1966, Lofts and Murton 1968, 1973 for reviews). Høst (1942) and Novikov and Blagodatskaia (1948) showed that during late autumn and mid-winter, male Willow Ptarmigan responded to artificially increased daylength by a rapid development of breeding plumage and gonadal activity. Within a few days after being transferred to long days, the birds began to replace their white winter feathers with feathers of the pigmented breeding plumage. The activation of the gonads was reflected by increased comb size and by the onset of aggressive behavior. All these events took place in unheated outdoor cages, with snow covered ground, and an ambient temperature far below the freezing point (Høst 1942).

The purpose of this investigation was to find out whether the development of breeding plumage in male Willow Ptarmigan is regulated by sex hormones, or if the plumage development and the coinciding activation and growth of the testes may be controlled through more or less separate mechanisms initiated by the same external stimulus (i.e. long days). To this end castration and testosterone treatment of male Willow Ptarmigan were performed, and the effects of such treatment, alone or combined, on photostimulated plumage changes and comb growth were observed.

METHODS

Forty-four farm-bred male Willow Ptarmigan were used for the experiment. The birds were individually caged with free access to water and a modified, pelleted chicken food. When the experiment started on 17 November 1976, all birds were exposed to a light regimen of short days (6L:18D) and had white winter plumages. Previously, they had all experienced a normal autumn with decreasing daylength, controlled by electrical timers and synchronized to the changes outdoors. The illumination was by 80W fluorescent lamps (4400–4600 Lum, 3600°K), each bird situated 1–1.5 m away from a lamp.

The birds were divided into groups as described in Table 1. Castration was carried out under Equithesin anesthesia by bilateral laparotomy between the last two ribs, the testes being removed intact by a pair of fine forceps. Photostimulation was performed by increasing the daylength from 6 to 18 h of light (18L:6D, i.e. long days). The light was always turned on at 0900. The experiment lasted until the beginning of February, when most of the intact photostimulated birds had developed fully pigmented backs. Testosterone treatments were given by daily injections in the pectoral muscle of 1 mg testosterone-oenanthate (Sigma) in 0.05 ml Sesame oil.

Plumage observations were carried out in three ways: 1) *Pigmentation and growth of developing*

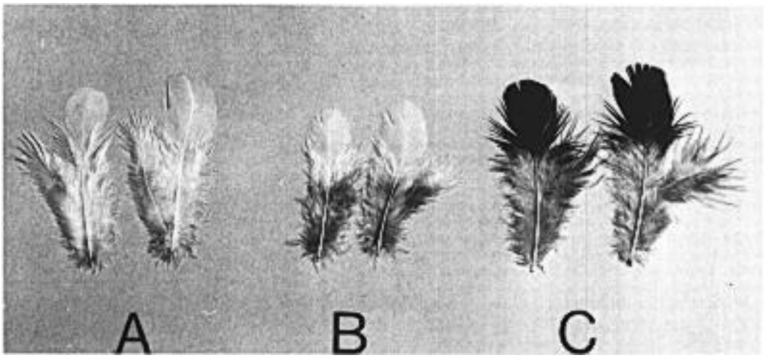

Fig. 1. Feathers plucked from the back of a male Willow Ptarmigan. **A**. from the winter plumage; **B**. from feathers regenerated after first plucking of a testosterone treated bird; **C**. from feathers regenerated after second plucking of a testosterone treated bird.

feathers. Before molting had started, about 60 feathers from one area in the neck and about 30 feathers from one area on the back were plucked on each bird, thereby stimulating regrowth of new feathers. In groups 2, 4, and 7 (Table 1), the feathers were plucked 7 days before the beginning of testosterone treatment. In group 9, the feathers were plucked 7 days after the beginning of testosterone treatment. The plucked feathers regenerated and were plucked a second time, and this took place before photostimulation in groups 3, 4, 6, 7, and 8. 2) *Time of onset of molting*. Molting was manifested by general loss of white feathers and the appearance of pigmented featherpulps outside the plucked areas. 3) *The percent of the birds' back and head appearing pigmented*. The development of pigmented plumage on the head and back was separately judged, and the percent pigmentation was subjectively assessed. The head is the area from above the shoulders, and the plucked area in the neck, therefore, belongs to the head region of the bird. The total height of the comb was measured to the nearest 0.5 mm.

RESULTS

Untreated, intact birds on short daylength (groups 1 and 3, Table 1) showed new feather pulps 7 days after plucking, both on the back and in the neck. All the feathers regenerated, and they were all white, both from the first and from the second plucking and regeneration.

Testosterone treatment affected the regrowing feathers in two ways: first, the feather replacement process was slowed down to a varying but considerable degree—

TABLE 1. The number of birds in each group, and the treatment they received throughout the experiment. The dates (day/month) indicate when the testosterone injections started, when the feathers were plucked, and when castration and photostimulation were performed. An asterisk indicates that the above listed treatment was not performed in that group.

Group	Number of birds	Feathers plucked[a]	Castrated	Testosterone-treated[b]	Photo-stimulated[c]
1	5	17/11 and 1/12	*	*	*
2	5	17/11 and 1/12	*	24/11	*
3	6	17/11 and 1/12	*	*	8/12
4	7	17/11 and 1/12	*	24/11	8/12
5	5	17/11 and 1/12	30/11	*	*
6	6	17/11 and 1/12	30/11	*	8/12
7	3	17/11 and 1/12	30/11	24/11	8/12
8	2	17/11 and 1/12	30/11	12/1	8/12
9	5	1/12	*	24/11	*

[a] One area of the neck and one area of the back were plucked two times (except group 9) to allow regrowth of new feathers.

[b] Testosterone treatment was given by daily injections in the pectoral muscle of 1 mg testosterone-oenanthate in 0.05 ml Sesame oil.

[c] Photostimulation was preformed by increasing day length from 6 to 18 h of light.

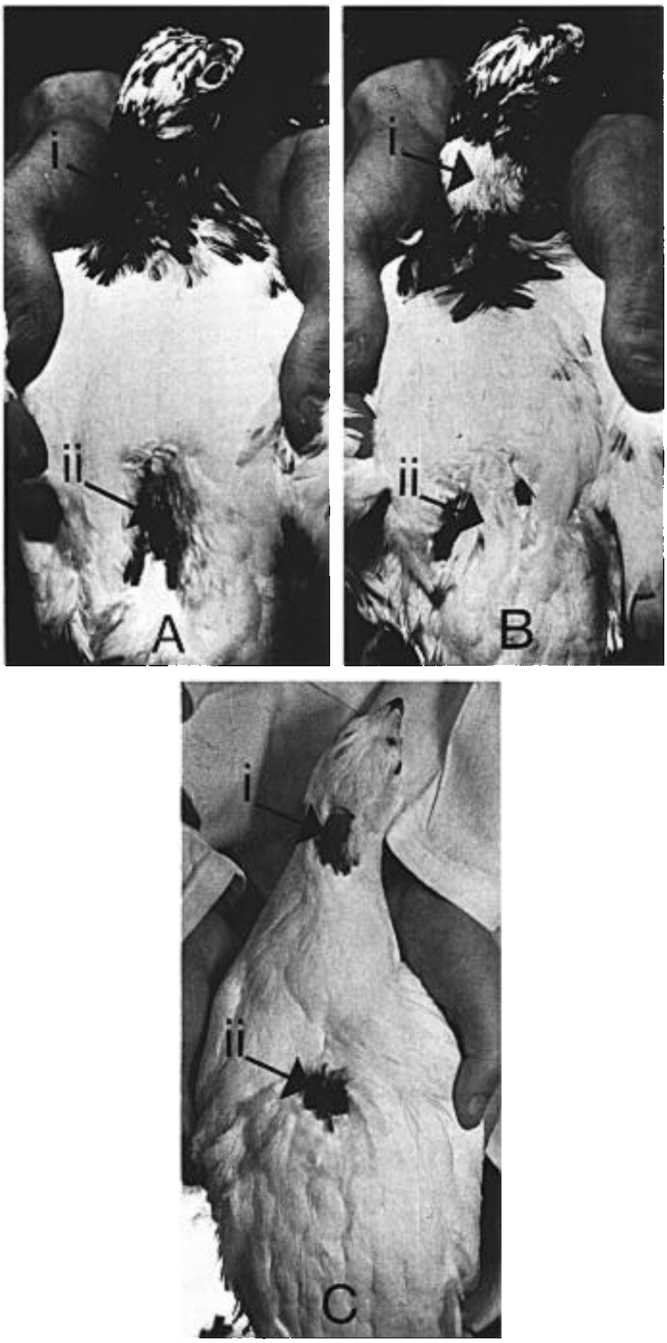

Fig. 2. Feathers regenerated on the plucked areas in the neck (i) and on the back (ii). **A**. photostimulated, testosterone treated male; **B**. photostimulated, untreated male; **C**. testosterone treated male on short daylength.

only a few to none at all regenerated, and the growth of the few that came was retarded; second, pigmentation was generally stimulated. In groups 2, 4, and 7, where feathers had been growing for a week before testosterone treatment started, there was no pigmentation of neck feathers. The proximal half of the regenerating back feathers, however, was pigmented (Fig. 1B). In group 9, where testosterone treatment started one week before plucking, the regenerating feathers were pigmented, but with a white 1–3 mm tip.

The second plucking and regeneration resulted in pigmentation of the whole feather in all the treated groups, both in the neck and on the back (Fig. 1C and 2A and C). In groups 3 and 4, the photostimulated molt began before the second regeneration was completed, leaving a white spot on the dark neck of the control birds (Fig. 2B, i), and a whole dark neck in the testosterone-treated birds (Fig. 2A, i).

Castration in no way affected the regeneration and growth of plucked feathers. However, the pigment-producing system was affected, and castrated birds regenerated pigmented feathers to a considerable extent from the very first plucking. These pigmented feathers on the plucked areas of castrates were not unlike the regeneration observed from the second plucking of the testosterone-treated birds (Fig. 2C, i and ii).

The intact birds of group 3 responded to the changing daylength by molting of white feathers and development of pigmented breeding plumage. The molt started 8–9 days after the change of daylength.

Neither testosterone treatment nor castration had any molting effect on the birds during short days. This was shown in groups 4, 6, 7, and 8 before photostimulation, and during the entire study in groups 2, 5, and 9, which remained on short days.

Both castration and testosterone treatment, however, affected the onset of photostimulated molt. The castrated birds of groups 6 and 8 showed no signs of molting until after 2–3 weeks of long days (i.e. molting was delayed). The testosterone-treated birds of groups 4 began to molt significantly earlier than untreated birds (6–7 days after photostimulation in testosterone-treated birds, 8–9 days in untreated birds). The castrated but testosterone-treated birds of group 7 behaved as the normal testosterone-treated birds. The birds of group 8 behaved as castrates and showed no normal male molt until 7 days after the testosterone treatment started. Then a normal molt ensued, and a normal male breeding plumage developed.

After the molting had started, the testosterone-treated birds of groups 4, 7, and 8 developed a breeding plumage not significantly different from the control birds of group 3. Before the testosterone treatment started the castrated birds of group 6 and group 8 showed a development much unlike group 3. Two to three weeks after transference to long days the birds started to develop a pigmented plumage, but in a way more like a female than a male ptarmigan. The replacement of white feathers was slow, and was initially not restricted to the head as in the male, but affected both back and head to nearly the same extent. These birds did not develop the conspicuous dark crop-region band normally present in the breeding plumage of the male (Johnsen 1929), and the pigmentation on the whole was more like that of the summer plumage.

Testosterone treatment always resulted in a rapid growth of the comb, and within 3 weeks the height of the comb increased 100% (Fig. 3). The birds on continuous short days did not grow larger combs unless they were testosterone-treated. Photostimulation resulted in a rapid comb growth, and within 4 weeks the height had

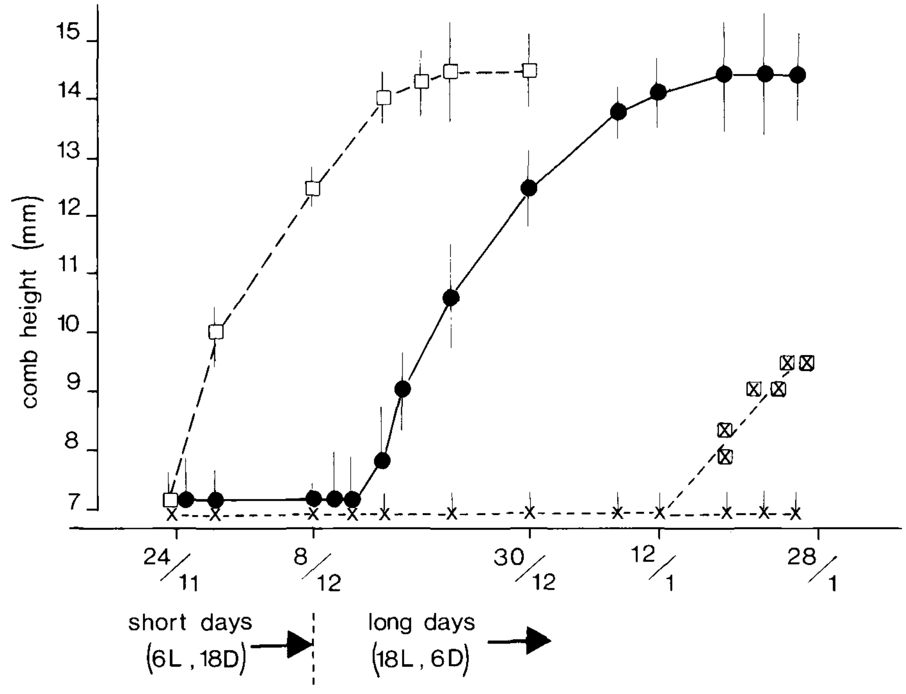

Fig. 3. Comb height variations of male Willow Ptarmigan (height in mm with vertical bars showing ± SE). One group received testosterone treatments from 24 November (☒, n = 7), one group was castrated on 24 November (☐, n = 8), and of these two received testosterone from 12 January (×). One group remained intact and untreated (●, n = 6). At 8 December, all groups experienced an increase in the daylength from 6 to 18 h of light.

increased 100% in the untreated intact birds of group 3. The castrated birds of groups 6 and 8 showed no comb growth at all after being photostimulated, but as soon as group 8 received testosterone a rapid growth ensued.

The pigmentation that resulted from castration and testosterone treatment of birds kept on short days differed from the breeding-plumage coloring resulting from photostimulation. While the normal breeding plumage has feathers with brown, reddish-brown, and black patterns, castration and testosterone treatment induced black and grey pigmentation on short days, and the feathers lacked the characteristic barred patterns.

Only the development of breeding plumage was affected by castration. When castrated birds had reached full pigmentation, they could no longer be distinguished from males wearing summer garb. The development into fall and winter plumage also occurred as in intact normal males. After about 2 weeks in white winter plumage, however, plucking again resulted in pigmented feathers, and photostimulation resulted in a feminine development of pigmented summer plumage.

At the end of the experiment, inspection revealed no testicular regeneration in the castrated birds. The birds were killed in a state where normal birds have enlarged testicles.

TABLE 2. A summary of the results from each group. A dashed line indicates that photostimulation was not performed, and therefore no plumage changes took place.

Group	Feathers regrown on plucked areas	Plumage changes after photostimulation	Comb
1	All white	—	Small—no changes
2	First plucking white, second pigmented	—	Growing after 24/11
3	All white	Molting into breeding plumage	Growing after 8/12
4	First plucking white, second pigmented	Like group 3, but molting began earlier	Growing after 24/11
5	All pigmented	—	Small—no changes
6	All pigmented	Long delay, then a very slow molt into a summer-like plumage	Small—no changes
7	All pigmented	Like group 3, but molting began earlier	Growing after 24/11
8	All pigmented	Like group 6 until 12/1, then like group 3	Small, no changes until 12/1, then growing
9	All pigmented	—	Growing after 24/11

DISCUSSION

The hormonal control of plumage changes in birds has long been a matter of confusion. Depending on the species involved and when experiments with hormones take place relative to periods in the bird's life (e.g. the annual breeding period), a great number of reactions has been recorded from the treatment of most of the normally occurring hormones. In addition, many other chemical and environmental stimuli affect the mechanisms of both molt and pigment production (see Witschi 1961, Ralph 1969, Payne 1972 for reviews).

The lack of comb growth in photostimulated, castrated Willow Ptarmigan was also reported by Nowikow (1939), and the dependency on testosterone for comb growth has now been documented for several avian species (see Parkes and Emmens 1944, Lofts and Murton 1973). The comb is an important secondary sexual character, and Gjesdal (1977) found a positive correlation between the comb height and social rank between male Willow Ptarmigan in captivity.

Most investigators have found that gonadal hormones inhibit molting in birds. Castration often triggers a premature molt, and in a number of species the birds enter a condition of continuous molt after castration. But for the more than 100 species, including Willow Ptarmigan (Høst 1942), where molting and changes in gonadal activity coincide, the action of gonadal hormones on plumage changes is less well understood (see Payne 1972). The present results show that the molting system is not influenced by testosterone as long as the birds are held on short days. After photostimulation, testosterone-treated birds molt earlier than control birds, and castrated birds do not show a normal male molt at all. The time lag between photostimulation and the first signs of molt for testosterone-treated birds is 6–7 days, which is the same time it takes for a plucked feather follicle to regenerate a new visible feather pulp. This indicates a daylength-dependent testosterone induction of molting. In the treated birds the plasma levels of testosterone are high when the daylength is increased, and a stimulation occurs even after the first long day. The control birds have to wait for their own testosterone production, and it is a reasonable inference that this becomes high enough within 2–3 days. The plasma level of luteinizing hormone (LH), which stimulates the testicles to produce testosterone, has been shown to increase the first day after photostimulation in Japanese Quails (*Coturnix coturnix*) (Nicholls et al. 1973, Gibson et al. 1975), White-crowned Sparrows (*Zonotrichia leucophrys*) (Follett et al. 1975, Lam and Farner 1976), and Willow Ptarmigan (Stokkan in prep.). The finding that regeneration of plucked feathers is retarded in testosterone-treated birds is not understood. The present results conflict with those of Nowikow (1939) who reported that photostimulated castrated Willow Ptarmigan molted into breeding plumage as normal birds. This could be attributed to an incomplete castration since this may result in a normal development of photostimulated breeding plumage, but a reduced comb size (Stokkan unpublished observations). The results of Nowikow (1939) are not quantified.

In male Rock Ptarmigan (*Lagopus mutus*), which also show seasonal dimorphism, testicular hormones seem to suppress the initiation of the molt from white to pigmented plumage (Salomonsen 1950–1951). MacDonald (1970) observed that one male Rock Ptarmigan implanted with testosterone did not change from white to pigmented plumage at the time when normal males did, but remained white through most of the summer, displaying sexual activity long after the normal breeding period was terminated. This difference whereby testosterone acts on the onset of molt between the two ptarmigan species may explain why male Willow Ptarmigan develop a pigmented breeding plumage, whereas male Rock Ptarmigan normally stay white all through the breeding period.

The present study shows that the pigment-producing system is affected by both testosterone treatment and castration independently of daylength. Sex hormones have been shown to affect the production of feather pigments in several species. Both quality and quantity are affected, and the effects have resulted from both gonadectomy and local and systemic administration of hormones (see Ralph 1969). Both testosterone treatment and castration stimulated pigment production, but there was a latency in the action of testosterone. This latency was shown in several ways. The birds of group 9 regenerated pigmented feathers after the first plucking, but they had a white tip. The back feathers of groups 2, 4, and 7 also had a white distal part (Fig. 1B), and the head feathers of these groups were not pigmented until they regenerated after the second plucking. In castrates, however, the feathers were fully pigmented after the first plucking and regeneration.

The different modes of action whereby castration and testosterone treatment affect pigment production suggest different mechanisms. Castration results in increased plasma levels of LH in male Willow Ptarmigan at this time of the year (Stokkan in prep.). Both testosterone (rat scrotum epidermis, Wilson and Spaziani 1976) and LH (weaver finch breast feather follicles, Hall and Okazaki 1966, Hall 1966) have been shown to stimulate melanin production through action on the tyrosinase enzyme system. Thus it could be argued that both increased levels of plasma testosterone, resulting from testosterone treatment, and increased levels of plasma LH, resulting from castration, could stimulate pigment production. The finding that castration and testosterone treatment resulted in regrowth of feathers displaying grey and black colors, which are different from those normally found in the male breeding plumage, suggests a hormone-influenced tyrosinase stimulation. Tyrosinase is the enzyme system catalyzing the conversion of L-tyrosine to DOPA-quinone, generally believed to be the rate-limiting step in the biosynthesis of melanin (Lerner 1953).

This study has focused upon the development of the male breeding plumage. The testes regress in June/July and the plasma levels of testosterone fall (Stokkan in prep.), but the birds still produce pigmented feathers until the end of October, when the winter plumage starts to develop. From the time that the castrates have completed the summer plumage until they again await the development of breeding plumage in winter, they cannot be distinguished from intact birds. Outside the breeding period, therefore, other hormones must control the molt and production of pigments. That such hormones may play a role in the control of seasonal plumages in Willow Ptarmigan has recently been shown by Braun and Höhn (1977). They found that plucked birds grew pigmented replacement feathers if they were injected with any of the hormones alpha-MSH, mammalian posterior pituitary extract, thyroxine, TSH or an FSH/LH mixture.

The complete understanding of the control of seasonal plumage changes of the Willow Ptarmigan is still an unsolved problem. However, the male breeding plumage must be regarded as a secondary sexual character, and the development of it is dependent on the levels of plasma testosterone.

ACKNOWLEDGMENTS

The author wishes to thank John Ness for excellent care of the birds. This study was supported in part by the Norwegian Research Council for Science and Humanities.

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EDITOR'S COMMENTS

With this issue we initiate what I hope will become a regular feature of *The Auk*: a "Commentary" section. This is intended to provide a forum for brief essays or points-of-view on various matters of interest to ornithologists, or exchanges relating to papers published in recent issues of *The Auk*. In this issue Harold Mayfield addresses some aspects of the role of amateurs in ornithology, speaking from the position of an amateur who has made exceptional contributions to the field. Harold prepared this essay at the invitation of the Editorial Board, and we have invited several other individuals to prepare such personal statements on several other topics of current interest. But "Commentaries" may be contributed as well as invited. If you have strong feelings about some matter of importance in ornithology and wish to submit an essay or position statement, please do so. Alternatively, we would welcome suggestions of topics that you would like to see addressed, and the names of individuals you think the Editorial Board might consider inviting to prepare such a Commentary. The ground rules are these: (1) contributions should generally not exceed 750 words in length, and (2) all contributed material will be reviewed by the Editorial Board, which will advise the Editor of the acceptability of the material.

One other matter: In the January 1978 issue of *The Auk* I drew attention to the rather lengthy time lag between acceptance of manuscripts and their final publication in *The Auk* (17.5 months, on the average, for the papers in that issue). Reducing this time lag has been a major objective during the past year, and we have now lowered it about as far as is practical. The average time lag between acceptance and final appearance of articles in this issue (taking into account the actual date of issue of the "January" issue) is 5.6 months; the time lag for Short Communications is about a month longer.

Because of the large number of inquiries concerning the late delivery of the October *Auk* and therefore of the 1979 dues notices, we feel that we should provide some explanation for this delay. First, the transfer of the editorial offices from Oregon State University to the University of New Mexico in late summer created numerous delays, particularly involving the completion of the index for volume 95. Second, after the October issue was sent to press we experienced additional delays at Allen Press, because their publishing schedule is tight, and material for *The Auk* now had to be worked into other scheduled jobs. Third, because our turn-around time for publication has been reduced significantly, some delays were experienced when some authors did not return galley proofs as expeditiously as possible.

The print order for the 1979 dues notices was submitted to Allen Press early in the Fall and the dates for submission of dues were established to account for a possible delay in publication. Unfortunately, we did not anticipate the magnitude of the delays. We apologize for the inconvenience this has caused the membership, and we trust that in paying dues members will have used their discretion in remitting the appropriate amount.

We should also note that this issue of *The Auk* was delayed for some of the same reasons noted above, but also to allow sufficient time for members to pay their dues and thus enable the Treasurer to establish the press run for the January *Auk*. We intend to return to a regular publication schedule as quickly as possible.—JOEL CRACRAFT, *Treasurer*; JOHN WIENS, *Editor*.

NESTLING MORTALITY AND THE ADAPTIVE SIGNIFICANCE OF EARLY LOCOMOTION IN THE LITTLE BLUE HERON

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ABSTRACT.—I studied the reproductive biology and ecology of the Little Blue Heron (*Florida caerulea*) from 1975 to 1977 in Mississippi and Alabama. Incubation began after the second egg was laid, producing an asynchronous hatching of later eggs. The primary cause of nestling mortality was starvation of late-hatching chicks because of their failure to compete successfully with older siblings for food. Late-hatching chicks grew as fast as early-hatching chicks when older siblings died. Nestlings from broods manipulated so that young were even-aged grew as fast as older chicks from uneven-aged broods. This suggests that the ability of adults to distribute food equally among nestlings, not the amount of food delivered, limited the growth of late-hatching chicks.

The developmental pattern of nestlings was dominated by the rapid growth of the feet and by the development of ambulatory skills by the age of 13 days. When the young were older than 19 days, both adults foraged away from the nesting area, returning to feed young during the day and brood at night. By this time the nestlings had developed thermoregulation, ambulatory abilities, and an escape response. Nestlings were essentially free of parental care after 21 days of age except for feeding, which continued until fledging at approximately 50 days of age. The rapid development of motor skills effectively shortens the nestling period from 56 to 19 days. I attribute the rapid development to an increased rate of food delivery (by releasing both adults to forage away from the nesting area), to increased food consumption (a consequence of sibling competition during feeding), and to decreased predation (by early maturation of the escape response). The pattern of nestling development is viewed as a preadaptation to large body size, as it allows a longer nestling period (= increased time for growth) than would be expected if young were dependent on adults for protection from predators until fledging. *Received 27 September 1977, accepted 11 October 1978.*

PATTERNS of avian development have received considerable attention (see Ricklefs 1968, 1973, 1977 for reviews) and some generalities can be made. Because of relatively high nestling mortality rates and efficient use of food resources, selective pressures have generally operated to shorten the nestling period by increasing growth rates to a physiological maximum (Ricklefs 1969). However, for large species reproductive strategies are complicated because of the long nestling periods and low growth rates correlated with increasing body size (Dunn 1975). Clearly there can be multiple solutions for increasing fitness under the conflicting demands of minimizing the duration of the nestling period and increasing body size. Decreased clutch size, low fledging weight, precocial development, and other morphological and behavioral characteristics are in part adaptations to shorten the nestling period.

In general, studies on avian reproductive strategies have treated the brood as a unit and have been concerned with the question of how selection has acted to maximize the return on parental investment. Because of this, the adaptive significance of nestling development has frequently been interpreted in terms of nest productivity rather than in terms of individual survival. Trivers' (1972, 1974) proposal that selection frequently results in parent-offspring conflict and sibling strife has helped stimulate a more refined theory of reproductive strategies (e.g. Brockelman, 1975,

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Graul et al. 1977). Still, only recently have these concepts been applied to data on nestling development (O'Connor 1977a, 1977b, 1978; Werschkul and Jackson in press).

In this paper I report on reproductive success, nestling behavioral and physical development, and parent-young interactions in the Little Blue Heron (*Florida caerulea*). I address these questions: (1) What are the causes and rates of nestling mortality? (2) Are the chances of survival equal for all young within a brood with respect to position in the hatching sequence? (3) In what way is the pattern of behavioral and physical development adaptive to the nestling environment? (4) Finally, are adaptations of the young to sibling competition limiting nest productivity?

METHODS

Observations were made from 1975 to 1977 on the reproductive biology and ecology of the Little Blue Heron in two mixed-species heronries in Mississippi and Alabama (for details on the heronry structure and species composition see Werschkul 1977a, 1977b). I made all observations in areas where Little Blue Herons nested without other species of wading birds. I tried to minimize the adverse effects of my presence on the nesting birds by dividing the heronry into sections and making observations in different sections within the heronry for the different aspects of the study, e.g. the areas where observations on nesting success were made were distinct from areas where nestling growth measurements were made. When data collecting required observations from the heronry for periods longer than 30 min, I restricted my activities to 0700–1000 on days with moderate temperatures and without heavy rains or high winds.

I visited nests every 2–7 days and measured nesting success as the number of viable eggs and/or young. I viewed the contents of each nest by using a mirror attached to a pole (Parker 1972). Nest visits continued until the young were 4 weeks old, when their ability to fly short distances prohibited accurate counts of the number of young. At 14 days young could climb out of the nest when I approached; if I was unsure of the exact number of young, I would record the nest as active but with an unknown number of young. I collected data on the relationship between position in the hatching sequence and nestling mortality from observations on nests used for growth measurements. Observations on the causes of chick mortality were made during nesting success measurements and from blinds.

I marked nestlings from 46 nests by marking their legs with permanent ink at hatching and later tagging them with USFWS bands and color bands. These nestlings were visited every 2–7 days and the following measurements made: body weight (to the nearest g on a triple beam balance), bill length (the upper mandible from the tip to base as marked by the feathers on the forehead), wing length (from the carpal-ulna junction to the distal end of the phalanges excluding feathers), tarsus length (from the junction of the tibiotarsus with the tarsometatarsus to its junction with the phalanges), and digit length (the middle toe from the webbing just below its junction with the tarsometatarsus to the distal end excluding the nail). I estimated adult sizes from measurements of museum specimens (N = 17) at Mississippi State and Louisiana State universities.

I manipulated 5 broods of size 3 and 10 broods of size 4 during the 1977 breeding season so that the young were even-aged. Pipped eggs and young under the age of 3 days were removed from nests, matched according to developmental progress, and placed back into other nests where eggs and/or young had been previously removed. I weighed these nestlings every 2–7 days.

The timing of endothermy was estimated by removing chicks from their nests, placing them individually in an incubator set at 25°C or 10°C, removing them after a 5- or 10-min period, and recording body temperature to the nearest 0.5°C by inserting a thermometer down the nestling's throat to the pectoral girdle. Data were analyzed by relating body weight to temperature.

Behavioral development of Little Blue Herons was studied during approximately 600 h of field observations. Blinds were constructed atop scaffolding, allowing me to view nests at close range and to identify individuals by differences in body markings. These observations were supplemented with experiments similar to those designed by Emlen (1963) for Herring Gull (*Larus argentatus*) chicks. A 46 × 61-cm piece of plexiglass was fixed as the top of a table at a height of 92 cm and this apparatus was placed outside the heronry. The plexiglass platform had a portion of the gummed paper covering removed to provide a "visual cliff" (see Emlen's Fig. 3, 1963). Prior to testing, birds were taken from their nests, hooded, transported to the platform, and placed on and parallel with the line dividing the paper-covered portion and the transparent part of the plexiglass. I would then lie underneath the platform so that I could view the bird from below and perform these tests: 1) *visual cliff*—the response of the nestling to the visual cliff; 2) *push resistance*—I placed the chick on the middle of the platform and slowly pushed it with a transparent shield towards the edge; 3) *edge withdrawal*—I placed the chick 5 cm from the edge of the platform; and 4) *jump-escape*—I withdrew from under the platform, walked 15 m from the platform, turned, waited 5–10 s, and ran slowly (ca. 2 m/s) back to the platform waving my arms. I scored my observations for these tests as: *visual cliff* test—no response (0), head turn (1), body turn (2); *push resistance* and *edge withdrawal* tests—no response (0), body turn (1), backwards push (2); *jump-escape* test—no response (0), jump during arm waving approach to platform (1), jump during initial testing or during withdrawal from platform (2). I repeated each test three times per chick unless the escape response made this impossible. Chicks were aged by bill length and grouped into age classes of 3-day intervals for analysis.

Data were analyzed using the SPSS Statistical Package (Nie et al. 1975) for descriptive statistics. I compared population parameters with the aid of the BMD Statistical Package (Dixon 1974). Analysis of covariance designs were treated as a regression problem with "dummy" variables (Neter and Wasserman 1974) and analyzed with an on-file program (LLS-SELECT) at the Mississippi State University Computer Center using the Linear Least Squares procedure of Daniel and Woods (1971) and the subset selection procedure of Lamotte and Hocking (1970). I calculated growth rates of body parts using Ricklefs' (1967) technique from data on the first- and second-hatched nestling.

RESULTS

Nestling mortality.—Of 926 nests observed during the 3-year study, 164 (17.7%) were deserted before the young reached the age of 28 days. Of these 164 desertions, 146 (89.0%) were abandoned before hatching was completed (Fig. 1). No nests with young over the age of 28 days were deserted. Of 18 pairs that deserted after hatching, 12 deserted after predation of juveniles, 4 deserted after loss of nest support, and 2 deserted from unknown causes. Predation on juveniles was nocturnal and concentrated in one area of the heronry. Only part of the nestlings were eaten, usually the head, suggesting that the predator was probably an owl or small mammal (J. Ogden pers. comm.).

Partial brood mortality was more common than loss of the entire brood. Of the sample population of 3,750 eggs, the loss of young because of entire brood failure was 664 (17.7%) while the loss of young from partial brood mortality was 1,031 (27.5%) (Fig. 2).

In general, incubation began after the second egg was laid, producing an asynchronous hatch (Table 1). The most common pattern of hatching was 2 eggs on day 1 followed by later hatchings every 1–2 days. Brood reduction generally resulted from the death of late-hatching chicks. Differences among mortality rates by position in the hatching sequence are significant ($\chi^2 = 20.87$; df = 4; $P < 0.01$)—mortality increased with each later position in the hatching sequence (Fig. 3). The primary reason for the higher mortality among late-hatching chicks was their failure to compete successfully with older siblings for food. This resulted in lower growth rates and eventual starvation (Fig. 4, Table 2). The growth rates of late-hatching chicks, however, were affected by the survival of older siblings. When early-hatching chicks survived, younger siblings apparently could not compete successfully for food, grew slowly, and eventually died. When older siblings died, however, late-hatching chicks did compete successfully for food, grew nearly as fast as early-hatching chicks, and survived well.

Death of early-hatching chicks was relatively uncommon in successful nests (Fig. 3). Among the first-, second-, and third-hatched, 20% (N = 83) failed to survive past the age of 19 days. The six of these nestlings that I was able to locate had died after falling from the nest, either injuring themselves or being unable to climb back to the nest (see also Meanley 1955).

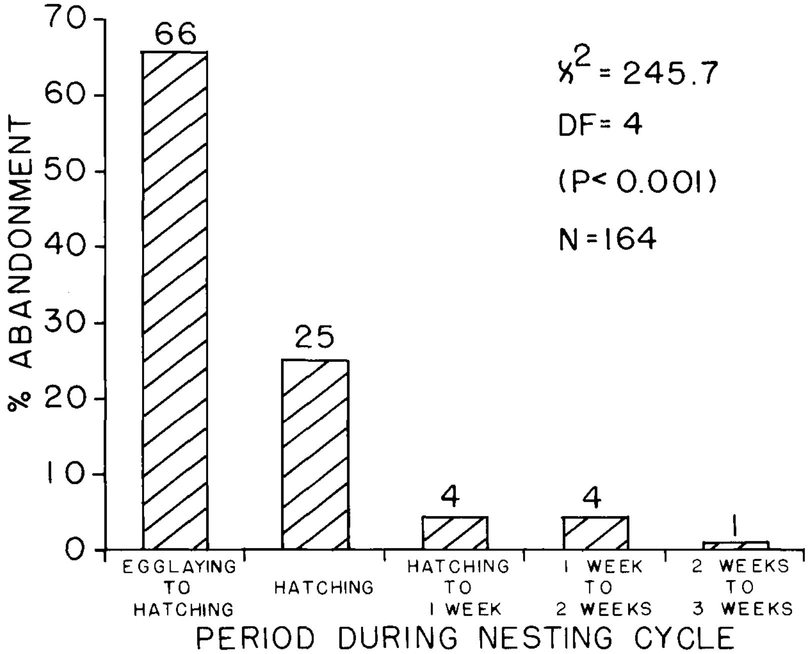

Fig. 1. Nest desertions by Little Blue Herons through the nesting cycle. Numbers above bar graph are percentage values.

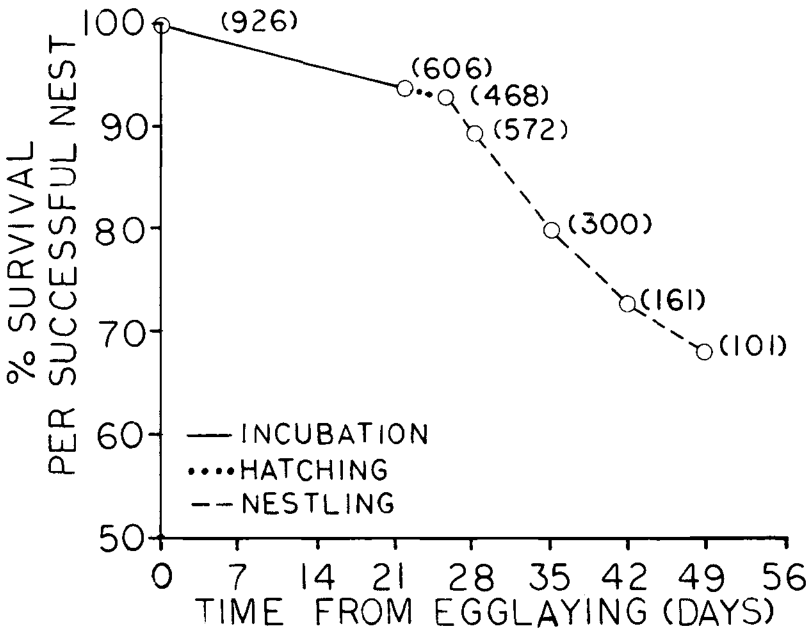

Fig. 2. Survival of Little Blue Heron eggs and nestlings per successful nest. Numbers in parentheses are sample sizes.

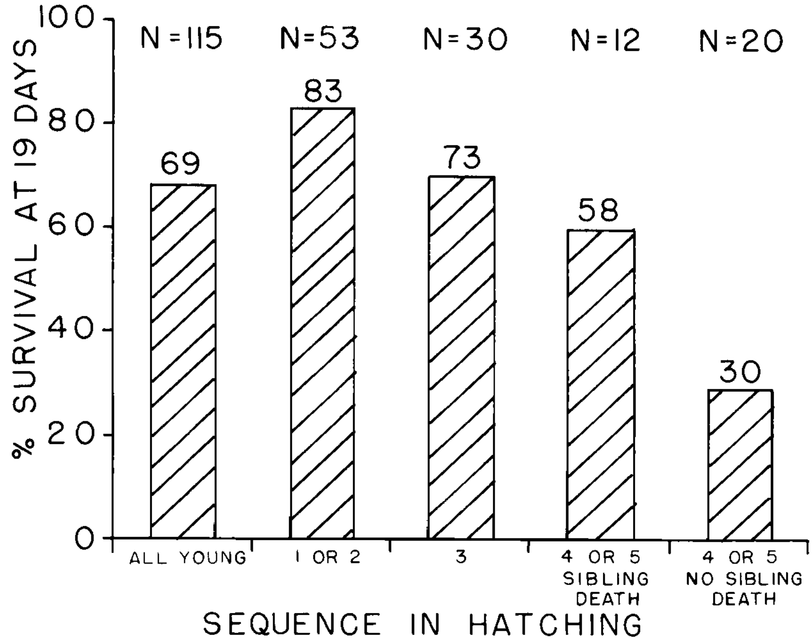

Fig. 3. Survival of Little Blue Heron nestlings by position in hatching sequence. Later hatchings (4 or 5) are divided into groups with and without death of older siblings. Numbers above bar graph are percentage values.

Because of the apparent effects of sibling competition for food, I was curious as to whether differences in growth rates among early- and late-hatching chicks resulted from insufficient food delivered to the nest to support all chicks or from an uneven distribution of food among nestlings. To distinquish between these alternatives, I manipulated 5 broods of size 3 and 10 broods of size 4 so that the young were even-aged. I assumed that young in even-aged broods had competitive abilities more nearly equal than young in asynchronously-hatched broods. Hence, if the growth rates of even-aged nestlings were lower than older chicks of uneven-aged broods, then the amount of food delivered limited the growth of late-hatching chicks. However, if the growth of even-aged chicks was equal to that of older chicks of uneven-aged broods, then food distribution limited the growth of late-hatching chicks. The growth rates of nestlings from even-aged broods of size 3 and 4 were not significantly different from those of the older chicks of uneven-aged broods (Fig. 4 and Table 2).

Table 1. Hatching sequence of Little Blue Herons.

Sequence in hatching	N	Time difference (days) in hatching from 1st hatched ($\bar{x}$ ± 1 SD)	Range (days)
2nd	34	0.59 ± 0.61	0–2
3rd	32	1.78 ± 0.91	1–4
4rd	18	2.67 ± 1.19	1–6
5th	8	3.38 ± 1.19	2–5

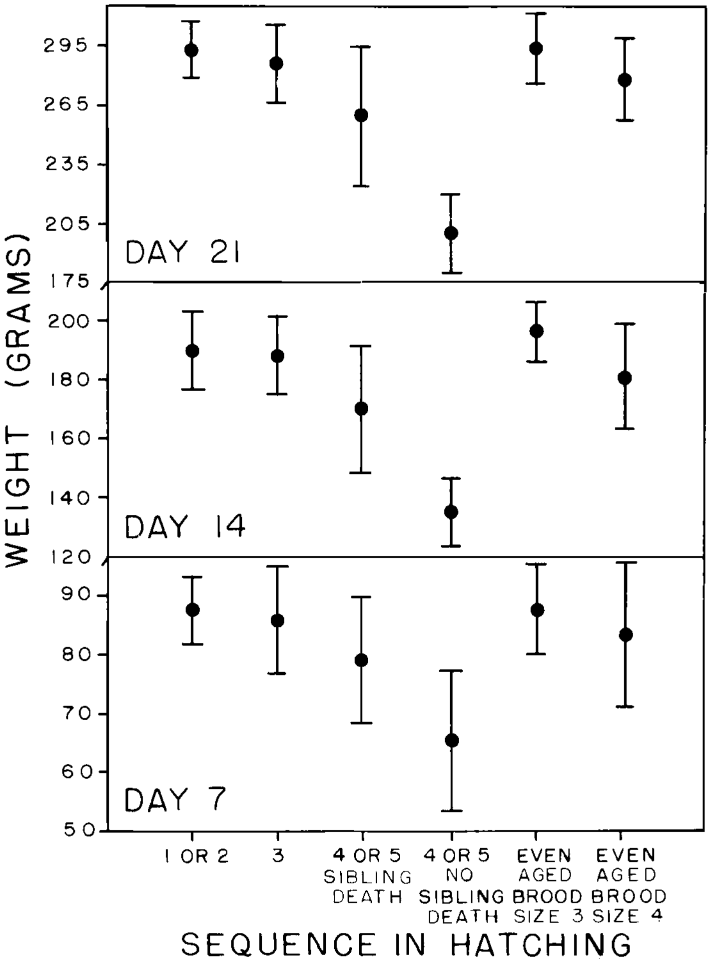

Fig. 4. Growth of nestling Little Blue Herons by position in hatching sequence for asynchronously-hatched broods and even-aged broods. Mean and 95% confidence interval are plotted. Regression equations for each group are given in Table 2. Division of later hatchings (4 or 5) same as in Fig. 3.

These results suggest that adults are unable to distribute food evenly among nestlings, rather than the amount of food delivered limiting the growth of late-hatching chicks.

Nestling development.—Nestling Little Blue Herons showed differential growth of body parts (Fig. 5), with a remarkably rapid development of the feet during the first 2 weeks. Four of the growth variables (digit, weight, wing, and tarsus) conform to the logistic curve and one (bill) to the Gompertz curve when data are fitted by Ricklefs' (1967) method (Table 3). Comparing the times required for 90% of the nestling's growth (t_{10-90} values), the digit shows the highest growth rates, followed by the wing, tarsus, and bill.

Endothermy was reached at a weight of about 225 g (age 16 days) during cold treatments (10°C for 10 min) and a weight of 160 g (age 11 days) for moderate temperatures (25°C for 5 min) (Table 4). However, these estimates should be con-

TABLE 2. Results of analysis of covariance comparing nestling growth vs. age, position in hatching sequence, experimental manipulation of hatching sequence, and death of early-hatching chicks.

Source	df	Mean sum of squares	F-value
Regression	6	360975.3	773.1**
Error	336	466.9	
Total	342		

Variables	B	STD error	*t*-value
X_1	14.82	0.25	59.2**
X_1X_2	0.07	0.38	0.2
X_1X_3	−1.06	0.94	1.1
X_1X_4	−0.03	0.32	1.0
X_1X_5	−1.84	0.48	3.8**
X_1X_6	−4.98	0.85	5.9**

$Y = 27.4 + 14.8X_1 + 0.07X_1X_2 - 1.06X_1X_3 - 0.03X_1X_4 - 1.84X_1X_5 - 4.98X_1X_6$
where: y = weight (g); X_1 = age (days) − 3; X_2 = 1 if even-aged, brood size 3, 0 otherwise; X_3 = 1 if even-aged, brood size 4, 0 otherwise; X_4 = 1 if 3rd hatched, 0 if otherwise; X_5 = 1 if 4th or 5th hatched, death of older sibling, 0 otherwise; X_6 = 1 if 4th or 5th hatches, no death of sibling, 0 otherwise.

** ($P < 0.01$).

sidered maximal, or what Dunn (1975) calls the *physiological* age of endothermy. The *effective* age of endothermy is generally earlier because of the synergistic effects of exogenous factors on body temperature. Depending on the weather and the age of nestlings, adult Little Blue Herons will brood or shade, nestlings will huddle or disperse, and individuals will sunbathe or gular-flutter as means of conserving or dispersing body heat (see also Bartholomew and Dawson 1954, Hudson et al. 1974). By the age of 11 days, nestlings were individually able to thermoregulate from 0800 to 2000 except during adverse weather. An adult brooded the young at night, during morning hours, and during adverse weather until the age of 19 days.

The rapid development of the feet and the timing of endothermy coincided with the behavioral changes needed for movement from the nest. After day 12, nestlings did not avoid a visual cliff and the beginnings of escape behavior were apparent (Fig. 6). By day 17 the results for the visual cliff and escape-jump tests were nearly reversed from day 3. The results of the push resistance and edge withdrawal tests reversed in a similar, though not so clear, manner.

The Forward (= threat) display is the common stereotyped behavior used by herons during territorial encounters (Meyerriecks 1960). Some components of the Forward display were evident in nestling Little Blue Herons at age 5 days (e.g. bill jabbing, head and neck held erect) though other components (e.g. feather erection, wings spread) did not appear until the age of 13 days. By the age of 18 days, although there were still obvious size differences between adults and young, Forward

TABLE 3. Growth parameters for Little Blue Herons, calculated by the methods of Ricklefs (1967).

				Growth rate	
Variable	Growth form	Asymptote	Ratio to adult	*K*	t_{10-90} (days)
Weight	Logistic	300 g	1.16	0.258	17.2
Digit	Logistic	58 mm	1.08	0.388	11.3
Wing	Logistic	74 mm	1.03	0.209	21.1
Tarsus	Logistic	79 mm	1.18	0.133	28.8
Bill	Gompertz	62 mm	1.26	0.088	31.8

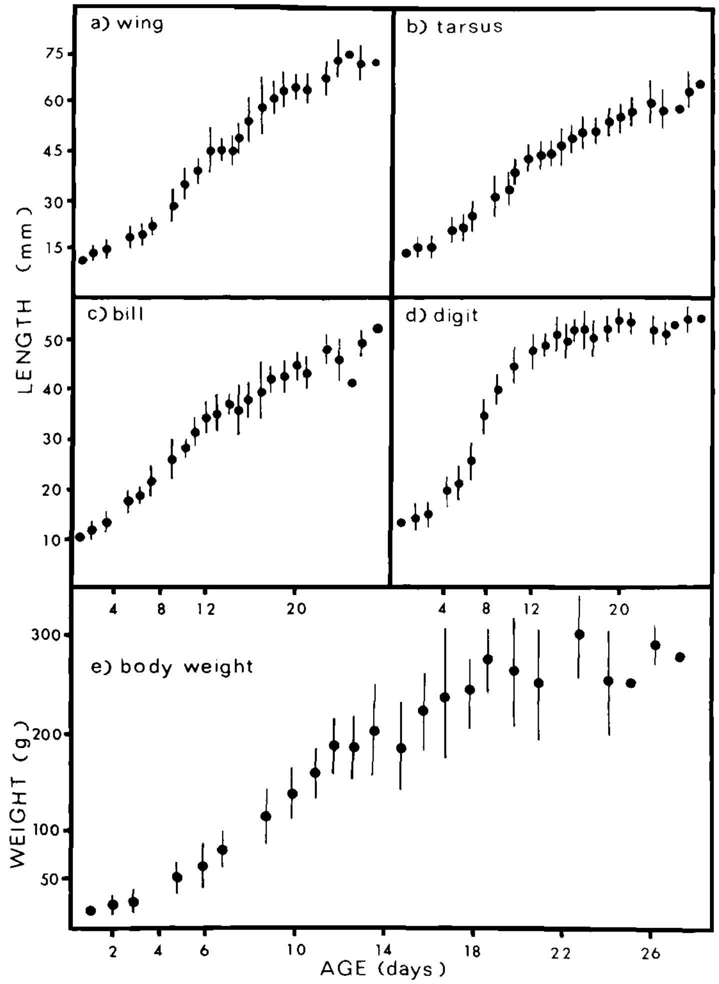

Fig. 5. Growth curves of body parts of nestling Little Blue Herons. Mean values ± 2 SD are shown.

TABLE 4. Results of analysis of covariance comparing body temperature vs. body size, temperature of chamber, and time in chamber.

Source	d.f.	Mean sum of squares	F-value
Regression	5	158.53	142.0**
Error	212	1.14	
Total	217		
Variables	B	STD error	*t*-value
X_1	5.18	0.35	14.7**
X_2	−2.79	0.79	3.5**
X_3	4.64	0.79	5.9**
X_1X_2	0.77	0.41	1.9*
X_1X_3	−1.82	0.41	4.1**

$Y = 25.7 + 5.18X_1 - 2.8X_2 + 4.64X_3 + 0.8X_1X_2 - 1.82X_1X_3$

where: Y = body temperature (C°); $X_1 = \log_{10}$ (body weight [g]); X_2 = 1 if chamber temperature 10°C, 0 if chamber temperature 25°C; X_3 = 1 if 5 min, 0 if 10 min.

** ($P < 0.01$).
* ($P < 0.05$).

displays by nestlings were usually successful in defending the nest site (see also Werschkul 1977c).

I assessed the responses of nestling Little Blue Herons to predators by observing their reactions to me during weighings. From the age of 1 to 6 days nestlings showed no apparent escape or protection responses to removal from the nest or handling. After the age of 7 days, Forward displays were frequently given when I approached and nestlings attempted to stab my hand with their bills when I reached into the nest. Nestlings first tried to escape at day 10, though they were easy to catch until day 14. After the age of 18 days, success at capturing nestlings depended on the location of the nest, the time of day, and the age of the chicks (see also McVaugh 1973). These observations parallel the relationship between nestling's age and predation rate. For the 12 nests suffering predation after hatching, 7 had an oldest nestling of 7 days or younger, 4 had an oldest nestling between the ages of 8 and 14 days, 1 had an oldest nestling between the ages of 15 and 21 days, and none occurred in nests with young older than 21 days.

Parent-young interactions.—I recorded the distance from the nest to parent between 1200 and 1300 through the nesting cycle (if a feeding was in progress the observation was discarded). The pattern of parent attentiveness after hatching was: brooding from day 1 to 10, one adult near the nest from day 11 to 18, and both parents absent from the nest after day 18 (Table 5).

After the age of 10 days young were fed once per adult visit. Before the age of 10 days young were fed more than once per adult visit. I assume adults deliver about the same amount of food to the nest on each visit and the multiple feedings before the age of 10 days represent one way adults provide food to young to match their ability to utilize and store food. Based on this assumption, I equate parental exchange rates, defined as the time between adult visits to the nest between 0600 and 2100, to feeding rates (Fig. 7). Parental exchange rates decreased after day 5, were nearly halved by day 11, and remained around 100 min until day 21. After day 21 they decreased until day 32, when quantitative observations stopped.

Feeding behavior changed with nestling development. During the first week food was regurgitated by adults into the nest where nestlings picked it up. Nestlings first started to grab the adult's bill at day 3 and this behavior was commonly observed after day 5. Bill grabbing and direct transfer of food predominated after day 7. At the age of 13 days chicks began to follow adults and were fed away from the nest. The change in feeding behavior from regurgitation into the nest, to bill grabbing, to active chase accentuated the impact of sibling food competition because of the nestlings' age differences. I did not quantify differential feeding of young, though I observed that older siblings were first to be fed and not all chicks were fed each feeding (see also Blaker 1969).

The young were capable of gliding flight after day 28 and sustained flight after day 35. After the age of 40 days, feedings were rare—a maximum of two per day. Adults continued to feed young until the eighth week, when they fledged. I was not always able to observe the exact date of fledging. However, I did note differences in fledging age of 9 days between nests and, in general, young from early-nesting birds stayed in the heronry longer than young from late-nesting birds.

Adult Little Blue Herons did not leave the nest when small avian egg predators such as Common Crows (*Corvus brachyrhynchos*) and Blue Jays (*Cyanocitta cristata*) entered the heronry although they did leave the nest when larger predators, like Red-tailed Hawks (*Buteo jamaicensis*), appeared. I found several partially-eaten

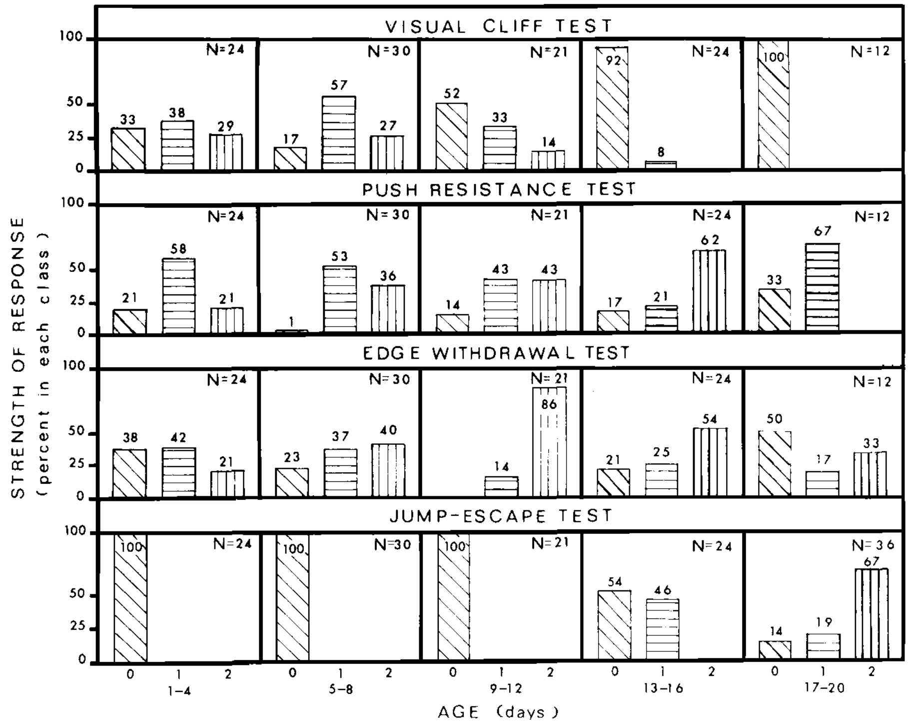

Fig. 6. Behavioral development of nestling Little Blue Herons. Numbers above bar graphs are percentage values.

adult Little Blue Herons on their nests after what I think was a raid by an owl. However, based on observations of adult behavior during the day, I doubt if the adults were protecting nestlings, but more likely were victims of nocturnal attacks. In general, herons have not been observed to defend the nesting area against large predators (Milstein et al. 1970, Krebs 1974, Werschkul 1977c), though they will defend against other herons and small egg predators (Werschkul 1977c, Burger 1978).

TABLE 5. Parent distances from the nest as a function of the age of the oldest nestling.

		Parent behavior (%)			
Age (days)	N	Brooding[a]	On nest[b]	Near nest[c]	Away from nest[d]
1–3	23	87.0	13.0	0.0	0.0
4–6	25	84.0	16.0	0.0	0.0
7–9	14	83.4	16.6	0.0	0.0
10–12	17	11.8	47.1	41.1	0.0
13–15	11	9.1	27.3	54.5	9.1
16–18	17	5.8	5.8	47.1	41.1
19–21	7	0.0	0.0	28.6	71.4
22–24	5	0.0	0.0	0.0	100.0
>25	23	0.0	0.0	0.0	100.0

[a] Includes shading.
[b] Within 1 m of nest.
[c] Between 1 m and 10 m of nest.
[d] Greater than 10 m from nest.

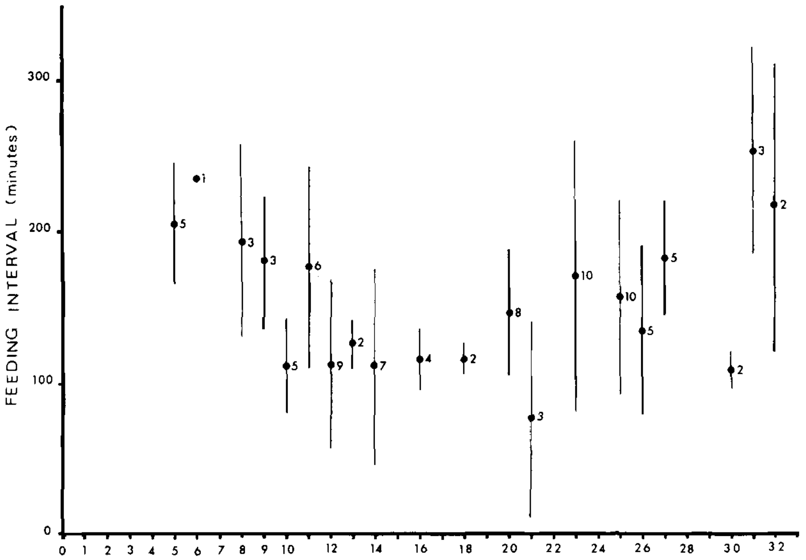

Fig. 7. Plot of feeding intervals vs. the age (days) of the oldest chick. Mean ± SD are shown. Numbers to the right of mean are sample sizes. Age is that of first-born chick.

Interactions among siblings.—I never observed nestlings to push younger siblings out of the nest (*contra* Meanley 1955). However, siblings would fight with one another before and after feedings, attempting to gain access to adults. At this time, nestlings occasionally fell from the nest site though they were usually able to climb back. It is probable that these exchanges between siblings represent one way a dominance order is established (D. Mock pers. comm.). A second form of interactions among siblings appears to me to be a form of play (Ficken 1977), where nestlings exchanged bill jabbing and grasping (possibly ritualized as Bill Duel in adults, see Mock 1976). I have observed minor injuries to younger siblings during these exchanges. Hence, these exchanges among nest mates may reinforce a dominance system established during feedings as well as provide an opportunity for young to develop the motor skills necessary after fledging for feeding and defense.

Discussion

Parental care for nestling Little Blue Herons can be divided into three phases (following Milstein et al. 1970): brooding (ages 1–10), guardian (ages 11–18), and post-guardian (ages 19–56). Age is determined from the hatching of the first chick. During the post-guardian phase both adults forage away from the nesting area, returning to feed young during the day and roost at night. Adults are able to leave the nesting area when young are older than 19 days because of the development of thermoregulation, rapid growth of the feet and the concurrent emergence of terrestrial locomotory skills, and the early escape response of the young. Except for food, nestlings are essentially independent of adults after the age of 19 days. By effectively shortening the duration of nestling dependence on adults, the pattern of nestling development serves as a preadaptation to large body size by allowing a longer time period for growth. In terms of the Little Blue Herons' life history, and probably that of many other wading bird species, this developmental pattern is one way the evolutionary conflict between selection for larger body size and reducing the duration of the nestling period is resolved.

Still, it would be a mistake to confuse selective pressures for rapid nestling development with possible evolutionary advantages from the emergent properties of rapid nestling development. The pattern of nestling development in the Little Blue Heron has not evolved in response to selective pressures on adult size but rather in response to selective pressures on young. Failure of nestling motor skills, often grouped as "accidental death" (see Meanley 1955, Summerour 1971), accounted for 100% of the known mortality I observed among early-hatching chicks from nests that were successful in raising at least one chick. This suggests that selective pressures favoring early development of terrestrial locomotion are strong—the high risk reflects harsh penalties associated with delayed maturity. The most likely advantages of rapid development of locomotory skills by nestling Little Blue Herons are to increase food delivery by allowing both adults to forage simultaneously, to avoid predators, and to increase competitive abilities during feedings.

Food delivery.—The ability of adults to forage simultaneously during the post-guardian phase should allow an increase in food delivery to nestlings (Owen 1955, Siegfried 1972). My observations on feeding intervals (Fig. 7) do not support this idea. On the contrary, the time between feedings increased during the post-guardian phase in the Little Blue Heron. It is possible that the amount of food delivered per feeding increased during this phase, but if this phase were timed to allow an increase in food delivery, one would expect increased energy demands by nestlings. Instead, nestling weight is near asymptote by day 18 (Fig. 5e) and the expected energy demands, for birds with an adult size of Little Blue Herons (Ricklefs 1968), are probably just after t_{50} or at 12–15 days.

Adults might increase their intake of food during the post-guardian phase if their body reserves were depleted during the guardian phase when food delivery to nestlings was high. I observed male Little Blue Herons to fast during nest construction and egg-laying, apparently to protect against promiscuous behavior by neighboring birds (Werschkul in prep.). Fasting, or a reduction in food consumption by adults during the guardian phase, would allow food delivery to parallel the energy needs of nestlings. Then with the emergence of chick independence at 18 days and the reduction in nestling energy demands, adults could increase their own intake. In this way, the development of early locomotory skills could increase food delivery to nestlings. However, this increased food delivery would be a result of rapid development rather than a cause.

Predator avoidance.—It is unreasonable to expect adult Little Blue Herons to protect nestlings against large predators since they are iteroparous and other types of parental care are necessary for the chick's survival (Skutch 1971). For this reason there are clear advantages for nestlings to develop ambulatory skills and an early escape response. The development of the feet and locomotory skills occurs by the end of the guardian phase and correlates with the emergence of an escape response at 13 days. Even during the guardian phase adults protect nestlings against other herons and from thermal stress, but not from large predators. The development of terrestrial locomotion decreases the vulnerability of nestlings to large predators from 30 days (age of first flight) to 15 days. Early development of ambulatory skills among nestlings dependent on adults for food is common when they are liable to predation

(Welty 1975) and there can be little doubt one of the ultimate selective advantages for the rapid development of the feet and escape response by Little Blue Herons is a decreased exposure to predators.

Sibling competition.—Nestling Little Blue Herons are active in obtaining food from adults by bill grabbing after day 5 and by following adults after day 13. These changes in feeding behavior allow greater monopolization of food, which in turn, intensifies sibling competition: the older and more mobile young are fed more often, the younger and less developed are fed less often. My study indicates a major cause of brood reduction is starvation, particularly of the youngest chick (see also Blaker 1969, Milstein et al. 1970, Siegfried 1972). Hence, natural selection should favor increased competitive abilities.

Other factors.—Additional factors probably selecting for early development of locomotory skills are restrictions on nest size and support of older and larger nestlings (W. Graul pers. comm.) and the frequent loss of nests late in the nesting cycle from construction deficiencies, loss of supporting structures, stick piracy, and/or poor weather (Werschkul 1977c, 1977d).

Concluding Remarks

In general, selective pressures on juveniles and on adults can differ and, in certain situations, may be in conflict. Selection for rapid nestling development and large adult body size is one example of this. For the Little Blue Heron, the resolution of this conflict appears to be the differential development of the physical and behavioral tools necessary for fledging (e.g. thermoregulation, locomotion, feeding). As a result, the period of nestling dependence (excepting food) has been reduced to 19 days, although the young continue to mature and do not "fledge" until day 56. There are probably numerous examples of this general type of conflict in avian evolution. Importantly, when selective pressures on juveniles and adults conflict, then adaptations by juveniles will constrain the direction of adaptations by adults, i.e. adaptations by juveniles are selective pressures on adults and vice versa.

Asynchronous hatching has traditionally been interpreted as one way parents adjust brood size to food availability (Gibb 1950, Owen 1955, Lack 1956, Siegfried 1972, Hussell 1972, O'Connor 1977b). When food availability is high, all young survive; when it is low, only the youngest die. My observations on Little Blue Herons suggest that late-hatching chicks survive only when an older sibling dies. In this way, late-hatching chicks are a form of insurance for adults against the death of early-hatching chicks as well as a way that adults can adjust brood size to food availability. Though never explicitly stated, the hypothesis that asynchronous hatching acts to adjust brood size to food availability assumes that when food is abundant chicks will consume only what they need and all chicks are fed. My observations on the growth of even-aged broods do not support this assumption and suggest that the ability of adults to distribute food evenly, not food availability, limits the growth of late-hatching chicks. It is possible that even-aged broods beg more than asynchronously-hatched broods and because of this are fed more (D. Mock pers. comm.). If this is so then the growth of even-aged broods may not be comparable with the growth of asynchronously-hatched broods.

In those species where asynchronous hatching, brood reduction, and sibling competition have been documented (Lack 1954, Emlen 1956, Ricklefs 1965, Parsons 1970, 1975), investigators have either ignored adaptive responses by nestlings or have looked at behavioral adaptations (Meyburg 1974). Morphological adaptations improving competitive abilities among siblings have recently been recognized (O'Connor 1977a) and no doubt are widespread. An important question raised by my observations on Little Blue Herons is in what way do these adaptations to sibling competition influence nesting success? Unfortunately, before the results presented here can be applied convincingly to this problem observations are needed on: (1) growth during years of differing food availability, (2) parental feeding effort and brood size, and (3) brood position, fledging weight, and post-fledging survival. Still, the success of even-aged broods suggests to me that the question of how parents minimize the adverse effects of adaptations by nestlings to sibling competition is of interest and may prove fundamental to understanding how parents use sibling competition to maximize their genetic contribution. Further, the evolution of reproductive strategies is influenced by factors other than high fertility (Brockelman 1975), and fertility may be lowered when unpredictable food resources during the nestling period create a high competitive environment among siblings.

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TERRITORY SIZE AND COMPOSITION IN RELATION TO RESOURCE ABUNDANCE IN LAPLAND LONGSPURS BREEDING IN ARCTIC ALASKA

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ABSTRACT.—The relationship of size and composition of breeding territories to productivity of arthropod prey in the component habitats was studied in a population of Lapland Longspurs (*Calcarius lapponicus*) nesting on arctic tundra near Barrow, Alaska. Territories are established quite synchronously around the time of snow melt in early June, before their resource value can be assessed directly. Twenty territories averaged 1.76 ± 0.46 (SD) ha in area. Large territories contained nearly equal amounts of wet, mesic, and dry habitat. Small territories contained less wet and dry habitat, but a much larger proportion of mesic habitat. Territory size was positively correlated with prey density in the year of measurement, due to an unusual abundance of prey in the relatively unpreferred wet habitat. Territory size was inversely correlated with indices of resource density based upon 3 and 7 years of data on prey productivity in the various habitats. These indices show average or expected prey density. The inverse correlation is increased when prey biomass data are weighted for prey selectivity by longspurs. No relationship between territory size and reproductive success was seen. *Received 25 April 1978, accepted 1 November 1978.*

THE relationship of territory size to resource abundance in solitary nesting species has been the subject of numerous reports and reviews (e.g. Stenger 1958, Brown 1964, Schoener 1968, Orians 1969, Holmes 1970, Cody and Cody 1972, Wiens 1973, Gill and Wolf 1975, Verner 1977, MacLean and Seastedt 1979). The contention that territory size is related to food resources is now well founded in theory, although far from universally accepted. Lack (1954, 1966) observed that year to year variation in territory size is frequently not correlated with fluctuations of food availability; he took this to indicate that territory size has probably not evolved to assure an adequate food supply for reproduction of the territory holder. Hildén (1965) suggested that birds may respond to proximate factors related to food abundance. If so, territory size should conform to expected food availability, but not necessarily to that found in any given year. Unfortunately, the long term data on food abundance required to test Hildén's hypothesis are rarely collected.

The present study concerns intra-population variation in the size of territories of Lapland Longspurs (*Calcarius lapponicus*) breeding on arctic tundra. We compare the size and composition of territories with habitat productivity measured in the same season (1975), and over a sequence of seasons taken to indicate average conditions.

STUDY AREA

The study site near Barrow, Alaska (71°18′N, 156°40′W), was about 2 km SE of the Naval Arctic Research Laboratory and encompassed an area of several km^2 centered on "The Beach Ridge." Extensive data exist on the breeding ecology of Lapland Longspurs (Custer and Pitelka 1977) and other insectivorous birds (Pitelka, 1959, 1974; Holmes, 1966a, b, 1970; Holmes and Pitelka, 1968; Pitelka et al., 1974; Safriel,

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1975) near Barrow. The insect prey of terrestrial birds have been identified, and the distribution and abundance of terrestrial arthropods in various habitats have been documented (MacLean and Pitelka 1971, MacLean 1973, Clement 1975, MacLean et al. 1977).

A description of the Barrow tundra ecosystem was given by Bunnell et al. (1975). The vegetation has been described by Britton (1957) and Webber (in press). Lowland sites are strongly dominated by the grass *Dupontia fischeri* and the sedges *Carex aquatilis* and *Eriophorum angustifolium*. Better drained sites support prostrate willows (*Salix rotundifolia, S. pulchra, S. phlebophylla*) and various forbs (e.g. *Saxifraga* spp., *Potentilla hyparctica*) mixed with grasses and sedges. The area shows little large scale topographic relief; microtopographic features are a complex of drained and undrained meadows, old beach ridges, and a variety of polygonal forms.

The Barrow area supports a variety of wader species, but longspurs are virtually the only passerine species breeding on the tundra (Pitelka 1974). Longspurs arrive at Barrow during the last week of May when the tundra is almost completely snowcovered. Melt-off takes approximately 3 weeks, and daily mean temperatures do not go above freezing until about 11 June. The snow is gone by 20 June; however, fresh snow can fall at any time during summer.

METHODS

Territory delineation.—Territorial males were live-trapped and marked with U.S.F.W.S. leg bands and 1–3 colored plastic bands. Most males on the study area were banded and individually recognizable. Unbanded males were identified by flight behavior, site specificity, and territorial song.

Display activities were used to delineate territories. Longspur displays consist of circular flights interspersed with glides accompanied by song. Display flights usually end at an elevated or snow-free spot on the tundra. These landing sites were marked with color-coded flags and distances between markers were later measured with a surveyor's transit. All undisputed landing sites and areas between outer display points were considered the exclusive area of a territorial male. Sites where two or more males were observed displaying were included in each of the territories. The largest possible polygon created by connecting straight lines to the outermost display points was usually considered to be the final territory size; however, if an area between two points was claimed by a neighboring male and was not defended by the bird whose territory was being measured, then the non-defended area was excluded from the territory. Thus, territory as used in this paper refers to the area within which male display activities were confined.

Twenty territories were delineated. A minimum of 30 min was spent each day between 2 and 22 June observing male activities on each territory. It was usually possible to watch activities on two or more territories simultaneously. Plots of apparent territory size vs. duration of observation revealed that 10 h of observation was sufficient to define the display areas of the birds, while fewer than 5–6 h led to underestimates of the size of the display area.

Microhabitat classification.—Following territory delineation, a 7.1-m grid was marked out on each territory. This grid provided one intersection point for every 50 m^2, giving between 218 and 566 points per territory. Each intersection point was visited and the site was classified into one of 17 categories based upon soil moisture and dominant plant species. These were later lumped for subsequent analyses into dry, mesic, or wet (saturated) habitats. The amounts of these habitat categories were tabulated for each territory.

Prey abundance.—The abundance of arthropod prey was assessed each season between 1966 and 1972, and in 1975, through the use of "sticky boards" covered with a resin. These are exposed on the tundra surface to capture arthropods that walk onto or land upon the board. MacLean and Pitelka (1971) reported results obtained between 1966 and 1969. Here we report further data. Sixteen sticky boards, each 1 m × 0.1 m, were placed in 11 vegetation types in 1975, when territories were recorded. Six of the boards were placed on the exact sites used in the earlier studies. Results of sticky board captures of adult crane flies have been compared with the numbers emerging into emergence traps and counted on transects across a variety of habitat types at the same time (Clement 1975). We believe that the sticky boards accurately reflect the relative abundance and habitat distribution of adult arthropod prey of Longspurs. The total amount of biomass captured on sticky boards is influenced by abundance, activity, and physical characteristics of the arthropods. Activity is influenced by temperature during the emergence period. Thus, comparisons between years and between disparate taxa must be made with caution. Sticky board data are used here primarily to compare the relative abundance of prey in the various habitat types.

Methods of counting and classifying the captured arthropods followed those of MacLean and Pitelka (1971). Only the crane flies (Diptera, Tipulidae) were identified to species. Others were grouped into large

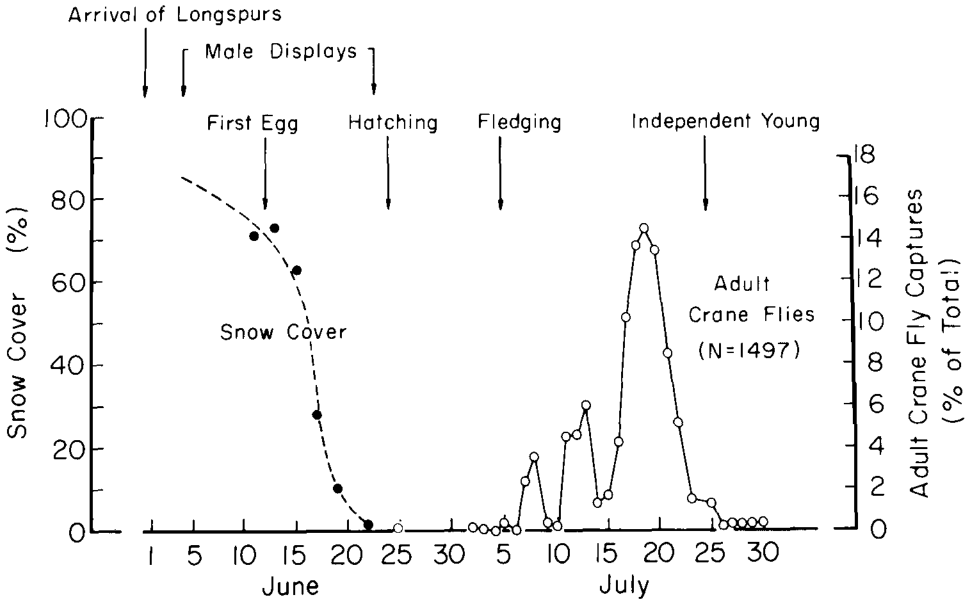

Fig. 1. Phenology of longspur breeding at Barrow, Alaska in 1975, in relation to snow melt and activity of adult crane flies on the tundra.

taxonomic categories (Table 3). Insects smaller than 2 mm (micro-Nematocera of MacLean and Pitelka 1971) were excluded from the counts, as they are not taken by longspurs.

Prey items fed to nestling longspurs were obtained by placing pipe-cleaner ligatures on the throats of nestlings (Hussell 1972). Nestlings older than 7 days were kept in the nest area by a wire mesh enclosure. Prey items were placed in 70% alcohol for later identification. Stomachs of nestlings found dead were also preserved. Classification of prey items followed that used for arthropod collections.

Weights of prey items were obtained from freeze-dried samples and from published reports (Table 3). Weights reported here are those of newly-emerged adults, while weights of crane fly larvae are those of the fourth (final) instar, which make up almost all of the larvae taken by foraging longspurs.

RESULTS

Territory size and variation.—Territorial display began in the first days of June, when the tundra was almost entirely snow covered (Fig. 1). Small patches of exposed ground served as foci of territorial activity. Only males that obtained territories within an 8-day period (4–12 June) were successful in attracting mates, although pair formation was observed as late as 16 June. Six of 28 males that established territories on the study area before 12 June and all three males that established territories after 12 June failed to attract males. One male (number 087, Fig. 2) attracted two females in succession, and mated bigamously. The total sex ratio (31 males, 23 females) indicates that females were in short supply in this population.

Territories of 20 male longspurs (Fig. 2) varied from 1.09 to 2.83 ha ($\bar{x}$ = 1.76, SD = 0.46). The birds did not occupy all of the study area, so that territories were not entirely contiguous. The overall density in the study area was about one pair per 3 ha, a value well below the maximum but above the minimum reported by Custer and Pitelka (1977) on an adjacent study plot for the period 1967–1973. This

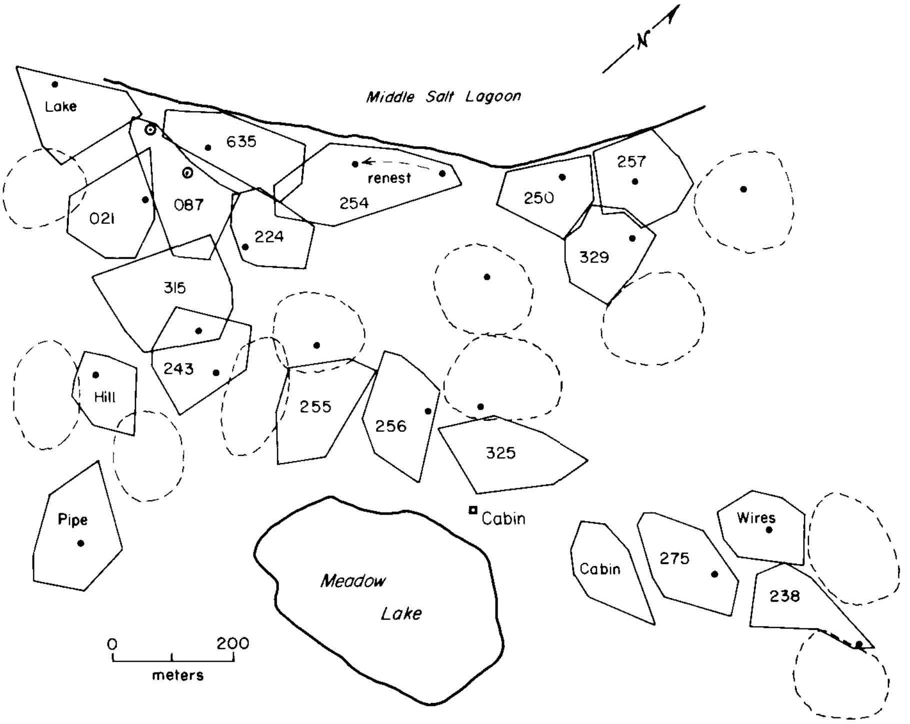

Fig. 2. The size and location of longspur territories in the study area. Dotted lines indicate territories present but not plotted. Nest locations are indicated by dots. The circled dots indicate the two nests of bigamous male 087.

supports their suggestion that the population was recovering from a low point reached in 1972.

Female behavior influenced territory size directly by selection of the nest site, and indirectly by date of pair bond formation. In three instances (territories 315, 254, and 238; Fig. 2), females placed their nests outside of the exclusive area of the males. The males then increased the areas covered by their display activities to include the nest sites. Two of these territories (315 and 254) were considerably larger than any others, and at least part of the large size was due to the female's choice of nest site.

Males continued to display after their females began to incubate eggs, and often flew from their own territories to pursue unattached females or neighboring females with incomplete clutches. Two males (territories 087 and Hill) that acquired mates later than other males were forced to spend much of their time driving off intruders. Thus, time spent in normal display activities was curtailed. Territory size delineation was dependent upon these displays, and in such cases competition for the female rather than the area may have reduced the size of the exclusive areas.

We divided the total sample into subsamples consisting of the largest and smallest 10 territories in order to compare the habitat composition of large and small territories (Table 1). Large territories contained nearly equal amounts of wet, mesic, and dry habitats. Small territories contained significantly less dry and, especially, wet habitats, but a much larger proportion of mesic habitats (Mann Whitney U-test,

TABLE 1. Habitat composition of the ten largest and ten smallest territories.

	Large territories (n = 10)		Small territories (n = 10)	
Habitat type:	%	Area (ha)	%	Area (ha)
Wet	32.8	0.69	17.0	0.24
Mesic	31.2	0.65	53.2	0.76
Dry	35.6	0.75	29.8	0.42
Total		2.10		1.42

$.05 > P > .02$). In fact, the actual amount of mesic habitat was, on the average, greater in the smaller territories.

Dry habitats consisted primarily of raised polygon centers, where *Luzula confusa, Poa arctica,* and a sparce lichen cover formed the dominant vegetation. Wet habitats in longspur territories consisted mainly of polygon troughs, where the grass *Dupontia fischeri,* the sedges *Carex aquatilis* and *Eriophorum vaginatum,* and the moss *Oncophorus wahlenbergii* were dominant. Continuous expanses of such habitat, forming wet meadows, were not occupied by territorial longspurs. The main mesic habitats were gently sloping meadows of *Carex aquatilis, Poa arctica* and *Salix* spp.

Eighteen nests in delineated territories were undisturbed by the research protocol; these produced 5.22 eggs and 3.72 fledglings per nest, for a mean fledging success of 71%. These values are slightly higher than those observed for the population as a whole (5.03 eggs and 3.03 fledglings per nest, based upon 34 nests). Five of the 34 nests were preyed upon during the nestling stage, one by a Snowy Owl (*Nyctea scandiaca*) and the others by Pomarine or Parasitic jaegers (*Stercorarius pomarinus, S. parasiticus*) or, in one case, perhaps by a least weasel (*Mustela nivalis*). Nineteen nestlings starved or died from a combination of starvation and exposure. Thus, of 53 nestling deaths, 64% were caused by predation and 36% resulted from starvation. No correlation existed between territory size and either clutch size or number of young fledged (Fig. 3A, 3B). Thus, the data show no reproductive advantage associated with territory size in 1975.

Arthropod abundance.—Table 2 summarizes the biomass of arthropod prey captured on sticky boards in wet, mesic, and dry habitats on the study area in seven different seasons, including 1975. The major component of biomass consists of adult craneflies: *Tipula carinifrons* in dry and mesic habitats, *Prionocera gracilistyla* and *Pedicia hannai* in mesic and wet habitats. This was particularly the case in 1975, when crane flies made up 63% of all biomass, compared with the 7-yr average of 48%. Much of the difference between 1975 and earlier years can be attributed to an unusual abundance of *P. gracilistyla.* In each of the prior seasons the number of *T. carinifrons* captured exceeded the number of *P. gracilistyla.* Dry habitats produced more biomass than wet habitats in five of these six seasons, and the average prey productivity of dry and mesic habitats was greater than that of wet habitats. In 1975, with the large abundance of *P. gracilistyla,* wet habitats were most productive. Overall, the biomass of adult arthropods captured on sticky boards in 1975 was well below the 7-yr average for this site. The peak of emergence in 1975 (Fig. 1) was slightly delayed compared to other seasons (MacLean and Pitelka 1971) due to a period of cold weather, with daily maximum temperatures below 4°C, that lasted for 3 days in mid-July and suppressed the emergence of adult Diptera.

Food of nestling longspurs.—Prey fed to nestlings consisted almost entirely of insects and spiders (Table 3). Crane flies are by far the most important component of the biomass of the nestling diet; over 60% of the biomass fed to nestlings in 1975 consisted of the crane fly species *Tipula carinifrons*. Hatching of longspurs preceded the peak crane fly emergence (Fig. 1), and pupae were more numerous than adults and larvae in the prey fed to nestlings. *Tipula carinifrons* and sawflies (Tenthredinidae), both larval and adult, occurred in the nestling diet in greater proportion than their capture on sticky boards (Table 3). *Prionocera gracilistyla* were not heavily used by longspurs, despite their great abundance in wet habitats.

Territory size in relation to prey abundance.—The prey capture data for wet, mesic and dry habitats (Table 2) were used to estimate the prey value of each of the 1975 territories. Since over 98% of the nestling diet consisted of the three crane fly species, sawflies, spiders, small Nematocera, and muscoid flies, only these seven groups were used in constructing the index. A biomass density index was calculated for each territory from the formula:

$$\text{Biomass Density Index} = \frac{\sum_{i=1}^{3}\sum_{j=1}^{7} a_i b_{ij}}{\sum_{i=1}^{3} a_i} \qquad (1)$$

where a_i is the area of moisture class i (wet, mesic, or dry) in a particular territory and b_{ij} is the biomass of insect j captured per sticky board placed in moisture class i. The values generated by this procedure express the relative prey availability of different territories.

Estimates of prey availability were compared with territory size using the Spearman Rank Correlation (Snedecor and Cochran 1967). There is a significant positive correlation between territory size and relative prey density in 1975 (Table 4). We believe that this is due to the unusual abundance of *Prionocera gracilistyla* in wet habitats in 1975.

MacLean and Pitelka (1971) reported densities of arthropods captured in 1967–1969 in wet, mesic, and dry habitats that included the sites sampled in 1975. Territory size in 1975 shows a strong negative correlation with expected prey density, calculated from the 3-yr average arthropod abundance data for wet, mesic, and dry habitats (b_{ij} of equation 1) (Table 4). The 7-yr prey-capture data for the Beach Ridge site used in this study (Table 2) include more temporal but less spatial variation than the 3-yr data used above. When the 7-yr averages are used to indicate prey abundance in the three habitat categories, a significant negative correlation between territory size in 1975 and expected prey density is again found (Table 4).

These correlations weight all prey in the seven major categories equally, without considering selectivity by foraging longspurs. Comparison of prey items obtained from nestling longspurs with sticky board captures (Table 3) shows considerable selection in favor of *T. carinifrons* and sawflies and against other prey categories. The ratio of biomass fed to nestlings to biomass captured on sticky boards (Table 3) was used as an index of selectivity to weight the importance of the various prey categories. This weighting factor emphasizes the nestling period, when food abundance is likely to be of particular importance. We assume that the habitat distribution of larval and pupal flies and sawflies follows that of adults captured on sticky boards (MacLean 1973, Clement 1975). Since only fourth (final) instar crane fly

TABLE 2. Biomass (mg) of arthropods captured on two sticky boards in wet, mesic, and dry habitats on the Old Beach Ridge study site, 1967–1972 and 1975. Biomass calculated from numbers of arthropods captured and mean biomass values given in Table 3.

		Tipula carinifrons	*Prionocera gracilistyla*	*Pedicia hannai*	Small Nematocera	Muscoid flies	Tenthredinidae	Araneida	Total
1967	Wet	1,614	282	211	1,365	247	58	77	3,854
	Mesic	1,640	339	68	1,252	379	16	31	3,725
	Dry	3,050	85	63	1,241	576	14	45	5,074
1968	Wet	318	113	416	3,128	707	110	94	4,886
	Mesic	712	367	236	3,416	1,000	52	15	5,798
	Dry	1,284	85	94	3,123	1,065	32	25	5,708
1969	Wet	229	141	191	740	1,669	167	482	3,619
	Mesic	318	56	83	730	1,196	74	98	2,555
	Dry	534	42	27	716	1,065	27	64	2,475
1970	Wet	458	42	126	1,551	710	61	372	3,320
	Mesic	521	28	72	1,453	912	32	200	3,218
	Dry	470	28	20	1,507	1,418	18	139	3,600
1971	Wet	902	691	252	887	1,067	88	560	4,447
	Mesic	1,322	409	189	764	2,159	63	174	5,023
	Dry	1,538	56	43	866	2,697	40	101	5,341
1972	Wet	2,669	3,640	656	289	866	124	—	8,564[a]
	Mesic	5,669	2,667	504	493	1,480	171	—	11,112[a]
	Dry	4,944	1,947	189	540	1,619	63	—	9,384[a]
1975	Wet	414	1,746	198	357	397	40	337	3,489
	Mesic	686	858	198	402	237	38	249	2,668
	Dry	850	270	14	609	189	43	119	2,094
Mean	Wet	943	951	293	1,188	808	93	320	4,597
	Mesic	1,552	675	193	1,216	1,052	64	128	4,871
	Dry	1,810	359	64	1,229	1,233	34	82	4,811

[a] 1972 spider data are missing. Total biomass estimated using habitat-specific means for the other 6 yr.

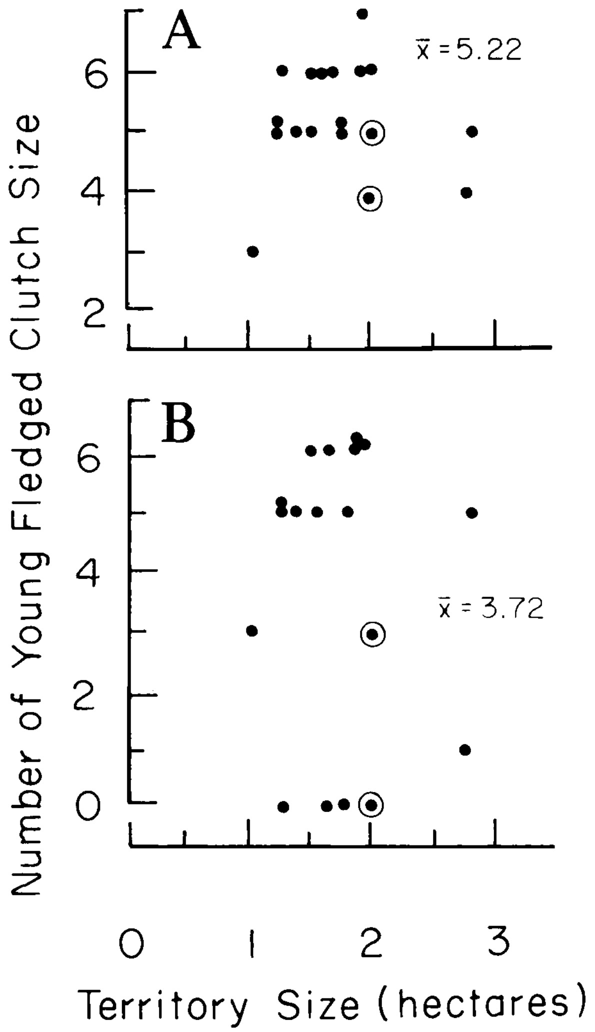

Fig. 3A. Relationship between territory size and clutch size at Barrow. B. Relationship between territory size and number of young fledged at Barrow. Values of bigamous male are circled.

larvae are taken in significant numbers by foraging birds, the larvae and pupae are taken from the same cohort represented by adults captured on the sticky boards.

Adjusted biomass density indices were calculated for each 1975 territory according to the formula:

$$\text{Adjusted Biomass Density Index} = \frac{\sum_{i=1}^{3} \sum_{j=1}^{7} a_i b_{ij} s_j}{\sum_{i=1}^{3} a_i} \qquad (2)$$

where s_j is the prey selectivity index for prey category j. Other terms are the same as in equation 1. If territory size is related to expected prey productivity, use of the adjusted biomass density index, which weights prey categories according to their importance in the diet, should emphasize the relationship. This is the case for all

TABLE 3. Major invertebrates obtained from esophageal ligature and stomach samples of nestling longspurs, and from 16 sticky-boards on the tundra surface in 1975.

		A. Obtained from nestlings		B. Sticky-board captures		
Prey item	Weight (mg)	Number	% of biomass	Number	% of biomass	A/B
Tipula carinifrons						
larvae	25.0	12	6.2			
pupae—male	21.8	95	36.9			
pupae—female	27.7					
adult—male	10.0	48	15.6	156	18.9	
adult—female	26.0			15	4.7	2.5
Prionocera gracilistyla						
larvae	30.0	—	—			
pupae—male	14.0	—	—			
pupae—female	32.0					
adult—male	12.0	17	6.9	177	25.7	
adult—female	30.0			25	9.1	0.2
Pedicia hannai						
larvae	5.0	5	0.5			
adult	1.8	66	2.4	228	5.0	0.6
Small Nematocera						
larvae	0.2	75	0.3			
pupae	0.4	23	0.2			
adults	0.3	880	4.3	4,561	16.6	0.3
Muscoid flies						
larvae	0.7	7	0.1			
pupae	0.9	57	1.0			
adult	0.9	221	4.2	914	9.9	0.5
Tenthredinidae						
larvae	6.0	81	10.2			
adults	1.8	140	4.7	67	1.5	9.9
Araneida	1.4	122	4.7	504	8.6	0.5
Other		33	1.8			

three sources of prey density data: 1975, 1967–1969, (MacLean and Pitelka 1971), and 1967–1972 plus 1975 (Table 4). Using the adjusted prey biomass density index, territory size in 1975 was inversely correlated with quality. The adjustment for prey selectivity removes the effect of the unusual abundance of *Prionocera gracilistyla* in 1975, since this abundance was not reflected in the prey fed to nestling longspurs.

DISCUSSION

The results of this study indicate that the size of breeding territories of Lapland Longspurs in arctic Alaska is related to the "expected" food density of the habitats comprising the territory. Territories that contain a large proportion of the most favored feeding habitats are, on the average, smaller than territories that contain a large proportion of wet habitats. The fact that this relationship applies most strongly to average or expected food density indicates that the birds respond to the habitat composition of the area rather than assessing food density directly. Similar patterns have been found in Ovenbirds, *Seiurus aurocapillus* (Stenger 1958), and in Sparrowhawks, *Accipiter nisus* (Newton et al. 1977).

Longspurs at Barrow begin territorial behavior when the tundra is mostly snow covered. This is necessary in order that the young will fledge while the easily-captured adult crane flies are abundant on the tundra (Fig. 1). The pattern of snow melt provides some information regarding the habitats occurring in a particular

TABLE 4. Spearman rank correlation coefficients of territory size in 1975 with estimates of prey biomass density, unweighted and weighted for prey selectivity by longspurs.

	Nature of data	
Year(s)	Sticky-board captures, not adjusted	Adjusted for prey selection by longspurs
1975 prey data (6 boards)	+0.54**	−0.40*
1967–1969 (12 boards) (MacLean & Pitelka)	−0.60**	−0.63**
1967–1972 & 1975 (6 boards)	−0.43*	−0.52**

* $P < 0.05$; ** $P < 0.01$.

area, but details of habitat composition and year-to-year variations in their productivity cannot be assessed. The information available to direct habitat selection increases as the season progresses (Wittenberger 1976), and adjustments to territory boundaries occur. Still more information is available by the time of egg-laying, and females may select nest sites close to productive feeding habitat. In three cases, two of them involving territories established quite early in the season, this took the female off the original territory of the male altogether. Thus, two levels of choice are available to the female: selection of a male (in part based upon the characteristics of the territory that he possesses), and selection of a site on (or near) the territory to place the nest.

It should be stressed that territory, as used here, refers to the area encompassing male displays. This is the usual operational definition of territory. The relationship of display area to foraging areas of the male and female was considered in a companion study on this same population (Tryon 1978, Tryon and MacLean MS). In the normal case, over 90% of the foraging of both male and female occurred on the territory early in the season, when territories were most actively defended. This value declined later in the season. The nest site became a strong focus for foraging activities, with less regard for territorial boundaries, when nestlings were being fed. Thus, the location of the territory and placement of the nest (in most cases) within the territory strongly influence access of the birds to potential feeding sites, particularly when feeding nestlings.

A large and high quality territory is beneficial to a male in attracting a female (or multiple females), and in assuring the success of the nest or nests. These are obviously related, since a female should not mate with a male whose territory is inadequate to allow successful reproduction. The observed inverse correlation between territory size and food density might result if (1) males recognize the resource value of their territories, and do not attempt to defend more resources than are required for successful reproduction, or (2) competition is most severe for areas of high quality (high food density) habitat, leading to a greater cost of defense per unit area of territory. The first of these alternatives is the "sufficient resource" hypothesis of Verner (1977). MacLean and Seastedt (1979) showed that this is unlikely, and that this hypothesis can be rejected without negating the central hypothesis that the basic function (cause for the evolution) of territoriality is the securing of adequate resources for reproduction. The high level of agression observed between territorial males, and the fact that areas temporarily vacated when a territorial male was trapped for banding were almost immediately occupied by neighboring or intruding males, argues that territory size is limited by competition for suitable habitat, or by the cost of defense of the area.

While competition for favorable habitat provides a mechanism of territory size determination, the fact that 36% of nestling deaths resulted from a combination of starvation and exposure indicates that the food value of the territory is important to the reproductive success of the occupants. We believe that it is food density in productive habitats, rather than total quantity of food, that is important to the birds. A large area of low productivity habitat is not the equivalent of a smaller area of highly productive habitat, in which food can rapidly be gathered for delivery to nestlings or fledglings. Further, it would be misleading to compare the total food requirements for reproduction with the total productivity of the territory. Each day the adults must supply the requirements of the growing young. Calculating from energetic and time budget estimates presented by Custer (1974), we estimate that each adult must gather one *Tipula* larva or pupa or two *Tipula* adults per min of foraging time to satisfy their own requirements plus the needs of five nestlings. The daily emergence of adult prey varies widely, depending upon both time of season and weather conditions. On favorable days the daily emergence far exceeds the requirements of the birds, but on unfavorable days the birds may be hard-pressed to collect sufficient food. On such days access to adequate areas of highly productive habitat without competition from conspecifics may be critical to successful reproduction.

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NUMBERS AND HABITAT SELECTION OF CASSIN'S AUKLET BREEDING ON TRIANGLE ISLAND, BRITISH COLUMBIA

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ABSTRACT.—Triangle Island, with approximately 360,000 breeding pairs, constitutes the largest Cassin's Auklet (*Ptycoramphus aleuticus*) colony in the world and contains 40% of the total breeding population of that species. Nesting habitat preferences were determined by stepwise multiple regression analyses. Cassin's Auklets preferred nesting in sparse shrubbery and short herbaceous vegetation on slopes and in the interior of the island. Their nesting densities ranged from 0.1 to 1.1 pairs per m^2 with an overall density of 0.37 pairs per m^2. Highest densities occurred on the open summit, around the edge of the plateau, on the southeast plateau, and on the southwest slope. They nested least densely on the central plateau of the island, where dense, tall salmonberry was the dominant vegetation, as well as on slopes where other burrowing alcids, Rhinoceros Auklets and Tufted Puffins, were present in large numbers. The latter two alcids were restricted to certain slopes and cliff tops while Cassin's Auklets nested on all slopes and on relatively flat areas of the island. Differences in nesting distribution between the three alcids may partly be explained by the lower wing-loading of Cassin's Auklets. *Received 1 March 1978, accepted 26 November 1978.*

CASSIN'S Auklets (*Ptychoramphus aleuticus*) nest on treed as well as treeless islands in British Columbia (Drent and Guiget 1961). On treed islands they nest predominantly at the edge of forests with little or no understory and burrow in bare or moss- and grass-covered ground. They nest on low islands as well as above cliff edges up to 100 m high. They are the most abundant nesting seabirds on Triangle Island, British Columbia (Vermeer et al. 1976). It was not until the summer of 1977 that a survey was conducted on the island to determine the total breeding population, thought to be the largest for the species in the world. Another large colony of 52,500 pairs occupies Southeast Farallon Island, California (Manuwal 1974a) where Thoresen (1964), Manuwal (1974a, b) and Speich and Manuwal (1974) studied its natural history and population structure. The objectives in this study were to document the breeding population of Cassin's Auklets on Triangle Island and its importance in relation to other known populations, to determine breeding densities of Cassin's Auklets among broad habitat units, and to identify the factors influencing those densities by means of regression analyses. The 1977 survey on Triangle Island and present inventories in British Columbia by the British Columbia Provincial Museum and the Canadian Wildlife Service, in Alaska by the Outer Continental Shelf Environment Assessment Program, and in California by S. M. Speich, made it possible to compare the Triangle Island population with the known population of Cassin's Auklets.

STUDY AREA AND METHODS

Triangle Island (50°52′N, 129°05′W), the outermost of the Scott Islands, is situated 46 km northwest of Cape Scott, at the northern end of Vancouver Island, British Columbia (see Fig. 3). Triangle Island is approximately 1.5 km long on its greatest dimension and is roughly triangular in shape. The perimeter is generally steeply sloped while the upper regions are more level, rising to a maximum elevation of approximately 200 m. The island was the site of an active light station from 1909–1919. Now only the

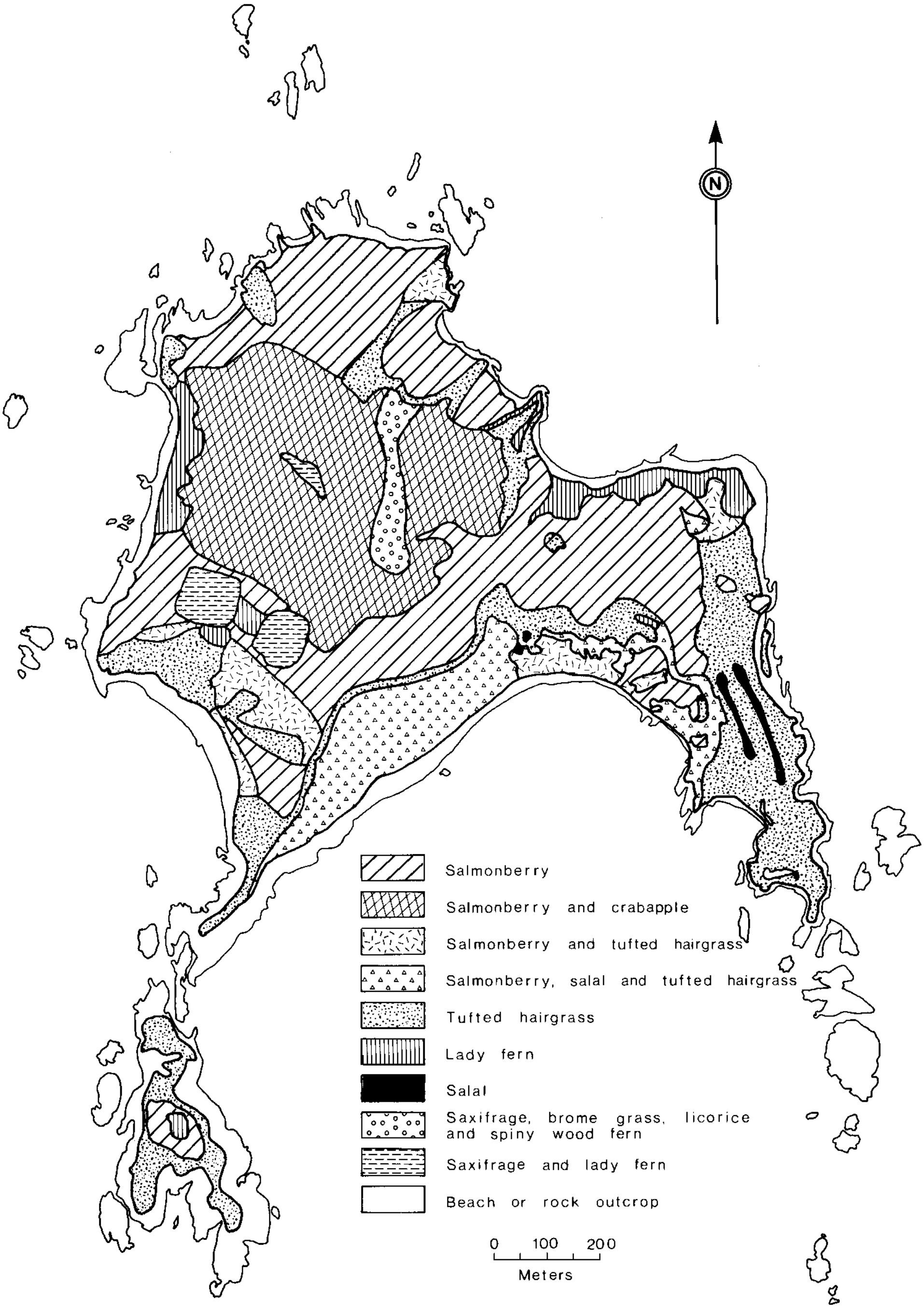

Fig. 1. Distribution of dominant vegetation on Triangle Island in 1977.

concrete shell, building foundations, and rusted train track remain. The climate is very humid and promotes a dense cover of vegetation over most of the island although strong winds prune larger shrubs to a continuously low and even height. There are no trees, and much of the island is covered by salmonberry (*Rubus spectabilis*) (Fig. 1). Lady ferns (*Athyrium filix-femina*) form large patches among the salmonberries. Tufted hairgrass (*Deschampsia caespitosa*) covers most wind-exposed ridges and slopes. Salal (*Caultheria shallon*) is abundant near rocky promontories. A more detailed description of the climate, flora, and fauna of Triangle Island has been given by Carl et al. (1951), while its bird fauna has been described in more detail by Vermeer et al. (1976).

Triangle Island was divided into 11 broad habitat units on the basis of their physical characteristics (Fig. 2). Those units were censused from 20 June to 31 July 1977, with the exception of the eastern portion of the south slope where 38 quadrats were censused in the summer of 1976. Quadrats of 5 m × 5 m were set out systematically 40 m apart on transects running up the slope from the beach. Transects were 50 m apart. On the edges around the island plateau, quadrats were established 70 m apart on a continuous transect that circled about two-thirds of the island. The plateau was sampled from quadrats 40 m inland of each plateau edge quadrat. One transect with quadrats spaced at 50-m intervals was run along the summit of the plateau. The number of alcid burrow entrances, major vegetation types, percentage plant cover, slope angles, and elevation were determined for each quadrat. Not all burrows were occupied, and some had more than one entrance. Therefore, in order to be able to estimate numbers of breeding pairs from the number of entrances the number of occupied burrows was determined in eight of the 25 m^2 quadrats mentioned earlier. Those eight quadrats represented a variety of exposures, vegetation types, and topographic situations in different parts of the island. Occupancy was determined by noting the presence of copious quantities of fresh feces at burrow entrances, and in the absence of the feces, by excavating the burrows to determine whether eggs or chicks were present. The substrate composition was determined at 26 different locations representing various vegetation types on the island. Nesting habitat areas were measured in different regions of the island. Areas of rock bluffs that were unsuitable for burrowing were excluded from those measurements. A report by the third author, providing detailed calculations of Cassin's Auklet breeding density, population, and nesting habitat, and showing 10 maps with transects and quadrats in 11 habitat units on Triangle Island, is on file in the Canadian Wildlife Service library at Delta, British Columbia.

The burrow density of Cassin's Auklets was multiplied by a factor of 25, the quadrat size, and was regressed by stepwise multiple regression on the amount of major vegetation types, amount of bare ground, slope angle, and elevation to determine if the birds preferred certain habitats for burrowing. Density of Cassin's Auklets burrow entrances was also regressed on that of Rhinoceros Auklets where the two species nested together on the eastern portion of the south slope. The stepwise procedure involved the reexamination at every stage of the regression for all variables incorporated into the model in previous stages (Draper and Smith 1966). The partial F-statistic for each variable in the regression at any stage was evaluated to check for the significance of each variable in the presence of others in the regression. This procedure evaluated the contribution made by each variable as though it had been the most recent variable entered. The SPSS stepwise regression program was used in the analyses. Any variables with $F \leq 0.01$ or tolerance level ≤ 0.001 were not admitted into the regression equation. A tolerance level of 0.001 implied that a variable may be entered if the proportion of its variance not explained by other independent variables exceeded 0.1%. The model was considered defined at the stage when the latest variable entered had a significant partial F-statistic at the 5% level or when an important variable became significant in the presence of other variables in the regression. The partial F-statistic is the ratio of the sum of squares contributed by a variable to the residual mean square of the regression. All variables in the reported equations were significant except for one. The F-statistic for the coefficient of determination (R^2) is the ratio of the total mean square of regression to the residual mean square. The R^2 values for all models were significant at the 1% level. Of many linear regression analyses made, only five equations are shown as they are thought to be representative of the nesting preference of Cassin's Auklets on Triangle Island. The nesting distribution of Cassin's Auklets, Rhinoceros Auklets (*Cerorhinca monocerata*), and Tufted Puffins (*Lunda cirrhata*), on the island were compared as the latter two species are also burrowing alcids that may compete with the Cassin's Auklets for nesting habitat.

RESULTS AND DISCUSSION

Breeding densities and populations.—In eight quadrats examined the number of occupied burrows was 36–58% of the number of burrow entrances, with a mean of

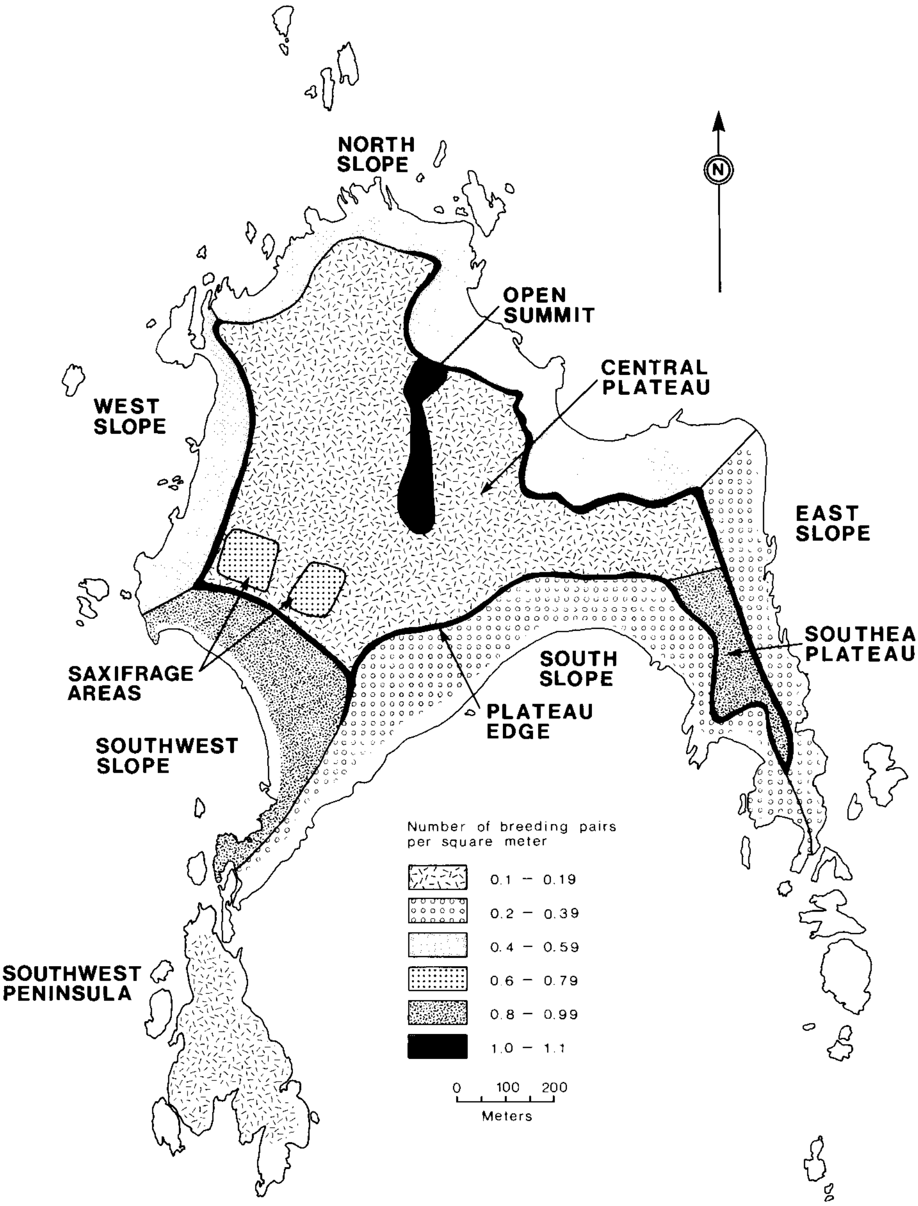

Fig. 2. Breeding densities of Cassin's Auklets according to broad habitat units on Triangle Island in 1977.

48%. Based on this average and 7,631 burrow entrances in 288 quadrats representing a total of 970,000 m^2 of nesting habitat, we calculated breeding densities of Cassin's Auklets on Triangle Island in 11 habitat units (Fig. 2). The densities varied from one habitat to another with an overall density of 0.37 pairs of Cassin's Auklets per m^2. Nesting was densest in areas with short herbaceous vegetation or sparse shrubbery such as the southwest slope with tufted hairgrass and low wind-pruned salmonberry interspersed with bare ground, the southeast plateau with tufted hairgrass and Alaska brome grass (*Bromus sitchensis aleutensis*), the open summit with Newcombe's saxifrage (*Saxifraga newcombeii*) and licorice fern (*Polypodium vulgara*) and spiny wood fern (*Dryopteris austriaca*), the saxifrage areas with Newcombe's saxifrage and lady fern, and the plateau edge around the island interior with a frequent and abrupt gradient between short vegetation such as tufted hairgrass and dense, tall salmonberry. Breeding densities were low in the central plateau of the island where 0.5–2.0-m tall, dense salmonberry with some Pacific crabapple (*Malus fusca*) and salal were dominant. Cassin's Auklets also nested in lower numbers on the southwest peninsula, where tufted hairgrass was dominant and where about 16,500 pairs of Tufted Puffins used most of the nesting habitat.

The total breeding population of Cassin's Auklets on Triangle Island was calculated to be 359,000 breeding pairs in 1977. The total breeding population in British Columbia outside Triangle Island consists of approximately 200,000 pairs (R. W. Campbell pers. comm.). About 250,000 pairs are found in Alaska (A. Sowls pers. comm.) and approximately 100,000 pairs breed south of British Columbia along the west coast of the United States and Baja California in Mexico (S. M. Speich and A. Thoresen pers. comm.). The known population of Cassin's Auklets, all situated along the North American west coast, therefore consists of approximately 900,000 pairs. British Columbia appears to contain approximately 60% of the known population of Cassin's Auklets, of which about 40% are found on Triangle Island. The next largest colonies are on Frederick Island on the west coast of the Queen Charlotte Island with approximately 65,000 pairs (R. W. Campbell pers. comm.); at Forrester Island, southeastern Alaska with 54,000 pairs (A. J. De Gange pers. comm.); and on Southeast Farallon Island with 52,500 pairs (Manuwal 1974b). The breeding center of Cassin's Auklets, with approximately 65% of the world's known population, ranges from Triangle Island to Forrester Island on the Alaska–British Columbia boundary (Fig. 3).

Habitat selection.—The burrow densities in the habitat units reflect the Cassin's Auklet preferences for certain habitat variables such as type of vegetation, slope angle, and elevation, and the inhibiting effects of unsuitable vegetation and other burrowing alcids competing for nesting space. The relationship between the Cassin's Auklet burrow density and the various habitat variables may be formally described by linear analyses. The south slope is ideally suited for regression analysis as it contains most of the variables that were expected to affect burrow density. Most of the vegetation types are found on the south slope, and Rhinoceros Auklets are present on the eastern portion of that slope. The estimated regression equation for Cassin's Auklets on the south slope is shown in Table 1.

Of the independent variables, slope angle, percent tufted hairgrass, density of Rhinoceros Auklet burrow entrances, and altitude were significant. Thus it appears that Cassin's Auklets prefer nesting in short hairgrass and away from Rhinoceros Auklets and steep slopes. Cassin's Auklets nests were most dense on a relatively flat area of the eastern part of the south slope, just below the plateau edge, where few Rhinoceros Auklets nested. In this case the significant negative partial regression coefficient for slope angle and positive regression coefficient for altitude may be attributed to the preference of this species to nest away from Rhinoceros Auklets, as Cassin's Auklets were observed to nest commonly on relatively steep slopes and low altitudes elsewhere on the island.

The significant explanatory variables on the southwest slope were bare ground

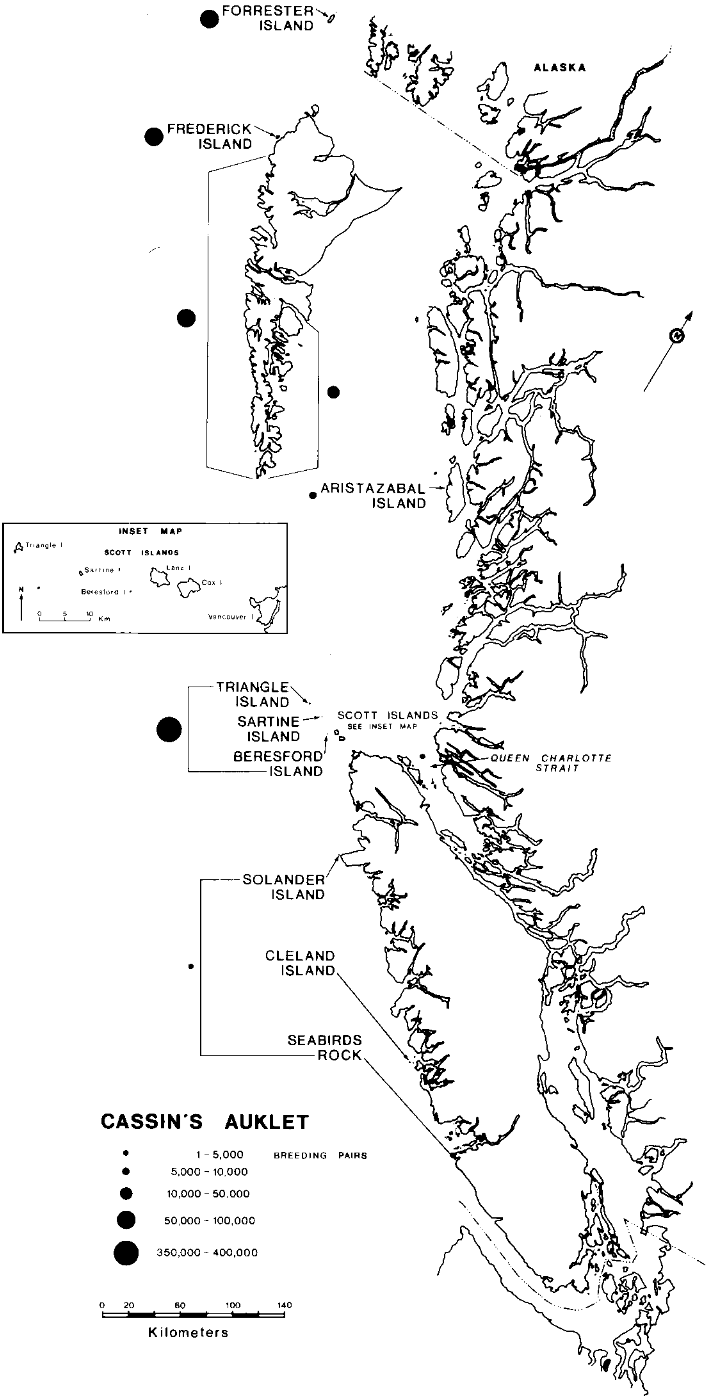

Fig. 3. Breeding populations of Cassin's Auklets in British Columbia and on adjacent Forrester Island, Alaska. Inset shows Triangle Island in the Scott Island Group.

TABLE 1. Linear regression equations for Cassin's Auklet burrow densities in different locations on Triangle Island, where D = density of Cassin's Auklet burrow entrances, SLO = slope angle, GRA = % tufted hairgrass cover, R = density of Rhinoceros Auklet burrow entrances, ALT = altitude, BG = % bare ground, SB = % salmonberry cover, F = % fern cover, and BGS = bare ground and saxifrage cover.

Location	Regression equations	Coefficient of determination	Degrees of freedom (residual)
South slope	D = 37.67 − 0.92 SLO + 0.24 GRA − 0.58 R + 0.13 ALT (F = 35.9) (F = 17.8) (F = 11.1) (F = 4.1)	$R^2 = 0.745$ (F = 24.1)	33
Southwest slope	D = 16.97 + 0.75 BG + 0.28 ALT (F = 13.7) (F = 8.6)	$R^2 = 0.463$ (F = 12.5)	29
Plateau edge	D = 28.84 + 0.38 GRA − 0.18 SB + 0.09 ALT (F = 9.8) (F = 4.0) (F = 2.0)*	$R^2 = 0.473$ (F = 13.4)	45
Central plateau	D = 31.84 − 0.26 SB + 1.15 BG (F = 20.8) (F = 4.1)	$R^2 = 0.511$ (F = 24.0)	36
Open summit	D = 68.32 − 0.64 SB − 0.72 F + 0.32 BGS (F = 25.4) (F = 8.3) (F = 4.9)	$R^2 = 0.875$ (F = 25.6)	11

* Not significant, but included as the SB variable is significant in the presence of the ALT variable.

and altitude (Table 1). Cassin's Auklets appeared to prefer open habitat there as at the eastern part of the south slope. Therefore the significant coefficient for altitude for the southwest slope may be related to the predominance of bare areas that occurred at higher altitudes. Although salmonberry was a major vegetation type, it had no significant inhibiting effect, perhaps because it was less dense and was short compared to elsewhere on the island.

At the plateau edge, tufted hairgrass and salmonberry were significant (Table 1). Salmonberry was tall and dense at the edge, hence the preference of the Cassin's Auklets to nest away from the salmonberry.

At the central plateau, salmonberry and bare ground were significant (Table 1). Salmonberry was most dense and tall and the highly significant negative correlation with salmonberry indicates avoidance of it by Cassin's Auklets. No burrow entrances were observed in quadrats completely covered with dense salmonberry. Neither were there any burrows on a trail cut through the salmonberry in 1975. However, in 1976 and 1977, fresh Cassin's Auklet burrows were common on the trail.

The burrow density of Cassin's Auklets on the partly open summit was also regressed on major vegetation types, amount of bare ground, altitude, and slope angle. As saxifrage, a short herbaceous plant, was sparsely distributed in bare areas it was combined with bare ground under one variable, BGS. Cassin's Auklets preferred bare ground and saxifrage away from dense salmonberry and ferns (Table 1). Cassin's Auklets therefore preferred nesting in open and short vegetation on all slopes and at all elevations of the island.

The slope substrate of Triangle Island is high in rock content, much more so than the less steeply undulating top of the island. The 25-cm top layer composition for 16 slope substrate samples averaged 44% rock, 33% soil, and 23% vegetation, while that of 10 plateau samples contained 3% rock, 60% soil, and 37% vegetation. Most of the rock material in the substrate consisted of pieces less than 3 cm long. The substrate generally did not appear to be a limiting factor to nesting as some of the highest Cassin's Auklet breeding densities were found in the soil containing most rock. No correlation was observed between the dominant vegetation types and their substrates. Therefore correlations observed between breeding densities of Cassin's Auklets and vegetation did not appear to be affected by their substrates.

Interaction and nesting differences between burrowing alcids.—Cassin's Auklet burrow entrances occurred in the same quadrats with those of Rhinoceros Auklets and Tufted Puffins on the eastern portion of the south slope and on the southwest peninsula. Cassin's Auklets, however, generally avoided high breeding densities of Rhinoceros Auklets. There were not sufficient quadrats on the southwest peninsula to determine whether there was a correlation between puffins and Cassin's Auklets, but Cassin's Auklet breeding densities there were among the lowest on the island. Cassin's Auklets burrows were commonly observed to be cut off by those of puffins and Rhinoceros Auklets. Perhaps Cassin's Auklets became displaced from the dense nesting areas of puffins and Rhinoceros Auklets by the extensive burrowing activities of those two species.

Cassin's Auklets were the most diversified nesters of the three burrowing alcids on Triangle Island. Rhinoceros Auklets nested in various types of vegetation on the eastern portion of the south slope and on the northeast slope, while the two main breeding concentrations of Tufted Puffins were located mainly in tufted hairgrass on steep slopes and cliff tops on the southwest peninsula and the east slope. Small groups of puffins also nested dispersed in tufted hairgrass on other slopes. The nesting pattern of Tufted Puffins suggested that they preferred steep slopes or cliff tops free of tall vegetation for flight departure from their burrows. Rhinoceros Auklets nested on gradual slopes and were not chiefly restricted to tufted hairgrass as were puffins. The Cassin's Auklet was the only species to nest on relatively flat areas in the island interior. Their initial flight when taking off was in a more horizontal plane than that of puffins and Rhinoceros Auklets, which dropped considerably in their initial flight along the nesting slopes. Cassin's Auklets have significantly lower wing-loading ($P < 0.01$) than Rhinoceros Auklets and Tufted Puffins (0.94 g/cm^2 vs. 1.46 and 1.49 g/cm^2, respectively). Lower wing-loading facilitates horizontal takeoff. The ability of the Cassin's Auklet to nest in relatively flat areas may be a consequence of its lower wing-loading.

ACKNOWLEDGMENTS

We thank J. B. Foster for permission to work on Triangle Island, an ecological reserve, and R. W. Campbell for providing information on Cassin's Auklet colonies in British Columbia. D. A. Manuwal, A. C. Thoresen, and S. M. Speich provided information on colonies in the United States and Mexico, and A. J. De Gange and A. Sowls provided such information for Alaska. L. Decker drafted the maps and D. R. Flook and D. A. Manuwal reviewed the manuscript.

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The revised, fourth edition of the **Council of Biology Editors Style Manual** has recently been published. This reference is indispensable to authors of scientific manuscripts, and is the foundation for the style followed in *The Auk.* Copies may be obtained (for $12.00, prepaid) from **American Institute of Biological Sciences, 1401 Wilson Blvd., Arlington, Virginia 22209.**

Members of the AOU are urged to submit **drafts of potential resolutions** to be considered for adoption by the Union at the 97th Stated Meeting at College Station, Texas in August. Subject matter should be pertinent to the scientific interests and objectives of the AOU. Please send drafts, with any helpful background information, by **1 June 1979** to the Committee on Resolutions, Warren B. King, Rm 336, National Museum of Natural History, Washington, D.C. 20560.

The **Second International Symposium on Avian Endocrinology** will be held in Benalmadena (Malaga, Spain) on 4–9 May 1980. Information will be available from the convener: Dr. August Epple, Daniel Baugh Institute of Anatomy, Thomas Jefferson University, Philadelphia, Pennsylvania 19107 USA.

LAND BIRD DENSITIES ON BAJA CALIFORNIA ISLANDS

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ABSTRACT.—Land bird populations were censused on four islands and three matching mainland sites in southern Baja California. Island densities (summed totals for all species) were more than twice as high as mainland densities in the dominant desert scrub habitat, and slightly higher in the secondary, riparian woodland habitat. Island-mainland ratios varied greatly in most species, ranging from 8.25:1 in the Black-throated Sparrow to 0.18:1 in the White-winged Dove. Contrary to the predictions of density compensation theory the consuming biomass of the various foraging guilds also differed greatly between island and mainland sites, island-mainland ratios ranging from 4.31:1 in the flower probers, to 0.15:1 in the large terrestrial granivores.

Environmental factors of food supply, predators, and climate apparently do not account for these differences in island vs. mainland densities. Instances of high island density are tentatively attributed to: a) higher mean adaptedness to local conditions due to isolation from the swamping and diluting effects of mainland interdeme gene flow, and/or b) overcrowding due to the blocking of normal, socially-induced dispersal movements by island coastline barriers (fence effect). Instances of low island density were encountered only in woodland species and are tentatively attributed to high extinction rates and tenuous population survival associated with the scarcity and small size of woodland habitat patches on islands. *Received 1 May 1978, accepted 28 October 1978.*

VARIATIONS in population density in ecologically similar but geographically separated land bird communities have received little attention because of the inadequacy of available census techniques, but several recent studies indicate that species densities, guild densities, and summed community densities may differ considerably between islands and closely matched mainland areas (Crowell 1962, Grant 1966, Diamond 1970, MacArthur et al. 1972, Emlen 1978).

In this paper I present data on island and mainland bird densities from the desert scrubland region of Baja California and then discuss possible explanations for the recorded differences in terms of a) extrinsic factors of climate, predation, and limited food resources, b) variations in mean adaptedness for local conditions as related to open vs. blocked gene flow patterns, and c) social spacing dynamics in open vs. blocked dispersal situations. A similar analysis has been made for lizard populations in the same area (Case 1975).

METHODS

The fieldwork, conducted between 5 and 28 April 1977, included bird censuses, vegetation measurements, and food resource (arthropod) sampling at four island and three mainland sites in southern Baja California (Table 1, Fig. 1). The sites were selected to provide island and mainland samples of each of the two dominant habitat types in the area (Fig. 2), a) the mixed desert scrubland that formed a rather uniform vegetational matrix over the lower slopes and bajadas, and b) the riparian, desert woodland that occurred in isolated strips and patches in arroyos and on sandy alluvial fans and coastal "bays." A third habitat type comprising the steep and relatively barren upper slopes of the hinterland was not sampled. Study sites were selected in island-mainland pairs along protected coasts where anchorage could be had for our boat within walking distance of good census areas. Island sites were selected first, and for each of these a mainland site was selected close by along a section of coast offering census areas with topography and vegetation as similar as possible to those on the island. For the most southerly island we found no good matching mainland situation.

Vegetation measurements were designed to detect and evaluate consistent differences in avian habitat

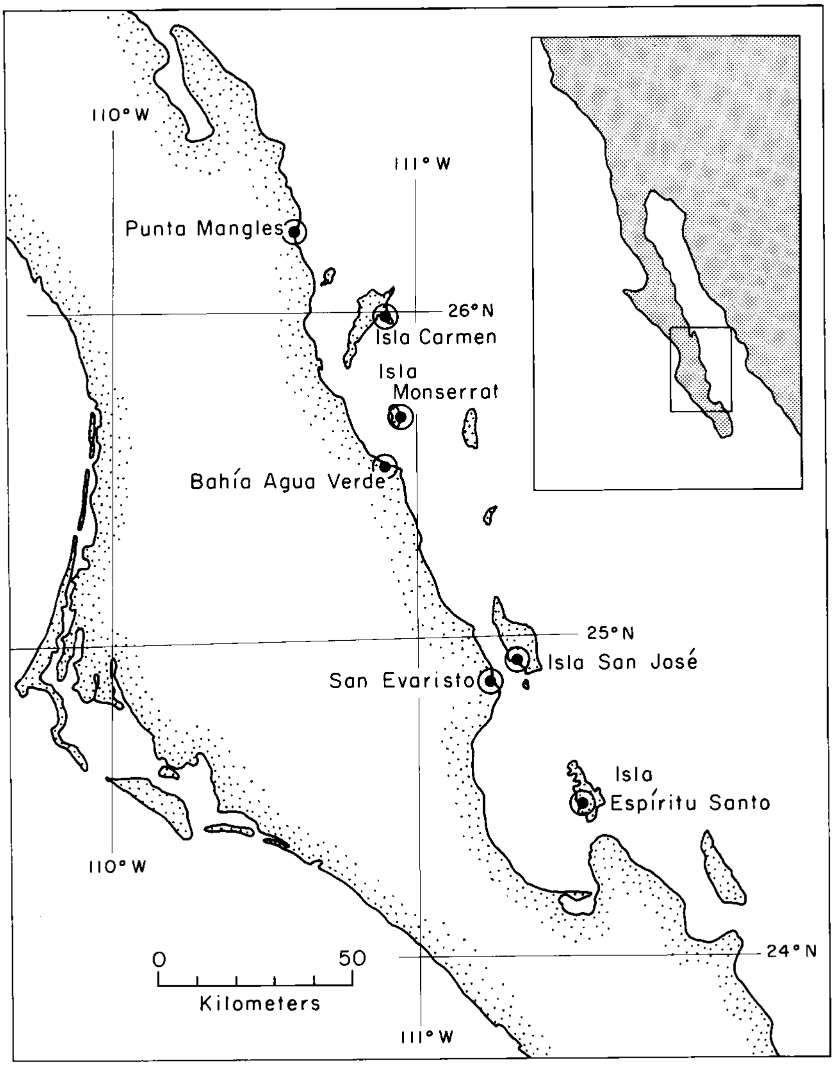

Fig. 1. Map of southern Baja California showing the locations of island and mainland study sites.

conditions between island and mainland sites (Table 2). At five or more representative stations of scrubland and woodland vegetation at each site I recorded: a) mean height and percent cover of trees (defined as woody plants 3–6 m high), high shrubs (1–3 m) and low shrubs (<1 m), b) height and percent cover of tall, medium, and low cactus types, and c) patchiness and mean density of the herbaceous ground cover. Procedures and conventions are described in the footnotes of Table 2. Common trees, shrubs, and cacti were identified to genus for ratings of relative dominance.

A rough index of arthropod abundance in tree foliage was obtained at each site by clipping and vigorously shaking representative branches of the dominant local tree species into a large plastic pail. Insects, spiders, etc. were counted as removed from the pail and the tally in each sample was related to the amount (weight) of foliage material sampled.

The bird censuses were early morning and late afternoon tallies of all detections in 60-m wide transect strips (30 m on each side of the advancing observer). Three experienced observers worked independently, totalling their counts for each locality after checking for interobserver variation. Procedures were similar

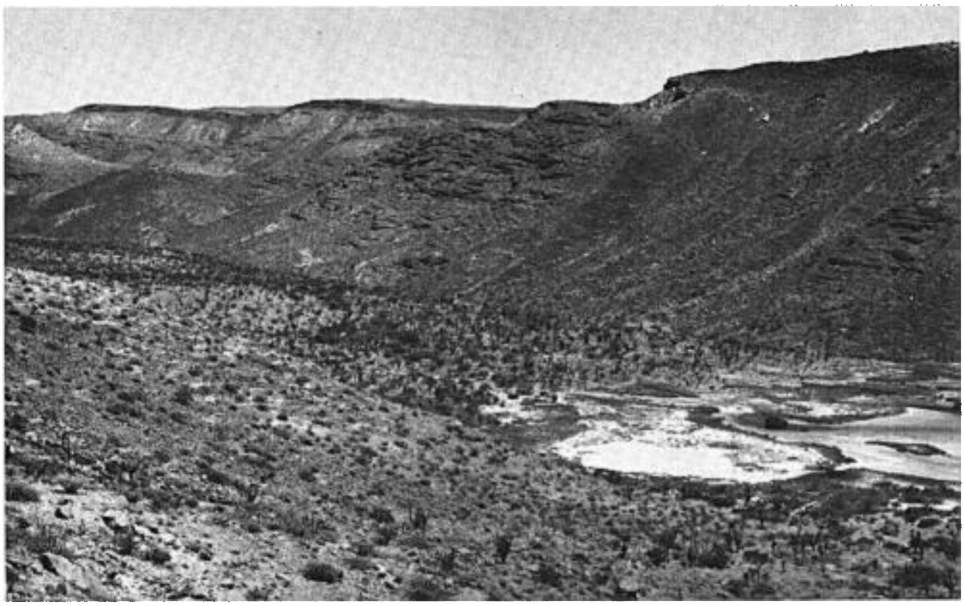

Fig. 2. Mixed desert scrub on the slopes and desert woodland (riparian scrub) in the bottomlands in a typical setting on Isla Espiritu Santo (photo J. J. Hickey).

to those developed for census work in Florida and the Bahamas (Emlen 1971), but as few species showed detectability attenuation inside the 30-m boundary in this open habitat, no density adjustments were made for low detectability species. From 8.4 to 16.0 km of transect line and 0.504 to 0.960 km^2 of transect strip were covered in two consecutive days at each site.

Population densities were calculated for each species in each of the two habitat types at each site and grouped for direct comparison of island and mainland conditions. Summed densities (total of all species) were calculated for each community and for each of eight foraging guilds in each community. For the

TABLE 1. Location and physiographic features of the seven study sites in Baja California, April 1977.

Site	Lat. N.	Long. W	Island distance offshore (km)	Island size (km^2)	Slope face	Alluvial[a] plains	Bajadas[a] & slopes
			Mainland sites				
Punta Mangles (2 km SW)	26°17′	111°26′	–	–	East	++ (fans)	++ (gentle)
Bahia Agua Verde (2 km S)	25°32′	111°03′	–	–	North	+ (fans)	+++ (steep)
San Evaristo (4 km S)	24°52′	110°41′	–	–	East	+++ (fans)	+ (steep)
			Island sites				
Isla Carmen (NE quarter)	25°59′	111°06′	6	151	SW	+ (fans)	+++ (gentle)
Isla Monserrat (E side)	25°41′	111°02′	13	7	SE	+ (arroyo)	+++ (steep)
Isla San José (W side)	24°55′	110°38′	5	194	West	+ (fans)	++++ (gentle)
Isla Espiritu Santo (W side)	24°29′	110°21′	8	99	SW	++ (fans)	++ (steep)

[a] +, ++, +++, ++++ indicate increasing amounts of the indicated feature.

latter I assigned each species to a single guild and calculated the guild biomass by summing the consuming biomass (density × body weight$^{0.633}$—Karr 1968) for all the member species. In the absence of local data on foraging behavior I was unable to make multiple assignments for single species as I have advocated for this type of study elsewhere (Emlen 1977).

RESULTS

COMPARISON OF ISLAND AND MAINLAND ENVIRONMENTS

Although the overall impression of a visitor to the Gulf of California is one of relatively uniform ruggedness, barrenness, and aridity, and although the study sites for this project were selected for similarity in topography and vegetation, the criteria used in the habitat measurements reveal considerable variation from site to site (Tables 1 and 2). For most of the vegetation parameters, however, variance was as great or greater in within-island and within-mainland series than between the two, and mean values showed no major or consistent island-mainland trends. In the scrublands woody vegetation averaged a little denser on the islands while cacti were slightly more numerous on the mainland. These ratios were reversed in the woodland habitats, where woody vegetation averaged denser on the mainland sites, presumably due to better ground water conditions associated with larger drainage basins, while cacti were denser on the islands. Annual grasses and herbs were slightly denser on the islands in the scrublands but denser on the mainland in the woodlands.

Food resources as sampled in the tree foliage invertebrates showed no major island-mainland difference (Table 2, last column). The widely variable values averaged higher in the mainland samples [86 ± 19 (SD) vs. 67 ± 30], but the second and third highest values were obtained on islands.

COMPARISON OF ISLAND AND MAINLAND BIRD COMMUNITIES

In terms of species richness, island and mainland resident communities were similar, with 20 species on the islands and 25 on the mainland (Table 3). Of the 25 species total, 8 were more abundant in the island communities, 10 were more abundant (5 found exclusively) on the mainland, and 7 were about equally common. Bird species diversity ($H' = p_i \ln p_i$) was higher on the mainland (2.54 vs. 1.97) due largely to a higher equitability ($J' = H'/H'$ max) of densities there ($J' = 0.85$ vs. 0.68). Migrants, a minor element in these desert communities at the time of our surveys in April, were more numerous on the mainland, where there were six species comprising about 7% of the total population. Only two migrant species were recorded in the island transects, where they comprised about 1% of the estimated population.

The summed density of resident birds was appreciably higher on the islands than on the mainland. The average for scrublands, the most extensive of the two surveyed habitats, was 303 birds per km^2 for the island communities and 136 for the mainland communities, a ratio of 2.23:1. In the more restricted woodland habitat, island communities had an average of 433 birds per km^2 and mainland communities 401, a ratio approximating equality.

Of the 25 resident species, 6 were widely distributed through both the scrubland matrix and the woodland patches at all sites, and 19 were specialists, restricted to or concentrated near special habitat features such as water sources, large trees, tree cacti, cactus thickets, or cliffs. The generalists as a group were numerically stronger on the islands in both scrubland and woodland with ratios of 2.47:1 in the former and 1.77:1 in the latter habitat type. The specialists, most of them woodland species,

TABLE 2. Vegetation characteristics of scrubland and desert woodland habitats at mainland and island survey sites.

	Scrublands on bajadas			Woodlands in arroyos and flats			Tree invertebrates
	Woody vegetation (percent cover)[a]	Cacti (percent cover)[a]	Herbs (density)[b]	Woody vegetation (percent cover)[a]	Cacti (percent cover)[a]	Herbs (density)[b]	Organisms per kg foliage[c]
Mainland sites							
Punta Mangles	26(4 + 18 + 4) F ≫ B = C = O J > B > S = F = L	8(tr + 8) Lam = P M = O	G > F 1	23(14 + 7 + 2)	0.2(0.2 + 0)	G > F 4	107
Bahia Agua Verde	8(3 + 4 + 1) L > O = F > C J ≫ A = R	tr(tr + O) P	G > F 18	—	—	—	81
San Evaristo	24(2 + 13 + 9) F > B = J = O J > F = B	3(tr + 3) P M > O	F > G 34	42(5 + 35 + 2)	9(1 + 8)	F > G 64	71
Mean	19(3 + 12 + 5)	4(tr + 4)	G > F 18	33(10 + 21 + 2)	5(1 + 4)	G > F 34	86
Island sites							
Isla Carmen	33(1 + 18 + 14) F > P > O J > F = B	1(tr + 1.2) P > Lop O > M	G > F 2	13(8 + 4 + 1)	14(tr + 13)	0	57
Isla Monserrat	19(4 + 13 + 2) F > O = C = L = B J > B = S	4(tr + 4) P O = Lam	G > F 30	—	—	—	97
Isla San José	60(11 + 40 + 9) F > O = C = J J > B = F = S	1(tr + tr) P ≫ Lam = Lop M > O	G > F 49	—	—	—	30
Isla Espiritu Santo	24(4 + 13 + 7)	1(tr + tr)	F > G 27	26(7 + 9 + 10)	1(tr + 1)	F > G 41	85
Mean	34(5 + 21 + 8)	2(tr + 1.5)	G > F 27	20(8 + 6 + 6)	7(tr + 7)	F > G 21	67
All sites	28(4 + 17 + 7)	2.6(0.3 + 2.3)	G > F 23	26(8 + 14 + 4)	6(0.5 + 5.5)	F > G 27	75

[a] Percent cover was determined at four or more representative points for trees (>3 m), high shrubs (1–3 m), low shrubs (<1 m), tree cacti (>3 m) and shrub cacti (<3 m) by summing the crown areas for all plants within a visually estimated 10-m (shrubs) or 30-m (trees) radius. Average crown areas were calculated for each plant type from rough measures of average crown diameters. Values for the woody vegetation cover at each site are recorded in this table as total cover, followed in parentheses by the values calculated for trees, high shrubs, and low shrubs. Values for cacti are the total cover, followed in parentheses by the values for tree and shrub cacti (tr = trace). Symbols under the percent cover values indicate the dominant (10% or more) plant species: woody plants—A = *Acacia* sp., B = *Bursera* sp., C = *Cercidium* sp., F = *Fouqueria* sp., L = *Lysiloma* sp., J = *Jatropha* sp., O = *Olneya* sp., P = *Prosopis* sp., R = *Ruellia* sp., S = *Simmondsia* sp.; cacti—Lam = *Lamaerocereus* sp., Lop = *Lophocereus* sp., M = *Machaerocereus* sp., O = *Opuntia* sp., P = *Pachycereus* sp.

[b] A rough index of herb abundance was calculated at each survey point by visually estimating the proportion (tenths) of the area within a 10-m radius of the observer that he subjectively classed, with the help of a reference chart, as dense, medium, sparse, or bare. The number of segments classed as dense were multiplied by 10; those classed as medium by 5; those as sparse by 2; and those as bare by 0. The sum of these products provided a density index potentially ranging from 0 to 100.

[c] Sum of all insects, spiders, larvae, etc. recovered from measured quantities of clipped tree twigs vigorously shaken into a large plastic container.

were slightly more numerous on the islands in scrubland situations (1.45:1) but less numerous in woodlands (0.38:1). The low woodland density on the islands is related to the absence of five and near absence of two mainland species. All 11 of the predominantly or exclusively mainland species were woodland rather than open scrubland birds.

Despite the similarity of habitat conditions most species showed marked differences in abundance between the islands and mainland (Table 3). Among the six generalist species two, the Black-throated Sparrow and the Costa's Hummingbird, were much denser on the islands (8.25:1 and 4.32:1, respectively); one, the Ladder-backed Woodpecker, was slightly denser (1.70:1); and three, the Ash-throated Flycatcher (0.87:1), the Verdin (1.16:1), and the Gnatcatchers (1.04:1), were roughly equal. None was clearly less common. Among the 14 regularly occurring specialist species (with more than 1.0 individual per km^2), 5 were found only on the mainland and 4 were definitely more common there, 3 species were more common on the islands, and 2 were about equally common.

A comparison of the summed densities for island and mainland foraging guilds suggests that the abundance or scarcity of other guild members in a community may not be important in determining a species' abundance. Thus the summed densities differed markedly between island and mainland communities in four of the eight recognized foraging guilds (Fig. 3). The island-mainland ratio (calculated as consuming biomass) for the flower probers, a one-species guild, was 4.31:1 (average for all sites in both habitat types). For the ground gleaning seed and small insect eaters, a four-species guild including the dominant Black-throated Sparrow, it was 3.33:1. Two guilds were less strongly represented on the islands, the large granivores with a ratio of 0.15:1, and the shrub-gleaning insectivores with 0.38:1. Four guilds had roughly equal representations, with island-mainland ratios ranging between 0.87 and 0.19 to 1.

Discussion

It is possible, of course, that the spring of 1977 was atypical and that the observed island-mainland differences were transitory. Assuming that they were representative, however, the striking differences in density and consuming biomass between island and mainland populations observed in this study must have a basis in one or more features of the environment or in some aspect or aspects of insularity *per se*. As my density estimates and habitat evaluations are too imprecise to permit detailed analysis of all the data, I will focus on the species and guilds with wide island-mainland differences, considering first the environmental factors of resource abundance, predation, and climate, then the nature of population responses to insular protection from interdeme gene flow and the effects of physical blocking of density-regulating dispersal movements.

Environmental Factors

Resource abundance.—Resources, particularly food supplies, are commonly regarded as the ultimate and often as the major proximate factor limiting population densities (Lack 1954), and many recent speculations on competition, displacement, ecological release, and density compensation are based on assumptions that resources are in limited supply.

TABLE 3. Land bird densities (birds per km^2)[a] on Baja California islands and opposing peninsular mainland sites.

	Scrubland habitat										Desert woodland habitat						
	Island sites					Mainland sites				Ratio	Island sites			Mainland sites			Ratio
Study sites[b]:	C	M	S.J.	E.S.	Total	P.M.	A.V.	Ev.	Total	I/M	C	E.S.	Total	P.M.	Ev.	Total	I/M
km of transect:	6.9	13.5	16.4	2.8	39.6	3.0	9.6	1.0	13.6		7.6	5.6	13.2	12.0	11.9	23.9	
Generalist residents [widely distributed species encountered at all study sites in the area (Matrix distribution)]																	
Costa's Hummingbird *Calypte costae*	4.8	7.3	24.2	17.8	14.6	5.5	1.7	+	2.5	5.84	11.0	83.0	41.5	11.1	9.8	10.5	3.97
Ladder-backed Woodpecker *Picoides scalaris*	+	2.5	7.1	11.8	4.6	+	1.7	16.6	2.5	1.84	4.3	26.7	13.8	5.5	11.1	8.3	1.67
Ash-throated Flycatcher *Myiarchus cinerascens*	12.0	9.8	40.5	+	22.2	16.6	12.1	66.4	17.1	1.30	30.5	38.5	34.0	51.1	43.3	47.3	0.72
Verdin *Auriparus flaviceps*	9.6	11.1	81.0	35.5	41.5	38.7	24.2	16.6	26.9	1.54	26.2	118.5	65.4	77.5	63.0	65.2	1.00
Gnatcatchers *Polioptila melanura* and/or *caerulea*[c]	9.6	13.4	42.5	47.5	27.2	27.7	31.0	+	28.1	0.97	52.5	94.8	70.4	67.7	64.2	65.9	1.07
Black-throated Sparrow *Amphispiza bilineata*	125.2	156.2	134.6	53.3	147.4	11.1	3.0	33.2	26.9	5.48	168.2	94.8	137.1	2.8	12.6	7.6	17.96
Total	161.2	200.4	330.0	165.8	256.5	99.6	101.8	132.8	103.9	2.47	292.7	456.3	362.2	215.8	194.1	204.8	1.77
Specialist residents [species concentrated in or restricted to special habitats or areas (Patchy distribution)]																	
California Quail *Lophortyx californicus*			11.1		4.6	+		49.8	3.7	1.27				48.5	20.9	34.7	0
White-winged Dove *Zenaida asiatica*	+		9.1	+	3.8	5.5	12.1	49.8	13.4	0.28	+	6.0	2.5	30.4	12.6	21.6	0.12
Mourning Dove *Zenaida macroura*			+		+				0	+			0	+		+	0
Roadrunner *Geococcyx californianus*					0	+		+	+	0			0	1.3	2.8	2.2	0
Gila Woodpecker *Melanerpes uropygialis*	+	1.2	28.4	+	12.1	+	1.7	16.6	2.5	4.87	4.3	26.7	20.1	15.3	30.7	22.9	0.88
Gilded Flicker *Colaptes auratus chrysoides*					0	+		+	+	0			0	1.3	11.1	6.3	0
Scrub Jay *Aphelocoma coerulescens*					0	11.1		+	2.5	0			0	+	18.1	9.0	0

TABLE 3. Continued.

	Scrubland habitat										Desert woodland habitat						
	Island sites					Mainland sites				Ratio	Island sites			Mainland sites			Ratio
Study sites[b]: km of transect:	C 6.9	M 13.5	S.J. 16.4	E.S. 2.8	Total 39.6	P.M. 3.0	A.V. 9.6	Ev. 1.0	Total 13.6	I/M	C 7.6	E.S. 5.6	Total 13.2	P.M. 12.0	Ev. 11.9	Total 23.9	I/M
Common Raven *Corvus corax*	2.5				0.5	+			+	+			0	+		+	0
Cactus Wren *Campylorhynchus brunneicapillum*					0	5.5		66.4	6.1	0			0	31.9	54.4	43.0	0
Canyon Wren *Catherpes mexicanus*				11.8	0.8	+			0	+		+	+	+		+	?
Gray Thrasher *Toxostoma cinereum*			1.0		0.5	+		+	+	+			0	7.0	1.3	4.2	0
Mockingbird *Mimus polyglottos*		1.2	16.3		7.1			+	+	+		59.3	25.2	1.3	23.7	12.5	2.03
Loggerhead Shrike *Lanius ludovicianus*	+		+		1.7			+	+	+	4.3		1.3		2.8	1.3	1.00
Yellow Warbler *Dendroica petechia*[d]					0				0			3.0	1.3			0	+
Hooded Oriole *Icterus cucullatus*			+		+	+	+		+				0	19.4		9.8	0
Cardinal *Cardinalis cardinalis*		2.5	20.3		8.8	+		+	+	+		+	+	23.6	4.2	13.9	0
Pyrrhuloxia *Cardinalis sinuatus*[d]		1.2			0.5				0	+			0			0	
House Finch *Carpodacus mexicanus*	2.5	13.4	2.0		5.8	5.5	3.5		3.7	1.59	21.9	17.8	20.1	4.2		2.2	9.31
Brown Towhee *Pipilo fuscus*					0	+		+	+	0			0	24.9	1.3	13.1	0
Total	5.0	19.4	88.1	11.8	46.3	27.7	17.3	182.6	31.9	1.45	30.5	112.7	70.6	209.0	184.1	196.5	0.36
Total residents	166.2	219.8	418.2	177.6	302.8	127.3	119.0	315.4	135.8	2.23	323.2	569.0	432.8	424.8	378.1	401.4	1.08

Table 3. Continued.

	Scrubland habitat										Desert woodland habitat						
	Island sites					Mainland sites				Ratio	Island sites			Mainland sites			Ratio
Study sites[b]: km of transect:	C 6.9	M 13.5	S.J. 16.4	E.S. 2.8	Total 39.6	P.M. 3.0	A.V. 9.6	Ev. 1.0	Total 13.6	I/M	C 7.6	E.S. 5.6	Total 13.2	P.M. 12.0	Ev. 11.9	Total 23.9	I/M
Migrants [Nonresident species present as winter or in-transit spring visitors]																	
Empidonax (sp.) *Empidonax* sp.			+			+		+						1.3	13.9	7.6	0
Phainopepla *Phainopepla nitens*						+		+						2.8	+	1.3	0
Orange-crowned Warbler *Vermivora celata*		+															
Black-headed Grosbeak *Pheucticus melanocephalus*			+	+		+		+				11.8	5.0	+	25.1	12.5	0.40
Green-tailed Towhee *Pipilo chlorurus*			6.1		2.5					+							
Lark Sparrow[e] *Chondestes grammacus*							70.9		50.0	0							
Brewer's Sparrow *Spizella breweri*								+							9.8	4.8	0
White-crowned Sparrow *Zonotrichia leucophrys*							+	+							1.7	0.7	0
Total	0	+	6.1	+	2.5	+	70.9	+	50.0	0.05	0	11.8	5.0	4.2	50.5	26.9	0.19

[a] A + in the data columns indicates the species was detected in the area but not recorded on the transect counts. A + in the ratio columns indicates presence on the islands and absence on the mainland.

[b] C = Isla Carmen, M = Isla Monserrat, S.J. = Isla San José, E.S. = Isla Espiritu Santo. P.M. = Punta Mangles, A.V. = Bahia Agua Verde, Ev. = San Evaristo.

[c] Two species of gnatcatcher not always distinguishable in the field are found in the area (Grinnell 1928, Banks 1963).

[d] Yellow Warblers and Pyrrhuloxias, although not recorded on the mainland in this study, are known to occur in the area.

[e] The Lark Sparrows at Bahia Agua Verde were in a single roving flock and the calculated density value is probably unrealistically high.

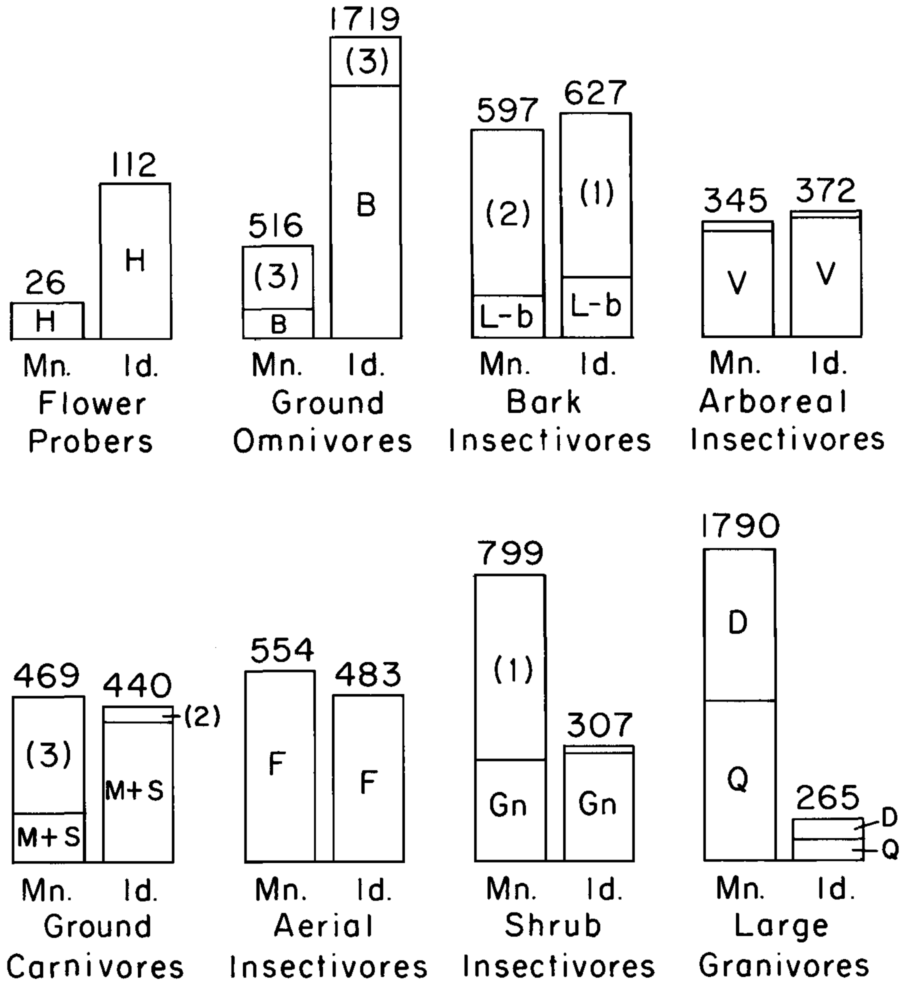

Fig. 3. Consuming biomass (see text) of the eight land bird foraging guilds on the Baja California mainland and islands. B = Black-throated Sparrow, Q = California Quail, D = White-winged Dove, M = Mockingbird, S = Loggerhead Shrike, V = Verdin, Gn = Gnatcatchers, Lb = Ladder-backed Woodpecker, H = Costa's Hummingbird, F = Ash-throated Flycatcher. Values in parentheses are the number of secondary species in the guild. Body weights for the consuming biomass values were taken from various sources including, notably, Miller and Stebbins (1964).

Resources were only roughly evaluated in this study, but no differences that could begin to account for the widely divergent island-mainland density ratios were detected. The sites were selected with specific attention to similarity in the vegetation and topography, presumed basic determinants of resource abundance and availability, and the subsequent measurements supported the correctness of these selections. The abundance of one resource base, that of the tree foliage gleaners, was measured and found to be roughly similar in the two situations. Seeds and small insects on the ground surface, the food base for the highly divergent ground omnivore guild, were not measured, but the abundance of annual grasses and forbs, the primary source of these food materials, was slightly less on the islands (Table 2), where the small ground-feeding omnivores were more abundant (Fig. 3). The correlation coefficient for grass-forb abundance vs. terrestrial omnivore biomass through the seven sites of the study was negative ($r = -.450$, $P = 0.31$).

The concept of density compensation and competitive release on islands with few species (Crowell 1962, MacArthur et al. 1972) is based on three assumptions: a) that the communities are resource regulated, b) that the niche space available is essentially filled to capacity in each case, and c) that the supply of resources is similar on the islands and mainland. A prediction of this model is that if and when these three qualifications are met, the total consuming biomass of birds in a foraging guild will be similar in the two situations, a reduced number of species in one situation permitting a compensatory increase of individuals in one or more of the persisting species. The third assumption of resource similarity appears to be reasonably supported for the Baja California island-mainland situation by my vegetation measurements. The large differences in consuming biomass seen in Fig. 3 therefore suggest that species in at least some of the foraging guilds are not resource regulated, and/or that some of the niche spaces are not filled to capacity. Errors arising from the crudeness of my guild categorizations and assignments and from the omission of non-avian consumer organisms are unfortunate but probably not great enough to invalidate these conclusions.

Looking at specific cases (Fig. 3), the Black-throated Sparrow with its 8.25:1 island-mainland ratio (mean for all sites in the two habitats—Table 3) faced nearly as much competing biomass on the islands (three additional species and 277 g of consuming biomass per km^2) as on the mainland (three species with 341 g per km^2). The Costa's Hummingbird with a 4.31:1 island-mainland ratio is the only regular flower prober on the islands or the mainland, and its only important part-time competitor, the Verdin, is also better represented on the islands (CB = 366 g and 316 g per km^2, respectively). The high number of Ladder-backed Woodpeckers on the island (1.70:1) could conceivably be attributed to density compensation, as there was only one other woodpecker species on the islands and two on the mainland; the biomass of the island competitor was slightly less (CB = 452 g per km^2) than the combined biomass of the two mainland competitors (494 g per km^2).

Among the specialist species with high island densities, the House Finch with a 4.39:1 ratio is a small ground seed and insect forager contributing to the already unbalanced ratio of this guild, as discussed above. The other two, the Mockingbrid and the Loggerhead Shrike, with ratios of 2.58:1 and 2.31:1, respectively, belong to the ground carnivore guild, which is otherwise better represented on the mainland (CB = 46 g and 315 g, respectively) and thus may reflect density compensation.

In addition to replacing reduced diversity with increased density of existing species on islands, resource-based compensation theory predicts that the niches of mainland species that are absent or rare on islands should be at least partially filled there by an ecological expansion of one or more of the island species. I found no evidence for such an expansion into the most obvious vacant or underexploited niches on the islands, the shrub-cactus niche of the mainland's Cactus Wren, or the large seed province of the mainland's California Quail and White-winged Dove populations. The quail was fairly common on the one island where it occurred, apparently a recent arrival; the dove was found at three of the four island sites but only in small numbers.

Predation.—Predators when abundant may operate as a limiting as well as a simple mortality factor on land bird populations. Avian predators were uncommon on both the islands and the mainland during the period of our study. Two hawks were seen on the mainland and three on the islands in 17 days of fieldwork. Shrikes were slightly more common on the islands; roadrunners and jays were absent on the islands (see Table 3). Ring-tailed cats (*Bassariscus astutus*), widely but sparsely distributed on the mainland, were present on at least one of the islands, San José. Small rodents were apparently widely distributed and comparably abundant at all sites. Lizards, at least potentially significant as nest predators, were appreciably more common on islands (Case 1975, personal observation). I have no way to appraise these pressures, but I see no evidence that the pressure was significantly lighter on the islands or that it was distributed in a way that could account for the assortment of density ratios recorded for the various species and guilds.

Climate.—Climatic differences between islands and neighboring coastal areas on the mainland cannot be discounted entirely as factors potentially affecting population density. However, I do not regard them as providing explanations for the large differences and irregular patterns of density distribution recorded in this study.

Water.—Fresh water is a rare commodity in this desert country, especially on the islands where catchment basins are small and arroyos steep and narrow. The low island densities of doves could be due to this factor, but House Finches, supposedly dependent on free water (Salt 1952) were substantially more abundant on the islands.

GENETIC FACTORS

Levels of adaptedness to local conditions.—The hypothesis of mean population underadaptedness proposed for the low densities of land birds in Florida *vis a vis* Bahama island pinelands (Emlen 1978) suggests that the southern Florida populations of widely distributed species were underadapted to their subtropical environment as a result of the swamping of incipient adaptations for local conditions by the annual influx (post-fledging dispersal) of birds carrying genes and gene combinations selected for other (more northern) conditions. Bahama populations were considered to have been shielded from this gene flow by the water barrier of the Florida Straits. Baja California should be and apparently is less susceptible to such peninsular swamping since it has more and higher barriers to gene flow. This is reflected in the large amount of subspeciation along the peninsula (19 of the 25 species considered in this study—American Ornithologists' Union 1957), and the high incidence of secondary centers of dispersal (Grinnell 1928).

In my Florida-Bahama comparison I also considered an interpatch gene flow hypothesis in explanation of the low population densities in northern Florida (Emlen 1978). In this hypothesis populations of a species in an environmentally patchy area were viewed as being prevented from evolving full adaptation for the environmental conditions of their patch by the continuing influx of genotypes from neighboring patches with slightly different characteristics. Populations in a relatively non-patchy area such as Grand Bahama, where more than 95% of the forested area is monotype pineland, would theoretically escape much of the constant dilution of adaptedness to which these Florida populations were subjected. This hypothesis could fit the Baja California setting, where the mainland has a wider assortment of accessible habitat and climatic patches in its highly dissected mountainous interior than do the islands.

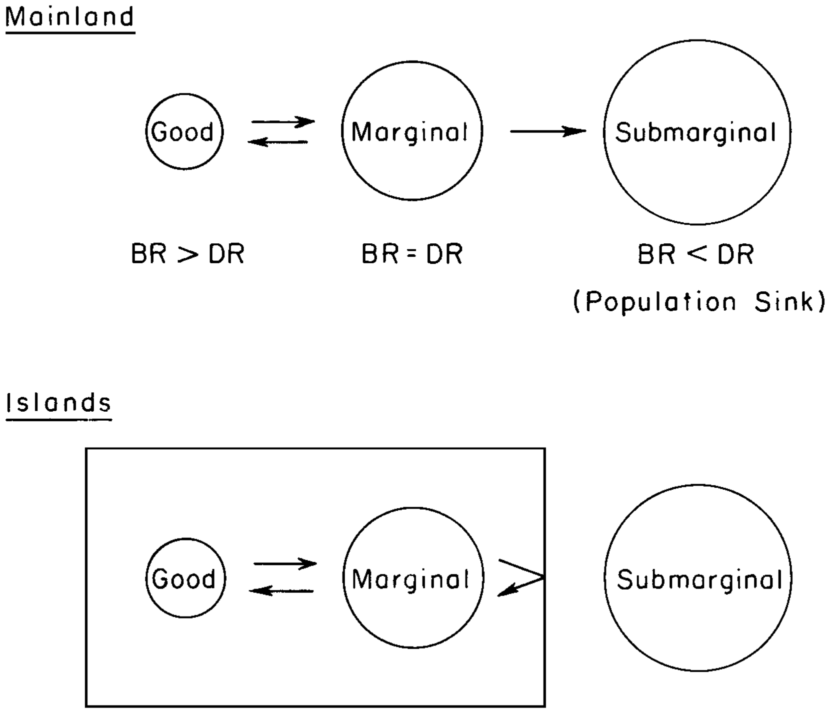

Fig. 4. Diagrammatic representation (hypothetical) of habitat availabilities (size of circles) and population movements (arrows) in mainland and island situations in the central portion of a species' range, where "good" situations are available for reproduction of population surpluses. BR = Birth rate, DR = Death rate.

SOCIAL FACTORS AND ISLAND BOUNDARIES

Physical constraints on normal dispersal movements.—A familiar but often neglected 'social saturation' model of population regulation (Howard 1920, Kluyver and Tinbergen 1953, Brown 1969, Emlen 1977, Verner 1977) assumes an adequate supply of resources and visualizes territorial behavior and other forms of local aggressiveness as initiating a dispersal of socially subordinate individuals out into inferior situations where survival is relatively poor and reproductive success curtailed. In this model densities in good areas are reduced below local, resource-determined carrying capacities by the socially induced emigration, while populations in marginal and submarginal areas are augmented, perhaps sustained entirely, by the influx of birds displaced from good areas. The pattern is depicted graphically in the upper part of Fig. 4.

Islands, with smaller residual areas of marginal and submarginal habitat than mainland areas, and with water barriers on all sides to block the escape of socially displaced birds, may under the same conditions experience a buildup of overall density as individual territories are squeezed or invaded under the pressure of expanding numbers. Territories have been recognized as resistingly compressible by most investigators since Huxley (1934), and a substantial 'silent minority' of nonterritorial floaters or of helpers may accumulate in and between territories at high densities (Stewart and Aldrich 1951, Smith 1978). This hypothetical island situation is depicted in the lower part of Fig. 4. The general pattern resembles that described by Krebs et al (1969) for populations of voles in large outdoor enclosures as the "fence effect" and discussed in a broader context by MacArthur (1972) as the "Krebs effect."

Conditions in Baja California provide the essential requirements of this model for the Black-throated Sparrow. The islands, despite their proximity to land, are effectively insulated against escape as indicated by the evolution of distinct breeding races on one or more of them (Banks 1963). They are mountainous, but the extent of low quality habitats for population overflow is far less than that available to mainland populations. Patterns of density distribution through the habitat types on the islands and mainland also support the fence-effect hypothesis: on the mainland where densities were low, sparrows spilled over into the woodlands from their preferred scrubland habitat only slightly (7.6 birds per km^2 in the woodlands, 26.9 in the scrublands) while on the islands under presumably high population pressures they were nearly as dense in the woodlands as in the scrub (137.1 and 147.4 birds per km^2, respectively). Unfortunately I have no data for the barren upland slopes. The same pattern of greater overflow into secondary habitats is indicated, though less strikingly, in the Costa's Hummingbird, a woodland species in which the secondary scrub habitat had 35% as many birds as the woodlands on the islands, 24% as many on the mainland.

The fence effect need not and probably does not apply to all of the 12 shared species with higher island densities; it obviously does not apply to the six with higher mainland densities. I will not attempt to analyze each case, but it is noteworthy that all but one of the six with high mainland densities are, like the five that do not reach the islands, woodland species (i.e. species that favor the smaller and more fragmented of the two available habitat types). Perhaps these woodland species, with larger available areas of secondary habitat for overflow, are more prone to disperse and thereby avoid some of the territory compression and density buildup conjectured for the scrubland species. Also, the position of the woodlands at the high productivity end of the habitat gradient should serve to enhance the buffering qualities of the alternate habitat (the scrublands) for the woodland species, and particularly the woodland specialists, against the rigid limits to dispersal presented by the island boundaries.

The fence effect hypothesis is essentially untested at this point. Intense field studies comparing social interactions, mating patterns, and breeding success in these island and mainland populations could presumably answer many questions posed by the concept.

LOW ISLAND DENSITIES

The genetic swamping and density dispersal mechanisms described above both relate to density regulation in mainland situations and are not applicable to species with low island densities. Low colonization rates in combination with relatively high extinction rates (MacArthur and Wilson 1967) may provide the best explanation for cases of low island densities.

All of the nine species absent from or with reduced population densities on the islands (island-mainland density ratios $<0.75:1$) were woodland species and thus closely restricted in the number and size of good habitat patches, especially on the islands. Demes restricted in this way are vulnerable to extinction by stochastic processes even under conditions of fairly frequent recolonization from nearby sources. I therefore tentatively attribute the apparent absence of the Roadrunner, Gilded Flicker, Scrub Jay, Cactus Wren, and Brown Towhee to the scarcity and small size of the wooded arroyos and alluvial fans on the islands. The California Quail is almost certainly a recent colonizer (natural or introduced) on the one island where it was found (San José). The White-winged Dove may owe its presence on three of the four surveyed islands to a recolonizing ability, associated with strong flight and wide-ranging habits. The two remaining species, the Hooded Oriole and Gray Thrasher, were each seen only once on the islands, individuals that may have been unestablished stragglers from the mainland.

ACKNOWLEDGMENTS

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COMMENTARY

THE AMATEUR IN ORNITHOLOGY[1]

HAROLD F. MAYFIELD[2]

NO branch of biology has felt the hand of the amateur like ornithology. Other branches have had amateur participation, but always more limited in scope. In botany interest has centered mainly on wildflowers, in entomology on butterflies and moths, and in malocology on shells, while in ornithology the influence has been pervasive.

From ancient times inquiring minds have found birds attractive subjects for study. Beyond all other creatures on earth, birds capture the eye with bright colors, the ear with music, and the imagination with the power of flight. Unlike many mammals and other forms of life, most of them are active in daylight in places where they can be seen and studied easily. For these reasons scholars long ago labeled ornithology the "scientia amabilis." Professional ornithologists usually have been captivated by birds long before they thought of themselves as biologists, and in this respect they differ from many of their colleagues, few of whom, for example, came to science through their love of fruit flies or rats.

Until the first quarter of this century ornithology was mainly the province of amateurs in America as well as in Europe. Before the invention of prism binoculars near the beginning of the century, most field observation took place down the barrel of a shotgun. Not surprisingly, sport hunters and taxidermists were prominent among those people with more than a casual interest in birds. Physicians calling on patients in horse-and-buggy days, with a gun under the seat and dissecting instruments at hand, were well situated to collect and preserve specimens. Clergymen and teachers, as the resident scholars in many communities, became also the bird experts. The Wilson Ornithological Society sprang from correspondence among teen-age egg collectors, and even the great professionals like Ridgway and Chapman often had no university training in biology.

In modern times the number of professionals, along with employment opportunities for them, has grown enormously, and the number of amateurs has fully kept pace. The literature has expanded accordingly and has reflected a widening spectrum of interests, from the superficial to the profound, loosely identified with "ornithology." To some professionals this brings a measure of embarrassment, lumping them with company they would prefer to disavow. Fieldwork is fun, and the public is not always able to distinguish what is purely recreational. In some quarters James D. Watson was dismissed lightly as a mere bird watcher before the elucidation of the double helix brought him the Nobel Prize in 1962. In the peck order of human society, indoor workers often look down on outdoor workers, and indeed, from the vantage point of controlled conditions in the laboratory, the outside world is deplorably untidy. Very recently "natural history" seemed headed for oblivion until restored to respectability in the name of ecology.

Although the scientist and the bird watcher may be hard to distinguish from a

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distance, the importance of ornithology to biology can no longer be questioned. Birds are the best studied class of vertebrates, and ornithology has led in many of the advances of biology. Observation of birds helped Darwin put the pieces together in arriving at the concept of evolution, and many recent refinements in evolutionary theory have come out of field studies of birds. Widespread recognition of the importance of ornithology came in 1973 when Konrad Lorenz and Niko Tinbergen shared a Nobel Prize for their pioneering role in the new discipline of ethology. It was no accident that the first Recovery Plans submitted under the Endangered Species Act of 1973 dealt with birds. And now a public far beyond the scientific community has become alerted to the significance of birds as indicators of the quality of the human environment. May I suggest that much of the vigor of ornithology has come from the amateur infusion?

The force of the amateur component is expressed in many ways. Most obvious is the financial support to institutions, scientific societies, and their publications. Notable especially in times of crisis is their function in educating the public and the legislatures on such issues as conservation and the teaching of biology.

Although research in this field as in all others is steadily becoming more sophisticated, amateurs continue to make major contributions to the advancement of knowledge. The Brewster Memorial Award for the "most important recent work on the birds of the Western Hemisphere" has been conferred 45 times beginning in 1921, and on one-fourth of those occasions it has gone to people not earning a livelihood as biologists. Although the last quarter of a century has brought a vast increase in the number of professionals and consequently a relative decline in the prominence of amateurs, Kenneth C. Parkes has calculated that 12% of the papers in the four leading American ornithological journals in 1975 were written by people not employed in biology (*in* J. R. King and W. J. Bock 1978, Workshop on a National Plan for Ornithology, Final Report, Panel on the Role of Ornithological Societies and the Amateur, Appendix vi). The size of this amateur element and the eagerness of its members are revealed in answers to a questionnaire addressed to "avian biologists" nationwide. In their responses 48% identified themselves as amateurs, and 90% of these expressed an interest in participating in research (King and Bock op. cit., p. 8).

In research the amateur brings to ornithology additional richness through diversity. Not seeking government grants nor academic status, the amateur is free to tread the byways of inquiry, without pressure for immediate results or conformity to current themes. In ornithology important problems are still accessible to the individual using his own resources. Discoveries are still possible without profound knowledge or elaborate equipment. The very complexity of biology has left unsolved mysteries within reach of any imaginative person. Compare, for example, mathematics, where basic simplicity and clarity has allowed centuries of progress to be piled layer on layer until the structure is so elaborate that mere comprehension of relevant questions is beyond the novice; or atomic physics and astronomy, where the equipment is so far beyond the reach of the individual that even the largest of institutions acquire it only through consortia.

Although solid work is performed by some amateurs on their own, the full potential of the whole group will not be developed without professional collaboration. This will become more important in the future as increasing specialization and depth threatens to move the frontiers away from the avocational ornithologist. In field observations many amateurs have skill few professionals can match, and their forte is the gathering of data, but the full value of their work will not be realized without professional assistance to see the facts within the larger conceptual framework of biology. Thus, the professional touch is often vital in pinpointing the information needed, planning the studies, and analyzing the results.

Some aspects of ornithology would seem to depend on amateur assistance indefinitely. It is difficult to imagine large-scale investigations of populations, migration, or reproductive success without the help of volunteers. The annual Christmas bird counts of the National Audubon Society have 30,000 people taking part and paying for the privilege. Selected volunteers work nearly 2,000 routes for the Breeding Bird Surveys coordinated by Chandler S. Robbins of the U.S. Fish and Wildlife Service. The greatest data bank on avian reproductive success in America is accumulating at the Cornell Laboratory of Ornithology mainly through the work of amateurs. These are some of the more conspicuous American examples, but the potential of amateur mobilization has been demonstrated best by the British Trust for Ornithology, whose projects already have included preparation of an atlas of breeding birds, coordination of all bird banding in the country, special censuses of farmlands and estuaries, and the accumulation of vast amounts of nesting data.

Perhaps the most important contribution of the amateur, and assuredly one that will not dwindle in the years ahead, is the nurture of young scientists. Nearly every scientific career in ornithology has been strongly influenced by early association with an enthusiastic amateur. Birds catch the imagination of the susceptible child and then the spark is fanned by an adult hobbyist. In each locality amateurs usually lead the bird hikes, prepare the check-lists, organize the bird clubs, and write for the newspapers. Not all of them contribute to the scientific literature but nearly all of them read some of it. A case in point is a small-town biology teacher who proudly counts among her former students five Ph.D.'s in biology, including at least two fellows of the American Ornithologists' Union.

The opportunity represented by amateurs was the subject of discussion in February 1978 when about 30 invited people met at Ithaca, New York, under the auspices of the National Audubon Society and the Cornell Laboratory of Ornithology. These people were unanimous in believing this was a great and growing resource that had scarcely been tapped for its potential value. Although a few amateurs carry out independent research of professional caliber, everyone agreed that most of this energy and enthusiasm could be harnessed and enhanced only with professional leadership.

A similar view was supported and amplified by the Workshop on a National Plan for Ornithology reporting to the National Science Foundation and the American Ornithologists' Union in March 1978 (King and Bock op. cit.). This group urged that the professional societies become prime movers in raising the participation of amateurs, local bird clubs, and nature centers. The recommendations pressed for new initiatives, with attention to better communications, training, and cooperative projects. To move in this direction, leaders of the ornithological societies in editing their journals and planning their meetings should give more thought to the breadth of the audience and accordingly direct a proper share of communications to the interested layperson. This calls for selecting a balanced fare and minimizing jargon and obscurity in presentations. All of this will require special effort in the face of forces pushing in the opposite direction.

In ornithology a symbiotic relationship has existed between the amateur and professional. Societies in the field, increasingly dominated by professionals, should recognize in the amateur segment a beneficial force. To preserve a fruitful relationship, they must continue to serve this portion of their constituency also. No other branch of science has this rich resource.

In arguing that ornithology is fortunate never to have drawn a clear line between the amateur and professional, I draw support from the view of science expressed by Jacob Bronowski in "A Sense of the Future" (1977, Cambridge, Massachusetts, MIT Press, p. 4): "Let no one tell you again that science is only for specialists; it is not. It is no different from history or good talk or reading a novel; some people do it better and some worse; some make a life's work of it; but it is within the reach of everybody."

ARETAS ANDREWS SAUNDERS, 1884–1970

(From a photograph taken in 1933)

IN MEMORIAM: ARETAS ANDREWS SAUNDERS

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"Aret" as he was called by his wife Grace and "Tubby" by his intimate boyhood friends, wished that he could be known as a naturalist. Saunders tried to learn and record as much as he could about birds, plants, insects, mammals, and other organisms in the field in order to clearly understand their relationships. He had an insatiable drive to observe plants and animals throughout the year, and to continue this year after year. He devised a unique method of recording bird song, leading to the publication of his useful and original *Guide to Bird Song*. Beyond that, however, he accumulated a vast amount of data on the daily and seasonal onset and cessation of singing, the time and site of singing, and variations in individual songs.

He was outstanding as a disciple of outdoor behavior study. He walked slowly and softly and as a result, saw much more. He had the patience to spend countless hours of observation in the blind or behind the camera. He felt strongly that birds should not be classified purely on the basis of morphological characteristics, but that behavioral characteristics such as singing and other actions should also be considered.

Aretas Andrews Saunders, the son of George A. and Isabel Andrews Saunders, was born in Avon, Connecticut, near Hartford, on 15 November 1884. During his boyhood he lived in Hartford and New Haven, where his father owned a bicycle store. His early interest in all phases of nature was encouraged by his Aunt Beth who gave and loaned him books that enabled him to identify plants and birds. His lifelong interest in mushrooms, begun in 1906, was aided by Hamilton Gibson's book on edible and poisonous fungi. Wherever he lived he explored the surroundings on foot or bicycle, becoming very familiar with the natural history of the region. He attended Yale University and Yale School of Forestry, graduating in 1907. During his college career, he took time off to work on an experimental rubber plantation in Nicaragua in 1905, and later on a forestry project in Alabama.

After graduating from Yale, he joined the U.S. Forest Service, spending several years in the Lewis and Clark, Gallatin, and Deer Lodge National Forests in Montana. His lifelong habit of recording copious natural history notes already well established, he observed and collected birds during his residency in Montana. The result of this effort was his book, *Birds of Montana* (1921).

In 1912 he left the Forest Service and began his career as a teacher in New Haven, Connecticut, teaching general science, geometry, physics, and trigonometry. For two summers he was instructor in ornithology at the Summer Biological Station at Flathead Lake, Montana. In 1914 he began teaching biology at Central High School in Bridgeport, Connecticut, where he taught until 1949. He married Grace Adams in 1916. They had a son, Stanley, who became an engineer for Eastman Kodak. During his early years as a teacher, Saunders worked in the summers as a farm worker, express company checker, and White Pine Blister Rust disease eradicator. He was a Sergeant in the Home Guard during World War I. In 1921 he began summer work at the Roosevelt Wildlife Forest Experiment Station in the Allegany State Park, a division of the New York State College of Forestry. His observations resulted in another publication, *Birds of Allegany State Park*. He also studied the birds of the marsh area of central New York and of the Adirondacks. During the

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summers of 1927 to 1940, he was instructor of ornithology at the Allegany School of Natural History. His *Guide to Bird Song,* was published during this period, as were *Butterflies of the Allegany State Park, Breeding Birds of the Allegany State Park,* and *Variations and Movements of the Red Eft.*

Saunders' background in music was important to his later efforts to describe bird songs. He learned on his own to play the mandolin and violin at an early age and later the flute and recorder. In church, he always volunteered for choir duty, offering his services singing bass or tenor as the situation dictated, and he sang in the Bridgeport Oratorio Society for years. After unsuccessfully attempting to record bird song using the traditional musical scales, he resorted to using a small tuning fork that he carried in his vest pocket. After hearing a bird song he plucked the fork, held it to his ear, and tried to approximate a position of the first note on the musical scale. He used a stop watch for accurate timing. These efforts resulted in the development of his unique method for pictorializing the sounds of birds in his *A Guide to Bird Songs.*

Saunders was also an accomplished artist. In his notes there were many sketches illustrating his observations. He obligingly covered the boards of other teachers with accurate full color drawings of regional birds, which often became permanent displays. Through the years, he gave many "chalk" talks on birds to varied groups, where he sketched on a board or paper the bird under discussion. Dominick D'Ostilio, a high school student who later illustrated Saunders' book *The Lives of Wild Birds,* said, "I don't know why he asked me to do it. He could easily have done the job himself." Knowing Saunders' interest in young people, it is not difficult to understand the choice.

Although Saunders had a pudgy figure, he was in good physical condition most of his life except for periodic troubles with asthma. Around 1938 he discovered that he was losing the ability to hear high notes. He spoke of watching a bird throw its head back with open mouth and vibrating throat and obviously sing its song, but did not hear it. This was disturbing to him, as he found that his migratory dates for certain birds that were first detected by song were later than in former years. He had me accompany him on certain dates to specific areas where certain birds had been recorded in previous years. My job was to hold my finger up as soon as the song began and drop it at the end. The most interesting example was the Blackpoll Warbler, which sings a high pitched song with notes on the same scale. The song starts softly with each succeeding note louder until the middle loudest note, after which the notes recede in loudness. Most of the time, he would hear the middle loudest note and no more.

During World War II, Saunders corresponded with many of his former students, stationed throughout the world. He acted as a liaison, informing all as to conditions at home and the whereabouts of others. In his letters, he expressed his philosophy of life and living repeatedly. Dominick D'Ostilio is eloquent in his review of Saunders' way of sharing his experiences:

> . . . that one should have pleasure and happiness in the study of living things. This is what he imparted in his narration, illustration, discussion approach to teaching. And he made things alive. There is no way to measure the total effect he had upon his students. They loved him for his congeniality and for his enthusiasm. His was the way to encourage others to get closer to nature—to know nature. His was the way of appreciating beauty in nature and finding value in

life. Again and again these letters bring out, "I'm all for the study of things that are alive." . . .

And what had he expressed about the knowledge we gain? You'll find it in the preface to his *A Guide to Bird Songs* (pp. v–vi):

> "I hope that those who use this book will find, thereby, even greater pleasure in the studies of live birds; that some of them will go on from bird listing to bird watching, and will perhaps find pleasure in contributing something to our greater knowledge of wild birds and their ways. If, among these, there are some who have a special ear for bird songs, I hope that they may try the detailed study of such songs, not merely for the purposes of identification, but to make contributions to a greater knowledge than we now possess."

And what has he expressed about the search for knowledge? You'll find this in a quotation from Henry Van Dyke which Mr. Saunders used to introduce his *The Summer Birds of the Northern Adirondack Mountains*:

> "You shall take pleasure in the time while you are seeking, even though you obtain not immediately that which you seek, for the purpose of a journey is not only to arrive at the goal, but also to find enjoyment by the way."

And what of his personal statement with respect to meaningful education? You'll find it in his "Suggestions Concerning Policies for the Allegany State Park," New York State Museum Handbook 17, on pp. 386–387:

> "In fact, education, rightly considered, is a recreation, and that man who has discovered this, and makes his recreation educational, has found a source of true happiness. To give to more and more persons this source of happiness is a far greater achievement than to give them mere recreation alone."

Mr. Saunders lived as that source of happiness in showing the way to more and more of his students.

In 1949, when he retired from teaching and moved to Canaan, Connecticut, he was awarded a grant from the Philosophical Society to study bird song. His studies concentrated upon certain birds in Florida, Georgia, North Carolina, West Virginia, Minnesota, Louisiana, North and South Dakota, and Oklahoma. The results of his studies were never published.

Saunders became an Associate of the American Ornithologists Union in 1906, a Member in 1920, and a Fellow in 1950. In 1954, he was a guest lecturer in ornithology at Cornell University. The Bureau of Sport Fisheries and Wildlife awarded him in 1961 a citation for reporting, for use in scientific investigations, observations on the distribution, migration, and abundance of North American birds for 35 years during the period 1911 to 1953. The National Audubon Society established an Aretas A. Saunders Memorial Fund in 1972.

Later in life, he developed Paget's disease—a progressively increasing porosity of the bone. Although it only affected the shin bone of one leg, it required him to use crutches. He had to give up driving. Nevertheless he persisted as best he could in getting out to observe nature. With the death of his wife Grace, 80, in 1964, Saunders lost interest or found that he did not have the energy for maintaining his lifelong habit of observing. He remarried within a year to a widow living next door. His second wife, Margaret, tried to make the last 5 years of his life comfortable. He died 7 April 1970 at the age of 85, after surgery on a broken hip caused by a fall.

I am indebted to Stanley Saunders who made available his father's unpublished autobiography *On Being a Naturalist* as well as other background material. In his possession at 195 Weston Road, Rochester, New York, are large amounts of his father's notes, diagrams, and tabulations. In addition I am grateful to Richard J. Clark, Dominick D'Ostilio, and Stephen W. Eaton for their assistance.

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SHORT COMMUNICATIONS

The Status of *Agelaius forbesi* Sclater

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During a visit to northeastern Brazil in 1880, W. A. Forbes encountered an all-black icterid that he described as locally distributed, but "common where it occurred, flying about in large flocks, like Starlings, in the neighbourhood of sugar-plantations. They were rather wary and not easily approached. The Brazilians called it 'Arumará'" (Forbes 1881: 340). Forbes mentioned having seen these birds at two localities in Pernambuco, Macuca and Vista Alegre, but stated that he collected only a single female, which he considered "apparently referable to a small form of" *Aphobus* (now *Gnorimopsar*) *chopi* (Vieillot). Sclater (1886: 345) noted that this specimen, which he considered to be immature ("Jr." of Sclater), was *not* referable to *chopi*. One the basis of bill shape he decided that it "must either be placed in *Agelaeus* [now spelled *Agelaius*] or in a genus by itself." He thereupon named it *Agelaeus forbesi,* sp. nov. Neither Forbes nor Sclater mentioned the actual provenience of the holotype, and Sclater erroneously gave the year of collection as 1881, an error perpetuated by Warren and Harrison (1971: 186). The specimen in the British Museum (Natural History), where Short has examined it, is labeled "Macuca," a locality visited by Forbes only in September 1880 (Forbes 1881: 322–323).

Pinto (1944: 577, footnote) erred in believing that Forbes *collected* this new species at two localities: "Os exemplares tipicos, colecionados em Macuca e Vista Alegre . . . ." Meyer de Schauensee (1966: 435) listed the Vista Alegre locality as a "sight" record of *forbesi,* but there remains a strong possibility that most of the birds seen by Forbes at both Macuca and Vista Alegre may have been, as he stated himself, *Gnorimopsar chopi,* an abundant and gregarious species. On the other hand, published descriptions of the ranges of *G. c. chopi* and *G. c. sulcirostris* appear to leave a small hiatus in northeasternmost Brazil, including Pernambuco. As there have been major habitat changes in the coastal forest belt of Pernambuco, both before and since Forbes' time, we may never know just which blackbirds he did see in such numbers at Macuca and Vista Alegre.

Hellmayr (1937: 181) corrected Sclater's identification of the holotype of *forbesi* as immature by describing it as an "adult bird just finishing its annual molt." Although the collector had marked the specimen label female and repeated this in his published account of its capture, Hellmayr questioned this, apparently influenced by his belief that *forbesi* was indeed referable to *Agelaius* in spite of some morphological differences—Hellmayr apparently thought that if it were an *Agelaius* female, it should not be black. Hellmayr also reiterated that the species was known from the holotype only.

So the situation stood until the early 1960's. In 1963 Parkes began work on his revision of the South American *Agelaius cyanopus* (Parkes 1966). While at the American Museum of Natural History, he found in that museum's "First Series" (a sample series of one or a pair of almost every New World species and subspecies) a *second* specimen of *Agelaius forbesi,* bearing no data other than "Pernambuco," originally identified and catalogued as "*Aphobus chopi.*" Although this specimen came to the American Museum with the Lawrence collection, there is no mention of it in any of the published works of George Lawrence. It was later reidentified and initialed by the late W. DeWitt Miller as "*Pseudagelaeus forbesi,*" and somebody else later pencilled out the "*Pseud-*" part. We cannot help but admire Miller's perceptiveness in identifying this specimen, but apparently he, like Lawrence, never published the record. In conversations with Eugene Eisenmann and Charles O'Brien, Parkes called attention to the rather mysterious possession by the American Museum of Natural History of a second specimen of a form supposedly known only from the holotype in the British Museum. Nothing seems to be known about the origin of Lawrence's specimen.

A few years later, Eisenmann and Parkes were serving as consultants during the final stages of preparation of Meyer de Schauensee's South American checklist (1966). The question of the status of *forbesi* was raised again at that time. As the specimen in the American Museum showed certain characters that seemed to combine aspects of *Agelaius* with those of *Gnorimopsar,* Parkes raised the possibility that the

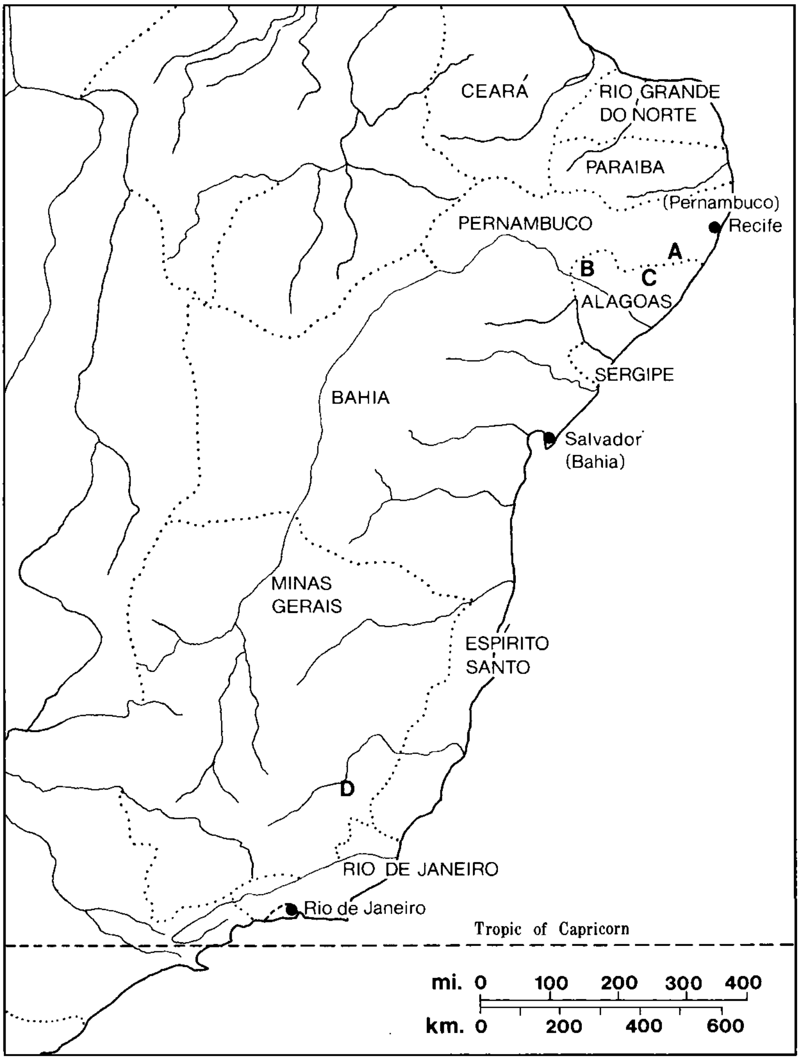

Fig. 1. Localities in Brazil where *Curaeus forbesi* has been collected. A. Macuca (type locality); B. Usina Sinimbú; C. Eugenho Riachão; D. Raul Soares.

two known *forbesi* might represent hybrids between those genera; *Agelaius* had already been shown to be one parent of an intergeneric hybrid (Selander and Dickerman 1963). On geographic grounds, the *Agelaius* parent of such a putative hybrid would have to have been *A. ruficapillus*. As it would be impossible to predict the color and pattern of such a hybrid, and especially of a female, one had to go chiefly by the structural characters, which did seem somewhat intermediate between *Agelaius* and *Gnorimopsar*. The brownish black color would not be incompatible with such a parentage. Eisenmann agreed that this was at least a possible explanation for the two known specimens of *forbesi,* and so informed Meyer de Schauensee, who added this theory in a footnote in proof.

The timing was unfortunate. In April 1967, just after the publication of Meyer de Schauensee's book, Parkes spent a day at the Los Angeles County Museum. To his amazement, he found a *series* of *forbesi*, mixed in with and identified as *Gnorimopsar chopi*. The specimens were from two areas of Brazil, one of them 1,400 km southwest of the type locality of *forbesi*. Parkes did not have time to measure the specimens, but wrote a note to the then curator, K. E. Stager, suggesting that these, the first known specimens of *forbesi* with adequate data, be called to the attention of E. R. Blake, then working on the first draft of the family Icteridae for the "Peters" Check-list. Stager sent Blake several of the specimens, and meanwhile Parkes, using the New York specimen and knowing that the hybrid theory was no longer tenable, was attempting to reassess the relationships of *forbesi*. On 9 August 1967, Parkes wrote Blake that he had restudied *forbesi*, and included the following sentences: "As you well know, there are a number of icterid genera with very large and very small species (in fact, there is a dramatic difference between the largest and smallest *sub*species of *Molothrus bonariensis*). Kick around the idea of *forbesi* being a small representative of *Curaeus*. I don't like the idea of that feather texture in *Agelaius*, but a small *Curaeus*? How about it?" Blake responded on 11 August 1967: "On study, *forbesi* simply can't be *Agelaius* × *Gnorimopsar*. On going over them again just now I'm virtually convinced the answer is, and can *only* be *Curaeus* as you suggest. Feather texture just right and *also* the bill, especially as to the flattened area on ridge of culmen. It's a natural but will look into it further."

Blake altered the manuscript for the "Peters" Check-list to include *forbesi* in *Curaeus*, and it so appeared in the published version (Blake 1968: 183). Although Blake included one of the localities from the previously unreported series in Los Angeles (Raul Soares, Minas Gerais), neither he nor anyone from the Los Angeles County Museum ever published an account of the rediscovery of the species, nor the rationale for transferring it from *Agelaius* to *Curaeus*.

Not long after Blake's list appeared, Short was investigating *Agelaius* and related genera in connection with his discovery of *A. xanthophthalmus* in Peru (Short 1969). Being unaware of the above history of the rediscovery of *forbesi*, he began an independent investigation of the relationships of this species. He was able to examine the holotype of *forbesi* at the British Museum (Natural History) at Tring, and assembled 10 of the original 11 specimens from the Los Angeles County Museum series (the 11th was exchanged to the U.S. National Museum of Natural History). This series had been collected in 1957 by H. F. Berla and E. Dante, and, as indicated above, had been considered to represent *Gnorimopsar chopi* until Parkes saw them in 1967.

Localities in the series assembled by Short include additions to those reported by Blake. Specimens of *forbesi* are now known from Macuca, southern Pernambuco (type locality); the Usina Sinimbú area in southern Alagoas, near Sergipe; Eugenho Riachão, in the Quebrangulo (= Victoria) region of north-central Alagoas; and the isolated Raul Soares region of southeastern Minas Gerais (320 km north-northeast of Rio de Janeiro, and 1,400 km southwest of Macuca). It is uncertain whether "Pernambuco" on the label of the Lawrence specimen refers to the state of that name, or to the vicinity of the city of Pernambuco, now called Recife. Thus, the presently known range of this blackbird includes coastal southern Pernambuco and Alagoas, and an area in southeastern Minas Gerais (Fig. 1). It is likely that a search of museum collections of *Gnorimopsar chopi* from this region would disclose additional specimens of Forbes' Blackbird.

Short made detailed comparisons between the series of *forbesi* and *Gnorimopsar chopi, Agelaius* spp., and *Curaeus curaeus*. In lateral profile the culmen of *forbesi* is straight, the bill is relatively shallow and sharply pointed, and the culmen is flattened in its center to the degree that lateral ridges border it. The bill is very different from that of *chopi* in being longer and less deep, and in completely lacking the diagonal ridge that crosses the base of the lower bill in *chopi*. In contrast, the bill does not differ markedly from that of *Agelaius cyanopus* and other *Agelaius*, allowing for the greater size of *forbesi*. Compared with the bill of *Curaeus curaeus*, that of *forbesi* is also similar but proportionately shorter. The wings of *forbesi* are short for its size, barely longer than the tail. Both *G. chopi* and *C. curaeus* have longer wings (longest primaries exceed the secondaries by 25–35 mm, versus 5–8 mm in *forbesi*) that are conspicuously longer than the tail. The wings of eastern Brazilian *A. cyanopus* and *A. ruficapillus* are but slightly longer than the tail, but *Agelaius* varies greatly in this respect, the migrant North American species having considerably longer wings proportionately. The long wings of *Curaeus curaeus*, a species of southern temperate regions, suggest the possibility of migration, and indeed, Hellmayr (1932: 103) says of the species in Chile: "After the breeding season the birds congregate in flocks, and are to a certain extent migratory." The tail of *forbesi* is somewhat graduated and relatively long, the outer rectrices being 12–18 mm shorter than the central pair. None of the other species has so graduated a tail; *C. curaeus* has a long and slightly rounded tail, barely showing graduation.

Like most Icteridae, *forbesi* is strongly sexually dimorphic in size (Table 1). Males average 9.7% longer in wing measurements, 9.1% in tail, 15% in culmen, and 1.8% in tarsus. These differences permit confidence in identifying the two unsexed specimens (AMNH 42121, LACo 60141) as females.

The color of *forbesi* is entirely blackish, but showing a brown tone, without the strong blue gloss of *G. chopi* and of species of *Agelaius*. Its color rather closely resembles that of *C. curaeus*. Characteristic of *forbesi* are lanceolate feathers with glossy shafts on the crown, nape, sides of head, malar region, and sides of the neck. The throat generally lacks these modified feathers, although several specimens, in-

TABLE 1. Measurements (mm) of *Curaeus* ("*Agelaius*") *forbesi*.

Museum & number	Sex	Date	Locality	Wing	Tail	Culmen[a]	Tarsus[a]	Longest minus shortest rectrix[b]
BMNH 1885.7.12.144 (holotype)	♀	Sept 1880	Macuca, Pernambuco	99	97	23.2	29.7	(molt)
AMNH 42121	?	—	Pernambuco	98	94	23.5	29.6	14.0
LACo 27135	♀	5 Feb 1957	Usina Sinimbú, Alagoas	99	94	22.8	29.5	17.5
LACo 27137	♀	16 Feb 1957	Usina Sinimbú, Alagoas	96	93	23.2	30.5	18.0
LACo 27140	♀	26 Feb 1957	Usina Sinimbú, Alagoas	97	93	21.6	30.2	14.0
LACo 60141	?	—	Raul Soares, Minas Gerais	95	93	23.5	29.8	11.5
LACo 60140	♂	—	Raul Soares, Minas Gerais	108	102	28.2	30.7	15.0
LACo 28308	♂	6 Sept 1957	Raul Soares, Minas Gerais (15 km N)	107	102	25.4	29.2	15.0
FMNH 283631	♂	9 Sept 1957	Raul Soares, Minas Gerais	105	108	26.2	29.6	18.0
LACo 27138	♂	7 Apr 1957	Quebrangulo, Alagoas	110	105	25.2	31.4	16.5
LACo 27139	♂	8 Feb 1957	Usina Sinimbú, Alagoas	106	99	25.9	32.0	17.5
LACo 27134	♂	22 Feb 1957	Usina Sinimbú, Alagoas	108	101	25.9	30.2	12.0

[a] Measured with dial calipers to nearest 0.1 mm.

[b] Measured with dial calipers to nearest 0.5 mm.

cluding the holotype, have a few such throat feathers, and their presence seems not to be associated with sex. No species of *Agelaius* has such modified feathers in the head region. In *Gnorimopsar* the feathers of these regions are not as lanceolate, but those of the crown and nape are glossier. The condition in *Curaeus curaeus* most closely resembles that of *forbesi,* but in *curaeus* the glossy shafts and lanceolate feathers are more restricted, appearing mainly on the crown, forehead, and ear coverts.

Assignment of *forbesi* to *Curaeus* seems the most satisfactory treatment on the basis of our present knowledge of these South American blackbirds. Similarities to *C. curaeus,* including modified head feathers, coloration, and bill shape, are noteworthy, whereas differences from *Gnorimopsar* and from marsh-inhabiting *Agelaius* are striking. The shorter wings and smaller size of *forbesi* compared with *C. curaeus* might be expected in a tropical representative of this genus, otherwise containing only the larger, longer-winged *curaeus* of temperate regions. The graduated tail of *forbesi* is not sufficiently different from the rounded or slightly graduated tail of *curaeus* to pose a problem in allying it with that species.

Ornithologists in the field in eastern Brazil should seek Forbes' Blackbird, to add to our very meager knowledge of the species. It should prove distinguishable from the Chopi Blackbird, with which it may associate, by its thin, straight bill and a combination of shorter wings and longer tail. At closer range, *Curaeus forbesi* should show "hackles" about the neck and appear sootier (brownish black), lacking the bluish gloss of *Gnorimopsar chopi*.

We are grateful to the authorities of the British Museum (Natural History), Los Angeles County Museum, and Field Museum of Natural History for permission to study specimens in situ and to borrow them. At various stages of this study, Eugene Eisenmann, Emmet R. Blake, Robert W. Storer, and John Farrand, Jr., have provided useful comments. The map was prepared by Nancy Perkins of Carnegie Museum of Natural History.

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Observations on Some Fruit-eating Birds in Mexico

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Fruit trees in the tropics provide the ecologist with an opportunity to examine a situation in which animal species share a common resource. Unfortunately, not much use has been made of this opportunity and literature on the subject is scarce. Accounts of avian utilization of fruit include those of Land (1963), Willis (1966), Diamond and Terborgh (1967), Leck and Hilty (1968), Terborgh and Diamond (1970), Leck (1971), and Howe (1977). The present study adds to the rather limited data base on the exploitation of particular fruit tree species by avian frugivores.

Observations were made from late May till early August 1975 near the Mayan ruins of Chicanná and Becán, near the town of Xpujil in the state of Campeche, Mexico. The vegetation here is a "semi-evergreen seasonal forest" (Beard 1955). From an unobstructed viewing station I observed birds coming to or leaving the fruit tree under study. The number of individual visits of a bird species was used as an assessment of fruit usage. Although this does not account for varying amounts of fruit consumed during a visit, previous investigators have found this to be a feasible and efficient method (Diamond and Terborgh 1967; Leck 1969, 1971, 1972).

Data were obtained on birds feeding on the fruit of five species of trees: *Neea psychotrioides* Donn. Sm. (Nyctaginaceae), *Ficus padifolia* H. B. K. (Moraceae), *Ehretia tinifolia* L. (Boraginaceae), *Metopium browneii* (Jacq.) Urban (Anacardiaceae) and *Talisia olivaeformis* (Kunth.) Radlk. (Sapindaceae). Characteristics of these fruits are given in Table 1. For each tree species, each hour of the day between approximately 0530 and 1800 was equally observed. For example, data often were collected from 0530 to 1800 on one day and from 1200 to 1800 on the next, making one 12-h "observation day." The variation in hours of observation per tree species was due to my relative success in locating suitable trees and to

TABLE 1. Fruit characteristics, number of trees observed, and hours of observation per tree species. Size refers to diameter except for *Metopium*, in which it refers to length and width.

	Fruit size (mm)			Color of fruit when ripe	Number of trees observed	Hours of observation
	N	$\bar{x}$	SE			
Neea	71	5.4	0.05	green	2	37.5
Ficus	86	7.7	0.06	green	2	50.0
Ehretia	122	8.0	0.08	red	3	112.5
Metopium	57	10.5 × 5.3	0.09 × 0.07	red	2	50.0
Talisia	107	16.1	0.19	green	4	70.0

TABLE 2. Percentage of visits by birds to each species of fruit tree. Percentages are based on the average number of visits per day of observation, thus correcting for the difference in length of time various tree species were observed. Other bird species observed feeding, but with small sample size (less than 25 visits), are not listed here.

	Neea	*Ficus*	*Ehretia*	*Metopium*	*Talisia*	Total visits
Cracidae						
Ortalis vetula	0	0	44.7	55.3	0	31
Psittacidae						
Aratinga astec	0	0	72.5	24.9	2.6	632
Amazona albifrons	0	0	3.2	77.2	19.6	31
Trogonidae						
Trogon citreolus	8.3	32.4	51.9	7.1	0.3	392
Ramphastidae						
Pteroglossus torquatus	23.5	28.4	40.5	6.9	0.6	148
Ramphastos sulfuratus	15.7	9.8	54.6	19.9	0	404
Picidae						
Centurus aurifrons	0.6	10.0	70.8	9.9	8.7	1,343
Centurus pygmaeus	0	1.5	30.0	55.8	12.7	98
Cotingidae						
Cotinga amabilis	0	100.0	0	0	0	27
Tityra semifasciata	19.8	7.4	30.6	42.2	0	66
Tyrannidae						
Tyrannus melancholicus	0	45.9	17.1	37.0	0	82
Pitangus sulphuratus	0	58.6	41.4	0	0	259
Myiozetetes similis	0	74.0	10.4	15.6	0	116
Megarynchus pitangua	24.6	59.0	1.6	14.7	0	26
Corvidae						
Psilorhinus morio	0	23.1	58.9	6.0	12.0	179
Cyano corax yncas	0	0	53.4	15.5	31.1	47
Cissilopha yucatanica	0	0	57.9	14.8	27.3	441
Turdidae						
Turdus grayi	0	40.8	59.2	0	0	179
Icteridae						
Icterus gularis	3.0	3.4	80.2	2.2	11.2	183
Icterus prosthemelas	0	0	30.2	0	69.8	33
Icterus auratus	0	0	2.0	0	98.0	34
Icterus chrysater	0	0	4.6	5.2	90.2	29
Icterus mesomelas	0	0	89.8	0	10.2	28
Dives dives	0	11.1	81.4	0	7.5	185
Thraupidae						
Euphonia affinis	42.8	57.3	0	0	0	39
Euphonia hirundinacea	0	99.4	0.3	0.3	0	322
Fringillidae						
Saltator atriceps	0	30.7	64.9	3.7	0.6	195

how long they stayed in fruit. All the trees were located in edge situations of forest and clearings. The greatest physical separation between any two individual trees was less than 2 km, and there were no discernible barriers or major habitat changes between tree localities.

None of the bird species equally distributed its visits to the five kinds of fruit trees, and most made over 80% of their feeding visits to only two of the trees (Table 2). Overall utilization of the fruit trees by avian frugivores was distinctively uneven, with the tree bearing intermediate-sized fruit attracting the greatest number of bird species (Fig. 1). Terborgh and Diamond (1970) concluded from their observations of 10 individual trees of six species that small fruits attracted the greatest number of frugivores and large fruits the least. In their study fruits less than 5 mm were designated "small" and those over 10 mm "large," a range in fruit size similar to that of the present study. However, my observations indicate that based on the single criterion of size, smaller fruits do not necessarily attract more species of avian frugivores (Fig. 1).

Although all the study trees were relatively close to one another and all were apparently available to any of the birds, the bird species showed a definite preference for one or two of the fruits. In addition to the obvious possibility that bill length or gape width of a bird might influence its choice of fruit, other features of the bird pertaining to feeding should be considered. For example, I often observed corvids

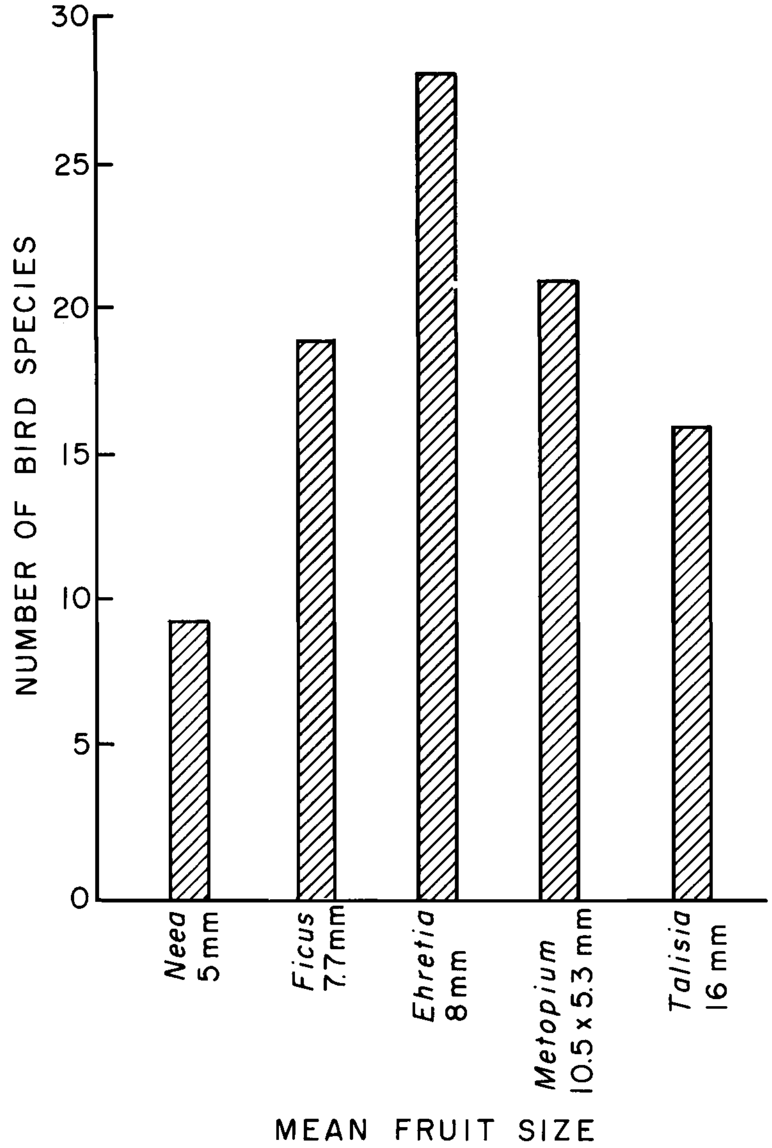

Fig. 1. Number of bird species using fruit in 3 days of observation of each fruit tree. Use of data from only 3 observation days allows comparison of frugivore diversity per tree species over a comparable time period. These totals include some species not listed in Table 2 since their total number of feeding visits was less than 25.

and icterids using their feet as well as bills to get at the inner flesh of the *Talisia* fruits. Perhaps it was lack of this manipulative ability that prevented many of the other birds from making much use of this fruit. Likewise, more attention should be focused on features of the tree other than fruit size, such as nutritional value and color. From my observations I am led to believe that the degree of accessibility of the fruit on the branches may be very important. Fruit on the tips of tiny branches was not accessible to large birds that fed from perches (e.g. the ramphastids and corvids), but was available to small birds (thraupids) or to birds that snatched fruit from the branches while on the wing (trogons, tyrannids). Thus spatial position in a fruit tree may be important even though the same kind of food is encountered at each location in the tree. While one may not expect to find as many morphological or behavioral feeding specializations in frugivores as are found in insectivores (Snow 1971), this is not to say that various adaptations of the bird species that are primarily related to other functions (e.g. feeding on an alternative insect food source, reproductive display) may not also have secondary effects in determining the kinds of fruit that the bird can most efficiently include in its diet. Future studies are required that would include more detailed data on the feeding method of the birds and on characteristics of the fruit other than size.

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Diet-Correlated Variations in Social Behavior of Wintering Tennessee Warblers

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From 14 December 1976 to 6 March 1977 we made extensive observations of the foraging and social interactions of Tennessee Warblers (*Vermivora peregrina*) wintering at Monteverde, located at 1,400 m on the Cordillera de Tilarán in northwestern Costa Rica (10°18′N, 84°49′W). Most Tennessee Warblers foraged for insects in the foliage of trees of all sizes. Like other winter residents they sometimes participated in mixed-species flocks, but more often they foraged for insects in pairs or small conspecific groups.

At any given time a small minority of the warblers fed on nectar, mostly at the flowers of the machete tree (*Erythrina lanceolata* Standl.:Leguminosae), scattered individuals of which stood at pasture edges and homesites. This small tree was conspicuous because its leafless branches bore pendant clumps of bright scarlet flowers. That wintering Tennessee Warblers feed on nectar is apparently common knowledge among ornithologists in Central America (e.g., F. G. Stiles and E. Morton, pers. comm., see also Peterson and Chalif 1973, A Field Guide to the Birds of Mexico, Boston, Houghton-Mifflin, p. 203).

Unlike their counterparts foraging for insects, nectar-feeding warblers were intolerant of conspecifics. Each individual defended its *Erythrina* and other trees within a radius of about 15 m by chasing conspecifics away. Agonistic encounters occurred during 55% of our 31 observations of nectar-feeding warblers. In approximately half of these encounters conspecifics were driven off, while in the other half a warbler was supplanted by hummingbirds (*Amazilia tzacatl* or *Campylopterus hemileucurus*) or, in one case, by a Black-throated Green Warbler (*Dendroica virens*), although the latter bird did not flower-feed.

On 13–14 January and 7–8 March in San José we observed Tennessee Warblers nectar-feeding in Poró trees (*E. poeppigiana*), which have far greater crown volumes than *E. lanceolata*. Entire Porós were apparently too large for one warbler to defend successfully. Typically, four or five birds spaced themselves within the crown of a tree, and any individual that entered another's portion of the tree was chased out of it. The volume of Poró canopy defended by a single bird at San José appeared similar to the total crown volume of the largest machete tree at Monteverde.

Tennessee Warblers arrive in Costa Rica between August and October (Skutch *in* Bent 1963, Life Histories of North American Wood Warblers, part 1, New York, Dover, pp. 85–86; Slud 1964, Bull. Amer. Mus. Nat. Hist. 128: 320). Individual *Erythrina* trees bear abundant blossoms for only 4–6 weeks, mostly during December–February. As trees go in and out of flower a scramble for trees worth defending probably occurs, with individuals that can successfully defend nectar sources shifting from tolerance to intolerance of conspecifics at least once and perhaps several times during a single winter.

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Discovery of an Oilbird Colony in the Western Drainage of the Ecuadorian Andes

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The Oilbird, *Steatornis caripensis,* has been recorded from many lower montane localities in the periphery of the Amazonian basin of mainland South America, in the coastal mountains of northern Venezuela, eastern Panama, and Trinidad. Many records, however, involve single individuals collected in the open, and comparatively few are of birds secured within, and showing the locations of, roosting and nesting colonies. Thus the precise distribution of these colonies remains largely unknown, even though the most conspicuous and accessible ones have become famous among ornithologists; one has been studied in great detail (Snow 1961, 1962). The occurrence of stray individuals far from known colonies could indicate that smaller groups roost and nest elsewhere, a possibility substantiated by recent evidence from highland Ecuador.

Several Oilbirds have been collected in the vicinity of Quito despite its high elevation (about 2,800 m) and its separation from the Amazonian basin by mountains of over 4,000 m (Salvatori and Festa 1900, Lönnberg and Rendahl 1922, Chapman 1926); one was captured alive and later preserved as a skin at the campus of Universidad Católica, Quito, on 3 July 1975. The source colony of these birds was unknown but it seemed unlikely that they came from southeastern Ecuador, some 400 km from Quito, where the only colonies in the country have been reported (Albuja and de Vries 1977).

Rumors of a nearer site first reached me in February 1976, when the geographer Francisco Terán claimed that a colony of fruit-eating "owls" lived in a gully near Puéllaro, a town only 25 km north of Quito, and added that these might be Oilbirds rather than owls because peasants in the neighborhood reputedly raided the colony and obtained nestlings from which they extracted oil. I visited the Puéllaro area on 7 and 9 October 1977, and with additional information from local people was able to explore the actual site.

It consists of an undetermined but small number of shallow caves formed by subsidence of pieces of volcanic tuff in the nearly vertical walls of a 175 m-long section of the Quebrada Santa Marta, a mountain torrent that has carved a trench 25–30 m deep with sides only 6–8 m apart, and which flows rather precipitously into the Río Guayllabamba. The general course of the quebrada follows an east-west slope, which is gentle with low banks in the stretch immediately above the trench and gradually becomes steeper so that below the trench the water rushes in a long series of rapids toward the Guayllabamba. The site is about 500 m downstream from the Quebrada Santa Marta bridge of the main road between the towns of Guayllabamba and Puéllaro, 63 km by road from Quito, at an elevation of about 2,160 m.

Despite the sheer tuff walls of the gully, native trees grow attached to cracks and raise their crowns well over the rims. Their foliage shields the gully from direct sunlight; this and the gully's steepness and depth make its lower recesses perpetually dark. The vegetation along the trench contrasts sharply with that growing in the surroundings; while native trees have persisted in the gully itself, cultivated fields of corn, tomatoes, and beans, pastures, and *Agave* and *Eucalyptus* hedges surround it. A permanently inhabited dwelling is only 100 m from the north rim, and directly above the darkest portion of the trench are the remains of an old foot bridge.

Most of the Oilbirds roost under the bridge's ruins. Their vocalizations can be heard whenever the foliage above is shaken or stones are dropped, and also at dusk when they begin flying near the bottom prior to leaving for their nightly foraging. On both of my visits the roar of the stream obscured the birds' voices but it seemed that at least six individuals roosted under the old bridge and another four nearby along the trench. One was seen leaving the site at 1845 on 7 October, but because of the trench's length, its foliage cover, and the growing darkness I saw no other birds that day or on the evening of 9 October. Rafael Narváez and I were able to lower ourselves into the trench with ropes on the second visit, and even though close inspection was limited to a section of the gully 20 m wide at a point some 50 m upstream from the bridge's remains, we found a group of six old nests in a shallow depression on the north wall about 12 m vertically below the edge and halfway between it and the bottom. Two of these nests were in poor condition but the others were unbroken, consisting of truncated cones of organic mud-like materials; the bases were 40–45 cm across, 40–45 cm high, and had flat tops 25 cm in diameter surrounded by a thin vertical rim 2–3 cm high. A piece from the top of one nest revealed that the materials had been deposited in concentric layers. The nests had been built on the sloping floor of a cavity 2 m deep that opened to the outside by an entrance 2.4 m wide and 2.0 m high. They were placed toward the rear of this cavity with their bases touching in a crescent.

While no specimens were secured, the location of these nests and their form of construction are typical of those reported for Oilbirds (Snow, op. cit.). The brief sighting of a flying bird on 7 October was enough to show that the bird's outline was like that of the bird captured alive in 1975, although no details of color could be seen. The voices heard were also similar to the sounds uttered by the captive specimen. Furthermore, I was able to locate the peasants responsible for the most recent raids at the colony, the brothers Delfín and Medardo Campaña, who described the birds fairly accurately as Oilbirds and readily recognized the preserved specimen. Mrs. Delfín Campaña smelled the latter and said its odor was exactly like that of the birds killed in their raids, which she cooked at home. These people reported that the birds fed mostly on the fruits of "Higuerón" (*Ficus* sp.), and that their breeding at the gully was timed to coincide with these trees' fruiting season in February and March each year. This, however, awaits confirmation because *Ficus* fruits have not been reported as food for Oilbirds elsewhere. While the Campaña family visited the colony regularly in the past and claimed to have killed about 40 birds including adults and juveniles in one raid 6 yr previously, the colony has not been disturbed in the last 2 yr because these people no longer own the ladder and ropes needed to climb into the trench.

The Puéllaro area must have supported significant stands of Andean forests; this is suggested by old records of birds typical of these forests such as *Otus albogularis* (Sclater 1860, Lönnberg and Rendahl 1922, Chapman 1926), *Thaluranía furcata, Trogon personatus* (Sclater op. cit.), *Semnornis ramphastinus* (Jardine 1855), *Tyranniscus nigrocapillus, Turdus serranus* and *Tangara vassori* (Sclater op. cit.), and likewise by recollections from early childhood of Puéllaro residents such as Francisco Terán. The forests have largely been destroyed but 'gallery' strips along steep gullies and ravines still remain, and continuous stands are found in the Guayllabamba gorge and adjacent areas at from 20 to 30 km to the northwest.

Presumably the Oilbirds at Quebrada Santa Marta follow the forest strips to reach the more extensive stands to forage each night, returning to their roost before dawn. These long trips might have caused a decrease in the numbers of birds there; the Puéllaro peasants claim that the colony was much larger in the past. The fact that a few individuals still persist can only mean that roosting and nesting safety are at least as important as foraging logistics for the long-term survival of colonies of these unique birds.

While the size of the colony at this site resembles that of the smallest colonies in Trinidad (see Table I in Snow 1962), its location is exceptional in that it is at considerable elevation (probably the highest yet found), on the western drainage of the Andes (the only one yet known), and in a region extensively disturbed by man. Furthermore it is probably the most accessible Oilbird colony that has been located, being less than a kilometer away from a major road and within short driving distance from a major city.

I thank Francisco Terán, whose interest originated this report, Rafael Narváez and Jaime Jaramillo for their assistance in the field, and the Ecuadorian Natural Area and Wildlife Department of the Dirección de Desarrollo Forestal for taking the initial steps toward preserving this small group of Oilbirds for future research and enjoyment.

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Caprimulgus indicus, Eurynorhynchus pygmeus, Otus scops, and *Limicola falcinellus* in the Aleutian Islands, Alaska

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The remains of a Jungle Nightjar, *Caprimulgus indicus* (UAM 3585, female by plumage, wing flat 216 mm), were found above the high tide mark on the beach of Buldir Island (52°23'N 175°56'E) on 31 May 1977. The specimen was identified as *C. i. jotaka* by Daniel D. Gibson, University of Alaska Museum. The species breeds from Transbaicalia to China and Japan and south to India and Ceylon; this northern subspecies breeds from Transbaicalia as far east as Amurland and Hokkaido, Japan, and is the only migratory race. It has straggled to Sakhalin and the southern Kuriles (Vaurie 1965, The birds of the palearctic fauna. Non-Passeriformes. London, H.F. & G. Witherby, Ltd. pp. 637–638). This is the first North American record of the species.

An adult female Spoon-bill Sandpiper, *Eurynorhynchus pygmeus* (UAM 3584, 34 g, moderate to heavy fat, ova to 2.2 mm), feeding at the wrack line, was collected at North Bight Beach, Buldir Island, on 2 June 1977. It was feeding with a male Ruff (*Philomachus pugnax*), two Ruddy Turnstones (*Arenaria interpres*), and a Mongolian Plover (*Charadrius mongolus*). The species breeds from the tip of the Chukotsk Peninsula to the base of the Kamchatka Peninsula and winters from southeastern China to the Indo-Chinese countries (Vaurie 1965, op. cit. p. 405). There is one previous Alaska and North American record: two specimens were collected from a flock of up to 10 birds on 15 August 1914 at Wainwright Inlet (Dixon 1918, Auk 35: 387–404).

The left wing of a Scops Owl, *Otus scops* (UAM 3618, wing flat 152 mm), was found behind North Bight Beach, Buldir Island, on 5 June 1977. It was identified as *O. s. japonicus* by Joe T. Marshall, National Museum of Natural History, who regards that subspecies as including *O. s. stictonotus*. The species has a wide range in Eurasia, from northwest Africa and Europe to Amurland and Japan. This subspecies is migratory and resident in Japan, breeding as far north as Hokkaido, and it has straggled to the southern Kuriles (Vaurie 1965, op. cit. p. 601). There is no previous North American record.

A female Broad-billed Sandpiper, *Limicola falcinellus* (UAM 3588, 30.5 g, little body fat, wing flat 104 mm, ovary identified), was collected on the beach at Clam Lagoon, Adak Island (51°55'N 176°35'W), on 19 August 1977, a first record for North America. It was feeding with a flock of Ruddy Turnstones and a Sanderling *(Calidris alba)*. The specimen was identified as *L. f. sibirica*, the eastern subspecies, by Lester L. Short, American Museum of Natural History. The species breeds in northern Norway, Finland, Sweden, northwestern Russia, and northeastern Siberia; this subspecies winters from southeastern Japan and China to Australia (Vaurie 1965, op. cit. pp. 406–407). There are also records from Sakhalin and the Kuriles (Yamashina 1974, Check-list of Japanese birds. Tokyo, Gakken Co., Ltd. p. 114).

These specimens were collected in connection with work for the Aleutian Islands National Wildlife Refuge, and they have been deposited at the University of Alaska Museum, Fairbanks. We thank Richard C. Banks, National Museum of Natural History, Joe T. Marshall, and Lester L. Short for their assistance with the identifications and Daniel D. Gibson for assistance with the identifications and help with the manuscript.

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Predators and Blackbirds: the "Uncertainty Principle" in Field Biology

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A persistent concern in field studies of birds is the possibility that the activities of the scientist may inadvertently influence the extent of predation on eggs and hatchlings. Data on this question are scanty as, in most cases, it is difficult if not impossible to determine predation rates on nests that have not been studied. The few studies that have dealt with this question have reached inconsistent conclusions. Gillett et al. (1975), for example, found that frequently disturbed sections of a colony of Glaucous-winged Gulls (*Larus glaucescens*) had a higher chick mortality and lower egg mortality than did undisturbed sections of the colony. Conversely, Robert and Ralph (1975) found egg mortality to be directly proportional to the amount of disturbance in a colony of Western Gulls (*L. occidentalis*), whereas chick mortality was inversely proportional to the amount of disturbance. In a third study, Willis (1973) investigated the effects of research activities on predation of Bicolored Antbirds (*Gymnopithys bicolor*) by noting that adults feeding at ant swarms had characteristic behavior patterns associated with each stage in the nesting cycle. By observing the behavior of banded adults, he determined which pairs were incubating eggs, feeding nestlings, or feeding fledged young, permitting estimation of survival rates of unvisited nests. The results of this study indicated no difference in predation rates between visited and unvisited nests.

In the course of a survey of the literature on Red-winged Blackbirds (*Agelaius phoeniceus*), I obtained indirect evidence that research activity on marshes may contribute to predation on Red-wing nests. In addition to data I obtained during a 2-yr study of a marsh-breeding population of Red-wings, I found data from 10 other marshes and 5 upland sites at which Red-wings were studied for 2 or more consecutive years and for which the proportion of successful nests (nests fledging at least one young) in each year was reported. As a predator normally removes the entire contents of a nest, the proportion of successful nests may be considered to be a rough estimate of the amount of predation (Lack 1954). As shown in Table 1, on 10 of the 11 marshes (data from the first year of the twelfth marsh were not available) the proportion of successful nests was lower in the second year of the study than in the first (binomial probability = 0.012). The average decline in the proportion of successful nests was 22.9% (range: 6–50%). Four marshes were studied for 3 or more consecutive years. The trend continues on these marshes; the amount of predation is again higher in subsequent years of the study than it was in the first year, but the increase is not as large as that between the first and second years of the study.

The impact of human activity on predation seems to be less for upland study sites than in marsh habitats. In three of five upland study sites the proportion of successful nests was slightly lower (mean = 7%) in the second year than in the first. On the remaining two study sites, however, the trend was reversed and a larger proportion of successful nests was found during the second year than in the first.

In 1975 and 1976 I studied Red-winged Blackbirds on a marsh in Princeton, New Jersey. During the second year signs of mammalian predation were abundant. Nests were frequently torn down, vegetation around nests was flattened, and in many instances bloody feathers lay floating on the water. During the first year of the study I rarely found such signs.

Research workers may influence a predator's ability to find nests in a number of different ways. Predators may learn to follow human scent from nest to nest (Snelling 1968), or repeated flushing of birds

TABLE 1. The proportion of successful nests in marsh and upland habitats during the first, second, and subsequent years of work at the same site. Names of sites are given only if the author worked at more than one location

Habitat	Location	Proportion of successful nests			Reference
		1st yr	2nd yr	3+ yr	
Marsh		.906	.643	.493	Brenner 1966
	Airport Marsh	.667	.558		Case & Hewitt 1963
	Inlet Valley Marsh	.700	.220		Case & Hewitt 1963
	Spencer Marsh	.836	.337		Case & Hewitt 1963
		.457	.390		Holm 1973
		.571	.258		Lenington 1977
	Clark's Pond	.662	.406	.413	Robertson 1972
	All Saint's Marsh	.676	.617		Robertson 1972
		no data	.560	.430	W. Searcy pers. comm.
		.339	.446		Weatherhead & Robertson 1977
		.612	.474	.394	Wiens 1965, Snelling 1968
		.350	.240		Young 1963
Upland		.330	.280		Dolbeer 1976
	500 ft site	.294	.230		Case & Hewitt 1963
	1,200 ft site	.368	.395		Case & Hewitt 1963
	Hyland Farm	.257	.219		Robertson 1972
	Hausman's Field	.400	1.000		Robertson 1972

may direct a predator's attention to nest locations. In addition, it is a common practice for blackbird researchers to place markers near nest sites as an aid in relocating nests. Predators could learn to associate such markers with a nearby meal. Presumably, the response of predators to human activity differs with the type of predator. Those such as mammals and snakes that hunt primarily using scent are most likely to take advantage of scent trails. Birds may be more responsive to visual cues.

In upland habitats, where the density of Red-wing nests is considerably lower than on marshes (Case and Hewitt 1963, Robertson 1972), it may be more difficult for predators to learn to find nests.

Whatever the proximal cause in the decline of the proportion of successful nests, it is clear that the very process of measurement is introducing changes in the phenomena being measured.

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Permeability of Magpie and Blackbird Eggshells to Water Vapor: Variation Among and Within Nests of a Single Population

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Circumstantial evidence from studies of domestic fowl indicates that permeability of avian eggshells is a genetically controlled character (Smith 1973, Wangensteen et al. 1974). If permeability of an avian eggshell is, in fact, largely an expression of the genome of the female producing the egg, it is likely that the majority of the variation in permeability in a sample of eggs (and in the population from which the sample is drawn) is attributable to genetic differences among various females. Consequently, it may be that little new information about the population can be obtained by collecting more than one egg laid by a single female (Sokal and Rohlf 1969: 206ff).

To evaluate the hypothesis that most of the variation in permeability of eggs in a population stems from differences among clutches as opposed to differences among eggs within clutches, we collected three eggs from each of 10 nests of Black-billed Magpies (*Pica pica*) located east of Fort Collins, Colorado (T8N, R67W, S36, Weld County; elevation 1,554 m). Three eggs also were collected from each of 10 nests of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) nesting at Latham Reservoir near Greeley, Colorado (T4N, R65W, S1-2, Weld County; elevation 1,402 m). In the laboratory the eggs were placed randomly in vented desiccators above anhydrous calcium sulfate to maintain a dry atmosphere (Ar et al. 1974). The desiccators were held in a constant temperature cabinet at 25°C, a temperature too low for embryogenesis to proceed (White and Kinney 1974). Each egg was weighed six times on an analytical balance at intervals of 24 h, and the rate of weight loss—which is attributable largely to the escape of water vapor (Ar et al. 1974, Rahn et al. 1976)—was computed using a linear regression procedure. Subsequently, the volume of each egg was determined by displacement of water (Lynn and von Brand 1945), and surface area was calculated using the equation derived by Hoyt (1976).

Since vapor pressure inside the eggs approximated the vapor pressure of pure water at 25°C (i.e. 3.167 kPa; Lomholt 1976, Taigen et al. 1978), and since vapor pressure of the atmosphere inside the desiccators was zero, the permeability of eggshells to water vapor was calculated using the equation

$$K_{H_2O} = \dot{M}_{H_2O}/(\Delta P_{H_2O} \cdot A)$$

where K_{H_2O} is permeability of an eggshell to water vapor ($\mu g \cdot day^{-1} \cdot Pa^{-1} \cdot cm^{-2}$), $\dot{M}_{H_2O}$ is the rate of water loss in the desiccator ($\mu g \cdot day^{-1}$), ΔP_{H_2O} is the gradient in vapor pressure across the eggshell (Pa), and A is the surface area of the eggshell (cm^2). All values for permeability were adjusted to sea level conditions (barometric pressure = 101.325 kPa).

Data for eggs of both magpies and blackbirds were subjected to one-way analysis of variance, Model II (Sokal and Rohlf 1969), which revealed that variation in permeability of eggshells to water vapor is significantly larger among clutches than within clutches (Table 1). We subsequently partitioned the variance using methods outlined by Sokal and Rohlf (1969), and found that fully 85% of the total variation in permeability of magpie eggs could be assigned to the "among clutch" component. For eggs of Yellow-headed Blackbirds, 56% of the total variation in permeability stemmed from differences among clutches. [Similar analyses were performed on data for conductance of magpie and blackbird eggs to water vapor ($\bar{\bar{x}}$ = 8.566 and 9.091 $\mu g \cdot d^{-1} \cdot Pa^{-1}$, respectively), and on surface area of eggs ($\bar{\bar{x}}$ = 22.5 and 12.9 cm^2, respectively), and similar results were obtained in every instance.]

TABLE 1. One-way Analysis of Variance (Model II) of data for permeability of eggs of Black-billed Magpies and Yellow-headed Blackbirds to water vapor [grand means ($\mu g \cdot day^{-1} \cdot Pa^{-1} \cdot cm^{-2}$): magpie = 0.410; blackbird = 0.703]

Source of variation	df[a]	Sum of squares	Mean squares	F-ratio	Expected mean squares	Estimate of variance component	% total variation
				Black-billed Magpie			
Among nests	9	1.0643	0.1182	16.82 ($P < 0.001$)	$\sigma_W^2 + 2.79\sigma_A^2$	$\sigma_A^2 = 0.0398$	85.04
Within nests	18	0.1268	0.0070		σ_W^2	$\sigma_W^2 = 0.0070$	14.96
				Yellow-headed Blackbird			
Among nests	9	0.6081	0.0676	4.62 ($P < 0.005$)	$\sigma_W^2 + 2.79\sigma_A^2$	$\sigma_A^2 = 0.0190$	56.54
Within nests	18	0.2632	0.0146		σ_W^2	$\sigma_W^2 = 0.0146$	43.46

[a] The total df is 27, instead of 29, because 2 eggs were damaged in transit to the laboratory

Permeability of avian eggshells to water vapor may increase during incubation (Sotherland et al. 1979), perhaps as a result of small decreases in thickness of eggshells attending recovery of calcium from shells by developing embryos (Simkiss 1967). Thus, it is possible that a portion of the variation in permeability among clutches we sampled is attributable to differences in the amount of time the various clutches had been incubated and in the amount of development that had occurred before eggs were collected. However, since none of the magpie eggs contained an embryo with a chorioallantois, it is not likely that variation in permeability among clutches could have been caused by ontogenetic changes in permeability of eggshells (Sotherland et al., ms). Therefore, the largest portion of the variation in permeability of magpie eggshells to water vapor probably can be traced to individual (genetically based?) differences among the females producing the eggs.

Eggs in many of the blackbird nests had undergone considerable incubation prior to collection, and were characterized by advanced embryos and well-developed chorioallantoic membranes. Thus, we cannot attribute inter-nest variation in permeability of blackbird eggshells to water vapor solely to genetic differences among females in the nesting population, because a portion of the variation in permeability may have resulted from ontogenetic changes in the eggshells.

Since there frequently are limits to the number of eggs that may be collected and/or handled conveniently in the laboratory, experiments must be designed carefully in order to extract the largest possible amount of useful and reliable information from the samples. Data summarized in Table 1 indicate that eggs of a single clutch are more similar than eggs from different clutches (particularly in the case of the magpies), and therefore that collecting more than one egg from nests such as these yields relatively little new information about the population in question (Sokal and Rohlf 1969). Furthermore, when there is a limit to the number of eggs that may be collected, the probability of making an inaccurate prediction about the population is increased by taking more than one egg from each nest, rather than by collecting one egg from each of many more nests. Figure 1A represents the most probable result of collecting eggs from three nests in a population. Values grouped in such a manner provide an accurate estimate of the population mean, but at the same time underestimate the population variance. Figure 1B represents the next most probable result of collecting eggs from three nests in a population. Although this procedure yields accurate estimates of both the population mean and the population variance, the effective sample size is very small (see beyond). Figure 1C illustrates the least probable outcome of collecting eggs from three nests in a population; the procedure provides inaccurate estimates of both the population mean and the population variance. If only one egg is taken from a nest, eggs may be collected from many more nests, and there will be a greater probability of obtaining accurate estimates of the population parameters (Figure 1D).

Another disadvantage of collecting several eggs from each of a few nests is that there are fewer degrees of freedom obtained by collecting eggs in this way than by collecting the same number of eggs but taking only one egg from each of several nests. Eggs collected by deliberately taking more than one egg from a nest cannot be considered statistically to be independent samples from a population: only the mean values for the nests from which eggs were taken can be considered as independent samples from the population. However, eggs collected by taking one egg from each of several nests are independent samples

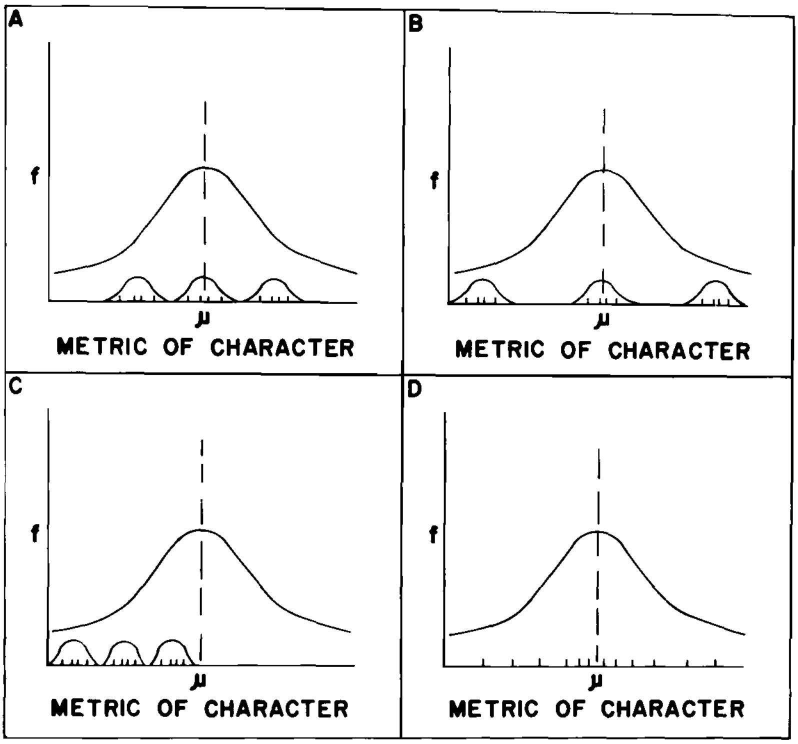

Fig. 1. Four possible results of collecting 12 eggs from a population. The large bell-shaped curves represent population frequency distributions; the three smaller bell-shaped curves in A, B, and C represent frequency distributions for individual nests. Small vertical lines along the abscissas are values of a character for individual eggs. A, B, and C are situations in which 12 eggs are collected by taking 4 eggs from each of 3 nests; D is a situation in which 12 eggs are collected by taking 1 egg from each of 12 nests. f = frequency; μ = true mean for the character.

from the population, because eggs acquired in such a manner have approximately the same probability of being collected. If each egg collected by taking several eggs from a nest is (erroneously) considered to be an independent sample from the population, the degrees of freedom will be increased artificially, and the estimate of the standard error will thereby be reduced. An inordinately low estimate of the standard error could lead investigators to conclude that a mean difference between populations is statistically significant when, in fact, no difference exists.

In summary, the majority of the variation in permeability of magpie and blackbird eggshells can be assigned to variation among clutches, which presumably reflects on genetic differences among females producing the eggs. Unless preliminary experiments have been performed to partition variation among and within clutches, it is best to assume that the "among clutch" component is the more important of the two. Thus, if a fixed number of eggs is to be collected, the most reliable sampling procedure is to take one egg from each of several nests rather than several eggs from fewer nests.

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Food-storing by Yellow-bellied Sapsuckers

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On four occasions during November and December in Nacogdoches, Texas we observed eastern Yellow-bellied Sapsuckers (*Sphyrapicus varius*) storing food. On 24 November 1977, an immature bird stored a whole pecan (*Carya illinoensis*) nut in a crevice of a dead pecan branch stub about 10 m above the ground. The sapsucker placed the nut in the crevice and pecked on it to wedge it into place. The bird had previously examined three other dead branch stubs and apparently found them unsuitable. While searching for a storage site with the pecan in its bill, the sapsucker repeatedly uttered its meow-like call.

On 8 December 1976, an adult male sapsucker removed a pecan from its covering, flew 15 m to a utility pole and wedged the pecan in a crevice 10 m above the ground near the top. He repeated the process three times.

On 13 December 1976, a juvenile male sapsucker fed on a southern magnolia (*Magnolia grandiflora*) fruit and then stored several 14 m above the ground in a crevice of an American elm (*Ulmus americana*). The next day the same bird stored red oak (*Quercus falcata*) acorns in the same elm tree. We did not observe sapsuckers preparing sites for food storage nor returning to feed on any of the stores.

Food storing has been reported in only six other North American picids, five of which are melanerpine (*Melanerpes erythrocephalus*: Kilham 1958, Wilson Bull. 70: 107–113; *Melanerpes carolinus*: Kilham 1963, Wilson Bull. 75: 227–234; *Melanerpes lewis*: Bock 1970, Univ. Calif. Publ. Zool. Vol. 92; *Melanerpes formicivorus*: MacRoberts 1970, Condor 72: 196–204; *Melanerpes aurifrons*: Martin and Kroll 1975, Wilson Bull. 87: 553). Alderson (1890, Oologist 7: 147) reported a Hairy Woodpecker (*Picoides villosus*) storing insects in an unused nest cavity. We believe this to be the first report of food storing by Yellow-bellied Sapsuckers, and it is of special interest because the genus *Sphyrapicus* belongs to the melanerpine assemblage of woodpeckers (Short and Morony 1970, Condor 72: 310–315).

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Seasonality, Clutch Size, and Hatching Success in the Cedar Waxwing

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This paper summarizes an analysis of Cedar Waxwing (*Bombycilla cedrorum*) nesting records obtained from the North American Nest Record Card Program at the Cornell University Laboratory of Ornithology. A total of 713 cards, ranging in dates from 1892 through 1974, was examined for seasonality, clutch size, and mortality. The sample size (713 nests) is relatively small because discrepancies within or lack of information on the cards frequently makes some records inapplicable to aspects of this study. Previous similar studies have used as many as 9,000 nest cards (e.g. Myres 1955, Snow 1955) on species that are commoner and more frequently reported in other nest record programs.

The majority of the nests are from northeastern United States and southeastern Canada. Biased geographical distributions may reflect the enthusiasm of different observers (Peakall 1970), and in this case more than half the reports are from Michigan. Nevertheless, a reasonable pattern appears that suggests that waxwing breeding activity centers in three states (Wisconsin, Michigan, and New York), each with more than 51 nest records. Ontario and Quebec are next most important, followed by five states with 6–10 records each (North Dakota, Minnesota, Ohio, Pennsylvania, and Virginia). British Columbia and 17 states had five or fewer records—the areas included California, the northwestern states, and states bordering the high activity regions described above. There is good agreement between the geography of our records and that of the Cedar Waxwing reports in the North American Cooperative Breeding Bird Survey (Robbins and Van Velzen 1969).

Peakall's recent work (1970) was used to determine clutch size and various aspects of nesting phenology. However, while Peakall calculated clutch completion dates, the values given in this paper are the estimated dates when the first egg was laid. This procedure allowed the use of a maximum number of nest records. Modifications were also made for the determination of clutch size. If only 1 visit was made to the nest, the record was ignored unless 4 or more eggs or 4 or more young were present. Nests with 2 or 3 eggs were used if 1 of the eggs subsequently hatched and there was no indication of damage to the nests. All nests of only 1 egg were excluded from analysis, as they probably reflected human disturbance. We used an incubation period of 12 days (Lea 1942) and a nestling period of 16 days; Lea (1942) and Putnam (1949) give this period as 15.5 to 15.9 days.

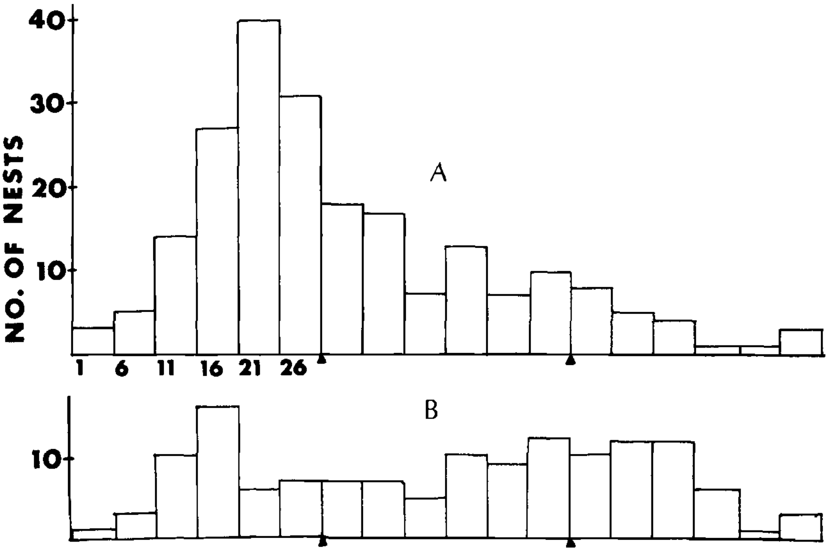

Fig. 1. Seasonality of nesting in the Cedar Waxwing. Plotted are the number of nests reported for each 5-day period, June through August. **A**. Nests prior to 1970, n = 218; **B**. Nests from 1970–74, n = 139.

TABLE 1. Annual hatching success for Cedar Waxwings.

Year	Nests	Eggs	Number hatched	Success (%)
1964	15	53	44	83
1965	17	104	75	72
1967	11	47	31	62
1968	15	55	26	47
1969	39	149	69	46
1970	10	39	14	36
1971	27	105	70	67
1972	48	165	93	56
1973	31	103	54	52
1974	28	102	59	58
Total	303	1,134	691	61

Only 357 cards could be used for analysis of the breeding season. From the pre-1970 data, 5-day groupings of clutch commencement clearly showed a 16–30 June breeding peak and a suggestion of a second peak in nest initiation at the end of July (Fig. 1A). Crouch (1936) and later researchers consider the waxwing as double-brooded. We note however, that the second "peak" is much less prominent or well defined than the first. For all years (1894–1974) only 36% of the nests recorded were started during the second part of the season, after 15 July. Thus, the term "double-brooded" should be used cautiously. Most interestingly, the pattern of post-1970 data shows a marked change (Fig. 1B). The graph of the 1970's shows little tendency towards an early peak; 44% of the nests began *after 24 July,* making the number of nests started in the first and second halves of the season nearly equal. For the pre-1970 years only 17% of the nests had the first egg after 24 July. This decline in the relative importance of the first clutch period is significant and not easily explained. We doubt that broad climatic changes are responsible. The Brown-headed Cowbird (*Molothrus ater*) frequently parasitizes the Cedar Waxwing (Rothstein 1976), and we suggest that the waxwing breeding season may be shifting away from higher parasitic pressures in the June cowbird breeding peak to a more favorable later season.

Cedar Waxwings typically lay a clutch of 3–5 eggs. From a New York State subsample (88 nests), clutches were: 2 eggs, 1%; 3 eggs, 13%; 4 eggs, 53%; and 5 eggs, 33%. (Six-egg clutches were reported rarely, from both and the United States and Canada.) The mean clutch size of a total sample of 338 nests was 4.2. There was no significant geographic variation; we examined the data for both north-south gradients in clutch size and for possible increases in clutch size toward the center of the breeding range. There was, however, a marked decrease in mean clutch size through the season, as shown for the monthly average clutch: June, 4.4 eggs ($n = 136$, $s = 0.7$); July, 4.3 eggs ($n = 110$, $s = 0.7$); August, 3.9 ($n = 87$, $s = 0.6$); and September, 3.8 ($n = 5$, $s = 0.5$). This decline is significant (for example, August vs. June, $P < .01$ with Student's t-test). Such decreases in clutch size with the breeding season are common for birds (Lack 1947, 1948); usually this decrease is assumed to be associated with a general decline in food supply toward the end of summer.

A total of 303 nest records could be used to determine hatching success rate. Overall hatching success for 1,134 eggs was 61%. Sixty-five records contained detailed information through the end of the fledging period. The percent of young that hatched and fledged was 55%. Geographic variation in breeding success was slight or statistically insignificant because of small sample size. Though no regional differences in nesting success were discernible, annual hatching percentages differed significantly (Table 1; $P < .05$, χ^2). Such yearly fluctuations in success are most reasonably attributed to weather differences. Clutch sizes showed no significant annual differences in this same 11-year period, so total recruitment was directly dependent on survival rates alone.

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The Nest and Eggs of the Black-and-yellow Silky-flycatcher (*Phainoptila melanoxantha*)

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The striking Black-and-yellow Silky-flycatcher (*Phainoptila melanoxantha*) is the only member of a genus confined to the mountains of Costa Rica and western Panamá. Although not rare, its habits are poorly known, and there exists no detailed account of its nest and eggs.

I found a nest of a Black-and-yellow Silky-flycatcher on 2 May 1972 at an elevation of 2,400 m on Volcán Poás, Alajuela Province, Costa Rica, while accompanied by F. G. Stiles and B. K. MacKay. The nest was located 1.5 m high in the central crotch of a 2-m sapling growing in the center of a dense thicket between the road and a large stand of montane forest. It contained two eggs. As our itinerary did not permit us to make further observations at the site, the nest and eggs were collected and are now in the collection of the Western Foundation of Vertebrate Zoology (No. 68,023).

The nest was a large, compact, open cup composed mostly of green moss interspersed with a few slender stems and fern fronds. It was lined with fine rootlets and plant stems. The outer diameter of the nest measured 22 × 16 cm, and it was about 12 cm in depth. The inner cup was 7 cm in diameter and 5 cm deep.

The two eggs measure 27.84 × 20.30 and 27.19 × 19.20 mm with empty dry shell weights of 0.274 and 0.260 g, respectively; they were subelliptical in shape (Preston *in* Palmer 1962, p. 13) and slightly glossy. They had a grayish-white ground color with a dense sprinkling of fine light gray, purplish brown, and dark brown spots over their entire surfaces. Each egg contained a slightly developed embryo.

I found an additional Black-and-yellow Silky-flycatcher nest on 26 April 1974 about 4 km E of Monteverde, Cordillera de Tilarán, Guanacaste Province, Costa Rica, while accompanied by H. Cernicek, M. Kiff, and C. Sumida. The nest was located in cloud forest within the Monteverde Cloud Forest Preserve at an elevation of 1,700 m. As in the case of the Volcán Poás nest, a male *Phainoptila* was perched on the top of a low shrub near the Monteverde nest. While I checked the nest contents, a female flew to within 2 m.

The Monteverde nest was empty, but apparently nearly completed. It was an open cup composed almost entirely of green moss; a lining had not yet been added to the inner cup. The nest was situated about 2 m high in the central crotch of a 3-m sapling growing in a thicket adjacent to a little-used trail. Unlike the Volcán Poás nest, which was located in such dense vegetation that it could not be seen from above or from the sides, the Monteverde nest was not well concealed and could easily be detected at a distance of 10 m.

M. Gochfeld (in litt.) informed me of another *Phainoptila* nest found by him, G. Tudor, and M.

Kleinbaum on 2 April 1969 near the summit of Volcán Poás. On a trail just within a stand of montane forest, they found a female Black-and-yellow Silky-flycatcher sitting on a nest located 4 m off the ground in a crotch of a slender sapling. The nest was just below the canopy of the tree and was clearly visible from below. It was an open cup, moderately compact in structure, and the bill, throat, and tail tip of the sitting bird (not flushed) were visible. Because the observers were unaware that the nest of *Phainoptila* was undescribed, no attempt was made to investigate its contents.

Sibley (1973) provided a detailed review of the taxonomic history and characters of the silky-flycatchers, including *Phainoptila.* Since its initial discovery, the taxonomic affinities of *Phainoptila* have been uncertain. Ridgway (1904) placed it in the Ptilogonatidae with reluctance, remarking that "the genus *Phainoptila* is doubtfully a member of this group . . . and might easily be referred to the Turdidae." Arvey (1951) thought that *Phainoptila* was the most primitive member of a group composed of the silky-flycatchers, waxwings, and palm-chats, all of which he lumped in the Bombycillidae. However, Skutch (1965) noted the behavioral dissimilarities between *Phainoptila* and other silky-flycatchers and echoed Ridgway's reservations about placing it with the ptilogonatid genera *Phainopepla* and *Ptilogonys.* Sibley (1973) found close agreement between the electrophoretic patterns of egg-white proteins of *Phainoptila, Phainopepla,* and the solitaires, *Myadestes.* He also summarized various morphological similarities between these genera and recommended that they be placed in the same family.

The appearance of the nest and eggs of *Phainoptila melanoxantha* supports a close relationship between it and *Phainopepla* and *Ptilogonys.* Published accounts of the nesting habits of *Phainopepla nitens* (Bent 1950), *Ptilogonys cinereus* (Rowley 1962), and *Ptilogonys caudatus* (Skutch 1965) indicate that, like *Phainoptila,* each of these species builds an open cup nest placed in the fork of a tree or shrub.

Aside from their somewhat blunter shape, the eggs of the Black-and-yellow Silky-flycatcher are simply larger versions of the eggs of *Phainopepla nitens* and *Ptilogonys cinereus* in the Western Foundation of Vertebrate Zoology collection. Judging from Skutch's (1965) description, the eggs of *Ptilogonys caudatus* are essentially identical to those of *P. cinereus.* The eggs of all four species are characterized by a pale gray or grayish-white ground color and a dense, almost uniform sprinkling of fine brown and lilac spots over their surface, although *Phainopepla* and *Ptilogonys* eggs occasionally bear a heavy wreath of markings near the large end. This egg color is so distinctive among passerine groups and at the same time so strikingly similar between these genera that it is reasonable to conclude that it indicates a close relationship between them.

I am grateful to my field companions in Costa Rica for their help in finding the nests described here, to M. Gochfeld for providing me with unpublished data, to A. Skutch and J. Wiens for helpful comments on the manuscript, and to E. Harrison and the Western Foundation of Vertebrate Zoology for financial support in Costa Rica.

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Molt Pattern as a Clue to San Blas Jay Ancestry

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In June 1970, while studying the San Blas Jay (*Cyanocorax sanblasiana nelsoni*) near Las Varas, Nayarit, Mexico (Hardy 1976, Wilson Bull. 88: 96–120), I caught two fledgling jays and brought them to an aviary in Los Angeles, California for study of ontogeny of plumage and softpart color (Hardy 1973, Bird-Banding 44: 81–90). They passed through the partial first prebasic molt, and assumed the typical first-year plumage. In corvids, the first prebasic molt involves only body and head feathers, and even on these parts is often partial, occurring in a complex, variable pattern. In the San Blas Jay most if not all body feathers are molted during the August–October period, and in wild birds, judging from skins, there is a head molt. The peculiar molt of these head feathers in my two captives that occurred in the spring of the first year of life, from late April to mid-May, was seemingly part of a protracted first prebasic molt. (Circumstances of captivity, such as diet, must have prolonged their fall molt.) An intriguing aspect of this head molt was its pattern. Unprecedented though it seems to be, its differential character may be phylogenetically significant.

In my earlier papers (Hardy 1961, Kansas Sci. Bull. 42: 13–49; 1969, Condor 71: 360–375) discussing phylogeny and systematics of the New World jays, I proposed the existence of two lines, the ornate and the inornate. The former consists mostly of lowland tropical species of the genus *Cyanocorax* plus, largely in temperate latitudes, *Cyanocitta,* the Blue and Steller's Jays. I showed how evolution in the ornate line had seemingly taken a course of simplification, producing in the highly derived forms of the line species superficially resembling the derived species of the inornate line. The ornate pattern is not found in other living corvids or presumably closely related families; therefore this pattern can be used to define the ornate line. On the other hand, as Joel Cracraft (a reviewer for this paper) pointed out, the ornate plumage is primitive within the lineage, and thus the loss of that plumage is a derived condition defining certain subgroups. The more primitive species of the ornate line, presumed to resemble most closely its ancestral forms, have prominent crests, bold markings on the face, including a triangular cheek patch and supraorbital spot, and pale tips on the rectrices (e.g. *C. dickeyi*, the Tufted Jay). Intermediate stages of derivation show reduction of the crest and pale tail tips or their loss after early ontogenetic stages, and an obfuscation of this bold pattern by increasing concentrations of melanin. As a result of this trend the pattern, rather than being represented by, for example, blue and white, is seen only in subtle contrast of black and dark blue or purple (*C. cayanus*). The furthest derived jays of the ornate line are dark brown or black and blue with only a trace here and there of pattern and essentially no crest (e.g. *C. morio* and *heilprini*).

In the two captive first year San Blas Jays, the spring molt of head feathers at the age of 10 months involved only a triangular malar-cheek patch and a supraorbital spot (Fig. 1) almost perfectly duplicating the primitive pattern as seen, for example, in the White-naped Jay, *Cyanocorax cyanopogon* (see Goodwin 1976, Crows of the World, Ithaca, New York, Cornell Univ. Press, p. 304). (It has been my fond hope since 1956 that some genius of a biochemist would discover a method for activating and diluting that most inert of substances, the pigment melanin, allowing the primitive head coloration pattern to be seen in the black-headed derived species of ornate line jays. The differential molt is an unforeseen answer to that hope.) Conservatively based on Haeckel's Law that ontogeny recapitulates phylogeny, the pattern revealed by this molt supports the idea that the bold plumage and ornamentation are primitive, not derived. This correlates with other expressions of Haeckel's Law in these jays; for example prominent crests only in subadult stages in the San Blas Jay, and white-tipped rectrices only through the first year plumage in the Yucatan Jay, *C. yucatanica.* Even among those who may view invocation of Haeckel's Law dimly, it surely will be seen that at the very least the facts do not correlate with complexity of ornamentation and plumage pattern being the derived state in this assemblage of bird species.

At the suggestion of Kenneth C. Parkes (another reviewer), I examined museum skins of many New World jays in search of further evidence of the molt. The search produced several instructive specimens. One skin of *C. sanblasiana nelsoni,* LSU 46226, essentially duplicates the molt character of the captives. A first-year bird, it was taken on 4 October 1958 at Agua Zarca, 6 Km N Puebla Juarez, Colima, by W. J. Schaldach, Jr. A molting adult specimen of the Brown Jay, *Cyanocorax (Psilorhinus) morio*, shows a similar pattern. It is LSU 48679, collected at Rancho Cielito, 2 mi. S Encino, Tamaulipas on 3 September 1965, by J. P. O'Neill. In this species the color pattern described is evident even in some non-molting birds in different shades of brown, rare specimens having the patches colored dull silver. In the present specimen the chin and throat feathers and the malar, post- and supraorbital feathers are

Fig. 1. Differential molt pattern of captive first year San Blas Jay. The paler cheek patch and supraorbital spot are in heavy molt, the color being the result of feather sheaths. Drawing from a 35 mm color slide.

ensheathed basally, accentuating the characters. Perhaps most intriguing of all is a molting specimen of the Tufted Jay, *C. dickeyi,* LSU 41147. An adult, it was collected at Rancho Telgas, N. of Rancho de los Orcones, E. of Huajacori, Nayarit, on 25 August 1963. Adults of this species have the bold putatively primitive pattern expressed in black and white. The molt at time of collection of this LSU specimen involved the chin and throat, a bar from front to back across the cheek patch and a spot on the posterior portion of the supraorbital patch. The San Blas Jay specimen confirms the non-anomalous character of the molt in that species but also shows that its occurrence in May in the captives represented abnormal prolongation of the first prebasic molt. The Brown and Tufted Jay specimens, in precisely the correct time of molt, reveal that differential timing of feather replacement in a peculiar pattern in species not having the ornate line plumage pattern hidden by melanic infusion matches that pattern found in the black-headed San Blas Jay.

In summary, a molt pattern found in the head color pattern of species thought to be less derived in an evolutionary line has been detected in the San Blas Jay, considered to be a derived form in which the color pattern is hidden. The molt thus correlates with other plumage and ornamentation features suggesting the evolutionary trend in phenotype change in the ornate line of New World jays.

I thank the following curators and their institutions for assistance in surveying their collections for specimens helpful in my study: M. A. Traylor, Field Museum; J. P. O'Neill, Museum of Natural Science, Louisiana State University; L. Baptista, Moore Laboratory of Zoology, Occidental College; F. Gill, Philadelphia Academy of Sciences; L. Short, American Museum of Natural History; L. Kiff, Western Foundation of Vertebrate Zoology; D. Niles, Delaware Natural History Museum; and R. Mengel, Museum of Natural History, University of Kansas.

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Great Horned Owl Predation on Leach's Storm-Petrels in Maine

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Owls apparently rarely prey on seabirds (Morse 1971, Auk 88: 426) and records of predation on storm-petrels seem especially scarce. Examples of predation on storm-petrels by the Short-eared Owl (*Asio flammeus*) include the diurnal White-rumped Storm-Petrel (*Oceanodroma tethys*) and the nocturnal Band-rumped Storm-Petrel (*O. castro*) on the Galapagos Islands (Harris 1969, Proc. Calif. Acad. Sci. 37: 95), the White-faced Storm-Petrel (*Pelagodroma marina*) on Selvagen Island, Madeira (Schweppenburg 1907, Ornith. Jahrb., Hallein 18: 39) and the British Storm-Petrel (*Hydrobates pelagicus*) on Skomer Island, Pembrokeshire, Wales (Glue and Morgan 1977, Bird Study 24: 111). Other examples include a probable Band-rumped Storm-Petrel that may have been taken by a Long-eared Owl (*Asio otus*) or a short-eared Owl on Baixo Island, Madeira (Schweppenburg op. cit.), the Leach's Storm-Petrel (*O. leucorhoa*) taken by the Barn Owl (*Tyto alba*) on Castle Rock, California (Bonnot 1928, Condor 30: 320), and the British Storm-Petrel killed by the Little Owl (*Athene noctua*) on Skokholm Island, Pembrokeshire (Alexander 1935, Bull. Brit. Orn. Cl. 55: 60).

On 6–8 July and 15 August 1977, 16 pellets of a Great Horned Owl (*Bubo virginianus*) were collected on Franklin Island, Muscongus Bay, Knox County, Maine. These pellets contained the remains of 14 Leach's Storm-Petrels, 7 Common Eider (*Somateria mollissima*) chicks, 1 Herring Gull (*Larus argentatus*) fledgling, and 3 meadow voles (*Microtus pennsylvanicus*). One of the petrels found in a pellet on 6 July 1977 had been banded on Haddock Island, 5.0 km west of Franklin Island, on 23 June 1977.

During the 3-day stay in July petrels were quite active over Franklin Island at night. Although Morse studied Great Horned Owl predation on nesting seabirds in Muscongus Bay and owl kills were found on both Haddock and Franklin islands, each having breeding populations of Leach's Storm-Petrels, no petrels were found in pellets by Morse.

I extend thanks to J. O. Whitaker for reviewing the manuscript. These observations were made while conducting research for the National Audubon Society under the direction of S. W. Kress.—*Received 19 December 1977, accepted 8 September 1978.*

Colonial Nesting as an Anti-predator Adaptation in the Gull-billed Tern

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It has often been noted that colonial nesting in gulls and terns permits joint defense of the nests against predators (Cullen 1960, Kruuk 1964, Patterson 1965, Lack 1968, Andersson 1976). However, other studies have suggested either that colonial nesting does not contribute to nest defense (Lemmetyinen 1971) or that nest defense is not the only effect of colonial nesting (Ward and Zahavi 1973, Hunt and Hunt 1976). In May 1972, while conducting a study of the breeding behavior of the Gull-billed Tern (*Gelochelidon nilotica*) (Sears 1976, 1978), I witnessed a dramatic illustration of the value of other colony members in the defense of a nest against predators.

My study was carried out during 1971, 1972, and 1973 on an unnamed spoil island 0.5 km south of the port at Morehead City, Carteret County, North Carolina. Each colony was almost free of vegetation, contained 20–30 nests, and contained about equal numbers of Gull-billed Terns, Common Terns (*Sterna hirundo*), and Black Skimmers (*Rynchops niger*). Observations were made from burlap blinds and by means of time-lapse photography.

Late in May 1972, an intense subtropical storm struck the area, bringing rain, high winds, and low temperatures. I did not visit the colonies from 21–27 May. On 28 May, I found only one nest still active.

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All other nests were empty, and their previous occupants had left the colony area. Many gulls were present, walking about the colony site and diving at the two remaining terns. The gulls became more active on 29 May, and at 1430 a Laughing Gull (*Larus atricilla*) dove and snatched up the 2-day-old chick. Eight Laughing Gulls and one Herring Gull (*L. argentatus*) were present by 1600. The Laughing Gulls all hovered over the tern nest, the Herring Gull walked up and took an egg, and the rest of the flock dove and scrambled for the remaining egg.

In contrast, in the intact colonies of 1972 and 1973, I rarely saw more than one or two gulls per day in the vicinity of the colony. A gull that approached the colony was usually chased by terns or skimmers, and I never saw a gull actually land in the colony. In 1973, nest success was almost 40% (17 broods/43 nests), many of these 26 nest failures were probably due to my presence rather than to predation by gulls (Sears 1978), and no nest failure was witnessed during the hatching period (18 failures occurred during the first half of the incubation period, 3 more occurred before hatching, and 5 occurred at an undetermined time).

I attempted to obtain a more objective description of the difference between the disturbance to a nesting pair in an intact colony and the disturbance to the pair deprived of its colony by making use of the continuous data provided by time-lapse photography. I focused on the oblique posture, a behavior that involves a harsh call and extension of the neck, and whose effect is to repel intruders (Sears 1976). Thus, performance of the oblique is a good indication of disturbance to the performing tern. In all, seven nests were observed for a total of 68.7 h.

The frequency of performance of the oblique posture at three nests of intact 1972 colonies prior to hatching was only 0.6 per h, and most of these were directed at fellow colony members. At three 1973 nests, the rate was 1.0 per h on dates prior to hatching and 1.9 per h on dates after hatching, again with most performances directed at other colony members. At the isolated nest, the rate of performance of this posture (to potential predators only) was 5.0 per h on 28 May and 14.0 per h on the day of successful attack by the gulls.

The great increase in the disturbance caused by gulls after the destruction of the colony and the rapid demise of the isolated nest in spite of the defensive efforts of both terns attest to the effectiveness of colony defense.

I thank H. C. Mueller, J. P. Ryder, R. W. Schreiber, M. L. Sears, and P. Stettenheim for constructive criticism of earlier drafts. The Frank M. Chapman Memorial Fund and the H. van Peters Wilson Fund of U.N.C. provided welcome financial support.

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A Nearly Synchronous Hatching of Barn Owls

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In May 1978 I observed a nearly synchronous hatching of a large clutch of Barn Owls (*Tyto alba*) in Hunterdon County, New Jersey. The site was a wooden nest box installed inside the upper level of a two-story garage-utility building with the access hole leading out over a driveway and parking area, which were in regular use.

Bent (1938, U.S. Natl. Mus. Bull. 170: 142) stated that "the eggs are laid at intervals of two or three days, and incubation begins soon after the first egg is laid; consequently the young hatch at similar intervals and vary greatly in size." According to Welty (1975, The Life of Birds, 2nd ed. Philadelphia, Saunders: 310) "In a brood of six young Barn Owls, the first to hatch will be about 15 days older than the last."

This year the adult owls took up residence in mid-March. The nest was not inspected in April for fear that early disturbance during egg-laying and incubation might jeopardize its success. The first inspection of the box on 9 May revealed 8 owlets all 1–2 days old, plus 3 eggs. Apparently a staggered hatching did not take place, as the chicks were of almost identical size and appearance. I believe these 8 chicks were the result of a nearly synchronous hatching, all within 48 h. On 14 May, 9 owlets plus 2 eggs were found. On 26 May and 4 June there were 10 owlets, but the egg was missing. On 25 June I visited the nest and banded all 10 owlets; the difference between the 8 first-hatched birds and the 2 that hatched later was still apparent. The 2 smaller chicks, although a bit thin, were lively, alert and healthy. On 7 July, 6 of the 10 had fledged, and on 13 July all had fledged.—*Received 5 September 1978, accepted 21 November 1978.*

Status of the Genus *Phalacrocorax* in Puerto Rico Including the First Records of *P. auritus*

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The only published record of a cormorant from Puerto Rico to date is one by Danforth (1926, J. Dept. Agric. P.R. 10: 35), who saw what he confidently felt was an Olivaceous Cormorant (*Phalacrocorax olivaceus*) flying over Cartagena Lagoon, southwestern Puerto Rico, on 17 October 1924.

On 17 January 1973 Roy Thomas and I observed a large, immature cormorant swimming on one of several fresh water ponds on the Cerromar Hotel golf course, approximately 6 km west of Dorado (Table 1, #2). Photographs were taken and sent to the Migratory Bird and Habitat Research Laboratory (MBHRL), U.S. Fish and Wildlife Service, where Chandler S. Robbins and Jay M. Shepard identified the bird as a Double-crested Cormorant (*P. auritus*). This represents the first record of *P. auritus* for Puerto Rico. Two slides have been accessioned into the collection of the MBHRL (numbers 120-1Ta, 120-1Tb).

The mounted specimen of record #3 (Table 1) was found at a restaurant (Richard's Place) near Loíza Aldea. J. Phillip Angle and John C. Barber of the National Museum of Natural History (NMNH) determined that this too was a Double-crested Cormorant, most probably an immature ♀ of *P. a. floridanus*. Its measurements were, bill length 54.0 mm, wing (chord) 280.0 mm, and tarsus (approximately) 56.0 mm. The specimen was returned to Richard's Place and three slides are in the collection of the MBHRL (120-2Ta, 120-2Tb, 120-2Tc).

This note contains eleven new cormorant records for Puerto Rico (Table 1). Sightings range from 25 July to 18 January, while months of peak occurrence are November through January. All individuals for which there are detailed descriptions were immature birds and apparently represent wanderers from

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TABLE 1. New cormorant records from Puerto Rico.

Record	Date	Observer	Species	Location	Reliability	Comments
1	Winter '72	Roy Thomas	?	Dorado Beach Hotel, Dorado	good	Seen on a large golf course lake (Mata Redonda)
2	17 Jan '73	H. Raffaele & Roy Thomas	*P. a.*	Cerromar and Dorado Beach Hotels, Dorado	excellent; photos taken and identification confirmed; photos in MBHRL	Seen at close range with a 25× scope on fresh water golf course ponds including Mata Redonda
3	Dec '73		*P. a.*	Loíza Aldea	excellent; photos taken and identification confirmed; photos in MBHRL	A mounted immature specimen; shot in a flooded sand extraction pit by a hunter
4	18 Jan '75	Wm. J. Bolte	?	Boquerón Refuge	good	Seen in mangroves on edge of Rincón Lagoon and in flight
5	25 Jul '76	Jim Williams	?	Cabo Rojo	good	Seen with head up and wings spread near a fresh water shrimp pond
6	9 Nov '76	Jim Sedgwick	*P. a.*	Lago Ponceña, Juana Díaz	good	An immature; seen swimming and in flight; appeared enormous next to 2 Pied-billed Grebes (*Podilymbus podiceps*) on the lake
7	11 Nov '76	Jim Sedgwick	*P. o.*	Dorado Beach Hotel	good	2 immatures on Mata Redonda; appeared not much larger than an American Wigeon (*Anas americana*) nearby
8	12 Nov '76	H. Raffaele	*P. o.*	Dorado Beach Hotel	good	2 immatures on Mata Redonda
9	29 Nov '76	Jim Sedgwick	*P. o.*	Lake #2, Juana Díaz	good	An immature; seen only 1.2 km from where he observed a *P. a.* on 11/9, but this seemed a smaller bird
10	4 Dec '76	Game Wardens of the P.R. Dept. of Natural Resources	?	Lago Ponceña, Juana Díaz	good	Shot by hunters, 2 birds seen a day or two before; measurements taken by hunters were: length 22" (56 cm) and weight 6 lbs. (2.7 kg); the specimen was reportedly eaten
11	Dec '76	Elizabeth Litovich	?	Dorado Beach Hotel	excellent	Immature; seen on golf course lake; photos taken

nearby breeding colonies, probably those in Cuba or the Bahamas. The large number of recent records suggest that cormorants either have long been overlooked in Puerto Rico or the degree to which they stray to the island and find suitable habitat has dramatically increased. Actually, it is probable that a combination of these two factors, the latter being more significant, account for the apparent change in status of these birds. All recent cormorant sightings, with the exception of that of Bolte, were from impounded or dredged fresh water lakes that weren't in existence a few decades ago, when most earlier observers studied the island's avifauna. Such localities, in addition to creating new and quite suitable habitat for cormorants, are more regularly surveyed by wildlife biologists than coastal mangrove lagoons, where a significant number of cormorants may occur annually but continue to go unnoticed. It is difficult, however, to conceive that this factor could account for such a substantial increase in cormorant numbers. These records could reflect increased cormorant populations in their source area.

Bond (1974, Nineteenth supplement to the check-list of the birds of the West Indies (1956), Philadelphia, Acad. Nat. Sci.) recently commented that "all cormorants reported from Puerto Rico, the Lesser Antilles and Tobago were probably vagrants of *P. olivaceus* from South America." This statement is in need of significant modification. It might be more accurate to say that although proof exists that *P. auritus* occur in Puerto Rico, there is little doubt that *P. olivaceus* also occurs as a stray (though this remains to be substantiated), both species apparently represented by wandering immatures from colonies in the Bahamas and Cuba. (Puerto Rico's Double-crested Cormorants probably come from the Bahamas or Cuba since this species is not known to breed in South America; therefore, it is likely that the island's Olivaceous Cormorants also derive from this area rather than South America.)—*Received 10 May 1977, accepted 27 November 1978.*

Observations at a Nest of a Partial Albino Red-headed Woodpecker

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Unusual individuals in a population always seem to arouse human curiosity, but too often that curiosity is quickly satisfied by preserving the specimen for posterity and future speculation as to its "fitness." We report here observations at a successful nest of an albinistic Red-headed Woodpecker (*Melanerpes erythrocephalus*). On 13 May 1977, M. Rogers discovered the partially albino Red-head (Fig. 1A) on the campus of the University of Alabama in Tuscaloosa. Its nest was in a partially dead sugarberry (*Celtis laevigata*) that stood in a parking lot 20 m from the nearest other tree. Live limbs of the tree extended to about 13 m, but the nest cavity was 8 m up in an 8.4-m dead stub of approximately 12 cm diameter. The albino bird's mate was normally pigmented (Fig. 1B).

When viewed with a 20× spotting scope at 20 m, the albino could be seen to have some color in primaries 4 through 9. The base of the bill was pink, the tip darker. The feet and legs were pink, though the eyes appeared dark. There were conspicuous black areas in the scapular region and along the rachis of the central rectrices. Other rectrices appeared nearly white and were quite worn. The albino bird's head was red, but when compared to that of its mate it appeared to be slightly pinker, as if the bases of the red feathers were whiter than normal.

Jackson climbed to the nest on 27 May and removed the three nestlings for banding. Their weight and physical development indicated their age to be approximately 8 days (Jackson 1970, Niobrara, Annual Report of the University of Kansas Museum of Natural History, 1968–69: 3–10). All three appeared normally pigmented.

On 27 May, Jackson and Schardien captured the normally-pigmented adult as it flew from the nest. The cloaca was swollen, suggesting that the normal bird was a male. On 28 May Jackson and Schardien found that the normally-pigmented bird was the parent roosting in the nest at night, further substantiating that it was the male and the albino the female (see Jackson 1977, Living Bird 15: 205–221).

During nest watches on 24 and 27 May and 5, 16, and 19 June we observed 16 of 42 feeding visits (38%) by the albino bird. This is within the range of variation found for the relative attentiveness of the

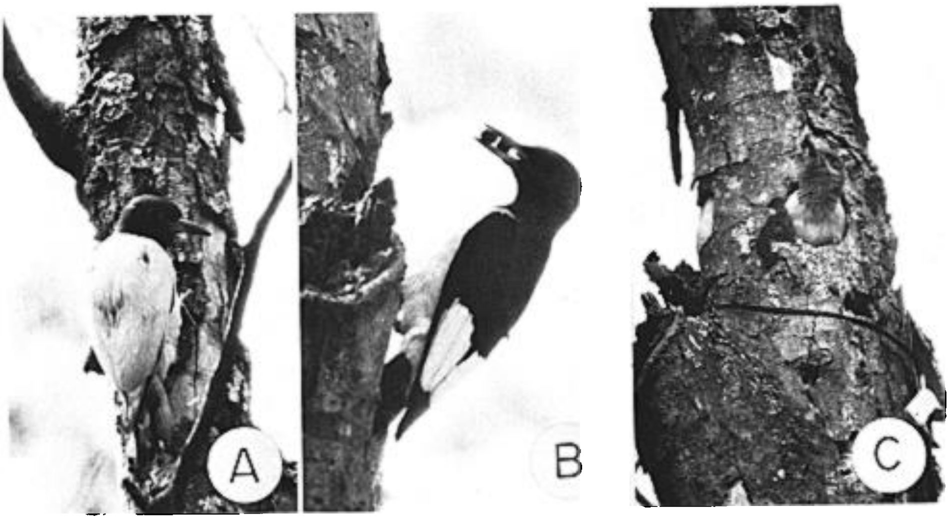

Fig. 1. (A) A female albino Red-headed Woodpecker, (B) her normal mate, and (C) a normally-pigmented nestling in the nest cavity just prior to fledging.

sexes in Red-headed Woodpeckers (Jackson 1976, Condor 78: 67–76). Both the albino and normal adult removed fecal sacs from the nest. Other behavior of the albino seemed typical for the species. Jackson and Schardien observed the albino flycatching from a perch on a utility pole and using the top of the pole as a "chopping block" at which to dismember its prey.

At least one of the nestlings fledged successfully on the morning of 19 June. This and the other young had juvenal plumage that seemed normal for the species.

We visited the site of this nest again in 1978, hoping to observe this unusual bird during another nesting attempt. Unfortunately the nest tree had been removed for a parking lot and we observed no Red-headed Woodpeckers in the vicinity.—*Received 5 September 1978, accepted 26 November 1978.*

Density and Volume Corrections of Eggs of Seven Passerine Birds

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Few measurements of the density of fresh eggs of passerine birds are recorded in the literature and, as far as I know, none showing the loss of density during the egg-laying period. The eggs used in this study were from nests located near Merrickville, about 50 km south of Ottawa, Ontario. Each clutch was probably laid by a different female. The Barn Swallow nests were in a single barn; the Red-winged Blackbird nests in three small marshes. (Scientific names of all species are given in Table 2.) The other nests were scattered over an area of about 6 km^2. The six Starling eggs were found on a recently mown lawn. The five Brown-headed Cowbird eggs were from four well-separated host nests and therefore probably laid by four different females.

The eggs were weighed, while sheltered from the wind in a transparent acrylic cylinder, with 10-g and 5-g Pesola balances reading to 0.2 g and 0.1 g, respectively. Length and breadth of the eggs were measured with dial calipers reading to 0.1 mm. To measure density, the eggs were placed in a solution of common salt (NaCl), the density of which was adjusted by the addition of fresh water and saturated salt solution until the eggs were just waterborne. The density of the solution was then measured with a hydrometer, graduated to 0.002 $g \cdot cm^{-3}$ and readable to 0.0005. Care was taken to mix the salt solution thoroughly and to see that the egg and hydrometer bulb floated at about the same level. As the egg and the hydrometer were in the same solution, the readings were not affected by temperature or impurities in the water. The eggs were rinsed in fresh water, dried, and numbered with small dots of red nail polish before being returned to the nest.

The above method of density measurement is accurate, and for small eggs, such as the Barn Swallow (for which a change in density of 0.002 corresponds to a change in weight of only 0.004 g), superior to methods based on weight and volume. Unfortunately it cannot be used satisfactorily for many eggs with very different densities, as this would involve too many large changes in the strength of the salt solution. Also there was some evidence that hatching success was reduced, particularly in the smaller eggs.

Loss of density during laying and incubating periods.—To determine the daily loss of density during the laying period, I measured the density of the eggs on the day they were laid and again 24 h later. Presumably other eggs in the clutch lost similar amounts during the 24-h period, but to avoid large changes in the strength of the salt solution they were not tested. I have assembled the results (Table 1) using the start of incubation (the laying of the last egg) as the base. Counting the days backward from the last egg rather than forward from the first egg gave distinctly better agreement between the density losses of eggs in different sized clutches. For instance, first eggs of the three 4-egg clutches of the American Robin and Red-winged Blackbird had a mean density loss of 0.0002 for the first day after the start of laying, whereas the two 2-egg clutches of those species had a mean loss of 0.0058. The data for the first day of incubation (Table 1) were obtained from the last egg laid. The mean daily density loss for the incubation period up to the time of pipping was calculated from weight loss measurements (Manning in prep.).

The gradual increase in the daily density loss of eggs of the American Robin and the Red-winged Blackbird during the laying period (Table 1) parallels the increase in incubation constancy of the latter species (Holcomb 1974) and is probably the result of that increase. After the clutch is complete, incubation constancy appears to vary little, and the cause of the difference between the density loss on the first day of incubation and the subsequent mean daily loss is obscure, unless it is associated with the increase in vascularity of the brood patch, which occurs after the third day of incubation (Holcomb 1975).

The Barn Swallow eggs lost density more rapidly than those of the American Robin and Red-winged Blackbird at the start of the laying period, but had a lower loss during incubation (Table 1). The first difference is no doubt associated with the longer incubation period of the swallow (Rahn and Ar 1974); the second may have been due, at least in part, to the position of the nest—immediately under a hot iron roof. Indeed, throughout the incubation period those swallows were seldom seen on their nests during the day, and the density loss of the first egg in a single nest in a cooler location was only 0.0005, though for succeeding eggs the losses were normal.

Density of fresh eggs.—It is evident from the foregoing that to obtain the density of fresh eggs they must be measured as soon as possible after they are laid. In many, probably most, species some incubation occurs before the clutch is complete and density measurements taken at that stage can be misleading. At the same time too many visits to a nest to check for newly-laid eggs is time consuming and undesirable. Therefore, there is likely to be a period of a few hours between laying and measuring. I have not attempted to correct the densities (Table 2) for the loss during this period, because the time of laying is not accurately known. For the Barn Swallow, American Robin, and Red-winged Blackbird the correction would average about 0.0002/h (Table 1). The Barn Swallows appeared to lay early, probably about 0600, which would indicate an average density loss of 0.0009 before measurement. This is a small amount, but it is more than twice the standard error (Table 2). The American Robins laid later and more irregularly, probably about 1200 on the average, so the correction would be 0.0005. The laying time of the Red-winged Blackbird seemed to be intermediate. The average density lost by the Starling eggs before weighing was probably less than 0.001, as the weather had been cold and damp.

TABLE 1. Mean daily loss of density (10^4 g·cm^{-3}) by eggs during laying and incubation. The number of eggs measured are in parentheses.

Species	Days before start of incubation					1st day of incubation	During incubation
	5	4	3	2	1		
Barn Swallow	41(2)	39(6)	37(10)	50(11)	62(12)	57(12)	86(44)
American Robin			17(5)	42(7)	58(9)	84(10)	123(26)
Red-winged Blackbird			16(3)	46(4)	65(5)	72(4)	119(59)

TABLE 2. Mean eastern standard time (EST) of measurement, weight, true volume, and density (with coefficient of variation) of fresh eggs. Means, standard errors, and coefficients of variation are based on individual eggs and total variances.

Species	N		EST, h[a]	Weight (*W*), g[b]	True volume (*W*/*D*), cm³ [b]	Density (*D*), g·cm⁻³	
	Eggs	Clutches				Mean ± SE	CV[c]
Eastern Phoebe *Sayornis phoebe*	9	2	9.7 (3.4)	2.13 ± 0.054	2.03 ± 0.052	1.0505 ± 0.00071	0.203
Barn Swallow *Hirundo rustica*	44	10	10.6 (2.3)	2.04 ± 0.026	1.94 ± 0.025	1.0518 ± 0.00037	0.233
American Robin *Turdus migratorius*	33	10	14.5 (1.6)	6.42 ± 0.082	6.07 ± 0.077	1.0577 ± 0.00053	0.270
Starling *Sturnus vulgaris*	6	—	—	7.06 ± 0.263	6.66 ± 0.247	1.0611 ± 0.00158	0.105
Red-winged Blackbird *Agelaius phoeniceus*	67	20	13.0 (3.3)	4.09 ± 0.041	3.88 ± 0.039	1.0551 ± 0.00029	0.224
Common Grackle *Quiscalus quiscula*	12	3	14.1 (2.8)	6.70 ± 0.146	6.32 ± 0.137	1.0606 ± 0.00065	0.212
Brown-headed Cowbird *Molothrus ater*	5	4[d]	9.4 (1.5)	3.44 ± 0.084	3.25 ± 0.078	1.0588 ± 0.00153	0.323

[a] Mean, standard deviation in parentheses.
[b] Mean ± standard error.
[c] Coefficient of variation.
[d] Host nests.

TABLE 3. The correction ($k\pi/6$) to the volume index (LB^2) needed to obtain the true volume of eggs, and the difference ($[1 - k]\pi LB^2/6$) between the ellipsoidal volume and the true volume. Means and standard errors are based on individual eggs and total variances.

Species	N		$k\pi/6$	$(1 - k)\pi LB^2/6$	
	Eggs	Clutches	Mean ± SE	Mean ± SE cm³	As percent of true volume
Eastern Phoebe	8	2	0.5117 ± 0.00480	0.046 ± 0.0194	2.23
Barn Swallow	46	10	0.5070 ± 0.00142	0.063 ± 0.0054	3.27
American Robin	35	11	0.5036 ± 0.00172	0.242 ± 0.0207	4.07
Starling	6	—	0.5130 ± 0.00227	0.138 ± 0.0306	2.07
Red-winged Blackbird	75	22	0.5065 ± 0.00098	0.127 ± 0.0076	3.33
Common Grackle	17	4	0.5091 ± 0.00213	0.184 ± 0.0278	2.89
Brown-headed Cowbird	5	4[a]	0.5181 ± 0.00314	0.033 ± 0.0189	1.02
All species	192	—	0.5071 ± 0.00068	—	3.27[b]

[a] Host nests.

[b] Mean weighted by egg numbers.

The regression equation for mean egg density (D) on mean egg weight (W) of the seven species is $D = 1.047W^{0.0067\pm0.00150}$ ($r = 0.89$). The observed densities (Table 2) average 0.0096 above those predicted from the observed weights by Equation 6 of Paganelli et al. (1974) and 0.0054 below those predicted by a similar equation given by Rahn et al. (personal communication).

Volume correction.—When the true volume of an egg is unknown, the length (L) × breadth² (B^2) may be used as an index (LB^2). To convert this index to true volume (V) it must be multiplied by $k\pi/6$, where $\pi/6$ is a constant (0.5236) giving the ellipsoidal volume and k is a variable, measuring departures from the ellipsoid (Barth 1967, Manning 1978). In the present case the true volume was calculated from weight and density (Table 2) and $k\pi/6$ determined as V/LB^2 (Table 3). Fresh eggs are not needed for this, and the egg numbers therefore differ in Tables 2 and 3. As $\pi/6$ is a constant and the effect of k, though very variable, is relatively small (Table 3), an average $k\pi/6$ for a species may be used to estimate the true volume of eggs, such as those in museum collections, the weight and density of which cannot be directly measured. Actually there are no significant differences among the species means in Table 3, and the best estimate is the weighted mean of the seven (0.5071). The two species with the largest series of measurements are the Barn Swallow and the Red-winged Blackbird. Although these two species are from different families, their mean volume corrections are similar, and it appears from measurements of asymmetry and bicone (Preston 1969), which are combined in the correction k, that this similarity may be general among passerine families.

The penultimate column of Table 3 gives the amount that must be subtracted from the ellipsoidal volume to obtain the true volume. The weighted mean of the coefficients of variation for these measurements is 59.2. This high figure is similar to the mean (65.6) obtained for the coefficient of variation of the volume correction calculated from Preston's data for asymmetry and bicone of 40 Canada Goose

TABLE 4. Partitioning of density variance between eggs within clutches and clutches as a whole. Density values are in 10^5 g·cm^{-3}.

	Degrees of freedom	Variance	95% confidence limits	% of total variance	Coefficient of variation
Barn Swallow					
Eggs	34	0.159	0.104–0.273	26.4	0.120
Clutches	9	0.443****	0.190–1.561	73.6 ± 11.1	0.200
American Robin					
Eggs	23	0.362	0.218–0.711	44.3	0.180
Clutches	9	0.454****	0.140–1.771	55.7 ± 17.0	0.201
Red-winged Blackbird					
Eggs	47	0.375	0.260–0.589	67.1	0.184
Clutches	19	0.184***	0.044–0.522	32.9 ± 13.7	0.128

*** = $P < 0.005$.

**** = $P < 0.001$.

TABLE 5. Partitioning of the volume correction ($k\pi/6$) variance between eggs within clutches and clutches as a whole. Values are in $cm^3 \cdot cm^{-3}$.

	Degrees of freedom	Variance	95% confidence limits	% of total variance
Barn Swallow				
Eggs	45	0.432	0.286–0.730	46.4
Clutches	9	0.499****	0.173–1.814	53.6 ± 15.6
American Robin				
Eggs	24	0.687	0.433–1.141	66.5
Clutches	10	0.346*	0.000–1.535	35.5 ± 19.3
Red-winged Blackbird				
Eggs	53	0.542	0.383–0.826	75.9
Clutches	21	0.172**	0.012–0.558	24.1 ± 12.8

* = $P < 0.05$.
** = $P < 0.025$.
**** = $P < 0.001$.

(*Branta canadensis*) eggs (Manning 1978). How much of the variation is attributable to instrumental and personal error is unknown in both instances.

Partitioning of variance of density and volume correction.—The clutch components of the variance of density and volume correction ($k\pi/6$) are significant in the three species tested (Tables 4 and 5), and as k corrects the ellipsoidal volume for the effect of asymmetry and bicone, it may be inferred that the variances of those measurements also have significant clutch components. As the number of eggs per clutch varied, the confidence limits for the clutch component of the variances are not exact (Sokal and Rohlf 1969). The same applies to the standard errors of the percentages of total variance, which were calculated according to Equation 4 of Swiger et al. (1964) for intraclass correlation. These two sets of statistics do, however, give an idea of likely variations. Judging by the confidence limits, there are no significant differences between species for the clutch components of the variances for either density or volume correction (Tables 4 and 5). The egg component of the density variance, however, is significantly higher in the Red-winged Blackbird than in the Barn Swallow (Bartlett's test; $P \approx 0.025$).

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BREWSTER AND COUES AWARDS, 1978

BREWSTER AWARD 1978

PIERCE BRODKORB

In 1963, when the first part of Pierce Brodkorb's "Catalogue of Fossil Birds" was published, it instantly became the standard work in paleornithology. Each succeeding part has been eagerly awaited, not only by paleornithologists, but also by many others in the related fields of systematics, evolution, and nomenclature of birds. Brodkorb has a prodigious knowledge of fossil birds, and has studied and reevaluated many previously described taxa. Thus, although the "Catalogue" is necessarily in large part a compilation based on existing literature, a substantial portion of that literature came from Professor Brodkorb's own pen. He and his students have been for many years among the most productive sources of new information about avian fossils, especially those of the New World. No fewer than 25 of the recognized genera in the four non-passerine volumes of the "Catalogue" bear Brodkorb's name as author.

Brodkorb is also a serious student of the intricacies of zoological nomenclature. The International Code of Zoological Nomenclature has mandated the determination of priority of usage of names at the family level. Brodkorb has won our gratitude for his willingness to undertake this difficult, time-consuming, and unpopular kind of research, and to incorporate his findings in his "Catalogue." He has produced, in a phrase, an indispensable reference work.

A paleornithologist worthy of the name must do more than just look at bones and books—he must try to place his findings within the context of the broad patterns of the origin and evolution of birds. Professor Brodkorb has done just that by summarizing his views in a chapter of "Avian Biology" (Academic Press, 1971).

As we find ourselves in a period of almost turbulant reexamination of the relationships of the higher categories of birds, the importance of fossil evidence is gaining new appreciation. Pierce Brodkorb's outstanding contributions to this aspect of ornithology well merit his receipt of the Brewster Award for 1978.

COUES AWARD 1978

JOSEPH J. HICKEY

More than any other individual, Joseph Hickey is responsible for pinpointing, documenting, and publicizing the deleterious effects of pesticides on breeding populations of raptors. In the late 1950's, he was among the first to appreciate the relationship between urban use of DDT and the catastrophic drops in robin populations. Shortly thereafter, he and his students documented the disappearance of Peregrines from the eastern United States.

Subsequently, Hickey organized a conference to assess Peregrine populations on a world-wide basis, and edited its proceedings. Later, he showed that Peregrines were threatened by pesticides, and that eggshell thinning and reduced reproductive success were correlated with high residues of DDE in Herring Gull eggs. Hickey has thus played a pioneering and pivotal role in virtually all aspects of research linking pesticide residues with decreased reproduction in birds.

Recognizing the importance of his and others' findings, Hickey actively turned his attention to publicizing the adverse effects on birds of the use of pesticides, through speeches, popular articles, and testimony in the famous Wisconsin hearings on the banning of DDT.

Considered in historical perspective, Hickey's contribution to basic ornithological knowledge and his willingness to take a strong scientific stand on the basis of his results stand as examples to be emulated by future researchers, and are ample justification for his designation as recipient of the 1978 Coues Award.

REVIEWS

EDITED BY WALTER BOCK

A Guide to the Birds of Venezuela.—Rodolphe Meyer de Schauensee and William H. Phelps, Jr. 1978. Princeton, New Jersey, Princeton University Press. xxii + 424 pp., 40 color and 13 black-and-white plates by Guy Tudor, H. Wayne Trimm, John Gwynne, and Kathleen D. Phelps, line drawings by Michel Kleinbaum. Hardback $50.00, softback $19.95.—South America has long been one of the most intriguing places to see or study birds, but books for the identification of its avifauna have been extremely slow in appearing. For the most part those that have appeared have been inadequately illustrated, a factor that severely limits their use by the amateur. The present volume, a pleasant surprise both in quality and compactness, covers Venezuela, one of the most interesting of the continent's countries.

The book is organized in typical guidebook style with acknowledgments, a note about travel to Venezuela, and introductory material about the country, followed by descriptions of the 1,296 species that are known to occur there. The plates are conveniently grouped in the center, and the end papers have a map of Venezuela depicting prominent features of the country's topography.

The illustrations in "The Birds of Venezuela" set it apart as the most useful book on South American birds. The plates prepared by Guy Tudor are no less than stunning. Upon receiving my copy I found myself staring at Tudor's plates for hours at a time. The *piece de resistance* is Plate 30, upon which 48 species of small flycatchers are depicted, *all* of them easily identifiable! The plates by John Gwynne are also excellent. Those by Wayne Trimm are adequate for identification, but the birds are rather stiff and their quality is variable. The line drawings by Michel Kleinbaum are very attractive and well done. Kathleen Phelps contributed two plates of some of Venezuela's more spectacular birds.

Guy Tudor's field work has paid off. He knows most of the birds he has depicted and it is obvious from his work. A few of his illustrations, however, are slightly misleading to me. The *Pygiptila, Thamnophilus,* and *Percnostola* antshrikes on Plate 22 are all too similar in shape, the *Mecocerculus stictopterus* on Plate 30 is too large and is depicted as an "upright" flycatcher rather than the more horizontally perching warbler- or vireo-type bird that it is, and the inclusion of the feet on the nightjars on Plate X seems unnatural. There are other small things with which I personally disagree, but all of these are totally overshadowed by the beauty, overall accuracy, and usefulness of the plates. Tudor's eye for design is often amazing, as in his treatment of the flying macaws on Plate 8. His depiction of hawks and eagles in flight is superb. Thanks in part to the large amount of reference material made available to him by his friends and associates, his renditions of these birds are extremely accurate and, by showing them from a side angle rather than an overhead angle, they are very useful. My main criticism of the illustrations is that the plates are often too crowded and the coverage of identifiable forms is often minimal. At least some attention is given to northern migrants, but more illustrations would help, especially for Venezuelans who may not have access to the many books on North American birds.

The text, although basically well done and accurate, is not outstanding. Each family account begins with a paragraph giving generalized information about the particular group. One item that does not appear in any Neotropical guidebook that would have been most helpful in "The Birds of Venezuela" is a guide to the families. Most North American or European birdwatchers are not familiar with the great diversity of South American birds, and without having some idea of what family a bird is in they would be hard pressed to know where to begin looking for it in the book. A general description of the variations in a family with silhouettes to illustrate these differences would be most useful. The species descriptions generally describe each bird in a typical "head-to-tail" fashion and are fairly museum-specimen oriented. Information on how to separate similar species is usually lacking. For many species the addition of a single note or statement would often serve to allow them to be easily and quickly identified. I also find disappointing the lack of useful information on vocalizations, especially when one of the foremost authorities on Neotropical bird sounds lives in Venezuela. The voice descriptions are, in general, of little value as they often describe sounds only in such terms as a "sharp penetrating chirp," a "metallic trill," or a "low whistle." Also, no differentiation is made between calls and songs. Voices are an important means of locating birds and should be accurately presented. Often a species is common in a given area, but with no knowledge of its voice a person may not find it. On the other hand, the authors have included a fair amount of information on habitat that will be quite useful to the reader. The inclusion of information on elevational ranges is important and valuable.

Much of the criticism I have of the text is reduced by the inclusion of an excellent series of plate notes by Guy Tudor. These notes, which are presented on the plate legends for each species, give the most useful marks for field identification. Tudor also includes comments on species not depicted on the plates. The effect of these notes is to make the center section of the book stand by itself as a small, extremely usable field guide.

The publishers have done an excellent job in printing. They are to be especially praised for the excellent reproduction of the color plates. The total quality of the book should be looked at carefully by other publishers of natural history books. In hours of looking through the text I have discovered few typographical errors. One point about which I am most concerned is why the hardbacked edition costs $30.00 more than the softbacked one. The cover and binding on my review copy are strong and well done, but certainly not worth $30.00! I purchased a softbacked copy for use in the field and it has held up well even after 2 months of being thumbed through on an almost daily basis by groups of Aguaruna-Jivaro Indians who were enthralled at seeing "their" birds depicted in color. My advice to purchasers is to buy the softbacked book and have it handsomely bound in leather, for about $5.00, on their next trip to South America!

The best book available on any area in the Neotropics is Ridgely's on the birds of Panama, but "The Birds of Venezuela" is certainly the best one available for a South American country. I hope that future authors of books on Neotropical birds will include more information on living birds and give more attention to field identification. Despite my criticisms of "The Birds of Venezuela," it is still an excellent book. The plates and notes by Guy Tudor are outstanding and make the book a must for any student of South American birds.—JOHN P. O'NEILL.

Guide to the Young of European Precocial Birds.—Jon Fjeldså. 1977. Skarv Nature Publications, Denmark. 283 pp., 39 color plates, 29 figures, many drawings. 200 Danish Kroner (ca. $33.00).—This is not so much one book as three—it is a guide to the identification of precocial chicks; a portfolio of color printings; and a systematic paper.

The text provides a broad overview of the biology of families with precocial young, and a general description of the chicks, that would be useful in introductory courses. Fjeldså's major thesis, which is largely verified, is that chicks of all species can be identified. Accordingly, each species is discussed in detail, with data on plumage characters, similar species, measurements of newly-hatched young, banding information, and general distribution. These accounts are generally good, although some questionable information is included. It is, for example, difficult to accept that newly-hatched Common Loons weigh 52–92 g, whereas Arctic Loons average 75 g. Previously unappreciated characters that permit the separation of allied forms are illustrated. Excellent black-and-white drawings depict chicks of many species; some show variation within a group or a species. There is a glossary of common names in several European languages.

The book is enhanced by a portfolio of 39 outstanding color plates showing the young of most species. Fjeldså's skill as an artist and a careful observer is undeniable, and the plates are the strong point of the book. Chicks are depicted accurately in lifelike postures, and in my copy the color rendition (except Plate 26) is excellent. I know of no other book with such a wealth of illustrative information on downy plumages. One minor slip appears in the Social Plover (*Chettusia gregaria,* Pl. 20), which is said to be identifiable by the presence of an undepicted hind toe.

Fjeldså's secondary thesis—the systematic aspect of this book—aims "to demonstrate the conservatism of downy plumage patterns and its (sic) usefullness (sic) in establishing phylogeny." The idea is not original. In 1915, P. R. Lowe emphasized the value of downy plumages, and they played a major part in Delacour and Mayr's classic revision of the waterfowl. Subsequently they have been used successfully to test relationships in a wide variety of taxa including ratites and tinamous (Jehl 1971, Trans. San Diego Soc. Nat. Hist. 16: 291–302), grebes (Storer 1967, Condor 69: 469–478), grouse (Short 1967, Amer. Mus. Novitates 2289), and shorebirds (Jehl 1968, Memoir 3, San Diego Soc. Nat. Hist.). Indeed Fjeldså's justifications for using downy plumages (p. 12) parallel arguments I advanced earlier (1968: 7).

The conservatism of downy plumages is convincingly demonstrated by a series of illustrations depicting the commonality of color pattern within a wide variety of taxa. These pattern diagrams are a major contribution because chicks are poorly represented in most collections, and patterns are difficult to reconstruct from prepared material. Note, however, that pattern interpretation is sometimes necessarily subjective, and thus the patterns should be used with caution.

Fjeldså's goal of using downy plumages to establish phylogenies is less successful. In a series of figures, he presents possible phylogenetic pattern transformations in grebes, waterfowl, grouse, and shorebirds.

This technique, too, is not new (cf. Jehl 1968, op. cit.), but Fjeldså is the first author to apply it so broadly. Unfortunately, he has chosen not to acknowledge, or has cursorily dismissed, the contributions of previous workers on chick plumages and, his taxonomic discussions are characterized by a lack of references of any kind. Thus, while his suggested grouse phylogeny (Fig. 13) is said to be supported by "anatomy studies, analyzed by cladistic methods," there are no supporting citations. In addition, the construction of the transformation diagrams is not explained, and one can only guess at their derivation. The result is phylogeny by fiat. Because of this cavalier treatment the reader is left interested but unconvinced, which is too bad because downy plumages unquestionably offer the possibility for fresh insights in phylogenetic studies. One example: Fjeldså points out (p. 106) that the few patterned species of rails are reminiscent of jacanas, rostratulids, heliornithids, psophiids, and perhaps hemipodes; this observation clearly requires further development.

Those interested in Fjeldså's interpretations of relationships in specific taxa—which mostly conform to previous results—should consult the text. Here I will only comment briefly on one aspect of shorebird relationships (Fig. 16). Basically, Fjeldså suggests that the downy pattern of "primitive" (not defined) calidridine sandpipers (*Aphriza, Calidris canutus*) can be derived from that of "primitive" (not defined) plovers (*Eudromias, Zonibyx, Oreopholus, Charadrius falklandicus*) via that of the turnstones (*Arenaria*). (Subsequently, the calidridines gave rise to two lines, the snipes and woodcocks, and the tringine complex.) I find this difficult to accept because the turnstone pattern is not easily derivable from either the plover or calidridine configuration. Further, recent studies by J. G. Strauch confirm P. R. Lowe's view that the plover and sandpipers are not particularly closely allied, and I (1968, Condor 70: 206–210) have argued that there is no strong evidence (including downy plumages) of close relationship between *Aphriza* and *Arenaria*. Fjeldså's interpretation, then, seems to conform more closely with the "classical" view of plover-sandpiper relationships than with data from downy plumages.

In my view, the turnstone pattern is reminiscent of the tringine sandpipers. Surprisingly, Fjeldså seems to agree (p. 136) for he notes that "the arrangement of bands on the back of Turnstone chicks may approach that in Godwits and Spotted Redshank." Fjeldså's interpretation is further confusing because while Fig. 16 suggests that *Arenaria* is an "intermediate," the figure caption states that it represents "a side branch with degenerate powder-puff down." I fail to appreciate how a tringine-like pattern with degenerate down can give rise to the complicated calidridine pattern with its highly specialized powder puff feathers, and how the calidridine pattern, in turn, reverted to the tringine state. A more reasonable view is that turnstones are tringine relatives. Fjeldså and I disagree on other details of wader phylogeny, and other taxonomists will doubtless find other areas of disagreement. At present, lacking detailed documentation, Fjeldså's phylogenetic ideas seem best considered as interesting working hypotheses.

Some comment on the production of the book is unavoidable. It is marred by abundant flaws in grammar, usage, and hyphenation. Capitalization is sporadically Germanic. The English meaning of words is often not appreciated. "Chickens" is used regularly (but not consistently) for "chicks," leading to such confusing combinations as "sandgrouse chickens." Button Quail are said (p. 99) to live "secretly (sic) in dense ground vegetation . . . are shy, escape . . . by running, and are very hard to blow up" (= flush?). Misspellings in scientific names and terminology as well as in common words occur on nearly every page. Proofing by a native English speaker would have eliminated these problems, which, initially, are a source of minor distraction but eventually become extremely annoying.

Taxonomic emphasis aside, the book invites comparison with Harrison's "Field guide to the nests, eggs, and nestlings of European birds." Those wishing a field guide will find Harrison's book more useful because of its size, format, broader scope, and low cost. Fjeldså's book is of significant value for its detailed descriptions of chick plumages and for its excellent portfolio—an important contribution in itself. I would hope that his taxonomic ideas, which are well worth pursuing, will be documented in more detail in subsequent publications.—J. R. JEHL, JR.

Parental Behavior in Birds.—Rae Silver (Ed.). 1977. Benchmark Papers in Animal Behavior, 11. Stroudsburg, Pennsylvania, Dowden, Hutchinson and Ross, Inc. xviii + 430 pp. $24.50.—Thirty-two papers published previously, mostly in standard journals, have been photocopied and arranged into five parts: initiation of breeding, pair formation and nest building, egg-laying, post-laying behavior, and post-hatching behavior. An introduction to the entire compendium and short introductions to each part contain numerous additional references. Two-thirds of the papers were published more than 20 years ago; only three were published within the last 10 years.

In assembling these papers Silver clearly examined an extensive literature and partitioned the information reasonably. However, in general I disagree with the papers chosen. Part 1 seems the weakest; all four papers are outdated. A. J. Marshall published important papers on the initiation of breeding more recently than 1957, and amazingly to me, no paper by Farner or King is included, even in the references! The four papers comprising Part 2 are good, but limited in scope. Breeding nexuses other than pairs are given short shrift, and no treatise on the use of nest materials in courtship is included. Three of the five papers comprising Part 3 are of very limited historical interest only, and no additional references are listed in the editor's comments. I find the information included under "laying" in "A New Dictionary of Birds" (Landsborough Thomson, Ed. 1964, London, Nelson) published 14 years ago far more complete. Post-laying behavior, Part 4, receives the most thorough coverage, but then one-third (11 of 32) of the papers are placed in this one of five parts. Here too antiquity of the papers chosen weakens the coverage. Host specificity in cuckoos is treated by a paper published in 1927; numerous recent papers cover the topic more thoroughly. Part 5 consists of eight papers; several are good choices. Although Skutch (1935) is of historical interest to the subject of communal breeding, I would have chosen a more recent paper that discusses attempts to understand the phenomenon (e.g. Brown 1974).

In summary, I cannot recommend that ornithologists buy "Parental Behavior in Birds" for reference or teaching. In its place I suggest the appropriate topics in Landsborough Thomson, Kendeigh's (1952) "Parental care and its evolution among birds," and papers in recent Proceedings of International Ornithological Congresses, which are written by authorities on the subject and often are reviews.—GLEN E. WOOLFENDEN.

A New Guide to the Birds of Taiwan.—Sheldon R. Severinghaus and Kenneth T. Blackshaw; Chinese translation by Lucia L. Severinghaus. 1976. Taipei, Mei Ya Publ. xiii + 222 pp., illustrated by Susan R. Blackshaw, 8 color plates, 107 line drawings, 1 map. $6.95 (available from Harrowood Books, 3943 N. Providence Rd., Newtown Square, Pa. 19073).—Greatly improved in every way over Dr. Severinghaus' earlier book (A guide to the birds of Taiwan, 1970), this guide provides identification material for the 201 (of 380+) species of birds most likely to be encountered in Taiwan (Formosa). Forty-three species are illustrated in color and another 100 in the line drawings. The color plates are fairly good and the birds can be identified with them, but reproduction is poor. The line drawings are mostly good, and adequate for identification. The text is brief, containing: length (in inches and centimeters), descriptive material, some comparisons with other species, habits, voice, status, distribution (geographical, seasonal, and altitudinal), and habitat. Most of the species covered could be identified using this text, with the exception of some difficult hawks, eagles, and warblers. The book is actually much shorter than its 222 pages since nearly half of it is taken up by the Chinese translation of each section. Some new information on status, distribution, habitat, and behavior is published here, making this the most up-to-date reference on Taiwan birds even though it isn't complete. An appendix lists some birds by behavior and habitat, another gives a complete list of the birds of Taiwan. Two organizations that would assist bird-watchers are specified so that visitors to this pleasant island will be able to get some guidance to its birding hot-spots and pleasures. Since all 15 of Taiwan's endemic species are covered in this book, all the birds of Taiwan can now be found in current bird books on Japan, Hong Kong, and SE Asia. The relevant extralimital books of most use in Taiwan are mentioned in the bibliography.

Hopefully this book will create interest in Taiwan's fascinating birdlife, so that the necessary conservation measures will be taken, aided by birding tourism and international efforts. The recent establishment of a high mountain reserve to protect the Mikado and Swinhoe's Pheasants is evidence of a swing in this direction. Dr. Severinghaus was instrumental in getting this area set up. Some laws were recently passed severely curtailing hunting and the sale of mounted birds, another hopeful sign. The authors have done a good job on this guide and anyone interested in Taiwan's birds will find it useful and essential.—BEN KING.

A Colour Guide to Hong Kong Birds.—Clive Viney and Karen Phillipps. 1977. Hong Kong, Government Press. 122 pp., 48 color plates, 8 line drawings, 1 map, paperbound. U.S. $4.50 (plus $1.50 for surface or $5.00 for air postage delivery in USA. Order from: Hong Kong Government Information Services, Sale of Publications Office, Beaconsfield House, Queen's Road Central, Hong Kong—checks or M.O.s payable to "Hong Kong Government").—This attractive and useful identification book covers 327 of Hong Kong's 375 species, 275 of which are illustrated in color, the remaining not illustrated. A list of the species not covered, with their last date of occurrence, is appended. The text for each species is on the page facing the plate on which it appears. Attractive and well-done, the colorful plates dominate the reader's attention, and by using them, one could readily identify most of the species depicted. A number of helpful flight paintings are included. There are some errors (all due to an inadequate specimen collection in Hong Kong). Instead of the Eastern Marsh-Harrier (*Circus aeruginosus spilonotus*), the Western Marsh-Harrier (*C. a. aeruginosus*) has been painted and described in the text as well; this is important as they are probably separate species, and the Western does not occur in eastern Asia. The crest of the Black-faced Spoonbill (*Platalea minor*) is tawny rather than white in breeding plumage, which further distinguishes it from the White Spoonbill (*P. leucorodia*). The plumes on a Little Egret's head are limited to the two long ones. The Chinese Babax is unrecognizable. The Common Buzzard (*Buteo buteo*) shown is a western Eurasian form that doesn't occur in eastern Asia.

The text for each species is brief, containing: status, seasonal distribution, field marks, habitat, habits, some songs, and often particular places to look for the bird. The textual material is mostly succinct and adequate for identification. However, as is usual for the simpler guides, many of the hawks and eagles could not be identified because so much of importance is left out. The order of species is partially standardized, the deviations being in favor of some larger and smaller bird groupings and other groupings by habitat. The 17 pages of introductory material contain information on how to use the book, how to identify birds, and places to look for birds in Hong Kong. The colored map on the inside covers is a good topographical one showing main roads and the birding areas mentioned in the text. Those who have not visited Hong Kong (and many who have) tend to picture it as a vast city split by a huge harbor and cannot imagine birding there. However, there are good places even on Hong Kong island and a great number of good areas on the mainland New Territories. On a recent visit (March 1978), we easily tallied 93 species in one day without trying for a big list. It is the only place in mainland China that is readily accessible and is well worth the visiting birder's time.

Comparison with "A new guide to the birds of Hong Kong" by M. Webster (1976—reviewed in Auk 94: 801) is necessary. The present book is highly recommended for the beginner or visitor to Hong Kong as its wealth of color plates covers most of the birds that are likely to be seen. More serious birdwatchers will want both books, as Webster's text is better for identification and contains descriptions of all species that occur in Hong Kong, as well as illustrations of most of them. Visitors to Hong Kong need not fear any longer that they will not have good books to help them identify the birds of this fascinating area.—BEN KING.

NOTES AND NEWS

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Chapman grants during 1978, totalling $44,754 with a mean of $492, were awarded to: George R. Angehr, role of interference competition in the organization of a guild of tropical hummingbirds; Martha Hatch Balph, relationship of plumage variability to social behavior in Pine Siskins; Ellen R. Becker, breeding biology and ecology of the Black Guillemot, *Cepphus grylle,* in Maine with special reference to the influence of territory size and habitat; Joan Bird, behavioral and ecological comparisons of Lesser Antillean Bullfinches: a study of the evolution of sexual dimorphism and monomorphism; Erik Joshua Bitterbaum, comparative ethology of the Purple and Gray-breasted martins; John G. Blake, avian species diversity in desert and semi-desert areas: 1. response to habitat complexity, 2. effect of habitat islands; Peter J. Blancher, importance of food supply in the distribution of two sympatric species of kingbirds (genus *Tyrannus*); Godfrey Roderick Bourne, reproductive costs in Barn and Cliff Swallows; Michael Braun, character convergence or hybridization: biochemical genetics of the Mexican Red-eyed Towhees; Deborah P. Buitron, social behavior and reproductive strategies of the Black-billed Magpie; Jeffrey T. Burns, mate-switching in House Wrens; R. Wayne Campbell, birds of British Columbia; Penn Richard Chu, geographic variation in song of island-mainland populations of the Carolina Wren, *Thryothorus ludovicianus*; C. Dwight Cooley, foraging efficiency and time-energy budget of the Loggerhead Shrike; Joel Cracraft, adaptive radiation add systematics of the moas (Dinornithidae); Robert J. Craig, comparative ecology of Louisiana and Northern waterthrushes; Timothy M. Crowe, systematics of francolins and bustards and distribution and status of birds rare and endangered in South Africa; Paul R. Cutright and Michael J. Brodhead, Elliot Coues: naturalist and pioneer historian; Margarete Dohmann, variation of the rectrices' coloration in different subspecies of the Grey Shrike species in regard to a possible eco-ethological signification; J. William Eley, review of the *Penelope purpurascens* and *Penelope jacquacu* superspecies groups, with emphasis on the taxonomy of *Penelope albipennis*; John T. Emlen, density distribution of Mississippi bottomland forest birds; Gary A. Falxa, Devora J. Ukrain, and David F. Whitacre, status and ecology of the Bat Falcon in southeastern Mexico; Elmer J. Finck, social organization of the Lark Bunting (*Calamospiza melanocorys*); Mary Kathleen Fite, vocal and territorial behavior of the American Dipper (*Cinclus mexicanus*); Darrel Blaine Ford, natal nest site characteristics and habitat compared to adult nest site selection in the Herring Gull, *Larus argentatus*; Paul S. Fromer, feeding ecology of the Northern Jacana, *Jacana spinosa*; Gary N. Fugle, dynamics of winter social organization in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*); Kimball Lewis Garrett, behavioral ecology of the White-headed Woodpecker, *Picoides albolarvatus*; Patricia A. Gowaty, evolution of mating system variability in Eastern Bluebirds (*Sialia sialis*); Judy Anne Gradwohl, ecology and spacing systems of birds in Antwren flocks; Peter W. Greig-Smith, effects of habitat modification on bird communities in the Seychelles; Judith Latta Hand, alignment of nests and territories by Western Gulls (*Larus occidentalis livens*): possible relation to thermal stress in the Gulf of California; Donna L. Hansen, comparison of breeding season behaviors of *Cinclus pallasii* and *Cinclus mexicanus*; Ross E. Harris, breeding biology and ecology of the Short-billed Dowitcher (*Limnodromus griseus*), and comparisons with sympatric shorebird species; Jeremy J. Hatch, territorial behavior of *Vestiaria coccinea*; Sarah Francis Heath, feeding ecology of limicoline bird species in the salt-pans of the Camarque, France; David Paul Hendricks, breeding biology of the Brown-capped Rosy Finch; Willard W. Hennemann III, role of the spread-winged posture in the thermoregulation of anhingas and cormorants; David F. Hennessy, regulation of snake mobbing by Scrub Jays and Mockingbirds according to apparent threat: form of behavior, snake species discrimination, seasonal variation, and inter- and intraspecific variation; David T. Holyoak, birds of south-east Polynesia; Paul A. Johnsgard, shorebirds in the collection of the American Museum of Natural History; Ellen Joan Johnson, nestling ecology of the Gray Catbird; David W. Johnston, an atlas of avian uropygial glands; Ronald L. Kalinoski, polygyny in the Bobolink: female-female aggression, male courtship, and male parental investment; James A. Kushlan, foraging ecology

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THE WILSON ORNITHOLOGICAL SOCIETY ANNOUNCES

PAUL A. STEWART AWARDS

The Paul A. Stewart Fund for Ornithological Research has been established by donations from Paul A. Stewart. Income from this endowment will be awarded annually to support research in ornithology, especially studies of bird movements based on banding and analyses of recoveries and returns and investigations pertaining to economic ornithology. Several Stewart Awards in the amount of $200 each will be available each year. Stewart Awards will be equally available to students, amateurs, and professionals.

LOUIS AGASSIZ FUERTES AND MARGARET MORSE NICE AWARDS

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is 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 contributions 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 are applicable 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 and facilities generally available at the colleges. High school students are eligible. In some years 2 Fuertes Awards of $200 each have been made, in some years, one. One Nice Award is made annually in the amount of $200.

Persons interested in those awards may write to **Clait E. Braun, Wildlife Research Center, P.O. Box 2287, Fort Collins, Colorado 80522.** Completed applications must be received by **1 March 1979.** Final decisions will be made by the Council of The Wilson Ornithological Society at the annual meeting of the Society, 12–15 April 1979.

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A symposium on **The Integrated Study of Bird Populations** will be held at Wageningen, the Netherlands, from 17–21 September 1979 on the occasion of the 25th anniversary of The Institute for Ecological Research of the Royal Netherlands Academy of Arts and Sciences. Invited speakers will address bird populations in relation to food supplies and territorial behavior, optimal foraging strategies, energetics of free-living birds, and Red Grouse and Great Tit population dynamics, and facilities will be available for display of posters on related subjects. Further information may be obtained from **I.A.C., Postbus 88, 6700 AB Wageningen, The Netherlands.**

The second **International Congress of Systematic and Evolutionary Biology** will be held at the University of British Columbia, Vancouver, Canada on 17–24 July 1980. A number of symposia will be offered, and sessions for contributed papers will also be organized. Those interested in receiving an information circular in the spring of 1979 should write to **Dr. G. G. E. Scudder, Department of Zoology, University of British Columbia, 2075 Wesbrook Mall, Vancouver, B.C. V6T 1W5 Canada.**

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EDITOR'S COMMENTS

With this issue we initiate what I hope will become a regular feature of *The Auk*: a "Commentary" section. This is intended to provide a forum for brief essays or points-of-view on various matters of interest to ornithologists, or exchanges relating to papers published in recent issues of *The Auk*. In this issue Harold Mayfield addresses some aspects of the role of amateurs in ornithology, speaking from the position of an amateur who has made exceptional contributions to the field. Harold prepared this essay at the invitation of the Editorial Board, and we have invited several other individuals to prepare such personal statements on several other topics of current interest. But "Commentaries" may be contributed as well as invited. If you have strong feelings about some matter of importance in ornithology and wish to submit an essay or position statement, please do so. Alternatively, we would welcome suggestions of topics that you would like to see addressed, and the names of individuals you think the Editorial Board might consider inviting to prepare such a Commentary. The ground rules are these: (1) contributions should generally not exceed 750 words in length, and (2) all contributed material will be reviewed by the Editorial Board, which will advise the Editor of the acceptability of the material.

One other matter: In the January 1978 issue of *The Auk* I drew attention to the rather lengthy time lag between acceptance of manuscripts and their final publication in *The Auk* (17.5 months, on the average, for the papers in that issue). Reducing this time lag has been a major objective during the past year, and we have now lowered it about as far as is practical. The average time lag between acceptance and final appearance of articles in this issue (taking into account the actual date of issue of the "January" issue) is 5.6 months; the time lag for Short Communications is about a month longer.

Because of the large number of inquiries concerning the late delivery of the October *Auk* and therefore of the 1979 dues notices, we feel that we should provide some explanation for this delay. First, the transfer of the editorial offices from Oregon State University to the University of New Mexico in late summer created numerous delays, particularly involving the completion of the index for volume 95. Second, after the October issue was sent to press we experienced additional delays at Allen Press, because their publishing schedule is tight, and material for *The Auk* now had to be worked into other scheduled jobs. Third, because our turn-around time for publication has been reduced significantly, some delays were experienced when some authors did not return galley proofs as expeditiously as possible.

The print order for the 1979 dues notices was submitted to Allen Press early in the Fall and the dates for submission of dues were established to account for a possible delay in publication. Unfortunately, we did not anticipate the magnitude of the delays. We apologize for the inconvenience this has caused the membership, and we trust that in paying dues members will have used their discretion in remitting the appropriate amount.

We should also note that this issue of *The Auk* was delayed for some of the same reasons noted above, but also to allow sufficient time for members to pay their dues and thus enable the Treasurer to establish the press run for the January *Auk*. We intend to return to a regular publication schedule as quickly as possible.—JOEL CRACRAFT, *Treasurer*; JOHN WIENS, *Editor*.

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The revised, fourth edition of the **Council of Biology Editors Style Manual** has recently been published. This reference is indispensable to authors of scientific manuscripts, and is the foundation for the style followed in *The Auk.* Copies may be obtained (for $12.00, prepaid) from **American Institute of Biological Sciences, 1401 Wilson Blvd., Arlington, Virginia 22209.**

Members of the AOU are urged to submit **drafts of potential resolutions** to be considered for adoption by the Union at the 97th Stated Meeting at College Station, Texas in August. Subject matter should be pertinent to the scientific interests and objectives of the AOU. Please send drafts, with any helpful background information, by **1 June 1979** to the Committee on Resolutions, Warren B. King, Rm 336, National Museum of Natural History, Washington, D.C. 20560.

The **Second International Symposium on Avian Endocrinology** will be held in Benalmadena (Malaga, Spain) on 4–9 May 1980. Information will be available from the convener: Dr. August Epple, Daniel Baugh Institute of Anatomy, Thomas Jefferson University, Philadelphia, Pennsylvania 19107 USA.

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