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A.O.U. Announcements

Fellows and Elective Members are reminded that nominations for Elective Member may be submitted to the Secretary on the prescribed form up until five months prior to the opening of the next Stated Meeting. The deadline for 1981 is **24 March.** Nominations for Fellow of the A.O.U. also must be received by that date. Nominations for Vice-President and Elective Councilors (3) may be made in writing to the Secretary at any time prior to the Annual Meeting.

The 99th Stated Meeting of the A.O.U. will be held at the **University of Alberta, Edmonton, Alberta, Canada** during the week of **August 24–27, 1981.**

The American Ornithologists' Union solicits applications for research grants from its **Josselyn Van Tyne** and **Alexander Wetmore Memorial Funds.** The Van Tyne awards will consider any aspect of avian biology; the Wetmore awards are limited to taxonomy/systematics. Grants are usually in amounts of a few hundred dollars. Preference is given to students and other persons without other sources of funds. Application forms may be obtained from **Dr. A. S. Gaunt, A.O.U. Committee on Research Awards, Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210.** Applications must be completed before **18 March 1981.**

EFFECT OF SEASON ON THE ENERGETICS, BODY COMPOSITION, AND CAGE ACTIVITY OF THE FIELD SPARROW

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ABSTRACT.—A linear correlation of existence metabolism (M_{kcal} = kcal·bird^{-1}·day^{-1}) with temperature (T = °C) was obtained for winter acclimatized Field Sparrows (*Spizella pusilla*) on a 10-h photoperiod (males: $M_{kcal} = 15.59 - 0.285T$; females: $M_{kcal} = 14.69 - 0.261T$). A curvilinear relationship was obtained for summer acclimatized birds on a 15-h photoperiod (males: $M_{kcal} = 16.40 + 0.0001T^3 - 0.0002T^2 - 0.3662T$; females: $M_{kcal} = 15.87 + 0.0036T^2 - 0.3911T$). Significant differences between summer- and winter-acclimatized birds occurred only at temperatures below 0°C. The lower limit of temperature tolerance was −13° to −14°C under a constant 10-h photoperiod and under fluctuating outdoor conditions and was somewhat lower under a constant 15-h photoperiod. The upper limit of temperature tolerance was about 41°C in the summer. With caged birds under fluctuating outdoor conditions, there was an increase in metabolized energy, existence metabolism, body protein, weight, and lipid content in the autumn and a decrease in the spring. During cold waves in winter, there was commonly an immediate drop in weight before increased metabolized energy brought recovery. In half of the birds, recovery was incomplete and mortality resulted. Coefficients of food utilization varied from 0.71 under a 10-h photoperiod to 0.79 under a 15-h photoperiod and from 0.72 to 0.86 under outdoor conditions. With death from cold or heat stress there was a loss of water, lipids, and proteins. The loss of water was greater under heat stress. Nocturnal activity (*Zugunruhe*) developed in a different pattern in spring than in autumn and was not accompanied by premigratory fattening in the spring. In several respects, the metabolic and behavioral responses of the Field Sparrow are intermediate between those of long distance migrants and permanent residents, indicating that they may be evolving from a migratory to a nonmigratory status. *Received 26 January 1980, accepted 17 March 1980.*

THE Field Sparrow (*Spizella pusilla*) is a partial migrant in eastern North America, with most of the population in the northern part of the breeding range migrating southward in the autumn, although scattered individuals may remain at least through the early part of the winter (Fig. 1). The present study is concerned with the metabolic capacity of the species to adjust to seasonal changes in climate in east central Illinois and how this correlates with migratory behavior. There have been several recent studies of seasonal variations in basal metabolism and causes of seasonal acclimatization (Dawson and Carey 1976, Carey et al. 1978, Weathers and Caccimise 1978, Southwick 1980). This research is concerned, however, with seasonal variations in existence metabolism, a preliminary survey of which, involving several species, was made by Kendeigh et al. (1977).

Analysis will first be made of how existence metabolism of seasonally acclimatized birds responds to changes in temperature under constant 15-h and 10-h photoperiods, and then how adjustments are made under fluctuating outdoor conditions. Variations in metabolism are correlated with cage activity, weight, and body components. The experimental work was done from 1959 through 1962.

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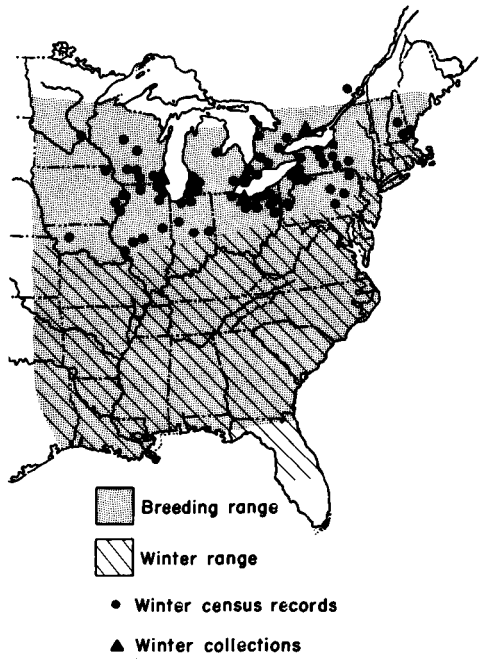

Fig. 1. Breeding and wintering distribution of the Field Sparrow in eastern North America.

METHODS

Capture and maintenance.—Wild birds were captured during the spring and summer and confined in an outdoor aviary until used. They were first fed a commercial seed mixture, which was then gradually changed to a homogeneous chick mash that was used in all experiments (University of Illinois chick starter No. 521, Kendeigh 1968). This chick mash had an energy value of 4.309 ± 0.020 kcal/g dry weight ($\bar{x}$ ± SE) (18.03 ± 0.084 kj/g).

Statistical differences were determined by the analysis of variance test. Differences were considered significant at the 5% confidence level. Regression lines were fitted by the least squares procedure, and standard errors of estimate are provided. Rates of metabolism are given in both heat units (M_{kcal} = kcal·bird^{-1}·day^{-1}) and in International Standard power units (M_{mW} = milliwatts). Conversion factors are: 1 kcal = 4.184 kilojoules (kj); 1 kcal·bird^{-1}·day^{-1} = 48.5 milliwatts (mW).

Indoor measurements.—For measuring existence metabolism under constant photoperiods indoors, the birds were placed singly in small (31 × 16 × 31 cm) metabolism cages as described by Martin (1967) and allowed a preliminary period of 6–9 days for acclimation. Measurements of food consumption were made over consecutive 3-day periods until the birds maintained constant weight (±0.3 g). The energy value of the excreta collected at the end of each period varied from 3.425 ± 0.005 kcal/g (14.33 ± 0.21 kj/g) in the outdoor experiments (see below) (n = 47) to 3.500 ± 0.005 kcal/g (14.64 ± 0.021 kj/g) in the 15-h photoperiod summer experiments (n = 48) to 3.534 ± 0.006 kcal/g (14.79 ± 0.025 kj/g) in the 10-h photoperiod winter experiments (n = 34). Total *excretory energy* subtracted from *gross energy* intake gave *metabolized energy,* which became *existence metabolism* when the bird maintained constant weight.

The summer acclimatized birds were first placed on a 15-h photoperiod (15L:9D) at 21°C. They were then divided into two groups, one group being subjected to progressively higher constant (±2°C) temperatures, the other to progressively lower temperatures. Lighting was provided by two 100-watt incandescent bulbs and controlled automatically (on at 0500, off at 2000). Relative humidity in the high temperature walk-in cabinet (31°C–42°C) varied between 40 and 60%, in the medium temperature cabinet (0°C–25°C) between 60 and 85%, and in the low temperature cabinet (−20°C–0°C) between 70 and 80%. Use was also made of a reach-in cabinet, lighted by 40-watt fluorescent bulbs, having a temperature range from 0° to −84°C. Snow or frost, instead of liquid water, was provided at temperatures below freezing.

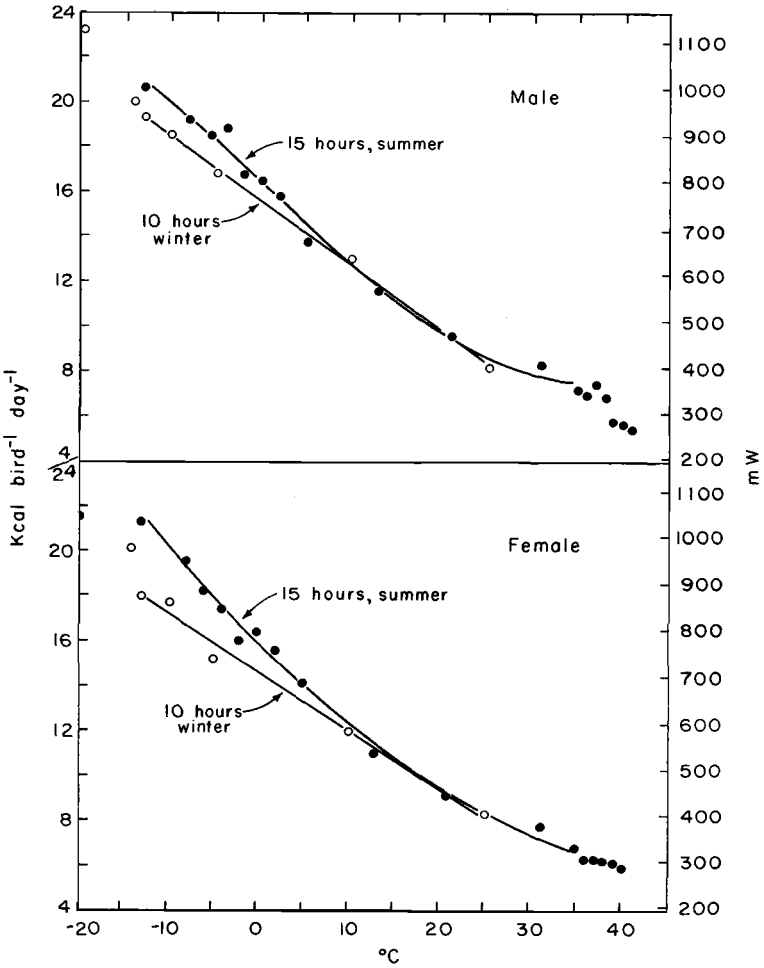

Fig. 2. Existence metabolism at constant temperatures and photoperiods.

For winter experiments, birds were transferred from the outdoor aviary in January and acclimated to a constant 10-h photoperiod (10L:14D; lights on at 0700, off at 1700) and 0°C for 4 days and then −5°C for another 6 days before the measurements were started at both low and high temperatures.

Usually 10 birds were started at each temperature in the summer experiments, but fewer birds (5–7) were available for the winter experiments. At extreme temperatures not all birds survived to complete the measurements. During the summer the birds were commonly run for 6–9 days at each temperature (extremes of 3 and 18 days), but in winter they were run for longer periods, usually 10–18 days (only 6 days at −14°C). Summer measurements began on 24 May and continued through the next 3 months; winter measurements were made between 15 January and 18 March.

The sexes were distinguished by dissection at the termination of the experiments. The average weight of the males in the experiment from −13° to 35°C was significantly heavier than the females in both summer (males, 12.8 ± 0.03 g, n = 84; females, 12.3 ± 0.04 g, n = 35) and winter (males, 15.2 ± 0.16 g, n = 15; females, 13.8 ± 0.17 g, n = 17). The winter weight of each sex was significantly higher than its summer weight. Weights did not vary with temperature except that above 35°C they declined, reaching 10.2 g in males and 10.4 g in females at 40°C in summer.

Outdoor measurements.—Metabolism cages, each containing a single bird, were placed out-of-doors under overhead shelter but exposed to natural changes in air temperature, as recorded nearby, and photoperiod. Convective losses from air currents were reduced by nearly full protection from north and

TABLE 1. Regression equations (± SE) of metabolism on temperature (T = °C) for the indoor experiments (−13°–35°C). For sample sizes, see text.

Photoperiod (h of light)	Sex	M_{kcal}	M_{mW}
		Gross energy	
10 (winter)	M	$22.18 - 0.359T \pm 0.95$	$1{,}076 - 17.41T \pm 46$
	F	$20.44 - 0.322T \pm 0.45$	$989 - 15.62T \pm 22$
15 (summer)	M	$21.62 + 0.0048T^2 - 0.5248T \pm 0.42$	$1{,}049 + 0.233T^2 - 25.45T \pm 20$
	F	$20.63 + 0.0057T^2 - 0.5401T \pm 0.45$	$1{,}001 + 0.276T^2 - 26.19T \pm 22$
		Excretory energy	
10	M	$6.52 - 0.68T \pm 1.05$[a]	$315 - 3.30T \pm 51$
	F	$6.36 - 0.0032T^2 - 0.0125T \pm 0.70$[a]	$308 - 0.155T^2 - 0.61T \pm 34$
15	M	$5.42 + 0.0018T^2 - 0.1644T \pm 0.16$	$263 + 0.087T^2 - 7.97T \pm 8$
	F	$4.58 - 0.0001T^3 - 0.0046T^2 - 0.1457T \pm 0.29$	$222 - 0.0048T^3 + 0.223T^2 - 7.07T \pm 14$
		Existence metabolism	
10	M	$15.59 - 0.285T \pm 0.23$	$756 - 13.82T \pm 11$
	F	$14.69 - 0.261T \pm 0.40$	$712 - 12.66T \pm 19$
15	M	$16.40 + 0.0001T^3 - 0.0002T^2 - 0.3662T \pm 0.42$	$795 + 0.0048T^3 - 0.010T^2 - 17.76T \pm 20$
	F	$15.87 + 0.0036T^2 - 0.3911T \pm 0.37$	$770 + 0.175T^2 - 18.97T \pm 18$

[a] Difference between sexes not significant.

west winds and partial protection from east and south winds. The birds were then provided with standard chick mash, and measurements were made over consecutive 3-day periods of food consumption, excreta, weight, and molt. Molt was quantified by counting the number and kinds of feathers dropped in the cage, following a procedure similar to that used by West (1960).

Four groups were run: 2 females from mid-August 1959 to February 1960, 3 males and 1 female from mid-August 1961 to mid-August 1962, 4 males and 2 females from mid-August 1961 until they died from cold stress during December and January, and 2 males and 2 females, which survived the 10-h photoperiod experiments indoors, from February to mid August 1962.

Cage activity.—In each different experiment at least part of the cages, usually all, had moveable perches and floors suspended from a spring and connected to a micro-switch and electric current so that movements of the birds were registered on Esterline-Angus 20-point recorders. The records were tabulated in terms of the number of different 4-min periods per hour in which the birds were active. A single recorded movement as well as continuous activity during a 4-min period constituted one unit of activity. The daily activity was separated into its diurnal and nocturnal components. In the experiments conducted indoors, this was based on the time that the lights were turned on and off, except that movements of the birds during the first few minutes after the lights were turned off were counted as a continuation of the diurnal activity. Out-of-doors with more gradual transitions between light and dark periods, nocturnal activity was counted as beginning when the birds first settled down for the night and as ending when birds that had shown no nocturnal activity began their diurnal activity. The times of sunrise and sunset or of civil or nautical twilight could not be used, because the differences in light intensities on clear and cloudy days affected the time of beginning or ending the nocturnal activity. Although not a precise method for quantifying total activity, variations in number of activity units per period of time have relative significance.

Carcass analysis.—Procedures followed practices described by Odum (1960). Briefly stated, carcasses, including feathers, were oven-dried at 105°C to constant weight to determine water content. Lipid determinations, mostly neutral fats, were based on ether extracts obtained in a Soxhlet apparatus. Kjeldahl equipment was used for measurement of nitrogen, and grams nitrogen times 6.25 gave grams of protein. The wet weight of the bird minus water, ether-soluble lipids, and proteins was assumed to be carbohydrate and ash.

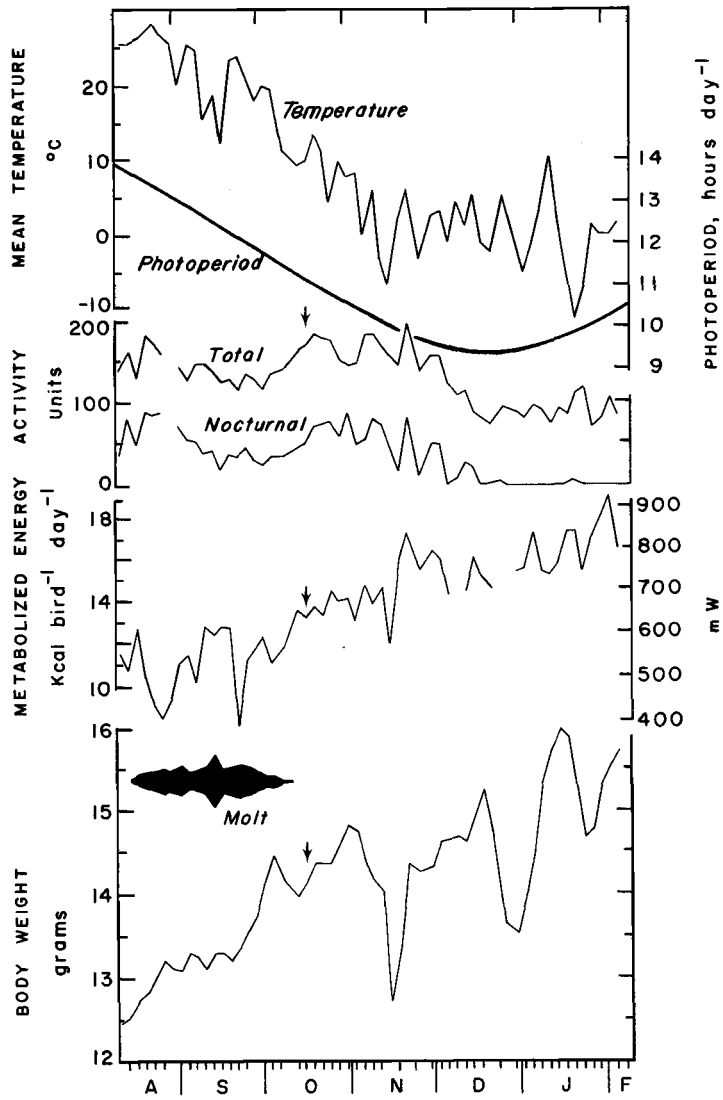

Fig. 3. Average variations in three caged females out-of-doors during the autumn and winter, 1959–60. The arrow indicates accidental death of one bird.

RESULTS

INDOOR MEASUREMENTS

Regressions of metabolism on temperature.—The regressions of gross energy intake, excretory energy, and existence metabolism on temperature varied curvilinearly in summer but linearly in winter (Table 1, Fig. 2). Rates were slightly but significantly higher in males than females, except for excretory energy under the 10-h photoperiod. This is correlated with their greater weights.

Existence metabolism was significantly higher in the 15-h summer birds than in

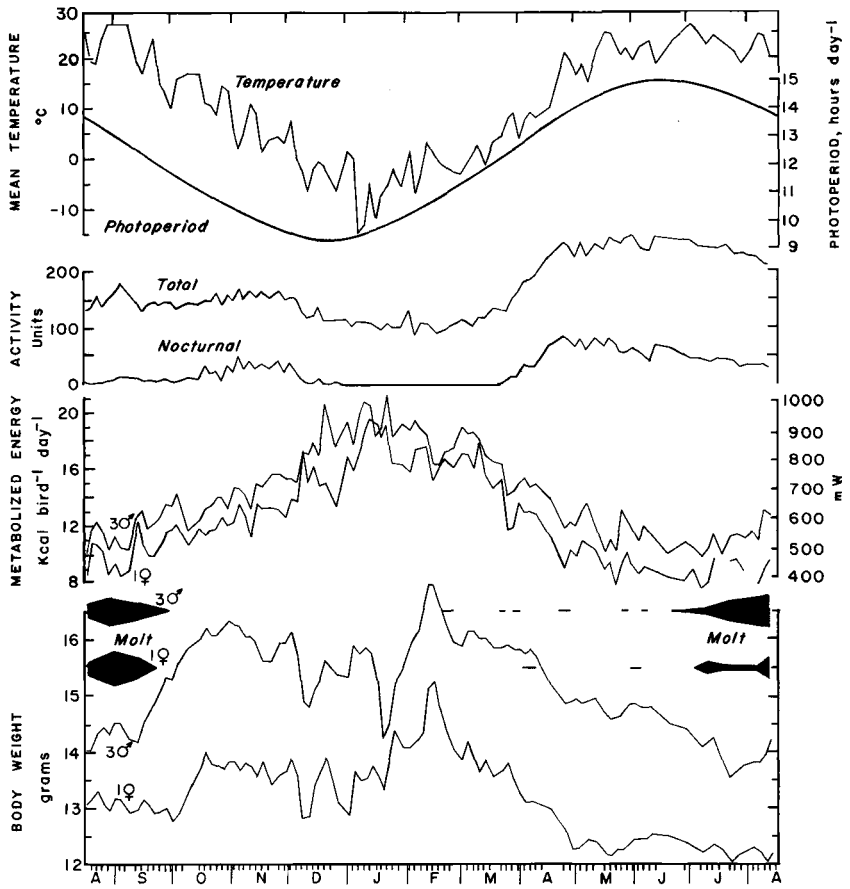

Fig. 4. Average variations in caged birds that survived a full year (1961–62) out-of-doors. "Activity" also includes birds involved in Fig. 5.

the 10-h winter birds at temperatures below 0°C (Fig. 2). The birds had 5 more hours available for activity and feeding on the longer photoperiod, but this relation to photoperiod is modified somewhat by differences in temperature acclimatization (see below).

Tolerance of extreme temperatures.—All birds survived 4 days at −13°C during the summer and only half (3 males, 2 females) survived 6 days at −20°C. Unfortunately, no runs were made at intermediate temperatures. During the winter, all birds survived 18 days at −13°C, but only 2 (1 male, 1 female) out of 6 survived for 6 days at −14°C. The 4 birds that died were females. The greater tolerance to low temperature of the summer birds may be related to the longer photoperiods to which they were exposed.

No attempt has been made to determine tolerance of birds to high temperature in the winter. During the summer, existence metabolism decreased in males at temperatures above 35°C, well below rates predicted from the regression equations (Fig. 2). As noted above, weight also decreased. Four of 8 males died during a 3-day

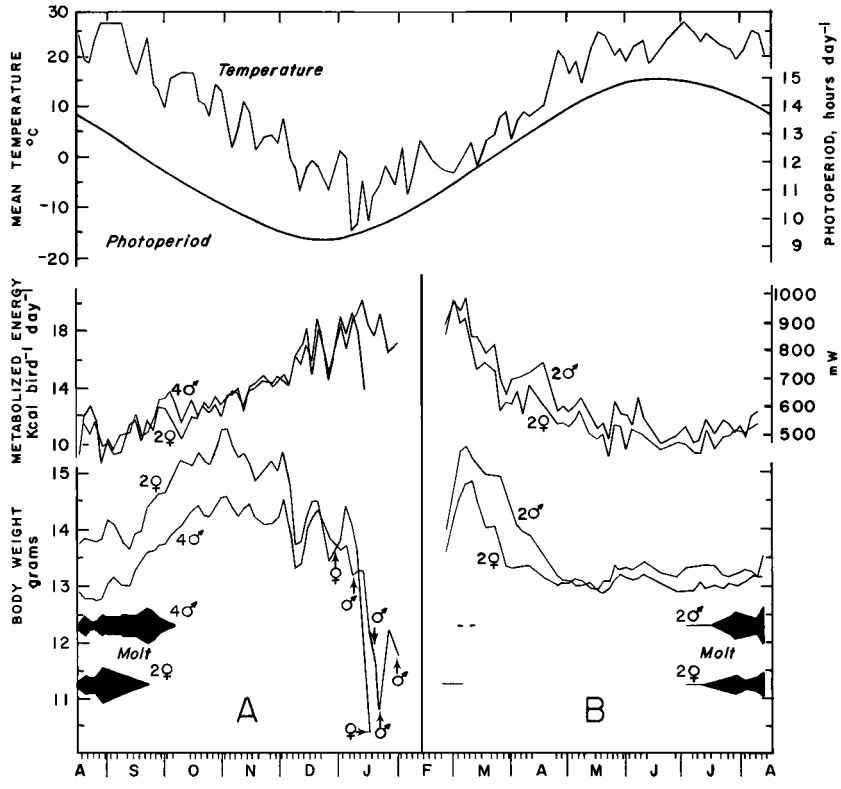

Fig. 5. Average variations in caged birds (A) that failed to survive out-of-doors (1961–62) and (B) that were placed out-of-doors after completion of experiments at constant temperatures and a 10-h photoperiod indoors.

period at 40°C and 2 died at 41°C. Both females survived 41°C; likewise their existence metabolism above 35°C decreased at approximately predictable rates. The number of records is small, but there is a suggestion that females tolerate heat better than males.

Cage activity.—Total 24-h activity of the birds under a 15-h photoperiod during the summer varied from 116 to 137 units over the temperature range of −2°–35°C. At higher temperatures, total activity decreased to 74 units at 41°C. For birds under 10-h photoperiods in the winter, total activity ranged from 67 to 98 units, with no significant differences between temperatures. Activity occurred throughout the light period, with seldom more than 1% of the total activity at either photoperiod occurring at night. Activity units per hour light were not significantly different between 10- and 15-h photoperiods, the greater total daily activity of the latter photoperiod being a reflection primarily of the more hours involved.

At the termination of the metabolic measurements of birds under the 10-h photoperiod in 1961, the photoperiod was increased to 15-h (18 March), while the temperature was maintained at 25°C. Within 3 days, nocturnal activity increased to 3% of the total and within 21 days it was 32%. Decreasing the photoperiod back to 10 h (6 April) for 40 days did not reduce the nocturnal activity.

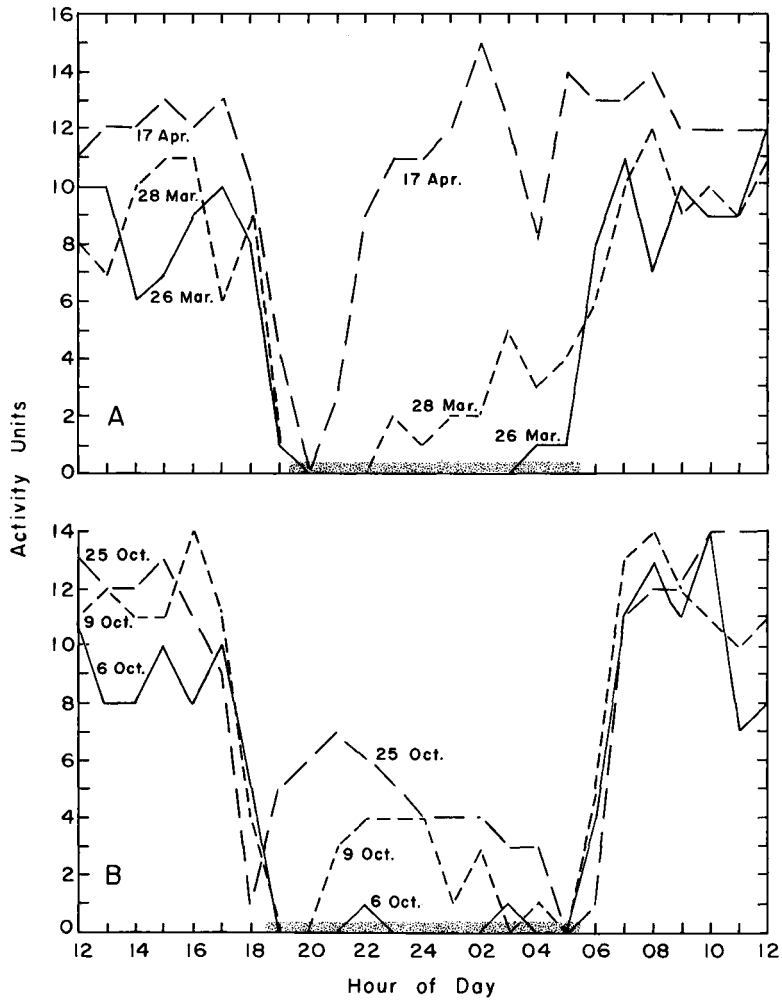

Fig. 6. Developing patterns of nocturnal activity (*Zugunruhe*) in (A) spring (n = 11) and (B) autumn (n = 13).

Outdoor Measurements

General responses.—With decreasing temperature and photoperiod in the autumn and increasing temperature and photoperiod in the spring, the general metabolic response was an increase in metabolized energy in the autumn and a decrease in the spring, with rates in the summer fluctuating around a constant level (Figs. 3–5).

Weights began to increase near the end of the autumn molt and peaked during winter. Weights declined during the spring with no evidence of fattening during the migratory period. The increase in weight during the autumn is more likely in response to falling temperatures than as preparation for migration.

There was considerable nocturnal activity of three females during August 1959 (Fig. 3), but during the autumn of 1961 nocturnal activity did not become significant until molting was completed (Figs. 4, 5). Nocturnal activity mostly ceased during

December in both years but began again in late March and continued through the summer.

Nocturnal activity in spring was more intense than in autumn and extended over a longer period. The two nights of most intense activity in October averaged 49 units; in April they averaged 87 units. In the autumns of 1959 and 1961, nocturnal activity was recorded on 63 and 49% of the nights. In the spring, the birds were active on 95% of the nights.

In spring, nocturnal activity first developed in the hours before dawn, and, as intensity increased, it began earlier and earlier (Fig. 6A). When unrest was at its maximum, nocturnal activity did not start until about 2 h after dark but continued into daytime activity without a predawn break. In the autumn, nocturnal activity began and continued more intensely near the middle of the night (Fig. 6B). There was little or no activity immediately after dark or for 1 or 2 h before onset of light.

Nocturnal activity in spring was not correlated with increase in weight as the result of deposition of fat, as commonly occurs in migrant species (Figs. 4, 5). Whether premigratory deposition of fat occurs in free wild birds was not determined. In the autumn (Figs. 3, 4, 5) the marked increase in weight in September and October coincides more clearly with the cessation of molt than it does with the onset of nocturnal activity, as has been shown also for other species (Farner 1960, King and Farner 1963, Helms 1963).

Specific responses to "cold-waves."—During the winter of 1959–60, the two females were exposed to a drop in temperature to −6°C in November and to −10°C in January (Fig. 3). In each instance there was a sharp decrease in weight and some minor fluctuations in metabolized energy, with recovery of both to higher levels in subsequent warm periods.

There were two waves of moderate cold temperatures (−6°C) in December 1961 (Fig. 4, 5). Metabolized energy rose slightly during the first wave but not enough to prevent a drop in weight. During the second, both metabolized energy and weight dropped. In each instance there was recovery during subsequent warm weather except for 1 female, which died in early January.

Temperature dropped to −15°C during the 9 January 1961 period and stayed below 0°C for the rest of the month. There was an immediate rise in metabolized energy sufficient to maintain weight in 3 males and 1 female, but this high rate was not maintained in 4 males and 2 females, so that their weights declined and death ensued.

Of 10 birds exposed to cold periods in December and January 1961–62, 1 male died during exposure to −15°C, 1 male during exposure to −13°C, and 2 males during warmer periods following these low temperatures. One female died during a warmer period after exposure to −6°C, and one female died during a warmer period following exposure to temperatures of −15°C and −14°C. It thus appears that mortality often comes from failure to recover fully from cold stress and not from the cold stress itself. These low temperatures approximate the lower limit of temperature tolerance for the birds indoors under a 10-h photoperiod. Likewise, the maximum levels of metabolized energy attained by the birds out-of-doors of 21.3 $kcal \cdot bird^{-1} \cdot day^{-1}$ (1,033 mW) in males and 19.7 kcal (955 mW) in females are comparable to the maximum rates of existence metabolism umder constant temperatures of 20.1 $kcal \cdot bird^{-1} \cdot day^{-1}$ (975 mW).

Because there is often a drop in weight initially when the bird is subjected to cold

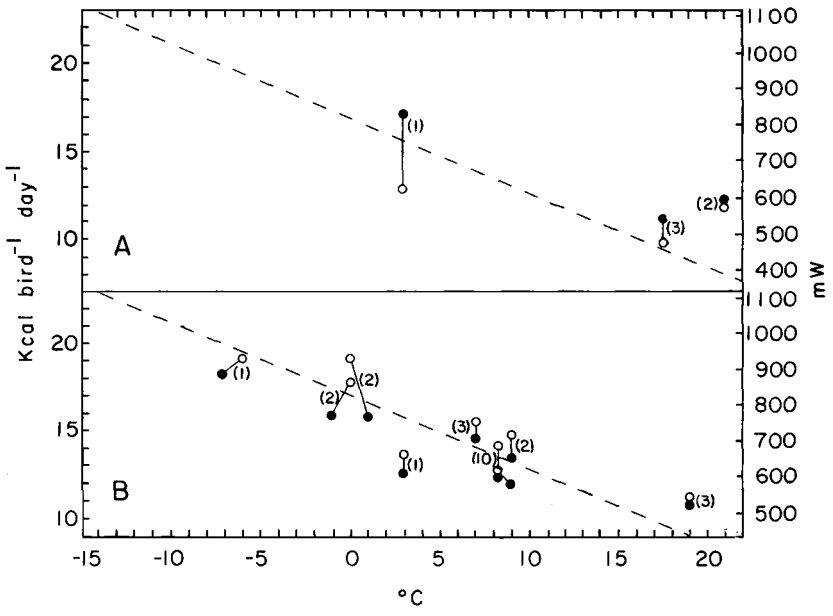

Fig. 7. Comparison of existence metabolism at equivalent temperatures (± 1.0°C) between an early date (dot) and a later date (circle) when there was (A) an intervening cold period and (B) an intervening period with the same or higher temperature. Data for (A) were obtained between late October and May, data for (B) between March and late May. Numbers in parentheses indicate number of birds in comparison. All data and regression lines include both sexes.

stress, resulting from inadequate increase in metabolized energy, it appears that body fats are the first resource that is mobilized to overcome cold. The males that survived the winter of 1961–62 were heavier than the males that did not survive. The females that survived the winter of 1959–60 were also heavy. The one female that survived the winter of 1960–61 was lighter, however, than the two females that died. Heavier weight (more fat) is therefore advantageous for surviving over winter, but the ability to mobilize and continue high rates of metabolized energy is probably more important.

One interesting difference between the birds that survived over winter and those that did not is that those that survived began nocturnal activity 13–15 days earlier in the autumn than those that did not. The mean starting date for survivors was 10 October (range, 6–12 October) and for the nonsurvivors 23 October (range 13–30 October). The significance of this is not clear but indicates that the two groups differed in other ways than in resistance to cold. Because the birds were captured from the wild during the spring and summer, it is possible that migrants on their way to more northern latitudes were included in the experimental groups as well as local residents. Even if all the birds were potential residents, the observed differences between individuals may indicate genetic differentiation in an evolving population.

Acclimatization.—Existence metabolism was higher over winter following periods of cold temperature than it was at equivalent temperatures preceding these periods. Likewise, existence metabolism was lower in the spring following periods of the same or higher temperatures than it was preceding these periods (Fig. 7). These

periods during which existence metabolism was measured were close enough together so that the slight differences in photoperiod were not a factor. There is thus some acclimatization to a higher rate of metabolism in response to winter cold, but it is not sufficient to offset the influence of a 5-h shorter photoperiod compared with the summer.

The regression of existence metabolism on temperature for outdoor birds, using all the data for both sexes in the above comparisons (October through May) and weighting each temperature by the number of records at that temperature, follows the equation ($n = 46$):

$$M_{\text{kcal}} = 16.92 - 0.422T \pm 1.2, \text{ or } M_{\text{mW}} = 821 - 2.05T \pm 58.$$

This regression has a steeper slope than for indoor birds at constant temperatures and a 10-h photoperiod (Table 1). In winter, birds under fluctuating temperatures are more responsive to a drop in temperature than under constant temperatures (10-h photoperiod), although this is not true during the summer.

COEFFICIENTS OF FOOD UTILIZATION

Coefficients of food utilization or metabolizable energy coefficients (metabolized energy/gross energy intake) varied between individuals, but there were no consistent variations correlated with sex or temperature. The average coefficient of all birds under a 10-h photoperiod was 0.71 and under a 15-h photoperiod significantly higher, 0.79. The coefficient for birds out-of-doors varied between 0.72 and 0.86.

CARCASS ANALYSIS

Differences between wild and caged birds.—Seasonal changes in body components were followed only in caged birds because of the difficulty of securing wild birds in the winter. The relationship between caged and wild birds was determined only during the summer.

Although there were small differences in body components between wild birds killed in early June and late July, they are statistically insignificant (Table 2A, B, C). Birds that had been confined in the small experimental cages for a few weeks had essentially similar live weights and protein content as wild birds during July, but water content was lower and lipids, carbohydrates, and ash were higher. Birds that had been held in the larger flight cages tended to be intermediate in component values, and only the higher lipid content was significantly different from wild birds.

Seasonal changes.—Caged birds killed in November compared with those killed in July were significantly higher in live weight and all body components except water (Table 2C, D, E, F). A marked increase in live weight from July to November has also been noted in free-living Field Sparrows (Baldwin and Kendeigh 1938: 436–437). The increase in lipids is the largest component in the increase in live weight, 53% in birds in experimental cages and 57% in birds in the flight cages. The increase in protein content may be largely accounted for by the heavier plumage after the autumn molt (Kendeigh 1934: 335). Water as percent of live weight was lower in the November birds.

Odum and Parkinson (1951) with the White-throated Sparrow (*Zonotrichia albicollis*), Blem (1973) and Barnett (1970) with the House Sparrow (*Passer domesticus*), Helms and Smythe (1969) with the Tree Sparrow (*Spizella arborea*) and Carey

TABLE 2. Carcass analyses. The values given are averages (in grams ± SE) with the figures in parentheses being percentages of total live weight.

Live weight	Fat-free dry weight	Water	Lipids	Proteins	Carbohydrate and ash
A. *Birds killed in the field 12–13 June 1962 (5 males, 1 female)*					
13.45 ± 0.29	3.82 (28.4)	8.96 ± 0.20 (66.6)	0.671 ± 0.075 (5.0)	3.10 ± 0.02 (23.1)	0.713 ± 0.024 (5.3)
B. *Birds killed in the field 19, 23 July 1962 (7 males, 5 females)*					
12.97 ± 0.21	3.59 (27.7)	8.77 ± 0.16 (67.6)	0.609 ± 0.037 (4.7)	2.95 ± 0.05 (22.7)	0.646 ± 0.014 (5.0)
C. *Birds from outdoor experimental cages killed 24 July 1962 (2 males, 2 females)*					
12.77 ± 0.48	3.64 (28.5)	7.67 ± 0.37 (60.0)	1.46 ± 0.23 (11.4)	2.88 ± 0.05 (22.6)	0.765 ± 0.034 (6.0)
D. *Birds from outdoor flight cages killed 24 July 1962 (3 males, 1 female)*					
13.22 ± 0.43	3.66 (27.6)	8.50 ± 0.22 (64.3)	1.06 ± 0.15 (8.0)	2.94 ± 0.06 (22.2)	0.709 ± 0.089 (5.4)
E. *Birds from outdoor experimental cages killed 8 November 1962 (5 males, 3 females)*					
15.74 ± 0.27	4.25 (27.0)	8.45 ± 0.15 (53.7)	3.04 ± 0.17 (19.3)	3.33 ± 0.06 (21.1)	0.923 ± 0.032 (5.9)
F. *Birds from outdoor flight cages killed 8 November 1962 (7 males, 4 females)*					
15.20 ± 0.21	4.15 (27.3)	8.86 ± 0.08 (58.3)	2.19 ± 0.13 (14.4)	3.24 ± 0.05 (21.3)	0.913 ± 0.030 (6.0)
G. *Birds that died from outdoor cold stress (4 males, 3 females)*					
10.60 ± 0.41	3.79 (35.8)	6.64 ± 0.26 (62.6)	0.172 ± 0.008 (1.6)	2.73 ± 0.13 (25.7)	1.09 ± 0.08 (10.3)
H. *Birds that died from indoor cold stress at constant temperature and 10-h photoperiod (4 females)*					
9.45 ± 0.23	3.19 (33.8)	6.07 ± 0.13 (64.2)	0.184 ± 0.022 (1.9)	2.37 ± 0.09 (25.1)	0.847 ± 0.053 (9.0)
I. *Birds that died from indoor cold stress at constant temperature and 15-h photoperiod (3 males, 2 females)*					
11.17 ± 0.31	3.66 (32.8)	7.25 ± 0.23 (64.9)	0.256 ± 0.032 (2.3)	2.69 ± 0.07 (24.1)	0.976 ± 0.044 (8.7)
J. *Birds that died from indoor heat stress at constant temperature and 15-h photoperiod (5 males)*					
8.14 ± 0.35	2.94 (36.1)	4.72 ± 0.18 (58.1)	0.475 ± 0.161 (5.8)	2.37 ± 0.10 (29.2)	0.566 ± 0.041 (7.0)
K. *Birds that died from starvation out-of-doors during the summer (1 male, 1 female)*					
8.88 ± 0.32	3.08 (34.7)	5.55 ± 0.16 (62.1)	0.246 ± 0.119 (4.0)	2.44 ± 0.03 (26.9)	0.634 ± 0.019 (7.1)

et al. (1978) with the American Goldfinch (*Carduelis tristis*) found small increases in fat-free dry weight in the winter; Helms et al. (1967) found no such increase in the Dark-eyed Junco (*Junco hyemalis*) in the winter, while Zimmerman (1965b) states that in the Dickcissel (*Spiza americana*) males have significantly higher amounts of protein during the breeding season. The Dickcissel has an incomplete prenuptial molt of body feathers. Absolute water content did not vary significantly in any of these species except the American Goldfinch.

Death from cold stress.—There was a significant decrease in weight before the birds died from cold stress. Compared with birds killed in November (Table 2E, G), the loss of 5.14 g in birds dying from cold stress is accounted for by 54.3% lipids, 34.3% water, and 11.7% protein. Of the amount present in the November birds, the loss of lipids is 94.3%, of water is 21.5%, and of protein is 18.0%. The apparent slight gain in carbohydrate and ash is statistically insignificant.

Birds that died in experimental cages indoors under a constant 10-h photoperiod and temperature did so at a significantly lower weight than birds outdoors under fluctuating conditions (Table 2G, H). This was caused by lower amounts of water, lipids, and protein, the differences between which were not statistically significant, and carbohydrate and ash, the differences between which were. These differences are similar to those obtained by Zimmerman (1965b) with the Dickcissel.

Birds under a constant cold stress and a 15-h photoperiod died at a significantly higher weight, water, and protein content than birds under a 10-h photoperiod and with greater lipid reserve than birds outdoors (Table 2G, H, I). These differences cannot be attributed solely to the difference in photoperiod, as the birds under the 15-h photoperiod were summer acclimatized and the others were winter acclimatized. In the Dickcissel, birds dying during the summer under a 15-h photoperiod had body components of nearly the same values as those under a 10-h photoperiod (Zimmerman 1965b).

It appears that death from cold comes as lipids approach exhaustion. Nonfat dry weight may not be utilized until the lipid reserve drops below a certain level (Odum et al. 1964), and there may be little loss of water until protein and glycogen begin to be catabolized (Wishnofsky 1958). Actually, the percentage of water in the birds at time of death was higher than in nonstressed birds.

Death from heat stress.—Birds that died under heat stress and a 15-h photoperiod, compared with those that died as a result of cold stress (Table 2I, J), had a considerably lower weight, as a result of a great loss of water, as well as significant losses of protein, carbohydrate, and ash. The same differences were noted for the Dickcissel (Zimmerman 1965b) and White-throated Sparrow (Kontogiannis 1967). Higher levels of lipids remained at death from heat than from cold in the Field Sparrow and Dickcissel but not in the White-throated Sparrow. The loss of water is of special significance, because at high ambient temperature a rise in body temperature is resisted primarily by evaporative cooling.

Death from starvation.—Two birds starved to death during the summer (Table 2K). Weight and body components were similar to those in the heat stressed birds, except that the loss of water was not so great. Body components of the starved birds were also somewhat comparable with the birds that died under cold stress.

Overall.—Some birds that died from heat stress had a total weight as low as 7 g, while several birds that had not been stressed averaged 15 g. When all the carcasses are considered, regardless of how obtained, the increase in body components per

TABLE 3. Comparison of adjustments for overwintering and migration (values for sexes are averaged).

	Dickcissel[a]	Field Sparrow	House Sparrow[b]
A. *Migratory status*	Long distance migrant	Partial migrant	Permanent resident
B. *Lower limit of temperature tolerance*:			
10-h photoperiod (winter)	−1°C	−13°C	−31°C
15-h photoperiod (summer)	−2°	−13° to −20°	0°
Out-of-doors (winter)	−3°	−13° to −14°	−25°
C. *Maximum existence metabolism winter compared with summer*	−14%	−12%	+29%
D. *Existence metabolism lower under 10- compared with 15-h photoperiod*	At all temperatures	Below 0° only	Absent
E. *Increase in maximum metabolism per hour at 10- compared with 15-h photoperiod*	29%	32%	84%
F. *Increase in metabolized energy under fluctuating compared with constant conditions*	—	Below 12° only	At all temperatures
G. *Change in winter compared with summer*:			
Total weight	Decreases	+19%	+9%
Lipids	—	+108%	+67%
H. *Survival over winter*	None	One-half	Nearly all
I. *Premigratory fat deposition*	Present	None	None
J. Zugunruhe	Present	Present	Absent

[a] Zimmerman (1965a).
[b] Davis (1955), Blem (1973), Kendeigh et al. 1977.

gram increase in total weight averaged approximately 0.65 g water, 0.11 g protein, and 0.22 g lipids.

DISCUSSION

The Field Sparrow is intermediate in its metabolic responses to seasonal changes in temperature and photoperiod between those shown for the Dickcissel (Zimmerman 1965a), a long-distance migrant from the tropics, and the House Sparrow (Davis 1955, Blem 1973, Kendeigh et al. 1977), a permanent resident in east central Illinois. The responses of these latter two species are representative of migrant and resident species generally (Dolnik and Blyumental 1964, Berthold 1975) and of the differences between related migrant and resident species in the same family (Columbidae, Riddle et al. 1932, 1934), in the same genus (*Emberiza* Wallgren 1954), and between races in the same species (*Passer domesticus,* Dolnik and Gavrilov 1975).

In order to survive winter at northern latitudes, a bird must be able to tolerate temperatures considerably lower than those that occur during the breeding season. The Field Sparrow can tolerate lower temperatures than can the Dickcissel but not as low as the House Sparrow (Table 3B). There is very little seasonal variation in tolerance to low temperature in the Dickcissel or Field Sparrow but considerable variation in the House Sparrow. The House Sparrow is able to do this partly because it increases its metabolic capacity in the winter (Table 3C). The Field Sparrow shows some metabolic acclimatization to cold, but this is insufficient at low tem-

peratures to offset the shorter photoperiods. By decreasing its level of metabolic activity in the summer, the House Sparrow conserves energy and is better able to tolerate high temperature but thereby loses some of its tolerance to low temperature.

Changes in photoperiod have little effect on total energy intake in the House Sparrow, because its rate of feeding increases to compensate fully for shorter periods of daylight (Table 3D). The Field Sparrow is able to do this only at temperatures above 0°C, while the Dickcissel does not do so at any temperature. At its lower limits of temperature tolerance, the Field Sparrow increases its rate of feeding under a 10-h compared with a 15-h photoperiod, about the same as the Dickcissel, but these increases are only slightly more than one-third as much as in the House Sparrow (Table 3E).

Fluctuating outdoor temperatures stimulate higher metabolic rates than do constant temperatures (Table 3F). In the Field Sparrow this is evident only below 12°C; in the House Sparrow it occurs throughout the range of temperatures, as is true also for the Evening Grosbeak (*Hesperiphona vespertina*), another northern overwintering species (West and Hart 1966).

Dickcissels held outdoors decreased steadily in weight in late autumn as temperatures became lower and photoperiods shorter (Table 3G). The Field Sparrow, however, increased in weight and lipid storage as much, if not more, than the House Sparrow.

None of the caged Dickcissels survived the east-central Illinois winter of 1961–62. One-half of the Field Sparrows survived the winters of 1959–60 and 1961–62 (Table 3H). Caged House Sparrows normally survive over winter out-of-doors. On its wintering grounds (Fig. 1), the Field Sparrow is not normally exposed to mean monthly temperatures below 0°C, although temperatures along the northern border may occasionally drop below freezing. In east-central Illinois, the normal mean monthly temperature during December is −1.0°C, during January is −3.2°C, and during February is −1.6°C. During the above three winters, mean daily temperatures during December dropped below 0°C to more stressful levels on an average of 18 days and below −13°C on 1.3 days, during January below 0°C on 20 days and below −13°C on 3.0 days, and during February below 0°C on 18 days and below −13°C on 0.3 days.

The Field Sparrow differs from the Dickcissel but not from the House Sparrow in having no premigratory fat deposition but is similar to the Dickcissel in showing *Zugunruhe*.

The Field Sparrow thus shows some metabolic and behavioral responses to seasonal changes similar to resident species, but usually not to as pronounced a degree, and some responses similar to those of migrant species. We would expect that a species evolving permanent residency from a migratory status would pass through a stage such as that exhibited by the Field Sparrow. A resident species changing into a migratory one might also pass through such a stage. As there is evidence that several species have spread northward during the last century or so and there is no species known to have changed from residency to migratory behavior, however, the first alternative is more likely to be occurring. No significant differences were detected between individual Field Sparrows correlated with migratory status. We cannot exclude, however, the possibility that the responses are stabilized and that the species will continue as a partial migrant, but this seems improbable to us.

ACKNOWLEDGMENTS

Thanks are due to various persons who helped capture birds and at times assisted in maintaining the experiment, especially to John L. Zimmerman, Floyd H. Blackmore, and Dwain W. Parrack; to Sue Lee for making the caloric determinations of excreta; and to Sally A. Olson for her work on carcass analysis. Acknowledgment is made to the National Science Foundation for research grants to the junior author and for a 12-month cooperative fellowship provided the senior author.

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GROWTH OF NESTLING IPSWICH SPARROWS IN RELATION TO SEASON, HABITAT, BROOD SIZE, AND PARENTAL AGE

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ABSTRACT.—At 7 days of age, nestling "Ipswich Sparrows" (*Passerculus sandwichensis princeps*) had attained 79% of the weight of breeding adults. Their weight at 7 days was uncorrelated ($r = 0.02$) with the exponential rate of weight gain during the period 0–7 days but negatively correlated ($r = -0.40$) with the rate at which this weight gain is damped. Nestling weight varied inversely with brood size and showed a midsummer minimum, especially with large brood sizes. Nestling tarsus length, growth rate, and damping rate each varied directly with brood size and had a midsummer maximum. Yearling adults raised nestlings with lower damping rates and higher weights than did older adults. Variation in nestling weight is thought to be influenced by sibling competition for food and the amount of time and energy invested by parents in nestlings at the expense of subsequent broods. The thermal consequences of brood size may contribute to the variation in tarsus length. *Received 2 August 1979, accepted 26 March 1980.*

THE weight and size of nestling birds has potential significance for their chances of survival (Perrins 1965) and the reproductive fitness of their parents. Here I attempt to describe the individual variation in the growth of nestling *Passerculus sandwichensis princeps* (recently designated a subspecies of the Savannah Sparrow, but hereafter called the Ipswich Sparrow) and to identify some of the causes of this variation.

Ipswich Sparrows are especially suitable for such study, as frequent disturbance of their nests on Sable Island, in the absence of terrestrial predators of any sort, does not greatly reduce nesting success. During this study, 0.75 nestlings left the nest per egg laid. A subsequent paper will examine the pattern of survivorship in young Ipswich Sparrows.

METHODS

The growth of nestling Ipswich Sparrows was measured during the summers of 1976, 1977, and 1978 on Sable Island, Nova Scotia as part of a study of the determinants of individual fitness. Ipswich Sparrows begin nesting in May and raise up to four consecutive broods, ending in late August or early September (Stobo and McLaren 1975). Often the age of one of the parents of the nestlings being studied was known from banding records. In the analysis, I assumed that the ages of a nestling's parents were uncorrelated, as there was no direct evidence to the contrary. Nestlings were studied in two major habitats, called Dense and Sparse. Dense habitat comprised grassy or heathy areas of well-consolidated terrain with representative plant species including bayberry (*Myrica pensylvanicus*), juniper (*Juniperus communis* and *J. horizontalis*), crowberry (*Empetrum nigrum*), meadow fescue (*Festuca rubra*), sedges (*Carex* spp.), and rushes (*Juncus* spp.). This habitat was usually in the vicinity of freshwater ponds. Sparse habitat, comprising the less consolidated sand dune areas, was vegetated almost entirely by various densities of marram grass (*Ammophila breviligulata*) and beach pea (*Lathyrus japonicus*). Although Sparse habitat lacked standing water, the vegetation was frequently wet from condensation and precipitation.

Nestlings were weighed daily between 1000 and 1400, from hatching until they were 7 days old

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(hatching = day 0). At hatching, individual nestlings were marked with colored thread tied around the leg, and at 7 days they were given an aluminum band. Nestlings were weighed with a spring scale to the nearest 0.5 g. The length of the right tarsus was measured to the nearest 0.1 mm with a vernier caliper when the nestlings were 7 days old. Nestlings discovered after hatching were weighed and measured when estimated by size and plumage to be 7 days old. Older nestlings were excluded, because broods break up and nestlings begin to leave the nest when 8 days old (Stobo and McLaren 1975: 45). The young birds fledge at approximately 3 weeks old, having spent about 2 weeks hiding in the grass.

The increase in weight of passerine nestlings is sigmoidal with time and may be described by the logistic equation (Ricklefs 1967). In my study, a least-squares method rather than the graphical method (Ricklefs 1967) was used to estimate the growth rates directly from the daily increments in nestling weight. For a similar method, see Crossner (1977). Because I did not know the final weight of each individual, I chose the first two coefficients of a polynomial regression to describe the trajectory of nestling growth. The difference equation,

$$\frac{\Delta W_i}{\Delta T_i} = r_a W_i - r_b W_i^2, \tag{1}$$

was used as an approximation to the logistic equation,

$$\frac{dW}{dT} = KW - \frac{K}{A}W^2. \tag{2}$$

W_i is the nestling weight on day i, beginning with day 0, and $\triangle W_i$ is the incremental change in weight ($W_{i+1} - W_i$) over the period $\triangle T_i$, which in this study was always 1 day. The logistic growth rate K (Ricklefs 1967) is here approximated by r_a, and the ratio K/A (growth rate/asymptotic weight) by r_b, which I will call the damping rate. Lack of equivalence between equations (1) and (2) occurs because of the problems of estimating the rate of exponential growth using interval measurements. Over a time interval of 1 day, equation (1) gives

$$\Delta W_i = r_a W_i - r_b W_i^2, \tag{3}$$

whereas the integrated form of equation (2) gives

$$\Delta W_i = \frac{(1 - e^{-K})(A - W_i)W_i}{W_i + (A - W_i)e^{-K}} \tag{4}$$

Equation (1) assumes parabolic growth within each discrete time interval. Equation (2) assumes linear growth only in an infinitesimally small increment of time and growth according to a dampened exponential function over any discrete time interval. Only when the time intervals become vanishingly small will equation (1) be exactly equal to the logistic equation. Consequently, my growth rate, r_a (with units of time^{-1}), is similar to but not identical to the logistic growth rate K. The damping rate, r_b, measures the rate at which the growth rate decelerates as the asymptote is approached. The ratio r_a/r_b is approximately equal to the asymptote A.

The rates r_a and r_b were estimated for each individual, using the curvilinear regression given by equation (1). Each individual was weighed eight times (days 0–7), providing seven points in the regression. If we let $W = X_1$, $W^2 = X_2$, and $\Delta W/\Delta T = Y$, then the least-squares estimators of r_a and r_b are

$$r_a = \frac{\Sigma X_1 Y - r_b \Sigma X_1 X_2}{\Sigma X_1^2} \tag{5}$$

$$r_b = \frac{\Sigma X_1 X_2 \Sigma X_1 Y - \Sigma X_1^2 \Sigma X_2 Y}{\Sigma X_1^2 \Sigma X_2^2 - (\Sigma X_1 X_2)^2}. \tag{6}$$

Four aspects of the growth of nestlings were analyzed; body weight at age 7 days, tarsus length at 7 days, growth rate (r_a), and damping rate (r_b). The general patterns of variation in these variables were investigated by four-way and five-way analyses of variance (ANOVA) with orthogonal design and fixed effects using the SPSS 7.0 computer package (Nie et al. 1975). First, each variable was compared among Years (1976–78), Months (June–August), Habitats (Dense, Sparse), and Brood Size (b/3–b/5). Nestlings were categorized according to the date when they were measured and banded at 7 days. Brood Size was defined as the number of nestlings in the brood during the second half of the nestling period. The uncommon broods of b/1 and b/2 were combined with b/3, and b/6 with b/5 in the analyses. Next, the parameter Parental Age (SY = second year, ASY = older) was included as the fifth main effect. The sample sizes were much smaller in the latter analyses because parental ages were often not known. SY adults were studied in both 1977 and 1978, while ASY adults were studied only in 1978.

TABLE 1. The weight (A) and tarsus length (B) of 7-day-old nestling Ipswich Sparrows subdivided according to natal habitat, brood size, and date of measurement. Variation in weight was analysed by ANOVA (Table 2). Values are mean ± SE g, with (*n*). All tarsus data were transformed to *z*-scores using the annual means and standard deviations. Variation in tarsus length was analyzed by ANOVA (Table 3). Values are mean ± SE; *n* is as in part A.

	Dense habitat				Sparse habitat				Monthly means			
Brood size:	b/3	b/4	b/5	Mean	b/3	b-4	b/5	Mean	b/3	b/4	b/5	Mean
					A. Body weight							
June	20.3 ± 0.28 (39)	20.2 ± 0.17 (88)	20.4 ± 0.16 (92)	20.3 ± 0.11 (219)	20.8 ± 0.28 (22)	20.5 ± 0.23 (41)	19.7 ± 0.49 (5)	20.5 ± 0.17 (68)	20.5 ± 0.20 (61)	20.3 ± 0.14 (129)	20.4 ± 0.16 (97)	20.4 ± 0.09 (287)
July	21.1 ± 0.25 (44)	20.3 ± 0.15 (93)	19.8 ± 0.17 (150)	20.2 ± 0.11 (287)	20.9 ± 0.47 (13)	19.4 ± 0.24 (62)	19.4 ± 0.28 (59)	19.5 ± 0.18 (134)	21.0 ± 0.22 (57)	20.0 ± 0.14 (155)	19.7 ± 0.15 (209)	20.0 ± 0.10 (421)
August	20.7 ± 0.21 (63)	20.4 ± 0.20 (60)	19.8 ± 0.32 (25)	20.4 ± 0.14 (148)	20.4 ± 0.52 (19)	20.5 ± 0.32 (37)	20.7 ± 0.58 (5)	20.5 ± 0.25 (61)	20.7 ± 0.20 (82)	20.4 ± 0.17 (97)	19.9 ± 0.29 (30)	20.5 ± 0.12 (209)
Habitat means	20.7 ± 0.14 (146)	20.3 ± 0.10 (241)	20.0 ± 0.12 (267)	20.3 ± 0.07 (654)	20.7 ± 0.24 (54)	20.0 ± 0.16 (140)	19.5 ± 0.25 (69)	20.0 ± 0.12 (263)	20.7 ± 0.12 (200)	20.2 ± 0.09 (381)	19.9 ± 0.11 (336)	20.2 ± 0.06 (917)
					B. Tarsus length							
June	−0.451 ± 0.177	0.050 ± 0.107	0.107 ± 0.096	−0.015 ± 0.068	−0.026 ± 0.246	−0.394 ± 0.141	0.078 ± 0.200	−0.240 ± 0.119	−0.297 ± 0.145	−0.091 ± 0.087	0.106 ± 0.092	−0.069 ± 0.059
July	0.180 ± 0.128	0.336 ± 0.081	0.088 ± 0.092	0.182 ± 0.058	−0.055 ± 0.255	−0.332 ± 0.137	0.006 ± 0.134	−0.156 ± 0.091	0.126 ± 0.114	0.069 ± 0.077	0.065 ± 0.076	0.075 ± 0.050
August	−0.300 ± 0.134	0.250 ± 0.079	−0.059 ± 0.154	−0.036 ± 0.073	−0.525 ± 0.224	0.015 ± 0.187	0.617 ± 0.084	−0.104 ± 0.139	−0.352 ± 0.115	0.160 ± 0.086	0.054 ± 0.137	−0.056 ± 0.066
Habitat means	−0.196 ± 0.086	0.210 ± 0.054	0.081 ± 0.063	0.067 ± 0.038	−0.208 ± 0.143	−0.258 ± 0.089	0.055 ± 0.117	−0.166 ± 0.064	−0.199 ± 0.074	0.038 ± 0.049	0.076 ± 0.055	0.000 ± 0.030

TABLE 2. Analysis of variance of the weight of 7-day-old nestling Ipswich Sparrows. The main effects in the analysis are year (YR) and month (MO) when measured, brood size (BS), and natal habitat (HB). F_1 was calculated using the residual mean square (R_1) after the extraction of all interaction terms. The sums of squares from the 3-way and 4-way interactions were added to residual R_1 to calculate R_2. F_2 was calculated using the more conservative residual R_2.

Source	df	Sum of squares	Mean square	F_1[a]	F_2[a]
Main effects	7	142.811	20.402	6.702***	6.578***
YR	2	26.187	13.094	4.301**	4.228*
MO	2	14.652	7.326	2.407ns	2.365ns
HB	1	21.214	21.214	6.969**	6.850**
BS	2	49.137	24.569	8.071***	7.932***
2-way interactions	18	121.887	6.772	2.224**	2.186**
YR × MO	4	28.441	7.110	2.336*	2.296ns
YR × HB	2	21.974	10.987	3.609*	3.547*
YR × BS	4	3.246	0.812	0.267ns	0.262ns
MO × HB	2	32.673	16.337	5.367**	5.275**
MO × BS	4	46.339	11.585	3.806**	3.740**
HB × BS	2	3.005	1.502	0.494ns	0.485ns
3-way interactions	20	92.039	4.602	1.512ns	
YR × MO × HB	4	42.382	10.596	3.481**	
YR × MO × BS	8	25.671	3.209	1.054ns	
YR × HB × BS	4	14.116	3.529	1.159ns	
MO × HB × BS	4	14.692	3.673	1.207ns	
4-way interaction					
YR × MO × HB × BS	4	28.304	7.076	2.324ns	
Residual R_1	867	2639.281	3.044		
Residual R_2	891	2759.623	3.097		
Total	916	3024.321			

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Some significant three-way and higher interaction terms occurred in the ANOVA's (Tables 2, 4, 6, and 8). Because these interactions are so difficult to interpret, however, their sums of squares were combined with the residual sum of squares (R_1) to form a new, larger residual (R_2). The F-ratios for the main effects and two-way interactions were recalculated using the larger residual mean square (R_2). The analyses will be discussed on the basis of the latter, more conservative set of F-ratios (F_2).

RESULTS

The weight of apparently newly hatched nestlings was approximately 2.0 g, but largely for practical reasons no special effort was made to determine the initial variation in body weight. The weight of 7-day-old nestlings [mean ± SE (n) = 20.2 ± 0.06 g (917)] was 83% of the weight of late-summer juveniles [24.3 ± 0.13 g (220)] and 79% of the weight of breeding adults [25.6 ± 0.55 g (108)] for sexes combined (from Stobo and McLaren 1975: 84).

The simple and first-order partial correlation coefficients were calculated for the three possible pairs of r_a (1), r_b (2), and weight at 7 days (3). Although weight was uncorrelated with r_a ($r_{12} = 0.021$, df = 590, $P > 0.05$) and negatively correlated with r_b ($r_{13} = -0.400$, df = 590, $P < 0.001$), the partial correlations ($r_{12.3} = 0.853$, df = 589, $P < 0.001$; $r_{13.2} = -0.878$, df = 589, $P < 0.001$) indicate that equation (1) adequately described weight gain up to 7 days. The growth and damping rates were highly correlated both in the simple ($r_{23} = 0.879$, df = 590, $P < 0.001$) and the partial ($r_{23.1} = 0.969$, df = 589, $P < 0.001$) correlations. This indicates very little variation in the ratio r_a/r_b, which is an estimate of the asymptote. Thus, when the growth rate r_a varies, it produces variation in the time required to reach the asymptote rather than in the asymptote itself.

TABLE 3. Analysis of variance of the tarsus length of 7-day-old nestling Ipswich Sparrows (Table 1B). See Table 2 for an explanation of the analysis.

Source	df	Sum of squares	Mean square	F_1[a]	F_2[a]
Main effects	7	25.464	3.638	4.033***	3.836***
YR	2	1.145	0.573	0.635ns	0.604ns
MO	2	3.697	1.848	2.049ns	1.949ns
HB	1	12.202	12.202	13.526***	12.867***
BS	2	9.579	4.790	5.309**	5.051**
2-way interactions	18	43.600	2.422	2.685***	2.554***
YR × MO	4	8.658	2.165	2.400*	2.283ns
YR × HB	2	1.698	0.849	0.941ns	0.895ns
YR × BS	4	7.220	1.805	2.001ns	1.903ns
MO × HB	2	2.196	1.098	1.217ns	1.158ns
MO × BS	4	10.940	2.735	3.032*	2.884*
HB × BS	2	11.971	5.985	6.635***	6.312**
3-way interactions	20	48.659	2.433	2.697***	
YR × MO × HB	4	14.132	3.533	3.917**	
YR × MO × BS	8	16.275	2.034	2.255*	
YR × HB × BS	4	12.936	3.234	3.585**	
MO × HB × BS	4	13.525	3.381	3.748**	
4-way interaction					
YR × MO × HB × BS	4	14.183	3.546	3.931**	
Residual R_1	867	782.096	0.902		
Residual R_2	891	844.937	0.948		
Total	916	914.001			

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** $P < 0.001$.

Nestling weight and tarsus length at 7 days and growth and damping rates for the period 0–7 days were compared, first among Years, Months, Habitats, and Brood Sizes, and then among these four parameters plus Parental Age. Although the Year terms in the ANOVA's were occasionally significant, they were generally ignored, because the sampling effort among the other parameters differed annually. Both the mean clutch size and mean brood size changed seasonally, with a peak in July. The seasonal changes in brood size are reflected in the sample sizes shown in Table 1.

The weight of 7-day nestlings is summarized in Table 1A. The four-way ANOVA of these data is given in Table 2. Nestlings from Dense habitat averaged 1% heavier than those raised in Sparse habitat. The mean weight of nestlings declined with increasing brood size. Nestlings raised in July were lighter than those from June or August, although the differences were not significant. The decline in nestling weight with increased brood size was slight in June, strong in July, and comparatively moderate in August. A significant interaction was also observed between Month and Habitat; the midsummer decline in weights was greater in Sparse habitat than in Dense.

At 7 days of age, nestling Ipswich Sparrows had a mean tarsus length [mean ± SE (n = 21.36 ± 0.037 mm (576); 1977 + 1978] that was 96% of the tarsus length of independent juveniles [22.43 ± 0.104 mm (35); 1977 only] and 95% of the adult tarsus length [22.49 ± 0.074 mm (82); sexes combined 1977 + 1978] as I measured them.

Early in the analysis I discovered that my method of measuring tarsus length had changed between 1976 and 1977. In 1976 I measured nestling tarsus lengths as having a mean ± SD (n) of 22.61 ± 1.00 mm (341). In 1977, however, it was 21.34

TABLE 4. The (A) growth rate r_a, and (B) damping rate r_b of 0–7-day-old nestling Ipswich Sparrows subdivided according to natal habitat, brood size, and date when 7 days old. See text for method of calculations of r_a and r_b. Variation in r_a and r_b was analysed by ANOVA (Tables 5 and 6). Values of r_a are means ± SE (n); values of r_b are (mean ± SE) × 10^{-2}, with n as in part A.

	Dense habitat				Sparse habitat				Monthly means			
Brood size:	b/3	b/4	b/5	Mean	b/3	b/4	b/5	Mean	b/3	b/4	b/5	Mean
A. Growth rate, r_a												
June	0.659 ± 0.0126 (17)	0.649 ± 0.0121 (64)	0.626 ± 0.0105 (47)	0.642 ± 0.0074 (128)	0.617 ± 0.0113 (9)	0.561 ± 0.0395 (11)	0.618 ± 0.0147 (5)	0.593 ± 0.0185 (25)	0.645 ± 0.0098 (26)	0.636 ± 0.0123 (75)	0.625 ± 0.0096 (52)	0.634 ± 0.0070 (153)
July	0.628 ± 0.0195 (24)	0.675 ± 0.0107 (66)	0.652 ± 0.0086 (92)	0.657 ± 0.0064 (182)	0.594 ± 0.0364 (8)	0.630 ± 0.0200 (30)	0.659 ± 0.0108 (43)	0.642 ± 0.0101 (81)	0.619 ± 0.0171 (32)	0.661 ± 0.0098 (96)	0.654 ± 0.0068 (135)	0.652 ± 0.0054 (263)
August	0.625 ± 0.0096 (55)	0.664 ± 0.0113 (44)	0.625 ± 0.0198 (20)	0.640 ± 0.0071 (119)	0.615 ± 0.0187 (19)	0.620 ± 0.0135 (37)	0.622 ± 0.0142 (5)	0.618 ± 0.0100 (61)	0.623 ± 0.0085 (74)	0.644 ± 0.0090 (81)	0.624 ± 0.0160 (25)	0.632 ± 0.0058 (180)
Habitat means	0.632 ± 0.0077 (96)	0.663 ± 0.0069 (174)	0.641 ± 0.0064 (159)	0.648 ± 0.0040 (429)	0.611 ± 0.0128 (36)	0.615 ± 0.0115 (78)	0.652 ± 0.0091 (53)	0.626 ± 0.0068 (167)	0.626 ± 0.0066 (132)	0.648 ± 0.0060 (252)	0.644 ± 0.0053 (212)	0.642 ± 0.0035 (596)
B. Damping rate, r_b												
June	2.97 ± 0.121	3.05 ± 0.090	2.85 ± 0.076	2.97 ± 0.055	2.63 ± 0.088	2.14 ± 0.286	2.98 ± 0.095	2.48 ± 0.144	2.85 ± 0.090	2.92 ± 0.094	2.86 ± 0.069	2.89 ± 0.054
July	2.75 ± 0.167	3.22 ± 0.071	3.15 ± 0.075	3.13 ± 0.052	2.35 ± 0.290	3.09 ± 0.149	3.15 ± 0.079	3.05 ± 0.078	2.65 ± 0.146	3.18 ± 0.067	3.15 ± 0.057	3.10 ± 0.043
August	2.78 ± 0.076	3.12 ± 0.068	2.99 ± 0.128	2.94 ± 0.050	2.73 ± 0.151	2.79 ± 0.090	2.84 ± 0.158	2.77 ± 0.072	2.77 ± 0.068	2.97 ± 0.058	2.96 ± 0.107	2.88 ± 0.041
Habitat means	2.81 ± 0.064	3.13 ± 0.046	3.04 ± 0.052	3.03 ± 0.031	2.62 ± 0.105	2.81 ± 0.088	3.10 ± 0.067	2.87 ± 0.053	2.76 ± 0.055	3.03 ± 0.043	3.06 ± 0.043	2.98 ± 0.027

TABLE 5. Analysis of variance of the growth rate r_a of nestling Ipswich Sparrows (Table 4A). See Table 2 for an explanation of the analysis.

Source	df	Sum of squares	Mean square	F_1[a]	F_2[a]
Main effects	7	23.482 ($\times 10^{-2}$)	3.355 ($\times 10^{-2}$)	5.466***	5.073***
YR	2	7.579	3.789	6.174**	5.730**
MO	2	4.317	2.158	3.517*	3.264*
HB	1	9.636	9.636	15.699***	14.570***
BS	2	5.770	2.885	4.700**	4.362**
2-way interactions	18	32.908	1.828	2.979***	2.765***
YR × MO	4	5.288	1.322	2.154ns	1.999ns
YR × HB	2	2.790	1.395	2.273ns	2.110ns
YR × BS	4	12.637	3.159	5.147***	4.777***
MO × HB	2	0.325	0.163	0.265ns	0.246ns
MO × BS	4	1.754	0.439	0.715ns	0.663ns
HB × BS	2	7.733	3.866	6.300**	5.847**
3-way interactions	18	36.393	2.022	3.394***	
YR × MO × HB	3	4.136	1.379	2.246ns	
YR × MO × BS	7	19.393	2.770	4.514***	
YR × HB × BS	4	6.502	1.626	2.649*	
MO × HB × BS	4	2.886	0.721	1.176ns	
4-way interaction					
YR × MO × HB × BS	1	2.376	2.376	3.871*	
Residual R_1	551	338.178	0.614		
Residual R_2	570	376.947	0.661		
Total	595	433.336			

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

± 0.80 mm (336), and in 1978 in was 21.38 ± 0.97 mm (240). This was corrected by transforming all tarsus lengths by the z-transformation (Sokal and Rohlf 1969), using the annual means and standard deviations. This necessarily made the Year term in the ANOVA nonsignificant.

The pattern of variation in tarsus length (Tables 1B and 3) was complex and very different from that observed for nestling weight. As with nestling weight, tarsus length was greater for nestlings raised in Dense habitat than for those in Sparse habitat. Nestling tarsus length was greater for nestlings raised in July, however, than for those raised in June or August (not significantly so), and mean tarsus length increased with increasing brood size. A significant interaction was observed between Habitat and Brood Size, but in each habitat broods of three had the smallest (or nearly so) tarsus lengths.

Very similar trends were observed for growth rate r_a (Tables 4A and 5), and damping rate r_b (Tables 4B and 6), as one might expect from the strong positive correlation between them. For both of these rates, nestlings from Dense habitat had larger mean values than those from Sparse habitat; means were largest in July, and in the three brood sizes the smallest mean rates were in broods of three. Very similar interactions between Habitat and Brood Size were found for both r_a and r_b.

The marginal totals in Tables 1B, 4A, and 4B show that the trends in nestling tarsus length are very similar to those in growth and damping rates. In contrast, the trends in nestling weight are different from, and generally the converse of, those found for growth and damping rates.

The size and growth of Ipswich Sparrow nestlings varied in an unpredicted manner with respect to parental age. The improvement in parental abilities expected to

TABLE 6. Analysis of variance of the damping rate r_b of nestling Ipswich Sparrows (Table 4B). See Table 2 for an explanation of the analysis.

Source	df	Sum of squares	Mean square	F_1[a]	F_2[a]
Main effects	7	18.960 ($\times 10^{-4}$)	2.709 ($\times 10^{-4}$)	7.162***	6.928***
YR	2	1.794	0.897	2.372ns	2.294ns
MO	2	4.861	2.430	6.426**	6.216**
HB	1	5.001	5.001	13.224***	12.791***
BS	2	7.708	3.854	10.191***	9.858***
2-way interactions	18	15.849	0.880	2.328**	2.252**
YR × MO	4	1.597	0.399	1.056ns	1.021ns
YR × HB	2	0.057	0.028	0.075ns	0.072ns
YR × BS	4	6.292	1.573	4.159**	4.023**
MO × HB	2	1.200	0.600	1.587ns	1.535ns
MO × BS	4	1.374	0.343	0.908ns	0.878ns
HB × BS	2	2.671	1.336	3.531*	3.416*
3-way interactions	18	14.384	0.799	2.113**	
YR × MO × HB	3	1.336	0.445	1.178ns	
YR × MO × BS	7	7.038	1.005	2.658*	
YR × HB × BS	4	1.733	0.433	1.146ns	
MO × HB × BS	4	2.327	0.582	1.538ns	
4-way interaction					
YR × MO × HB × BS	1	0.088	0.088	0.232ns	
Residual R_1	551	208.387	0.378		
Residual R_2	570	222.859	0.391		
Total	595	257.668			

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

accompany increased age did not result in larger or more quickly growing nestlings. The offspring of both male and female ASY adults averaged lighter than those of younger adults, especially at the largest brood size (Table 7). For both parental sexes, a significant Age by Month interaction occurred when the mean weight of nestlings raised by SY parents declined as the summer progressed, whereas the offspring of ASY parents were lightest in July. This interaction may have occurred because the broods of ASY parents were largest in July (Ross 1979). These weight differences were not paralleled by differences in the tarsus length of the offspring of SY and ASY adults. Significant interactions in tarsus length, however, were found for both Age by Brood Size and Age by Month among female parents. The biological meaningfulness of these interactions is reduced because of the lumping of heterogeneous subsets resulting from the limitations of the sampling effort and from the larger clutches and earlier nesting of ASY adults (Ross 1979). The growth rates of nestlings raised by males or females of either age did not differ significantly. In contrast, the damping rates of nestlings raised by ASY adults were significantly greater than those of nestlings raised by SY males or females. In summary, the nestlings of ASY adults began to grow as quickly as those of SY adults, but their weight gain was curtailed sooner, resulting in lower body weight at age 7 days.

DISCUSSION

The growth rate r_a is clearly a measure of the rate of increase in biomass. Although r_a is not identical to the logistic growth rate K of Ricklefs (1967), the two are positively correlated. The damping rate r_b is much less easy to interpret, because its units (weight^{-1}·time^{-1}) do not have any simple biological interpretation. Because

TABLE 7. Mean ± SE (n) values for four nestling growth parameters for nestling Ipswich Sparrows subdivided according to the known age of a parent. The given probabilities are for the differences between age groups within sexes from a larger ANOVA. See text for definitions.

Parental sex	Parental age	7-day nestling weight (g)[a]	7-day nestling tarsus length (z)[a]	Growth rate, r_a	Damping rate, r_b ($\times 10^{-2}$)[a]
Male	SY	20.8*** ± 0.13 (164)	0.194ns ± 0.078 (164)	0.637ns ± 0.0074 (108)	2.88* ± 0.053 (108)
Male	ASY	19.2 ± 0.25 (82)	0.105 ± 0.134 (81)	0.635 ± 0.0100 (62)	3.02 ± 0.071 (62)
Female	SY	20.5** ± 0.14 (145)	−0.071ns ± 0.082 (145)	0.640ns ± 0.0077 (125)	2.95*** ± 0.062 (125)
Female	ASY	20.1 ± 0.24 (76)	0.088 ± 0.107 (76)	0.637 ± 0.0093 (68)	3.05 ± 0.061 (68)

[a] ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** $P < 0.001$.

r_b is the coefficient of the squared term in equation (1), variation in r_b would indicate greater variation in the second half of the growth trajectory than in the first. The damping rate measures the rate at which the instantaneous growth rate decreases as the asymptote is approached and therefore may indicate the rate at which energy is diverted from simple biomass accumulation to tissue differentiation.

A lack of a positive correlation between the growth rate and the asymptotic or near-asymptotic weight is widely found in studies of passerines. Growth rates presented by or calculated from Ricklefs (1968, and pers. comm.), Hussell (1972), Dyrcz (1974), Crawford (1977), and Crossner (1977) all fail to show distinct trends. Ricklefs (pers. comm.) has indicated that there may be no inherent relationship between the growth rate and asymptotic weight of nestling Starlings (*Sturnus vulgaris*), but positive correlations may arise between the two in each nutritional situation. Thus Ricklefs' K and my r_a may not be adequate indices of the overall quality of a nestling's existence unless they are set in a larger framework.

The trends observed in weight and tarsus length may result from certain aspects of the nestlings' nutritional and thermal environment. The decrease in nestling weight in larger brood sizes (Table 1A) probably reflects the well-known problem of sibling competition for a food source limited by the parental foraging abilities (Royama 1966, Seel 1970, Hussell 1972, Askenmo 1977, Schifferli 1978). Because nestling weights were higher in the Dense habitat than in the Sparse habitat for broods of four and five, especially in July when over half of the young from Sparse habitat were raised, a slight amount of the variation in nestling weight may be attributable to differences in food availability between the habitats.

Newly hatched nestlings are poikilothermic, gradually achieving homoiothermy near the end of the nest period as they develop the plumage and physiological mechanisms required for thermoregulation (Dawson and Evans 1957, 1960; O'Connor 1975a,b). Because the rate of heat loss depends on the surface/volume ratio of the brood and is correlated with brood size (O'Connor 1975b), nestlings will be more prone to hypothermia at lower brood sizes. Temperature directly modifies the rate of bone growth by influencing both arterial dilation and metabolic rates (Brookes and May 1972). Skeletal development in the limbs and tail of white mice

(*Mus musculus*) is much more sensitive to environmental temperature than is thoracic skeletal development (Garrard et al. 1974). Consequently, the overall trend for tarsus length to increase in larger broods (Table 1B) may result from brood size-dependent variation in the nestlings' body temperature. The significant Month by Brood Size interaction (Table 3) may have arisen because July was a warmer, sunnier month than June, whereas nests were more shaded under tall grass in August.

Variation in the growth rate (Table 4A) and the damping rate (Table 4B) may be due to both nutritional and thermal factors. Each nestling in a large brood would receive a smaller share of food than in a smaller brood, but improved thermal conditions would mean that less energy was expended on thermogenesis. July may be both the warmest and most food-rich month, and such conditions could produce faster growth and development.

In many passerine species older male and female parents have improved reproductive performance through a combination of increased reproductive effort and increased parental success (Klomp 1970, Perrins and Moss 1974, Rheinwald et al. 1976, Crawford 1977, De Steven 1978, Harvey et al. 1979, Ross 1979). Although it is commonly assumed that the foraging abilities of passerines improve with age (e.g. Lack 1968: 297), such an improvement has been demonstrated only for non-passerines (Orians 1969, Recher and Recher 1969, Buckley and Buckley 1974, Groves 1978). Crawford (1977) found that both yearling Red-winged (*Agelaius phoeniceus*) and Yellow-headed (*Xanthocephalus xanthocephalus*) blackbirds raised lighter nestlings than did older adults. Growth and damping rates that I calculated from the mean trajectories of weight gain for both species were larger for the offspring of yearlings. Thus age-related changes in the parental skills of passerines seem likely.

Table 7 suggests that ASY Ipswich Sparrows do not provide a greater quality of parental care than do SY birds but actually reduce the amount of food delivered to their nestlings. Stobo and McLaren (1975) found that late in the nestling period the female Ipswich Sparrow reduces her attendance at the present brood and produces a subsequent nest and clutch of eggs before the independence of the former nestlings. Throughout the nestling period, the male increases his rate of food delivery and takes a major share in the care of the young after they leave the nest. By this division of labor, a pair of Ipswich Sparrows may raise up to four broods in a summer.

I found that when either of the parents was SY in age, more time was taken to produce the next nest and clutch after the previous brood had been successfully raised to 7 days than when either parent was ASY (Ross 1979). In contrast, there was no significant difference between the parental age classes in the time required to renest and relay after the clutch or brood was predated or abandoned. This suggests that the age effect relates to the willingness of an individual female to begin the next clutch or of an individual male to take greater responsibility for the brood in progress, rather than to differences in sexual competence or egg formation. These age differences contributed to a greater production of eggs and 7-day-old nestlings by ASY adults than by SY adults in a summer (Ross 1979).

The probability of survival of young Great Tits (*Parus major*) is correlated with their weight at fledging (Perrins 1965). Therefore, the lower weights of the nestlings raised by ASY Ipswich Sparrows would seem maladaptive. The probability that an individual would return to Sable Island (the sole breeding place of the Ipswich Sparrow) at age SY, however, was independent of the nestling's weight, tarsus

length, r_a, r_b, habitat, date of hatching, brood size, or parental age during 1976–78 (Ross and McLaren, in prep.). After they leave the nest, young Ipswich Sparrows spend approximately 2 weeks hiding in the grass before they achieve independence from their parents. This period may allow them enough compensatory feeding to shore up their half of the parent-offspring conflict (Trivers 1974). Adults certainly benefit if they can increase the number of offspring by reducing the care of each to the barest minimum. Differences in nestling weight related to parental age probably reflected modifications to the parents' allocations of energy to offspring in an attempt to increase parental fitness.

ACKNOWLEDGMENTS

I wish to thank Ian McLaren for his advice throughout this study. Field assistance was given by Susan MacCormack, Douglas Nakashima, and Judith Robins. This study was funded by grants to I. A. McLaren from the National Research Council of Canada, the Canadian Wildlife Service, and the Canadian National Sportsman's Fund. I was supported by postgraduate scholarships from the National Research Council of Canada and Dalhousie University.

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TERRITORY SIZE DIFFERENCES IN RELATION TO REPRODUCTIVE STAGE AND TYPE OF INTRUDER IN HERRING GULLS (*LARUS ARGENTATUS*)

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ABSTRACT.—Breeding Herring Gulls defend three territory types, which vary in size depending on the stage in the reproductive cycle. Territory types are a function of the nature of the conspecific intruders and consist of a primary territory defended against neighbors, a secondary territory defended against non-neighbors, and a unique territory defended against all intruders under all conditions. In all three territory types, defense activity is highest at the nest. The unique area is smallest, the primary territory is intermediate in size and nonoverlapping with neighbors, and the secondary territories are largest and overlapping. The defense of each territory type is discussed in terms of the costs and benefits to the territory defender during each stage in the reproductive cycle. I suggest that one advantage of breeding synchrony within subcolonies is to prevent egg and chick loss due to territory size differences of the unsynchronized pairs. *Received 12 September 1979, accepted 6 March 1980.*

ORNITHOLOGISTS have been fascinated by the existence and adaptive significance of territory since Howard (1920) first described it. Although authors initially concentrated on documenting its occurrence, they later began classifying territories according to their use for foraging, nesting, or both (Nice 1941, Tinbergen 1953, Brown 1964). Many species of gulls breed in large colonies and defend breeding territories, but they obtain all their food away from the colony. Kirkman (1940) and Huxley (1934) suggested that the nesting territories of gulls resemble rubber discs, because their size varies under different conditions.

Subsequently, authors have shown that territory size varies as a function of age (Dhondt and Huble 1968, Ralph and Pearson 1971), time of day (Weeden 1965), and stage of the breeding cycle (Stenger and Falls 1959, Weeden 1965, Stefanski 1967, Falls 1969). Nonetheless, in most studies, territory size has been determined for a short period of time during only part of the reproductive cycle rather than from daily observations throughout the cycle. In gulls, territory size has often been obtained by measuring the distance to the closest neighbor. This distance may not be a good measure of territory size, because only in dense gull colonies might the nest be located in the center of the territory. Furthermore, territories are usually not round but are irregularly shaped.

Hunt and Hunt (1976) measured territory in Western (*Larus occidentalis*) and Glaucous-winged (*L. glaucescens*) gulls and found that it increased during the chick phase. Under some conditions, differences in territory size resulted in differences in reproductive success. Glaucous-winged Gulls with larger territories had higher reproductive success, as their chicks were not killed by neighbors. Hunt and Hunt did not mark the birds in their study for individual identification, however, and they determined territory boundaries on the basis of all encounters without considering whether they occurred with neighbors or non-neighbors. Furthermore, they did not look for specific territory size differences as a function of stage in the reproductive cycle.

Kirkman (1940), and later Patterson (1965), suggested that territory owners respond differently to conspecific neighbors than to non-neighbors. This aspect was

not stressed in either study, and their birds were not individually marked. Quantitative data on the reactions of gulls to intruding neighbors and non-neighbors are generally lacking in the literature. Investigators working with passerines have long known that males respond differently to the songs of neighbors as compared to non-neighbors (Weeden and Falls 1959, Emlen 1971). Such responses involve individual recognition, with the strength of the responses depending upon the location of the intruder relative to the territory and the territory-holder. These responses have not been directly related to shifts in territory size. The ability of gulls to recognize and respond differently to neighbors and non-neighbors could result in differences in how space is used and defended around nests.

In this paper I describe shifts in Herring Gull (*Larus argentatus*) territorial boundaries and territory size with respect to reproductive stage (pre-incubation, incubation, chicks) and type of intruder (neighbor, non-neighbor) and comment on the adaptive significance of these shifts. I hypothesize that territory owners would defend space differently depending upon their stage in the reproductive cycle and upon the type of intruder.

STUDY AREA AND METHODS

I observed the territorial behavior of Herring Gulls during 1976 and 1977 on Clam Island, New Jersey, where a colony of 800 pairs nested on *Spartina patens* and under bushes. Clam Island is a low salt-marsh island located behind a barrier beach in Barnegat Bay. Data from 1976 were used to generate hypotheses about the territorial defense of Herring Gulls to be tested in 1977.

In 1977, 15 color-marked pairs were observed from a blind for 8–12 h a day, 4 to 6 days a week, from before egglaying (15 April) to fledging (15 July). Additional pairs that nested adjacent to the study area were color-marked so that the neighbors of all study animals could be determined. To color-mark gulls, I suspended a cup filled with dye from a small frame over the nest. A string connected to the cup allowed me to dump the dye on the gull once it resumed incubation. Gulls immediately flew, and I continued to pull the apparatus from beside the nest. Thus, the returning gull resumed incubation without any apparent effects. A neighbor was defined as either member of a Herring Gull pair whose territory abutted the primary territory of the pair being examined, while a non-neighbor was defined as any other conspecific.

I recorded the presence and location of every intruder on maps, the outcome of each encounter, the sex of the intruder when it was a neighbor, and the reaction and reproductive stage of all nearby territory owners. The sex of neighbors was determined by noting the copulatory position of all pairs observed to copulate at least twice. The sex of intruders was determined only when size differences were extreme. Aggressive interactions were recorded on data sheets listing the sex and status of the intruder and the outcome of the interaction. The exact location of each encounter was plotted on a scaled map. These daily maps of all territorial encounters could be related to the reproductive stage of each pair. Because the pairs were fairly synchronous, this resulted in about 10 pre-incubation, 20 incubation, and 32 post-incubation (chick phase) maps for each pair. During the entire study period, aggressive interactions varied from 2 to $60 \cdot day^{-1} \cdot pair^{-1}$ ($\bar{x} = 1.32 \pm 0.54$ encounters$\cdot pair^{-1} \cdot h^{-1}$).

The areas of all individual territories were determined with a computer by tracing the defended areas onto a console that entered data directly into the computer. For the analysis, I drew a line that connected the outermost points of each territory type. This was straightforward for the unique and primary territory types, as these boundaries were relatively fixed and territorial clashes occurred at the boundaries. Furthermore, many nonattack defense behaviors (such as grass-pulling and upright posturings) occurred at the boundaries between neighbors. These defense behaviors confirmed the location of the precise boundary. The boundaries of secondary territories were less precise but could be computed, because the secondary boundary of one pair was the unique boundary of its neighbor. Furthermore, there were no points of defense for any pairs that were more than 2 m from other defense points. Such distant points were defended very early in the season (March), when territories were initially being established, but I did not include these data.

In order to test the hypothesis that territory size relates to the distance to the closest neighbor, I measured the distance from the center of a nest to the center of the four closest neighbors. The distance

TABLE 1. Behavior of territory owners with respect to reproductive stage and type of intruder. N = neighbor who is intruding, and NN = non-neighbor who is intruding. Shown are the types of intruders that a territory owner will chase as a function of stage.

Reproductive stage	Type of territory		
	Unique	Primary	Secondary
Pre-incubation			
Either member of the pair	N, NN	N, NN	NN[a]
Incubation			
Incubating bird[b]	N, NN		
Nonincubating	N, NN	N, NN	NN[a]
Chick phase			
Either member of the pair	N, NN	N, NN	NN[a]

[a] Chases only when the neighbor whose primary territory the secondary territory overlaps does not chase it.
[b] Chases only when its mate is not present.

of each of these neighbors (and combinations thereof) was then correlated with the computed mean primary territory size for each pair.

Data from 1976 generated the following hypotheses to be tested in 1977: (1) territory owners respond differently to neighbors than to non-neighbors, (2) three territory types are defended, and (3) these territory sizes vary with reproductive stage.

RESULTS

Three defended areas were discernible for each pair of Herring Gulls: a primary territory, a secondary territory, and a unique territory (Fig. 1). The primary territory was usually defended against all conspecific intruders. The secondary territory (larger than the primary territory) was defended against non-neighbors (except when the defender was incubating) whenever a neighbor did not chase the intruder. The unique territory, the smallest area, was defended against all intruders at all times. Table 1 summarizes the defense behavior of members of a pair, which varied seasonally depending upon reproductive constraints. Either member defended during the pre-incubation phase, while during the incubation period the nonincubating mate did the chasing. When its mate was not present, the incubating territory holder left its nest only to chase conspecifics (neighbor and non-neighbor) from its unique territory. During the chick phase, both members of each pair chased intruders from all defended areas. Territory owners chased intruders (only non-neighbors) from their secondary territory only when their neighbor (in whose primary territory the intruder landed) did not chase the intruder. Neighbors did not chase these intruders when only the incubating bird was present.

These interactions can be illustrated by an intruder that lands at X in Fig. 1: (1) If the intruder were a neighbor of pair 1, pair 1 would chase the intruder, because it would be in the primary territory of pair 1. (2) If the intruder were a non-neighbor, either a nonincubating bird from nest 1 would chase it, or (if no one from nest 1 chased it) a nonincubating bird from either nest 2 or 3 would chase it, as it would be in their secondary territories.

When plotted seasonally for the 15 pairs, the mean size of the secondary territory was always larger than that of the primary territory (Fig. 2), and the mean size of the unique territory was always smaller than that of the primary territory ($F = 28.6$; df = 2,161; $P < 0.001$). Territories generally increased in size in early June following hatching. This was possible because one pair deserted its territory due to egg

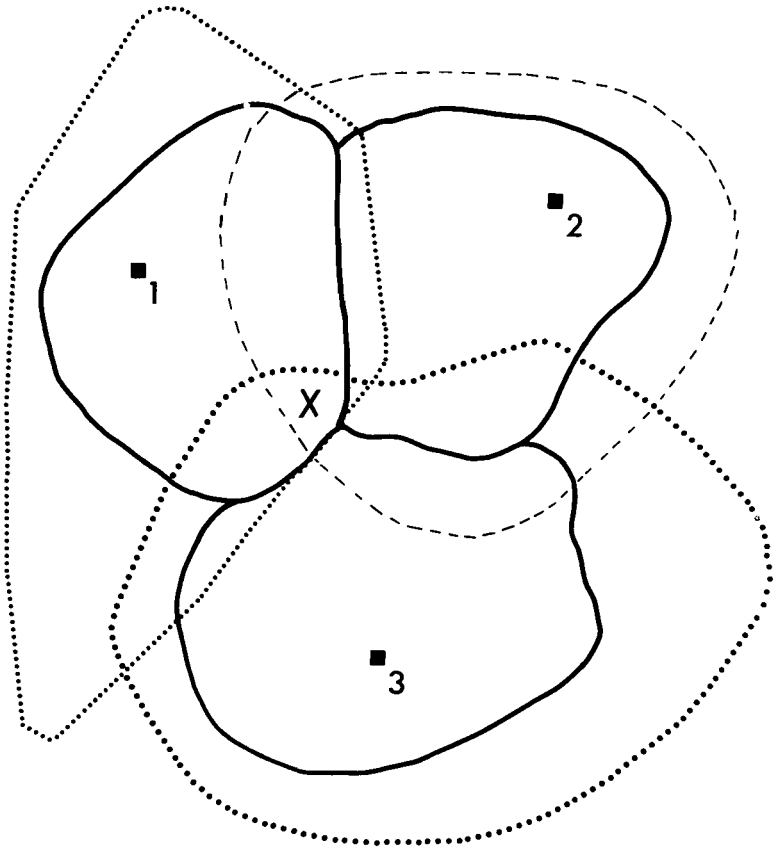

Fig. 1. Representation of territory types in Herring Gull. Solid line = primary territory; small dotted line = secondary territory of pair 1, large dotted line = secondary territory of pair 3, and dashed line = secondary territory of pair 2. The unique territory for pair 1 = the area bounded by the solid line on the left and the dashed and dotted lines within the solid line on the right. Square = the nest location; X = the point at which an intruder has landed (see text).

loss, and some previously unused space was occupied. Both events normally occur in gull colonies unless space is extremely limited.

Because mean territory size varied seasonally, gulls appeared to defend territories of different sizes at different periods in their reproductive cycle. To test this, I analyzed the data by reproductive stage (Fig. 3). Significant differences occurred within and among reproductive stages and territory types ($F = 53.9$; df = 6,271; $P < 0.001$). In general, all three territory types were significantly different in size during each reproductive stage (Table 2A). The variation in size as a function of reproductive stage for each territory type is shown in Fig. 3. Secondary territory size varied among all stages (Table 2B). The unique territory, however, was similar in size in the pre-incubation and incubation stages, and the primary territory was similar in size during the pre-incubation and chick phases (Table 2B).

Four pairs from nearby territories outside the study area lost their eggs to predators (crows and conspecifics) during the incubation period. All contracted the size of all three of their territories so that there were no significant differences among their primary, secondary, and unique territories ($F = 26.3$; df = 1,50; $P < 0.01$).

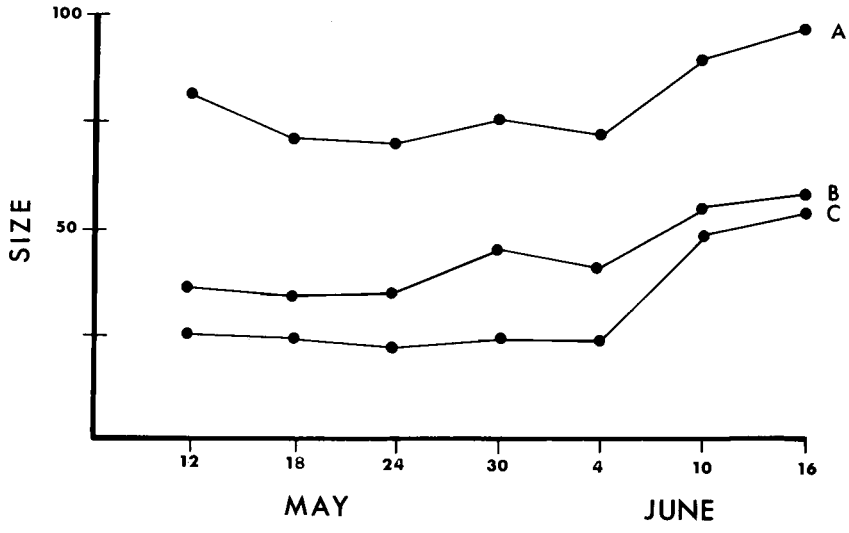

Fig. 2. Seasonal differences in primary (B), secondary (A), and unique (C) territories in Herring Gulls.

They reduced their unique ($\bar{x}$ = 20 ± 5 m^2) and primary ($\bar{x}$ = 22 ± 4 m^2) territory sizes to that of the unique territory of normally incubating pairs. The secondary territory stayed slightly larger ($\bar{x}$ = 26 ± 8 m^2), as the birds still chased non-neighbor

TABLE 2. Statistical values for differences in the sizes of territory types defended as a function of reproductive stage and territory type.

Stage and type	*t* value	df	*P*<
A. Reproductive stage			
Pre-incubation			
Unique and primary	3.75	28	0.001
Unique and secondary	10.45	28	0.001
Primary and secondary	3.93	28	0.001
Incubation			
Unique and primary	0.67	28	NS[a]
Unique and secondary	3.06	28	0.005
Primary and secondary	2.65	28	0.05
Chick phase			
Unique and primary	4.83	26	0.001
Unique and secondary	13.42	26	0.001
Primary and secondary	9.12	26	0.001
B. Territory types			
Secondary			
Pre-incubation and incubation	6.86	28	0.001
Pre-incubation and chick	3.02	26	0.005
Incubation and chick	7.92	26	0.001
Primary			
Pre-incubation and incubation	3.81	28	0.001
Pre-incubation and chick	1.97	26	NS
Incubation and chick	4.95	26	0.001
Unique			
Pre-incubation and incubation	0.66	28	NS
Pre-incubation and chick	4.93	26	0.001
Incubation and chick	5.43	26	0.001

[a] NS = not significant.

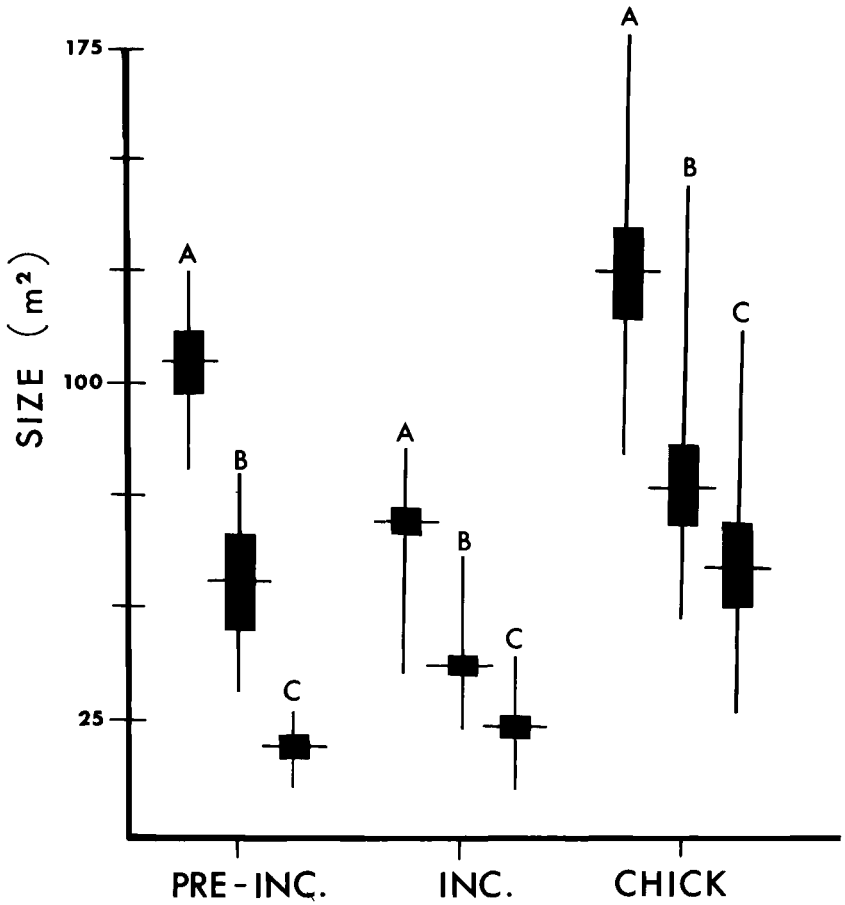

Fig. 3. Differences in primary (B), secondary (A), and unique (C) territory size as a function of reproductive stage. Shown are mean (horizontal line), range (vertical line), and SD (vertical bar).

intruders. These pairs reverted to courtship and did not concentrate on territorial defense until they had relaid. Once they had complete clutches, they again began defending a primary and secondary territory and attempted to enlarge these areas.

I then tested the hypothesis that territory area relates to the distance to the nearest neighbor, as is assumed in many papers on territoriality. The distance to the closest conspecific neighbor did not correlate with the primary territory size ($r = 0.174$). The best measure of the primary territory size for the 15 pairs was the distance to the second nearest neighbor in any direction other than that of the first nearest neighbor ($r = 0.831$, $P < 0.01$). The correlations of territory size with the mean inter-nest distance of the closest two neighbors ($r = 0.58$, $P < 0.05$) and closest three neighbors ($r = 0.64$, $P < 0.01$) were lower.

To determine the threat of egg cannibalism that neighbors provide to one another, I constructed 15 nests at the primary territory boundaries of 15 pairs in another area of the colony. Each test nest contained three Herring Gull eggs, and all were eaten within 2 h: 2% by crows, 11% by conspecific non-neighbors, and 87% by the resident territory owner (equally by both sexes).

Discussion

I did not examine territorial behavior before pair formation or reformation (assuming most pairs had been paired in previous years), because it is difficult to mark individuals without making them shift locations. Cursory observations indicated that secondary territories were very large and became distinguishable from primary territories when neighbors settled and were no longer able to displace the territorial pair.

Overall, the mean primary territory size for the 15 pairs examined did not correlate significantly with the distance to the nearest neighbor. My results indicate that the distance to the second nearest neighbor provides the best indication of territory size. Given the territorial requirements of Herring Gulls (adequate space to raise chicks), this is understandable. When the first nearest neighbor is very close (where dense vegetation or rocks present a visual barrier between nests; see Burger 1977), then the second nearest neighbor must be far enough away to provide adequate territory space. When the nearest neighbor is at an intermediate distance, then the second nearest neighbor is also at an intermediate distance. Thus, the second nearest neighbor provides the best measure of territory size.

In the present study, differences in the defense of the territory of Herring Gulls existed with respect to the type of intruder as well as to the stage in the reproductive cycle. These differences reflect the functions of the three territory types as well as the magnitude of the threat posed by the type of intruder. During the pre-incubation phase, the pair must establish a primary territory large enough for subsequent reproductive activities. Thus, they chased both neighbors and non-neighbors at greater distances than required for successful courtship and mating. It is adaptive for them to defend bigger secondary territories to prevent intruders from establishing a territory between the present neighbors. If an intruder established a station (future nest site) a few meters into a neighboring gull's primary territory, the new intruder would annex some of the defending gull's primary territory as well as some of its neighbor's. Thus, a gull is not defending a neighbor's nest but is protecting its own territory by creating a buffer zone. The defense of a secondary territory during the pre-incubation phase is required only when their neighbors are absent.

During the incubation phase, one member of each pair is always present and is incubating. At this time, their reproductive investment (eggs) is best protected by remaining on the eggs. But anticipatory to the chick phase, the pair must maintain an adequate primary territory. If the parents allowed the territory to shrink to the size of the nest, they might be unable to expand it to the necessary size required by mobile chicks. Adults remain on the eggs until violations of their unique territory occur. A larger secondary territory is maintained to prevent intruders from establishing territories. These intruders are not immediate threats to the nest and eggs, but they will be when the eggs hatch. Courting neighbors are ignored, as these neighbors will be incubating when the defending, incubating pair's chicks have hatched.

During the chick phase, all three territory types increase significantly in size. This is possible because of the loss of the chicks of one pair (and reduction of territory size) and the availability of some unused area. Both events regularly occur in a gull colony, and gulls normally expand their territory into these unused areas. During this chick phase, parents provide room for chicks to wander about without being killed by neighbors during territorial clashes or by non-neighbors who are canni-

balistic. Cannibalism is well known in Herring Gulls (Parsons 1971, Davis and Dunn 1976), and so it is advantageous for parents to chase all non-neighbors. Time and energy invested at this time directly relate to chick survival (see Hunt and Hunt 1976), particularly as it is too late in the season for pairs to relay (Burger, unpubl. data).

Methodologically, the computing of the three territory types depends upon the quantity of data recorded. The exact territory boundaries will become more precise with more data. Nonetheless, I found that after 6 or 7 days of recording territorial clashes during each phase (pre-incubation, incubation, chick) the territorial boundaries did not shift markedly with additional data.

In gulls, where cannibalism is often the most important cause of chick mortality, I suggest that breeding synchrony may be the result of the decreased mortality of eggs and young in synchronous areas as compared to asynchronous areas. As shown above, reproductive losses in Herring Gulls would be higher in areas of low synchrony directly as a result of egg and chick losses to neighbors and indirectly by the increases in aggression necessary to defend areas against courting pairs. During the egg-laying period, pairs often leave their eggs uncovered until they lay the second or third egg. Courting individuals often wander about the perimeter of their territory, and eat any uncovered eggs they encounter. I also found that males and females ate unattended eggs in their secondary territories. If marked differences in chick size facilitate parental recognition of chicks not their own, then asynchrony would contribute to chick cannibalism.

Biologists normally assume that breeding synchrony is a function of social facilitation during the pre-egg-laying phase (Darling 1938, MacRoberts and MacRoberts 1972, Burger 1979). The adaptive significance of synchrony relates to reducing the percentage of chicks taken by predators and to the early egg laying found in synchronous areas. In terns, the biomass of prey taken per day by nocturnal predators is constant throughout the breeding season, despite a hundredfold increase in biomass available (Nisbet 1975). If there is no recruitment of predators into the area (M. Gochfeld, pers. comm.), a high degree of synchrony results in an abundance of food for only a short period of time, making it impossible for predators to eat as high a proportion of young as under asynchronous conditions. Highest survival of chicks in early egg-laying gulls has been found by Paynter (1949), Paludan (1951), and Vermeer (1970), while highest survival in the mid-egg-laying period was found by Brown (1976) and Kadlac and Drury (1968). I suggest that in a species like the Herring Gull in which cannibalism accounts for most egg and chick losses, and neighbors account for much of the cannibalism, it is adaptive to by synchronous for protection against conspecifics, as well as for the usual antipredator devices.

ACKNOWLEDGMENTS

I thank M. Gochfeld for many discussions on synchrony and for helping with the computer analysis and the manuscript. M. Conover, G. Hunt, B. Murray, G. Shugart and J. Verner provided helpful comments on the manuscript, and I thank them. The research was funded by the Research Council of Rutgers University.

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PATTERNS IN THE AMINO ACID COMPOSITIONS OF AVIAN EPIDERMAL PROTEINS

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ABSTRACT.—I used statistical analysis to compare the amino acid compositions of avian epidermal proteins. Comparisons were made of individual monomers from a single tissue of the morphological parts of various tissues, and of unfractionated tissues, at both the intra- and interspecific levels. The results imply a chemical basis for tissue protein structural heterogeneity, document tissue specificity, and indicate design relationships between protein distribution and tissue function. The amino acid composition of keratins provides information on the evolutionary relationships of natal down, feather, scale, claw, and beak. *Received 11 June 1979, accepted 3 June 1980.*

THE hard, keratinaceous structures of the avian epidermis differ morphologically and in their functional requirements. Nevertheless, the structural proteins of feathers, claw, down, scale, and beak commonly referred to as keratins are the products of closely related genes (Brush 1974, 1975) and share a common molecular configuration. Physical evidence indicates that the polypeptides that form these structures have a common β-pleated sheet structure and are organized into microfilaments (Fraser et al. 1972, Brush 1978). These in turn form filaments that consist of interacting chains, as modeled by Fraser and his colleagues (Fraser et al. 1971, Fraser and MacRae 1976). The supramolecular organization of the filaments has been studied with the electron microscope. The solubilized proteins are of two basic sizes, are tissue specific, and are extremely heterogeneous in electrophoresis (Brush 1975, Brush and Wyld MS). The feather proteins have an average molecular weight of 10,500 and those of the claw, scale, and beak of 14,500. The latter are enriched dramatically in glycine and show increased amounts of hydrophobic residues (e.g. Tyr, Leu, Phe) when compared to the lower molecular weight monomer in the feather and down (Walker and Bridgen 1976). The keratins of all the structures are relatively high in Cys, Pro, and Ser, and deficient in His, Met, and Lys.

The presence of a large number of similar protein monomers in a given tissue makes amino acid sequence studies difficult. This is especially true in keratins, where a family of closely related structural genes is involved. Simple separations based on charge (i.e. electrophoresis or chromatography) or solubility (i.e. Zn-acetate fractionation) are almost always incomplete. Absolute purification is difficult for those proteins whose sequence similarity is probably the result of only a few nucleotide changes. Yet full sequence data are available for pennacious feather keratin polypeptides of two species and for chicken down. Perhaps more progress has been made in the analysis of tryptic peptide maps and amino acid compositon of feather keratin monomers, techniques that require less preparation and are more rapid than sequence studies (Busch and Brush 1979). Relatively few species, however, have been examined, and only feathers of the contour plumage have been investigated. More extensive fractionations based on relative solubility of related groups of monomers have been carried out for a broad range of tissues in a half-dozen species (Brush in press). The fractions, which presumably share certain chemical properties, were not compared extensively by amino acid analysis. Thus the available amino

TABLE 1. Comparison of amino acid compositions of avian keratins. Values are given as average SΔQ. The range of values in a given comparison is included in parentheses. The large difference in the *Dacelo* beak value is discussed further in Brush (in press). The major tissues are feather (FKM), scale (SKM), and down (DKM). Details of intraspecific tissue differences and species differences in contour feather appear in Tables 3 and 4.

	SΔQ (range)	Reference
A. Intraspecific-Chemical		
1. Monomers		
Tern-FKM	48.8 (5.3–185)	Busch & Brush 1979
Turkey-FKM	35.7 (4–86)	Busch & Brush 1979
Gallus-FKM	44.5 (2–89)	Kemp & Rogers 1972
Gallus-FKM	9.2 (1–24)	Akahane et al. 1977
Gallus-SKM	11.5 (5.3–13)	Walker & Bridgen 1976
Gallus-DKM	25.3 (4.8–68)	Walker & Rogers 1976
2. Chemical fractionation		
Gallus-feather: ethanol ppt.	27.4 (13.3–55.2)	Harrap & Woods 1964
Gallus-scale: Zn ppt.	76	Brush in press
Dacelo-beak: Zn ppt.	421	Frankel & Gillespie 1976
B. Intraspecific-morphological		
1. Feather parts (rachis, calamus, barb, medulla)		
Gallus contour feather	15	Kemp & Rogers 1972
Gallus contour feather	15.4	Crewether et al. 1965
Anser contour feather	14	Crewether et al. 1965
Turkey contour feather	23	Crewether et al. 1965

acid composition data of avian epidermal structures are scattered and incomplete. Analyses from several laboratories are available for selected tissues of common species. Until now, little effort has been directed toward specific comparative morphological or systematic studies. The use of the amino acid compositions of the entire complex of solubilized proteins or partly purified preparations may provide significant information regarding the evolutionary relationships of the proteins, although this approach lacks the fine resolution of sequence data. Further, in concert with other data it may provide insights into structural problems, functional requirements, and evolution of these tissues. In this study I used a number of statistical methods to analyze and compare the amino acid compositions of avian epidermal proteins. This information was used to construct dendograms that, in association with other biochemical and structural information, provide a basis for speculation on the design and evolution of the epidermal structures of birds.

METHODS

Several statistics may be used to compare the similarities of protein amino acid compositions. These are designated as the difference index (DI) (Metzger et al. 1968), the composition divergence (D) or deviation function (Harris and Teller 1973), and the composition coefficient (SΔQ) (Marchalonis and Weltman 1971, Dedman et al. 1974). The value of the coefficient lies in its ability to estimate similarity in sequence from similarity in composition (Black and Harkins 1977; Woodward 1978; Cornish-Bowden 1978, 1979). Not all the available methods have been evaluated with equal rigor. The DI was assessed independently by Woodward (1978). He compared the distribution of DI values among both related and unrelated protein pairs and concluded that a DI of less than 10 indicated relatedness (e.g. homology), that values over 27 indicated unrelatedness, and that DI's of pairs in the region 10–27 could not be judged reliably. Unfortunately, this presents an ambiguity in an area of intense interest to systematists. These studies conclude that each index has a reasonable predictive value and is a relatively reliable screening test for the detection of protein similarities. A major problem occurs in comparing molecules of different chain length, and various statistical compromises have been provided. In regard to most

TABLE 2. SΔQ values from feather keratin monomers of emu (*Dromaius novaehollandiae*) and gull (*Larus novaehollandiae*) that have been fully sequenced (O'Donnell and Inglis 1974). The average SΔQ value for all available monomers from tern (*Sterna hirundo*) and turkey (*Meleagris gallopavo*) was 86 (Busch and Brush 1979). The average SΔQ for all values in this table is 140.6 ± 41. These values represent minimal values to estimate interspecific differences in presumably homologous monomers.

	Larus	*Sterna*	*Dromaius*	*Meleagris*
Larus novaehollandiae	—	150	109	105
Sterna hirundo		—	181	101
Dromaius novaehollandiae			—	96
Meleagris gallopavo				—

parameters it is difficult to choose among them. The SΔQ value of Marchalonis and Weltman (1971) has been widely applied and is empirically useful.

I applied all these techniques to an extensive sampling of the available amino acid compositions of avian keratins from various structures. Amino acid compositions were obtained from the literature or from analysis in my laboratory. When necessary, data were converted to residues percent (e.g. residues/100 residues) as a common unit value. I attempted to identify problems such as the reproducibility of analysis by comparing data on similar material from different laboratories (Table 1). Technical differences among the various laboratories may be reflected in variation and reproducibility of reported values. All values for amino acid residues were rounded to a single decimal place for calculations.

The SΔQ is basically the sum of the difference between each amino acid squared:

$$S\Delta Q = \Sigma_j(X_{ij} - X_{kj})^2 \quad (1)$$

where X_j is the content of a particular amino acid of type j, and the subscripts i and k identify the particular proteins that were compared. SΔQ gives a direct estimate of the number of sequence differences from composition and is most accurate in comparisons of polypeptides of equal length. It is based on residues/100. The other method of choice is the SΔn statistic, which is more sensitive to differences in polypeptide length (Cornish-Bowden 1977). It is defined as one-half the individual differences among residues squared. In this case the comparison is based on total chain length rather than a normalized value:

$$S\Delta n = \tfrac{1}{2}\,\Sigma(N_{iA} - N_{iB})^2 \quad (2)$$

where N_{iA} and N_{iB} are the numbers of amino acid residues of the ith type in proteins A and B, respectively. The summation is carried out over each type of amino acid distinguished in most composition measurements. A correction factor is applied (Cornish-Bowden 1979; equation 5) if the proteins differ by approximately 20 or more residues. The SΔn is an estimator equal in reliability to SΔQ; indeed the two are interconvertible (see equation 3). The SΔn statistic has probably the most rigorous theoretical development, and is superior in comparisons of proteins of unequal length. There is good agreement between knowledge of how it ought to behave and its function in practice when applied to related proteins. There are not as many empirical tests of the SΔn as exist for the SΔQ. The values are related by the factor:

$$S\Delta Q = \frac{2 \times 10^4\, S\Delta n}{N^2} \quad (3)$$

where N is the total polypeptide length (Cornish-Bowden 1977). It is possible to apply either statistic to a given data set with internal consistency as the molecular weights of the major monomers are known and their distribution is tissue specific (Brush and Wyld in press). The values of the SΔn calculations were used in all studies of tissues with polypeptides of different lengths.

Complete sequence data are available for very few avian keratins. The complete sequences of individual feather keratin monomers (FKM) from a gull, *Larus novaehollandiae,* and Emu, *Dromaius novaehollandiae* (O'Donnell and Inglis 1974), chicken down (Walker and Rogers 1976), and a partial sequence of chicken scale monomer (SKM) (Walker and Bridgen 1976) were compared by diagonal index matching and sequence-nucleotide (REH) comparison (Holmquist et al. 1972, Moore et al. 1976). Comparisons were also made with the same samples using the SΔn statistic (Cornish-Bowden 1977).

TABLE 3. Amino acid composition differences among tissues of *Gallus gallus*, estimated with the SΔn values, which includes an appropriate correction for chain length differences. Values for similar tissues analyzed in different laboratories are included.

	Feather			Down				Scale (scute)			Reticulate scale	Beak	Claw
	a.	b.	c.	d.	e.	f.	g.	h.	i.	j.	k.	l.	m.
a. Feather (Akahane et al. 1977)	0	16.1	8.99	44.1	43.4	6.3	9.2	369.0	333.4	280.5	1,308.2	296.2	313.8
b. Feather (Harrap & Woods 1964)		0	1.5	34.8	34.3	14.8	17.9	307.9	265.5	224.8	1,213.2	230.6	240.8
c. Feather (Kemp & Rogers 1972)			0	30.5	29.0	8.1	11.0	318.6	275.3	223.2	1,220.1	241.2	253.3
d. Adult down				0	25.3	40.0	33.2	302.6	263.1	207.1	1,220.1	229.9	232.2
e. Natal down					0	24.1	37.2	310.7	259.4	208.0	1,072.1	215.8	230.0
f. Natal down (Walker & Rogers 1976)						0	10.5	348.3	299.7	249.7	1,187.9	260.3	286.0
g. Natal down (Kemp & Rogers 1972)							0	351.1	303.7	258.7	1,311.0	268.1	286.0
h. Scale (scute) (Walker & Bridgen 1976)								0	24.2	33.6	587.1	35.0	29.1
i. Scale (scute) (Kemp & Rogers 1972)									0	28.9	551.5	8.5	8.3
j. Scale (scute) (Brush & Wyld 1980)										0	566.3	26.6	23.0
k. Scale (reticulate) (Brush & Wyld 1980)											0	570.2	557.6
l. Beak (Frankel & Gillespie 1976)												0	4.0
m. Claw (Fraser et al. 1972)													0

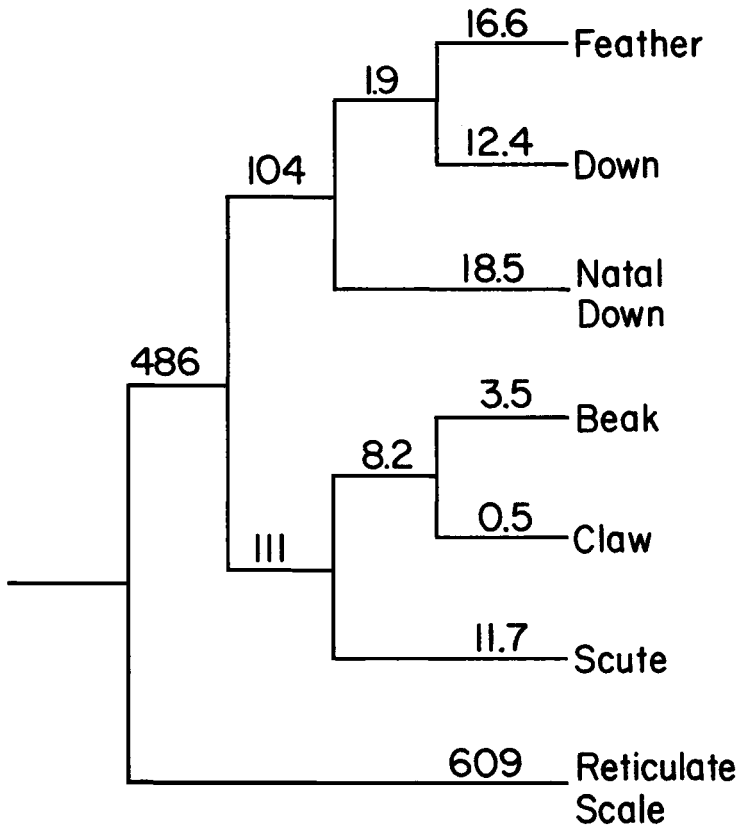

Fig. 1. Dendogram of avian keratin tissues based on amino acid compositional differences as estimated by SΔn. Branching sequence and limb lengths established by Fitch-Margoliash (1967) algorithm. This was the best-fit tree, with SD = 216, and F = 29. The high SD was a result of the large distances between the two tissue groups and the great distance to reticulate scale.

RESULTS

Avian epidermal structures can be categorized by a hierarchical sequence of chemical-morphological organization. Detailed comparisons of the amino acid compositions at each level can supplement other investigations. The degree of similarity in composition reflects both genetic relatedness and functional requirements.

Intraspecific differences in monomers.—The structural details of feather keratin monomers isolated from several species were given by Busch and Brush (1979). The compositional differences were used here as an indication of the range of values of variation within the primary molecular structural element among the available species (Table 1A). The isolated monomers represent the simplest structural element and each is the product of a separate gene. Individual monomers from other tissues showed similar difference values, which implies that sequence differences among monomers account for the electrophoretic and chemical heterogeneity. The chemical fractions, generally isolated by their solubility, are always electrophoretically heterogeneous (Brush in press). The chemical fractions are operational groups defined by specific physical-chemical properties (Table 1A and 1B).

TABLE 4. Comparison of amino acid compositions of adult contour feathers from a variety of species. Values are reported as SΔn. The mean interspecific value was 61.7 for 28 measurements. The average of all feather values to *Gallus* scute was 290 SΔn units. Data from references listed in Table 2; values for *Ardea* and *Tadorna* from this laboratory. Values for *Gallus a* from Akahane et al. (1977) and *b* from Harrap & Woods (1964).

	Sterna	*Melea-gris*	*Gallus a*	*Gallus b*	*Larus*	*Dromaius*	*Ardea*	*Tadorna*
Sterna	0	43.7	53.3	37.5	58.6	114.7	69.6	12.8
Meleagris		0	21.0	3.1	43.6	45.4	93.5	61.7
Gallus a			0	21.0	52.1	33.7	98.7	83.0
Gallus b				0	41.4	56.8	92.0	52.4
Larus					0	56.2	97.0	73.7
Dromaius						0	118.5	118.4
Ardea							0	73.9
Tadorna								0

At the morphological level the elements of the feather, such as rachis, calamus, and barbs, can be separated mechanically, recognized unambiguously, and associated with specific functions. Comparisons of amino acid compositions of feather parts are presented in Table 1B. The values were similar in magnitude to those obtained from chemically produced fractions. This indicates again a molecular heterogeneity associated with structure and, presumably, with functional requirements.

Monomer differences between species.—Complete sequence data are available for isolated monomers of only two species (O'Donnell and Inglis 1974). These can be compared with the presumably homologous monomer isolated from other species (Table 2). The values are greater than within-species differences. Presumably these differences represent sequence divergence in the monomers accumulated since these taxa shared a common ancestor. Thus, differences among monomers of each tissue within species are structurally or functionally derived, while those in homologous monomers in different species reflect genetic divergence.

Tissue differences.—The keratin tissues of an individual take several morphologically distinctive shapes. The most obvious are contour feather, bills, claws, and scales. Further, some represent different phases in development—natal and adult down, for example. The amino acid compositions of these structures can differ significantly (Table 3). In this table the composition values were calculated with the SΔn formula. For the previous data the SΔQ was used. Values for the comparisons of all tissues of *Gallus gallus* are given in Table 3. A dendogram based on these values is presented in Fig. 1. Note the close clustering of the feather-down complex and the small distances among the scale-claw-beak complex. The distance that separates these two clusters are vast by comparison. The reticulate scale is even more distant, which probably reflects the evolutionary origin of this structure (Brush and Wyld 1980).

Interspecific comparison of feather composition.—Average values among comparisons of the same tissue performed in different laboratories give an estimate of the reproducibility of the amino acid composition analysis. The average SΔn value for unfractionate *Gallus* contour feather keratin was 8.8, for down 23.9, and 28.9 for scute. The magnitude of these differences approached those measured among chemical fractions or gross morphological elements.

The only SΔn values available in quantity were for adult contour feathers (Table 4). These values are comparable with previously published SΔQ values, but are considerably more extensive. These values correspond roughly with generally ac-

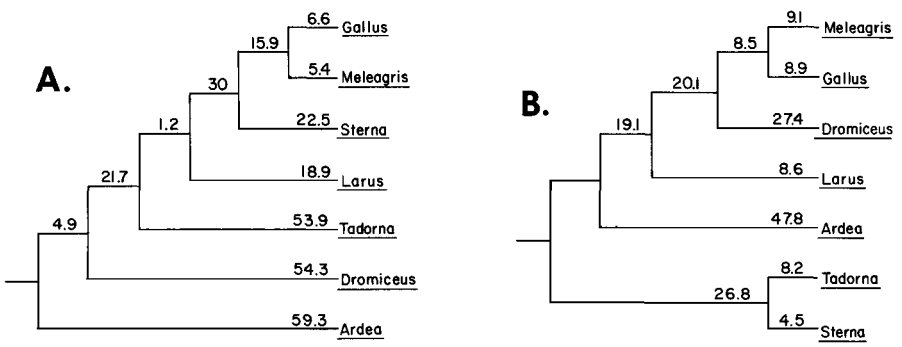

Fig. 2. Phylogeny based on amino acid composition analysis of unfractionated feather keratins. **A.** The Fitch-Margoliash techniques gave a branching order that was more like the generally accepted classification. Tests of "goodness-of-fit" gave an SD = 21, F = 51. **B.** The Farris-Wagner (Farris 1970) algorithm had an SD = 21, F = 17. The origins, significance, and use of these values is discussed by Prager and Wilson (1978).

cepted taxonomic opinion (Fig. 2). The possibility of basing phylogenies on amino acid composition analysis was recently explored (Cornish-Bowden 1979). Clearly, amino acid composition is only one dimension useful in interspecific comparisons. Electrophoretic comparisons of solubilized feather proteins are also of considerable promise (Brush 1976, Knox 1979).

DISCUSSION

The solubilized SCM-keratin monomers of avian epidermal structures can be characterized by their electrophoretic pattern in polyacrylamide gels. When compared under various conditions, the morphologically diverse tissues within an individual have many bands in common, but each contains unique polypeptide units. That is, recognizable tissue-specific patterns exist that involve both common and unique bands and differences in concentration. The distribution and relative amounts of each monomer unit reflect structural and functional differences. There are also species-specific influences that modify the tissue pattern. There is a significant difference between the size of the basic keratin polypeptide in feathers and that in scale, beak, and claw, but, unlike the keratins of the integument of other amniotic vertebrates (Fraser et al. 1972, Wyld and Brush 1979), no significant size heterogeneity of polypeptides occurs within single avian structures. Overall, the keratin structures share many biochemical and organizational properties (Brush and Wyld MS).

In order to establish the existence of a hierarchical sequence of amino acid difference values, I began with the system in which the component molecules were presumed to be most closely related. The isolated SCM-monomers of a single tissue such as feathers or scales within species provided such information (Table 1). There are 8–10 major structural genes, and probably an equal number of minor genes, that produce the feather and scale keratins (Rogers 1978). Comparison of the polypeptides within species indicates the degree of sequence variation among the products of a single genome (Table 1). These data were then expanded to include other fractionation procedures, individual monomers isolated from different species, the unfractionated solubilized proteins from morphologically distinct portions of the

same structure in various species, and the solubilized proteins from different tissues within and among species. Several patterns emerged from the amino acid composition analysis based on these comparisons.

Average differences among the isolated monomers from tissues within species were small and presumably represent a limit of minimal sequence differences. By all criteria they represent groups of closely related proteins but differ among tissues. Presumably this reflects differences in the functional requirements of each structure.

Although the average difference values for monomers varied among the tissues, each monomer in an electrophoretic or chromatographic series was most like its immediate neighbor. Distances between neighbors increased along the series. Simultaneously, the cumulative differences increased as one progressed through the pattern. This supports the hypothesis that the electrophoretic heterogeneity of the elements is based on structural differences and agrees with differences produced by other types of fractionation.

The single available calibration that relates $S\Delta Q$ to actual sequence difference is in the comparison of Band III for Silver Gull and Emu contour feathers (Table 2). The data for monomers of known sequence were compared with bands of similar electrophoretic mobility from other species. The estimated sequence difference (average = 141) was large relative to intraspecific comparisons of isolated feather keratin monomers. Thus, it appears that intraspecific keratin monomers were more alike than the monomer from another species with an identical electrophoretic mobility. The $S\Delta Q$ values indicated that the proteins were homologous. The major differences in sequence are presumably the result of divergence. The second point illustrated by this comparison is that proteins with similar electrophoretic mobilities may indeed have different sequences. This can be a source of confusion in electrophoretic comparison of complex protein mixtures (Brush 1979). Extrapolation of the sequence data indicates an average difference of about nine residues among the monomers within a species. The differences are cumulative, as indicated by matrix analysis along a chromatographic or electrophoretic series. One can conclude that, although differences among the monomers that form a single tissue are minimal, those monomers whose chemical behavior is most similar have smaller differences than polypeptides with greater chemical differences (e.g. position in elution sequence). This inference is supported further by observations based on sequence (Walker and Rogers 1976) and peptide map studies (Busch and Brush 1979). The latter have been especially informative because fine differences are resolved with a minimum of material. The compositional differences imply significant sequence differences among closely related polypeptides.

The conservative nature of change in closely related monomers is supported by the intraspecific comparisons of the various parts of feathers (Table 1B). The barb, rachis, medulla, and calamus within several species have average $S\Delta Q$ values lower than among the isolated feather monomers. These structures were also distinguished by their electrophoretic pattern. Thus, the unfractionated protein mixtures from different morphological parts appear more similar than the fractionated monomers prepared from the whole extract of the same structure. Values for structures from different stages varied intraspecifically. Chick and adult scale, for example, were very similar, while natal down and adult contour feathers differed by a magnitude similar to the interspecific isolated feather keratin monomer values. Pennaceous feather and natal down proteins differ in other parameters such as electrophoretic pattern and solubility as well (Brush in press, Brush and Wyld MS). The implication

is that morphologically different parts within tissues retain a high portion of their structural elements in common. Further, the combined sequence difference among these units is small. The proportional distribution of monomers or related groups of monomers must affect gross compositional differences. Such distributional differences would tend to minimize apparent differences in unfractionated samples. These arguments, and the reproducibility of values for similar structures analyzed in different laboratories, imply that the difference in SΔQ values for tissue monomers may approach the limits of resolution of the analytical system.

The difference values for tissues within species were greater than values for the same tissue between species. This reflects the conservative nature of keratins in terms of taxonomic divergence over time and the specific requirements of function and design of the tissues within a species. The compositional differences for unfractionated solubilized keratin monomers of homologous structures from different species averaged about twice that for the parts within species. The differences among tissues of an individual and the feather generations from the same species were larger. This implies that the tissue-specific differences are related to both functional and morphogenetic differences. The molecular heterogeneity provides a basis for the morphological diversity and functional requirements of the epidermal structures.

This system of analysis is not free of problems. For example, comparisons among tern (*Sterna hirundo*) feather keratins showed that monomers number VI and VII differed by almost 185 SΔQ units, enough to be considered unrelated proteins. Closer examination of the data indicated that the difference was due mainly to the enrichment of a single residue (Gly) in FKM-VII. This monomer is also likely to be the one found in the high-Gly portion of the Zn-Acetate fractionation procedure (Brush in press). If this is the case, then the system is sensitive to differences in individual residues. Enrichment by repeats in the sequence may be taxonomically uninformative but a structural necessity. Similarly, there are technical problems associated with the detection and quantification of specific amino acid residues. Fortunately, none of these occurs in significant numbers in the keratins. It is also apparent that the statistical analyses were sensitive to differences in only a small number of residues. Together, these factors could produce inaccurate comparisons and may account for lowered reproducibility among laboratories. Nevertheless, adequate internal consistencies exist in the data from various laboratories and in patterns of the results to make the data useful. Further, the behavior of fractions in separation by solubility was consistent with the amino acid compositional data. Chain length differences can be accommodated by the SΔn formulation.

The phylogeny of the keratin tissues constructed from amino acid compositional data provides a basis for studies of their relationship (Fig. 1). The values for contour feather and two types of down cluster together. There is little indication that natal down is signficantly different enough to be considered a primitive structure or a precursor to adult feathers. One can only conclude that all feathers appear to be derived structures unique to birds. The "harder" structures, e.g. scale, beak, and claws, cluster together and are relatively distant from the feathers. Again this reflects structural differences related to function. Both these groups are vastly separated from reticulate scale. On the basis of these and additional data, we suggest that the reticulate scale is homologous to the reptilian scale and the other hard tissues and feathers are derived in birds (Brush and Wyld 1980).

Computer analysis of the scanty sequence data show the proteins of different tissues to be distantly related in comparison to polypeptides within structures. Se-

quence changes are mostly the product of conservative nucleotide changes and are not unexpected, given the present models of the evolution of these structures (e.g. Maderson 1972a,b). Neither computer method was used to establish limb lengths in the relationship dendograms. Despite limited data, the hypothesis that homologous morphological structures are more alike at the biochemical level than morphologically different structures was supported.

In summary, it is apparent that tissues considered homologous by morphological criteria have strong compositional similarities. Compositional differences are greater between tissue types within species than between the homologous tissue in other species. I conclude that protein composition is determined largely by the structural and functional requirements of a tissue and less by species differences due to anagenic changes. Future emphasis should be placed on studies of tissue differences rather than phylogenetic relations based on a single factor in a tissue. One remarkable aspect of the keratins is the tremendous organizational flexibility, as shown in the morphological manifestation of structure produced by a group of related gene products whose chemistry and supramolecular interactions are only now being perceived.

Although amino acid compositions have been useful in indicating trends in the structure and evolution of avian keratins, some unanswered questions remain. Composition data are valuable in probing the nature of the structural heterogeneity of polypeptides within tissues. They provide insight into possible relationships and homologies among structures, and the relative contribution of functional requirements and species difference. Finally, they are an important factor in addressing problems in design and evolution of epidermal structures. For example, amino acid compositions were instrumental in demonstrating differences in the protein of reticulate scales and scutes and their relationships to other structures (Brush and Wyld 1980). Further, we have established that the scale and claw are very similar in amino acid composition and may be primitive. Beak proteins are more like claw and scale than feathers, but differ significantly and are probably derived. In each case, some further definitive test is possible. The molecular approach may provide a framework for explaining the function-structure relationships of morphological entities at the protein level. Consistencies exist among the amino acid composition, molecular morphology, chemical fractionation behavior, and other molecular data (e.g. electrophoretic heterogeneity and molecular sizing) that, when considered together, are mutually supportive. These parameters reflect trends in the design and evolution of the structures that relate to traditional questions of structural design, homology, and taxonomic relationships. The heterogeneity and tissue-specific nature of avian epidermal keratins is now well documented. The available data indicate that the proteins have significant consequences for the functional design of tissues. Questions of the relationships of synthesis, distribution, and organization of the proteins in relation to tissue morphology and functional requirements can be approached further on both the molecular and ultrastructural levels.

ACKNOWLEDGMENTS

Ms. April Ladden performed preliminary statistical analysis of the composition data. Ms. Erika Kares has provided continued laboratory support and had considerable input into the phylogenetic reconstructions. Dr. Jean Wyld read and commented on several drafts of the manuscript. Dr. Pam Todd of the Biochemistry Department, University of Melbourne, assisted with the computer comparisons of sequence data. Several anonymous reviewers provided careful, positive criticism; I am particularly grateful for

their time and efforts. Support was provided from a grant from the National Science Foundation (DEB-76-20967). Funding for the amino acid analyses was made available from the University of Connecticut Research Foundation.

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OFFSPRING REDUCTION IN MACARONI AND ROCKHOPPER PENGUINS

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ABSTRACT.—Mortality of Macaroni Penguin (*Eudyptes chrysolophus*) and Rockhopper Penguin [*E. chrysocome* (*crestatus*)] eggs and chicks was investigated at Marion Island. Two eggs were laid at each nest, but no pair reared more than one chick. Egg mortality exceeded chick mortality in both species. Both eggs hatched at 6% of Rockhopper Penguin nests and at no Macaroni Penguin nests. When both eggs hatched, one chick died of starvation within 12 days. Chicks were successfully reared from 43% and 34% of all eggs laid by Macaroni and Rockhopper penguins, respectively. Egg mortality was greater and occurred earlier, and chick mortality was lower, in Macaroni than in Rockhopper penguins.

Offspring reduction was closely related to egg dimorphism and differential egg mortality. In both species the first laid (A) egg was markedly lighter than the second (B) egg. Mortality of A-eggs was 99.7 and 88% and of B-eggs 44 and 32% in Macaroni and Rockhopper penguins, respectively. Chicks were raised successfully from 3% of all A-eggs laid by Rockhopper Penguins. No A-egg chicks were reared by Macaroni Penguins. The B-eggs, a better investment, were treated preferentially, and the smaller A-eggs were often disregarded. The A-egg functions as an insurance against the loss or failure to hatch of the B-egg in most Rockhopper Penguin clutches but serves no obvious function in the majority of Macaroni Penguin clutches. *Received 23 July 1979, accepted 26 March 1980.*

BIRDS of many species may lay more eggs per clutch than the number of chicks that they are able to raise to independence, and it is generally assumed that the necessary reduction in the number of offspring occurs through brood reduction—the differential mortality of chicks in relation to their position in the hatching sequence (e.g. Ricklefs 1965, Lack 1966, O'Connor 1978, Howe 1978). *Eudyptes* penguins lay a standard clutch of two eggs, in which the first laid (A) egg is markedly smaller than the second laid (B) egg (Gwynn 1953), but rear only one chick per clutch (Warham 1975). Accounts of mortality in Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins [*E. chrysocome* (*crestatus*)] indicate that the adjustment in offspring numbers occurs primarily through differential egg mortality—the loss or failure of eggs in relation to their position in the laying sequence (Gwynn 1953, Warham 1975).

No account of egg and of chick mortality in either the Macaroni or Rockhopper penguin has been comprehensive. Reports of egg mortality either do not state the number of nests at which both eggs were lost (Gwynn 1953) or, in cases involving the loss of only one egg, do not indicate whether it was the A- or B-egg that was lost (Warham 1963, Duroselle and Tollu 1977). There has been no quantitative assessment of chick mortality. Warham (1963, 1971) reported that in both species both eggs may be hatched at some nests but that the proportion of nests at which this occurs and the period of sibling coexistence were not known.

The mortality of eggs and chicks of Macaroni and Rockhopper penguins was investigated at Marion Island (46°45'S, 37°45'E) in the austral summers of 1974–75 and 1976–77. Particular attention was paid to differences in the pattern of mortality between the two species and differences in the degree and timing of the mortality of A- and B-eggs and ensuing chicks.

METHODS

The duration of phases in the breeding cycle is similar in the two species. At individual nests, the egg period lasts 40 and 39 days in the Macaroni and Rockhopper penguins, respectively, and in both species the chick-rearing period lasts 70–71 days.

Mortality was assessed during five phases: (1) the laying phase, the 4-day interval between the laying of the A- and B-eggs; (2) the incubation phase, from the laying of the B-egg until the first of the eggs hatches; (3) the hatching phase, from the hatching of the first egg until the second egg hatches or clearly fails; (4) the guard phase, the 3 weeks immediately following hatching during which the male parent remains at the nest guarding the chick; and (5) the postguard phase, from the end of the guard phase until the chick leaves the colony.

Mortality was assessed at several colonies with populations ranging from tens to hundreds of pairs. Study populations all bred on broken, sloping lava terrain. This restricted the effect of human disturbance but made it impossible to analyze the effect of location (edge to center) on mortality. Mortality in the laying phase was assessed in 1976, when the contents of individually numbered nests were monitored daily. Most birds permitted nest inspection and handling of the eggs without leaving the nest site. My movement through colonies was slow and careful. If birds left their egg(s), I remained close by to deter predators until the parents returned. There was no appreciable difference in the reaction of birds in the two species to human disturbance. When there was any doubt whether my activity had affected egg loss, the record for that nest was discarded. Males of both species return to their nest site in the latter part of the egg period and remain at the nest irrespective of its contents until some time after all the chicks in the colony have hatched. Egg mortality during incubation and hatching phases was assessed by inspecting the contents of individually numbered nests a few days before hatching was due and then monitoring their contents daily until after hatching was completed.

Chicks were weighed within 24 h of hatching and daily thereafter until they were fed (indicated by a marked increase in chick weight compared with egg weight at the end of incubation), until brood reduction had occurred, or until the chick died or became independent and went to sea. During the guard phase, chicks remained at the nest, and any missing from the nest were assumed to have been killed and removed by predators. Chicks were given numbered plastic flipper tags when about 15 days old. Some Rockhopper Penguin chicks moved into inacessible cavities at the end of the guard phase and could no longer be monitored. The number of singly reared A-egg chicks was increased by removing some B-eggs from nests that had retained both eggs through the incubation period.

RESULTS

Egg mortality.—Egg mortality was substantial in both species, and 72% of all Macaroni Penguin eggs and 60% of all Rockhopper Penguin eggs were lost or failed to hatch. The pattern of egg mortality in the two species differed in several ways (Table 1). Total nest failure through the loss of both eggs was greater in Macaroni than in Rockhopper Penguins. Egg mortality occurred earlier in Macaroni Penguins, and at no Macaroni Penguin nests were both eggs retained until the end of the incubation phase. Both eggs remained at 30% of all Rockhopper Penguin nests, but, because of mortality in the hatching phase, both eggs hatched at only 6% of all nests (Table 1).

Mortality of A-eggs was 99.7 and 88%, and of B-eggs it was 44 and 32% in Macaroni and Rockhopper penguins, respectively (Table 1). Loss of the A-egg during the laying phase amounted to almost 54% in the Macaroni Penguin but was less than 2% in the Rockhopper Penguin. Macaroni Penguins also lost more single eggs than Rockhopper Penguins during the incubation phase. Mortality in the hatching phase was confined to Rockhopper Penguins and was largely due to the loss of A-eggs from the nest after the B-egg had hatched. A-eggs found beside Rockhopper Penguin nests during this phase almost all contained well developed embryos and some of the eggs were pipped.

TABLE 1. Mortality of Macaroni and Rockhopper penguin eggs at Marion Island.

	Macaroni Penguin			Rockhopper Penguin		
	A-egg %	*n*	B-egg %	A-egg %	*n*	B-egg %
Laying phase						
Number of nests sampled		24			53	
Loss of A-eggs before B-eggs laid	53.6		—	1.9		—
Combined laying and incubation phases						
Number of nests sampled		300			258	
Loss of both eggs	44.0		44.0[a]	26.0		26.0
Loss of single eggs	55.7		0.3	39.1		4.7
Both eggs retained until one hatched	0		0	30.2		30.3
Hatching phase						
No. nests (with 2 eggs) sampled		0			35	
Loss of single eggs	—		—	77.0		3.0
Both eggs lost	—		—	0		0
Both eggs hatched	—		—	20.0		20.0
Total egg mortality	99.7		44.3	88.0		32.0
% all eggs lost or failed		72			60	

[a] Includes five B-eggs that were addled and one where the chick died in the egg. The proportion of addling in Rockhopper Penguins was not ascertained.

Most of the eggs lost simply disappeared, either stolen directly from the nest by Lesser Sheathbills (*Chionis minor*), Skuas (*Catharacta skua*), or Kelp Gulls (*Larus dominicanus*) or dislodged from the nest by the parents and then taken by scavengers. No replacement eggs are laid (Gwynn 1953, pers. obs.).

Brood reduction.—No Macaroni Penguins hatched both eggs. At 18 Rockhopper Penguin nests where two chicks hatched, only one of the brood survived. Coexistence of the siblings ranged from 2 to 12 days. At 17 nests where an A- and a B-egg hatched, 16 B-egg chicks and one A-egg chick survived. In one nest two A-eggs hatched (the result of the capture of a dislodged A-egg after the B-egg was lost). At this nest the first chick to hatch survived, and the second chick died 12 days after hatching.

Three principal factors affected the length of time two chicks coexisted: (1) the degree of hatching asynchrony; (2) the difference in size and weight of the chicks when the second chick hatched; and (3) the time elapsed before the chicks received their first meal. Typically, the B-egg hatched first and the B-chick was fed before the A-chick hatched. The A-chick was not usually fed and died from starvation within 4 days. The period of sibling coexistence was increased when both chicks hatched on the same day. One A-chick hatched, and was fed, before the B-chick hatched. Though equal in weight to the B-chick, it was smaller in size and was dominated by the B-chick in competition for food and soon died. The only A-chick that outlived its B-sibling was at a nest where the chicks were not fed until the B-chick was at least 132 h old. The B-chick was by that time too weak to compete with the later-hatched A-chick and died of starvation.

Chick mortality.—The overall chick mortality was 22% in Macaroni and 61% in Rockhopper Penguins (Table 2). The principal differences were the absence of brood reduction in Macaroni Penguins and the markedly greater mortality of Rockhopper Penguin chicks during the postguard phase.

TABLE 2. Percentages of chick mortality and hatching and overall breeding success of Macaroni and Rockhopper penguins at Marion Island. Sample sizes are given in parentheses.

Species and chick type	Hatching success[a]	Chick mortality			Breeding success[a]
		Through brood reduction[b]	In guard phase[c]	In postguard phase	
Rockhopper Penguin					
A-egg chicks[a]	12.0	94.0 (17)	8.0 (26)	50.0 (18)	3.2
B-egg chicks	68.0	6.0 (17)	18.0 (62)	43.0 (40)	31.7
Macaroni Penguin[e]					
B-egg chicks	55.7	— —	14.9 (67)	8.8 (57)	43.2

[a] Success per 100 eggs of each type.
[b] Brood reduction affected 50% of Rockhopper A-chicks, 6% of B-chicks, and no Macaroni Penguin chicks.
[c] Mortality in the guard phase excludes mortality through brood reduction.
[d] Two broods of two A-chicks have been treated as cases of single A-chick survival.
[e] Only one Macaroni Penguin A-egg chick hatched. The chick died within 48 h.

Chicks from A- and B-eggs of both species were usually viable and could be successfully reared by their parents, although in natural circumstances no Macaroni Penguins reared an A-egg chick. The great majority of chicks that survived until independent were, however, from B-eggs (Table 2). The mortality rate of Rockhopper Penguin A-chicks hatched and raised singly was 46%, the same as that of B-chicks.

The cause of death was known in few cases. Most chicks simply disappeared, the majority probably killed and removed by Subantarctic Skuas. Chick mortality in the postguard phase was greater in Rockhopper Penguins because, being smaller than Macaroni Penguin chicks, they were preyed upon by skuas until they were older.

Breeding success.—The number of chicks reared to independence per pair was 0.43 in the Macaroni Penguin and 0.35 in the Rockhopper Penguin (Table 2). Differential mortality was such that only 3% of all Rockhopper Penguin A-eggs, and none of the Macaroni Penguin A-eggs, gave rise to successfully reared chicks.

DISCUSSION

The results confirm that in the Macaroni and Rockhopper penguins offspring reduction occurs primarily through differential mortality of the eggs and that only one chick may be reared from each clutch.

Differential egg mortality is an expression of parental investment (sensu Trivers 1972). The B-eggs of both species contain more provisions than A-eggs and give rise to larger hatchlings, which complete growth earlier and are heavier at independence than those from A-eggs (Williams MS). The B-eggs, therefore, form a bigger and better investment than the A-eggs. In both species the B-egg is treated preferentially, and the A-egg is often disregarded (Warham 1963, Downes 1955, Burger and Williams 1979). Tinbergen (1951) has demonstrated a similar preference for relatively large eggs in other bird species.

The two prime causes of differential egg mortality are displacement from the nest and theft by a predator. Displaced eggs are normally ignored if the B-egg remains in the nest (Downes 1955). Egg mortality is greatest during incubation when the

positioning of the egg with respect to the broodpatch appears to be critical. Penguins possess a single elongated broodpatch against which the eggs are positioned one in front of the other. The posterior position, in which the egg is tucked between the adult's feet, is the safest. The egg in the anterior position is more often exposed and more accessible to predators and is also more readily dislodged from the nest than is the posterior egg. The B-egg occupies the safest posterior position significantly more often than the A-egg in the Rockhopper Penguin (Burger and Williams 1979) and probably also in the Macaroni Penguin.

Differential egg mortality is more pronounced in the Macaroni Penguin than in the Rockhopper Penguin. The difference in egg mortality may be attributed partially to the greater safety of eggs in Rockhopper Penguin nests. Macaroni Penguins normally incubate in a more erect posture, which provides less security for the eggs, than the posture used most frequently by Rockhopper Penguins. Rockhopper Penguins prefer to nest against natural features such as rocks or grass tussocks. At such sites materials are usually available for nest building, and disturbance, which can lead to egg loss through displacement, is limited. Macaroni Penguins breed at high density on open areas where disturbance is more frequent and may come from any direction and where fewer materials are available for nest building. The difference in egg security resulting from these dissimilarities may be compounded by the effect of egg dimorphism. Preferential treatment of the B-egg and disregard for the A-egg should be more developed in the Macaroni Penguin, in which egg dimorphism is more marked (Gwynn 1953, Williams MS), than in the Rockhopper Penguin. The great loss of A-eggs by Macaroni Penguins during the laying phase may also be due to the eggs being dislodged from the nest during nest scraping, which precedes the laying of the B-egg and which is more pronounced in this species than in the Rockhopper Penguin (Williams 1977).

Eudyptes penguins are not the only birds that, though laying a two-egg clutch, invariably raise only a single chick. A similar situation occurs in some species of boobies (Nelson 1978), cranes (Miller 1973), and raptors (Newton 1978). Many other bird species, including most other penguins, lay two-egg clutches but may raise one or two chicks from each clutch. Except for Macaroni and Rockhopper penguins (and probably all other *Eudyptes* penguins), birds with two-egg clutches normally retain both eggs in the nest until one or both hatch. Offspring reduction then occurs through desertion of one egg or, if both eggs hatch, through the death of the weaker chick by starvation or sibling aggression. Thus offspring reduction takes place only after the "surplus" egg has already functioned as an insurance against both the loss and the failure to hatch of the "preferred" egg. An insurance function for *Eudyptes* A-eggs has been claimed by Lack (1968) and Howe (1976), and this is the case for a minority of Rockhopper Penguins, for at 35% of the nests the A-egg is retained until the end of the incubation phase (Table 1). Egg mortality in Macaroni and Rockhopper penguins is greatest during the first half of the incubation phase (Gwynn 1955, Warham 1963, pers. obs.), and the A-egg may still function as an insurance against B-egg loss if it is retained through this stage. This seems to be the case in about 60% of Rockhopper Penguin nests but at very few Macaroni Penguin nests (Downes et al. 1959, pers. obs.). Thus, at our current level of appreciation, the A-egg serves no obvious function in the clutches of the great majority of Macaroni Penguins and in a substantial minority of Rockhopper Penguins.

ACKNOWLEDGMENTS

This study was sponsored financially and logistically by the Antarctic Division of the South African Department of Transport. Additional support was provided by the South African Scientific Committee for Antarctic Research and the University of Cape Town.

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FEEDING ECOLOGY OF THE BARN OWL IN CENTRAL CHILE AND SOUTHERN SPAIN: A COMPARATIVE STUDY

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ABSTRACT.—We examined the food habits of the Barn Owl (*Tyto alba*) in the mediterranean-climate areas of central Chile and southern Spain. In both areas most prey were small mammals (95% and 87% in Chile and Spain, respectively). Spanish Barn Owls frequently fed on reptiles and amphibians (4.5% of the diet), whereas such prey were not consumed by Chilean Barn Owls. The most noticeable difference involved mean body weight of small mammal prey (70.7 g in Chile vs. 21.2 g in Spain), which was associated with the different weight ranges of small mammals present in the two areas (40–320 g in Chile vs. 2.5–390 g in Spain). The narrower diet and specialization on mammals by Chilean Barn Owls was probably accounted for by the greater availability of larger small mammals and also perhaps by their greater overall density. In spite of the different prey weights taken by the owls, their body weights were similar in the two areas. These results are discussed in relation to the species configuration of the owl communities in Chile and Spain. *Received 1 February 1980, accepted 14 April 1980.*

MUCH information has been published on the diet of the Barn Owl (*Tyto alba*) in different parts of the world (Clark et al. 1978). Recently, its food habits have been documented in central Chile and southern Spain (Jaksić and Yáñez 1979, Herrera 1973, respectively). These are areas of very similar climate, physiognomy, and resources, characterized by the presence of a chaparral-like shrub vegetation (di Castri and Mooney 1973). By comparing the diet of the Barn Owl in these two distant but nevertheless similar areas, we expect to gain some insight into the ecological factors that may affect its food habits in different parts of its range.

STUDY AREAS AND METHODS

The diet composition of Barn Owls in central Chile was obtained by pooling data reported by Reise (1970), Schamberger and Fulk (1974), Fulk (1976), and Jaksić and Yáñez (1979) and unpublished material kindly provided by D. Torres. The largest part of southern Spanish data were taken from Herrera (1973); unpublished information from a few supplementary localities was added. All these data were combined to form a single sample for each region. Both study areas fall clearly within the limits of the mediterranean-type climate (di Castri and Mooney 1973), with dry-hot summers and rainy-mild winters.

For central Chile, 3,594 prey items were identified in 2,545 pellets from 18 localities enclosed in a geographical area between latitudes 30°30′–34°36′S and longitudes 70°31′–71°40′W. The vegetation of the entire region, disregarding agricultural lands, is that of typical central Chilean scrubland (chaparral), an assemblage of shrubby species described in Thrower and Bradbury (1977). Habitat types where we sampled pellets were generally moderately to slightly disturbed by human activities. About 15% of the pellets, however, were deposited near areas of intense agricultural practice. Spanish food data, totaling 14,407 prey items in nearly 3,500 pellets, came from 26 localities fairly evenly distributed between latitudes 36°30′–38°30′N and longitudes 4°–7°W. Various habitat types are represented in this area, ranging from arable land in the bottom of large valleys to fairly undisturbed evergreen oak woodlands (*Quercus ilex*) and schlerophyllous shrublands in mountain and hill areas. These latter habitat types were the best represented in terms of number of prey items; hence, the diet composition of Spanish Barn Owls should be representative of individuals occupying habitats subjected to moderate or little human influence.

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TABLE 1. Gross diet composition of the Barn Owl in central Chile and southern Spain. Trophic diversity (H'NGG) and evenness (JNGG) in relation to the number of prey items contributed by each higher taxonomic category are also shown. N = number of prey items.

	Central Chile		Southern Spain	
Prey type	N	%	N	%
Mammals	3,417	95.1	12,492	86.7
Birds	130	3.6	590	4.1
Reptiles	—	—	121	0.8
Amphibians	—	—	539	3.7
Invertebrates	47	1.3	665	4.6
H'NGG	0.22		0.56	
JNGG	0.14		0.35	

In addition to computing the dietary percentage of different prey categories in the two areas, we further characterized Barn Owl food habits by the following parameters: (1) MWSM, mean weight of small mammals in the diet, which is the grand mean obtained by summing the products of the numbers of individual prey times their weight (g) and dividing by the total number of mammalian prey in the sample. Mean weights of adult small mammals in central Chile were reported by Schlatter, Toro, Yáñez, and Jaksić (1980) and Schlatter, Yáñez, Núñez, and Jaksić (1980); mean weights of adult small mammals in southern Spain were obtained from van der Brink (1968) and the mammal collection of Estación Biológica de Doñana, as detailed in Herrera (1973). (2) H'NGG, trophic diversity in relation to the number of individuals contributed by each higher taxonomic unit (mammals, birds, reptiles, amphibians, invertebrates). (3) H'NM, trophic diversity in relation to the small mammal component of the diet (rodents, lagomorphs, insectivores, marsupials, chiropterans). The latter two parameters were computed by means of the Shannon's information function as described in Herrera (1974); corresponding values of evenness ($J = H'/H'\max$) were also obtained.

Weight and wing length data for sympatric owl species in central Chile were taken from the ornithological collections of the Museo Nacional de Historia Natural (Santiago), Instituto Central de Biología de la Universidad de Concepción, Museo de Historia Natural de Valparaíso, and Instituto de Zoología de la Universidad Austral (Valdivia). All data for southern Spain were from skins preserved in the collection of Estación Biológica de Doñana unless otherwise stated.

RESULTS

General composition of the diet.—Small mammals were the main prey of Barn Owls in both central Chile and southern Spain (Table 1), accounting for nearly 95% and 87% of total prey items, respectively. Reptiles and amphibians were absent from the diet of Chilean Barn Owls, whereas these two groups made up 4.5% of all prey items in southern Spain. The importance of bird prey was similar in both regions, while invertebrates were represented more frequently in southern Spain than in central Chile (4.6% vs. 1.3%, respectively).

Among mammals (excluding chiropterans), the importance of rodents in the diet of Barn Owls was greater in Chile than in southern Spain (95.5% vs. 77.5%), where insectivores contributed an important fraction of the prey (22.5%; see Table 2). This latter group is not present in Chile. The only prey species found in both regions are the cosmopolitan house mouse (*Mus musculus*), Norway rat (*Rattus norvegicus*), black rat (*R. rattus*), and European rabbit (*Oryctolagus cuniculus*), this latter only recently introduced to central Chile (Jaksić et al. 1979). Norway rats and European rabbits were rarely consumed by the Barn Owl in either Chile or Spain; this is probably related to the large size of both species (see Table 2), as the specimens found in pellets were juveniles. Black rats appear more frequently in the diet of Chilean than in that of Spanish Barn Owls (6.8% vs. 0.6%), and the reverse is true for the house mouse (7.3% vs. 47.4% of total prey in Chile and Spain, respectively).

TABLE 2. Composition of the small mammal component of the diet of the Barn Owl in central Chile and southern Spain. Trophic diversity (H'NM) and evenness (JNM) in relation to the small prey are also shown. *N* = number of prey items. MWSM = mean weight of small mammal prey ± standard deviation; this figure is calculated on the basis of all small mammals with known weight; rabbits are computed as juveniles.

Prey species	Central Chile			Southern Spain		
	N	%	Weight (g)	*N*	%	Weight (g)
RODENTIA	*3,237*	*95.5*	—	*9,572*	*77.5*	—
Abrocoma bennetti	134	4.0	219	—	—	—
Akodon longipilis	208	6.1	76	—	—	—
Akodon olivaceus	390	11.5	40	—	—	—
Apodemus sylvaticus	—	—	—	1,702	13.8	27.3
Arvicola sapidus	—	—	—	18	0.1	216.0
Eliomys quercinus	—	—	—	39	0.3	82.5
Mus musculus	248	7.3	17	5,857	47.4	20.0
Octodon degus	101	3.0	230	—	—	—
Oryzomys longicaudatus	939	27.7	45	—	—	—
Phyllotis darwini	958	28.3	66	—	—	—
Pitymys duodecimcostatus	—	—	—	1,861	15.1	27.5
Rattus norvegicus	1	<0.1	320	27	0.2	390.0
Rattus rattus	232	6.8	158	68	0.6	180.0
Spalacopus cyanus	26	0.8	112	—	—	—
LAGOMORPHA	*1*	*<0.1*	—	*5*	*<0.1*	—
Oryctolagus cuniculus[a]	1	<0.1	1,300	5	<0.1	1,100.0
MARSUPIALIA	*153*	*4.5*	—	—	—	—
Marmosa elegans	153	4.5	40	—	—	—
INSECTIVORA	—	—	—	*2,774*	*22.5*	—
Crocidura russula	—	—	—	2,371	19.2	6.6
Suncus etruscus	—	—	—	403	3.3	2.5
CHIROPTERA	*26*	—	—	*141*	—	—
Unidentified	26	—	—	141	—	—
H'NM		1.93			1.41	
JNM		0.78			0.61	
MWSM (g)		70.7 ± 52.3			21.2 ± 24.0	

[a] Juveniles (180 g in central Chile; 150 g in southern Spain).

Size of small mammal prey.—The mean body weight of small mammal prey (MWSM) differed greatly between the two regions (Table 2), the figure being more than three times greater in Chile ($P < 0.001$, weighted-variance t-test; see Sokal and Rohlf 1969). Because the largest prey taken in Chile and Spain were of equivalent size, the much smaller MWSM in Spain was, then, a consequence of the greater comsumption of low-weight insectivores and rodents there. The small house mouse (20 g, nearly 50% of total prey), particularly, affects substantially the MWSM value computed for Spanish Barn Owls. In central Chile, the smallest prey available was the house mouse (17 g), but it accounted for only 7.3% of the total diet. The most important prey types there were the leaf-eared mouse (*Phyllotis darwini*) and the rice rat (*Oryzomys longicaudatus*), with body weights of 66 g and 45 g, respectively. Together, they accounted for 56% of total prey.

For both central Chile and southern Spain, the small mammal species preyed upon by the Barn Owls corresponded to the spectrum of available prey in the two regions, disregarding some local, endemic taxa (Herrera 1973, 1974; Jaksić and Yáñez 1979). The large number of prey items and localities considered, together with information derived from extensive small mammal trapping in the two areas, support this contention. Hence, it is possible to analyze some characteristics of the

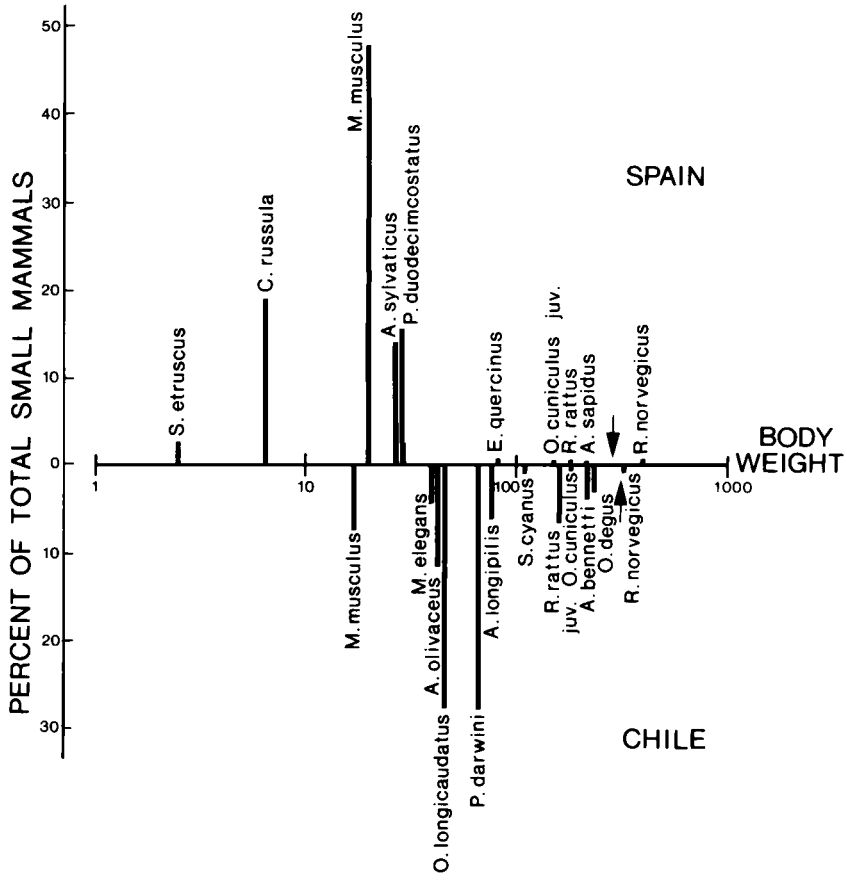

Fig. 1. Relative frequencies (%) of small mammal prey in the diet of Barn Owls in central Chile and southern Spain (excluding bats), ordered along a logarithmic axis of body weights. Arrows denote mean body weight of Barn Owls in the two areas (Table 3); generic names of small mammal species are shown in Table 2.

prey in central Chile and southern Spain on the basis of the sampling made by the Barn Owls. Ordering small mammal species along a gradient of body weight in both areas (Fig. 1), it is apparent that the Barn Owl faces very different situations in the two regions with regard to frequency distributions of available small mammal prey. In southern Spain there are two distinct groups of small mammals (2.5–27.5 g, and 82.5–390 g), with no species in the 30–80-g range. The "light" species group is totally lacking among Chilean small mammals (the cosmopolitan house mouse being the exception), whereas the "heavy" group is nearly as equally well represented as in Spain, largely by the same species. Most important, a group of four "medium" species (40–80 g) exists in central Chile, precisely in the gap of the Spanish weight distribution. It is clear, then, that the striking difference in the mean body weight of prey between the two regions can be attributed to the differential availability of prey-weights in both areas.

Trophic diversity.—The previous results show that Chilean Barn Owls have a narrower diet containing more mammalian prey than do their Spanish counterparts.

TABLE 3. Owl assemblages in central Chile and southern Spain. Owls from the two areas were primarily matched by taxonomic relatedness, secondarily by size similarity. Only resident species in typically mediterranean habitats were considered. Sample sizes for means are shown in parentheses; both sexes were combined. Difference in wing length between populations of the Barn owl in central Chile and southern Spain is statistically significant ($t = 6.29$, $P < 0.001$), but difference in body weight is not ($t = 1.58$, $P > 0.12$).

Central Chile			Southern Spain		
Owl species	Mean body weight (g)	Mean wing length (mm)	Owl Species	Mean body weight (g)	Mean wing length (mm)
Bubo virginianus	1,500 (2)	351 (17)	*Bubo bubo*	1,886 (8)	469 (14)
Asio flammeus	350 (2)	325 (19)	*Strix aluco*	426 (10)	263 (17)
Tyto alba	307 (8)	302 (16)	*Tyto alba*	281 (20)	283 (34)
Athene cunicularia	247 (3)	193 (25)	*Athene noctua*	148 (30)	157 (41)
Glaucidium brasilianum	74 (4)	108 (12)	*Otus scops*	69 (2)[a]	152 (2)[a]

[a] After Dementiev and Gladkov (1966); average of female and male means.

This is also apparent from a comparison of H'NGG values, which are more than two times higher in southern Spain; the same holds true for evenness values (Table 1). Consequently, the relative contribution of the various higher taxonomic categories to the Barn Owls' diet is more unequal in Chile than in Spain. The diversity and evenness of the small mammal component of the diet (H'NM) do not show as great a contrasting difference as in the previous case, although they are noticeably higher in central Chile. This means that the diet of Barn Owls in this latter area was based upon a more diverse array of small mammal species, which in addition were more equally represented (Table 2).

DISCUSSION

Our results reveal that the diets of the Barn Owl in central Chile and southern Spain differ in several important respects. Chilean Barn Owls concentrate more on small mammals, which tend to be larger than those preyed upon by Spanish Barn Owls. The latter more frequently include nonmammalian prey in their diet, and the diversity of small mammals consumed is less than in central Chile.

The trophic diversity for Chilean Barn Owls is intermediate between the very high H'NGG values shown by southwestern Spanish populations and the extremely low figures exhibited by populations in nonmediterranean, western European localities (Herrera 1974). In these latter areas the Barn Owls fed almost exclusively on an abundant supply of voles (*Microtus* spp.; see Uttendörfer 1939). Although of the same order of magnitude, the diversity of small mammals (H'NM) in the diet of Barn Owls in Chile was slightly lower than in temperate, western Europe, but was noticeably higher than in mediterranean Spain (Herrera 1974). The concurrent, opposite variation of H'NGG and H'NM values observed in western Europe has been interpreted as a response of the Barn Owl to changes in the abundance and density of small mammals, which become much lower in the mediterranean areas of southwestern Europe (Herrera 1974, Herrera and Hiraldo 1976). The same argument may also explain some Chile-Spain differences. Species diversity of small mammals appears to be similar in central Chile and southern Spain, but density is probably higher in central Chile. Schamberger and Fulk (1974) obtained figures of 0.06, 0.13, and 0.34 individuals/trap-night in three habitat types in central Chile,

and year-round trapping by Jaksić and Yáñez (1978) in the same general area gave a monthly average of 0.03 individuals/trap-night (range between 0.02 and 0.07). In southern Spain trapping success usually ranges between 0.00 and 0.04 individuals/trap-night, as revealed by several years of small mammal trapping in many habitat types and nearly 20 localities (R. C. Soriguer, unpubl.). These differences in small mammal densities, if substantiated by more detailed studies in the future, may partly explain the dissimilarities in trophic diversity between Chilean and Spanish Barn Owls. If Barn Owls forage in an optimal manner, greater small mammal density would theoretically favor a concentration of predation on this group, while discouraging predation upon other energetically less profitable types like reptiles, amphibians, and invertebrates (Schoener 1971, Pyke et al. 1977, Krebs 1978).

There are, however, two factors that complicate an acceptance of this explanation. These are the interregional differences in the size distribution of small mammal species and the configuration of the community of coexisting owl species. These two factors, together with the differences in small mammal density discussed above, most likely operate simultaneously to generate interregional dietary differences, but presently it is not possible to assess the relative importance of either of them.

As shown above, in southern Spain there are two distinct groups of small mammal species. The "heavy" group is shared with central Chile, and in both areas it represents a negligible fraction of total prey items (made up mostly of juvenile individuals). Species in this group are close to, or greater than, the body weight of the Barn Owl (Table 3 and Fig. 1) and presumably exceed its upper limit of handling capacity. If one disregards this set of heavy species, the Barn Owl is left with a group of "light" prey species in Spain and a group of "medium" species in Chile. Accordingly, the Chilean Barn Owls feed on mammalian prey of presumably higher energetic reward than their Spanish counterparts, provided that the body size of the owls is similar in both areas (Table 3) and assuming that pursuit and handling time of heavier Chilean small mammals is not disproportionately higher. Under these circumstances, in terms of optimal foraging theory (Pyke et al. 1977, Krebs 1978), it is not necessary to propose greater overall density of small mammals in central Chile to account for the narrower diet of Barn Owls there. An "average" Chilean small mammal is energetically more profitable than a Spanish one, relative to other alternative prey of smaller size (bird, reptile, amphibian, invertebrate). Therefore, the optimal diet of Chilean Barn Owls should contain fewer nonmammalian prey than the diet of Spanish Barn Owls, as it in fact does (Table 1).

There is a well-known relationship between predator and prey sizes (Hespenheide 1973, Wilson 1975) that also appears to hold in intraspecific comparisons (Schoener 1967, Roughgarden 1974). It is therefore surprising that a three-fold difference in MWSM between Chilean and Spanish Barn Owls is not related to any significant difference in mean body weight of both owl populations (Table 3). This may be related to the similar configuration of the set of sympatric owl species in the two regions. Both assemblages are equivalent in species number and show a similar patterning in the relative distribution of body sizes (weight and wing length). The Barn Owl is the only species occurring in both areas, although two other congeneric species pairs exist. For the Spanish assemblage, detailed food data for all species reveal a clearcut interspecific segregation in type and size of prey associated with a close relationship between owl and prey sizes (Herrera and Hiraldo 1976). Marti (1969, 1974) described a similar pattern for the owl species in a grassland habitat.

No equivalent information is available for the Chilean assemblage as a whole, but the analysis of the subset formed by the three most common species (Barn Owl; Burrowing Owl, *Athene cunicularia*; Great Horned Owl, *Bubo virginianus*; see Jaksić et al. 1977) suggests a similar situation. These species exhibit clear differences in mean prey size, corresponding closely to differences in owl size. Herrera and Hiraldo (1976) proposed that the owl assemblages in mediterranean habitats exhibit a well-defined resource partitioning, based on prey type and size. If this pattern has evolved in response to interspecific competition, there should be strong selection against deviations in body size from the "species' norm" due to the competitive pressures of adjacent owl species. This should be especially important for a species like the Barn Owl, which is situated in the middle of the size range (Table 3) and is presumably subjected to strong diffuse competition from neighbors.

Because responses of individual owl species to changes in environmental conditions depend upon community relationships, further studies on Chilean owl species are needed for interregional comparisons of community patterns. Such comparisons also require more detailed knowledge of prey populations and of factors responsible for the marked difference in the prey-weight distribution between central Chile and southern Spain.

ACKNOWLEDGMENTS

We are grateful to the Curators of the following mammalogical and ornithological collections: José Yáñez (Museo Nacional de Historia Natural, Santiago), Roberto Schlatter (Instituto de Zoología, Universidad Austral, Valdivia), Ana Avalos (Museo de Historia Natural de Valparaíso, Valparaíso), and Tomás Cekalović (Instituto Central de Biología, Universidad de Concepción, Concepción). Dr. Miguel Delibes and Pedro Jordano made valuable comments on an earlier version of this paper; Dr. Ramón Soriguer provided unpublished information on small mammal density in southern Spain.

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POSTNATAL DEVELOPMENT OF LEACH'S STORM-PETREL[1]

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ABSTRACT.—Thirty-one nestling and 2 adult Leach's Storm-Petrels were collected on Kent Island, New Bruswick. The ages of the nestlings were estimated by comparing weights and wing lengths to those of chicks of known age obtained by other investigators on Kent Island. The specimens were dissected into 10 components for each of which we determined the water, lipid, ash, and nonlipid ash-free dry contents. The body proportions of the petrel neonate are similar to those of the neonates of starlings, terns, and quail. Water levels in the tissues are consistent with precocial development. The size of the neonate relative to that of the adult is large (16%) compared to other species, and the postnatal growth increments of body components (ratio of adult to neonate) are correspondingly small, ranging from ratios of between 3 and 4 for the viscera, head, and legs, to 8 for the integument, 14 for the wings, and 59 for the pectoral muscles.

The pectoral muscles increase to 5% of body weight within 10 days, after which they apparently play a major role in heat production. Correlated with their early maturation, as indicated by decrease in water content, the pectoral muscles grow slowly throughout the latter part of the postnatal development period. Their growth rate at that time may constrain the overall rate of growth of the chick.

Our results suggest, first, that with respect to many aspects of development petrels resemble semi-precocial species more closely than semi-altricial species (as defined by Nice). Second, the slow growth of petrels is consistent with their precocious mode of development; explanations based upon reduced energy requirements of slowly growing chicks (cf. Lack) are not required. *Received 4 September 1979, accepted 31 March 1980.*

THE Procellariiformes are a varied group of pelagic seabirds that breed on remote islands or in other inaccessable places. Most of the small species dig burrows for nesting, all lay a single large egg, and many species have prolonged periods of incubation and development. In addition, nestlings of most procellariiform birds accumulate large amounts of fat, which diminish before fledging. Lack (1968) described the unique features of clutch size and development in the Procellariiformes as adaptations to the food supply. Adult albatrosses, shearwaters, and storm-petrels forage at great distance from the breeding colony and return infrequently to feed the young. Food supplies are thought to be variable and their availability greatly affected by weather. The one-egg clutch of all Procellariiformes, indeed of most pelagic seabirds, suggests adaptation to minimize the food required by the brood. Lack suggested that slower growth may further reduce food requirement and allow procellariiform birds to exploit more distant or sparse food resources. Fat stores presumably enable chicks to survive occasional long intervals between visits from their parents.

In comparisons among birds of diverse orders, variation in growth rate has been related to adult body size and to the precocity of the chick at hatching: chicks of larger species tend to grow more slowly than those of smaller species (Lack 1968, Ricklefs 1968); chicks that are self-sufficient (precocial) at hatching grow much more

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TABLE 1. Relative size and water indices of organs in one neonate and two adult Leach's Storm-Petrels, and growth increment and allometric constants of these components.

Component	Percentage nonlipid weight				Water index		Growth increment		Allometric constant (b)[c]
	Wet		Dry						
	Neonate	Adult	Neonate	Adult	Neonate	Adult	Ratio[a]	Log_e[b]	
Integument	15.4	23.0	23.5	38.1	2.4	0.5	8.1	2.1	1.28
Body	35.7	26.1	34.8	19.9	4.3	2.3	4.0	1.4	0.84
Stomach	4.3	2.9	2.9	1.5	6.7	3.7	3.6	1.3	0.85
Intestine	6.1	3.2	4.2	1.8	6.5	3.5	2.8	1.0	—[d]
Heart	1.5	1.7	0.9	1.0	—[e]	3.1	6.2	1.8	0.86
Liver	5.4	4.4	4.8	3.3	4.8	2.4	4.5	1.5	1.00
Head	16.0	11.3	12.6	7.9	5.5	2.6	3.8	1.3	0.70
Legs	11.7	7.5	13.3	7.3	3.5	1.6	3.5	1.2	0.73
Pectoral muscles	1.2	13.4	0.6	9.4	—[e]	2.6	59.0	4.1	1.96
Wings	2.6	6.6	2.3	9.7	4.9	0.7	13.7	2.6	1.52
Total	—	—	—	—	4.1	1.5	5.4	1.7	

[a] Ratio of the mass of the adult component (n = 2) to that of the neonate (n = 1), based on nonlipid wet masses.
[b] Natural logarithm of the growth increment.
[c] b is the exponent in the equation $Y = aX^b$ relating component mass Y to total mass X, based on nonlipid wet masses; based on 31 chicks and 2 adults.
[d] Component extremely variable.
[e] Components were too small to estimate water content accurately.

slowly than chicks that are dependent (altricial) (Ricklefs 1973; 1979a, b). As in precocial and semi-precocial species, procellariiform neonates have a thick down and are thermally independent at an early age. But because their eyes are closed and they do not leave the nest, Nice (1962) tentatively classified them as semi-altricial. She noted, however, that the relative sizes of their egg yolks were more consistent with those of semi-precocial species. If procellariiformes were semi-altricial, their potential growth rates presumably would be comparable to those of species in groups having altricial or semi-altricial development (songbirds, raptors, doves, herons, cormorants, etc.), and their realized (= slow) growth rates could be limited by rate of feeding. If the growth rate of procellariiform chicks were limited by availability of energy or nutrients, it should be possible to demonstrate that their food requirements are reduced relative to the requirements of more rapidly growing altricial and semi-altricial species. With this goal in mind, we initiated a study of development in Leach's Storm-Petrel (*Oceanodroma leucorhoa*) in New Brunswick, Canada. This paper describes postnatal growth. Elsewhere (Ricklefs et al. 1980) we consider energetics, and subsequent papers will cover feeding, fasting, and embryonic development.

Leach's Storm-Petrel (family Hydrobatidae) has an extensive breeding distribution in the North Atlantic and North Pacific oceans (Palmer 1962). The North Atlantic subspecies is *O. l. leucorhoa*. Its breeding in eastern North America has been described by Bent (1922), Gross (1935), Palmer (1962), and Wilbur (1969). Other studies have been published by Ainslie and Atkinson (1937) and Ainley et al. (1975). The most complete general account is that of Palmer (1962), who summarized many of the unpublished findings of C. E. Huntington on Kent Island, New Brunswick.

METHODS

The study described in this paper was conducted at the Bowdoin Scientific Station on Kent Island, New Brunswick between 24 and 38 July and between 1 and 8 September 1972. We collected 31 chicks

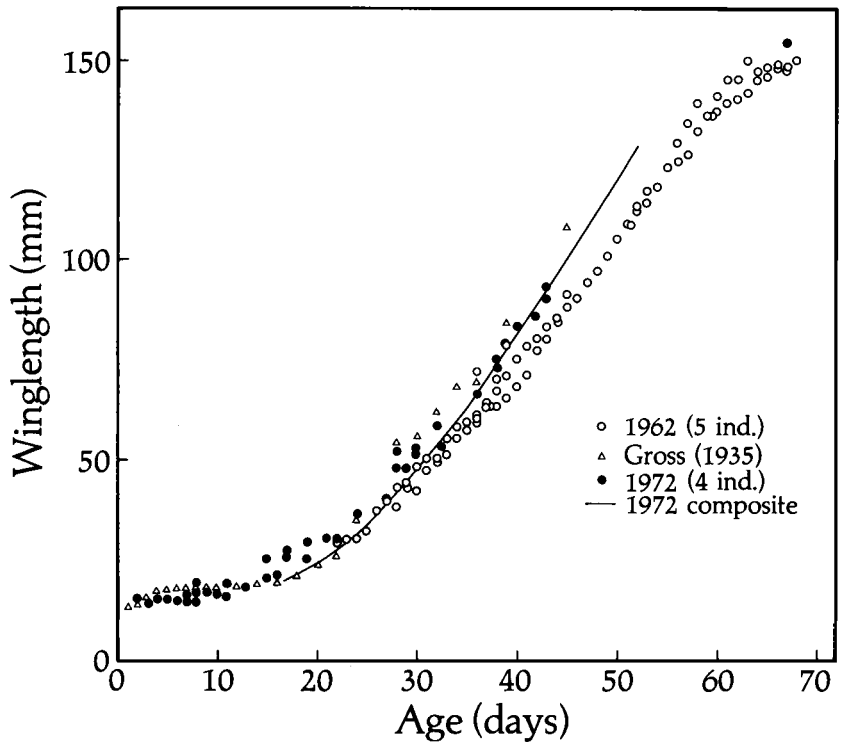

Fig. 1. Relationship between wing length and age based on Gross (1935) and unpublished data of C. E. Huntington (1962) and J. McEnroe (1972). The solid line was estimated from growth increments of 13 chicks over 5-day intervals (see text). Day of hatching = 1.

and 2 adults. The specimens were frozen and processed later according to the methods of Ricklefs (1975). Briefly, thawed specimens were measured and then dissected into 10 components: integument (skin and feathers, including subcutaneous fat), stomach (contents removed), intestines (contents not removed), heart, liver, head, legs, wings, pectoral muscles, and body (carcass). Each component was dried to constant mass at 40–45°C under vacuum, extracted in a 5:1 mixture of petroleum ether and chloroform, which removes both triglycerides (storage lipids) and phospholipids (structural lipids), and ashed in a muffle furnace at 550°C. The primary data for each component were the masses of the wet, dry, nonlipid (= lean) dry, and ash components. From these we calculated the following: water = wet − dry; lipid = dry − nonlipid dry; nonlipid wet = wet − lipid; water index = water/nonlipid dry. The amount of mineralized bone was estimated by the expression bone = ash − (water × 0.02), in which the subtracted quantity represents approximately the level of dissolved ions (g ash/g water) in tissues lacking bone (Ricklefs unpubl.).

We estimated allometric constants (b) relating component mass (Y) to total mass (X) by least squares fitting of a and b in the equation, $\log Y = \log a + b \log X$. We used the graphical method of Ricklefs (1967a) to fit Gompertz equations, having the form

$$M(t) = A \exp(-\exp[-K(t - t_i)]),$$

to curves relating mass [$M(t)$] to age t. The constant t_i is the age at the point of inflection (maximum growth rate), K is the growth rate constant, and A is the asymptote or mass plateau. We determined that the Gompertz equation gave a better fit to the data than either the logistic or von Bertalanffy equations (see Ricklefs 1967a).

Ages of chicks were assigned by criteria derived from unpublished measurements of mass and wing length obtained by C. E. Huntington and J. McEnroe on Kent Island. Details are given in the results section.

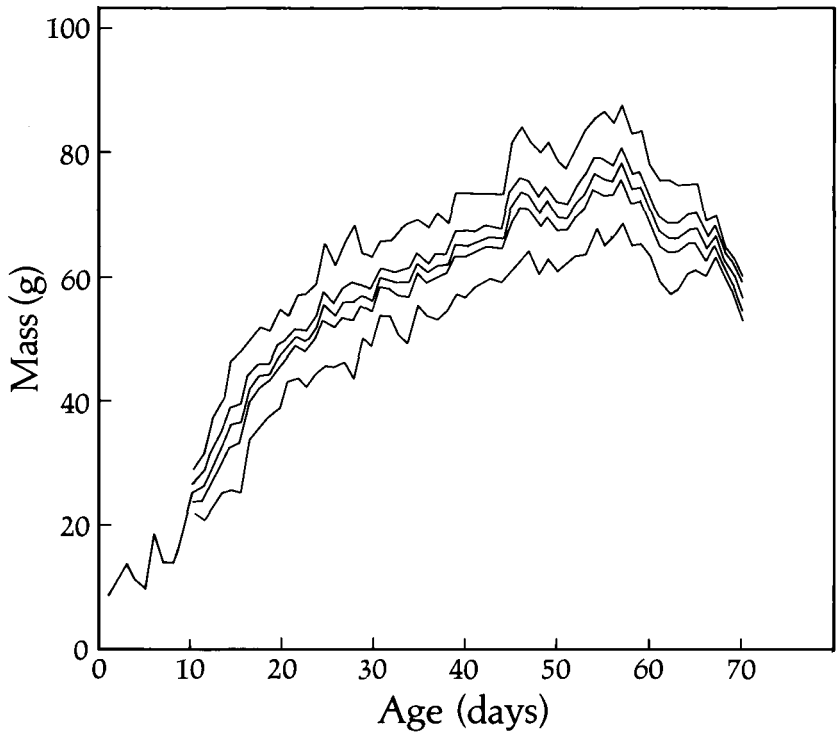

Fig. 2. Relationship between mass and age based on 19 chicks weighed by C. E. Huntington on Kent Island in 1962. The lines bounding the mean are ±1 standard error and ±1 standard deviation. Sample sizes varied between 1 and 2 for days 1–9, 6 and 11 for days 10–14, 12 and 19 for days 15–62, and less than 10 for days 63–69.

Results

General biology.—Adult petrels have a mass of about 45 g (Palmer 1962). The average mass of 45 partially incubated eggs on Kent Island, New Brunswick was 8.8 g (Gross 1935). Thirty-three relatively fresh eggs (spec. grav. $\geq$ 1.0), weighed on Baccalieu Island, Newfoundland on 10 and 12 June 1978, had an average mass of 10.7 g (SD = 1.0 g and SE = 0.2 g) (W. A. Montevecchi pers. comm.). The egg hatches after between 38 and 46 days ($\bar{x}$ = 42.4, SD = 2.2, n = 14; C. E. Huntington pers. comm.), and the chick leaves the nest 63–70 days after hatching (C. E. Huntington in Palmer 1962).

The eyes of the neonates are closed. At hatching, the chicks are covered with a thick down (protoptile plumage). A second (mesoptile) down begins to grow during the second week, and adult-type (teleoptile) feathers appear during the fourth week in most feather tracts (Palmer 1962). The young are brooded less than 5 days. The eyes usually open before the end of the second week after hatching.

Adult-neonate comparison.—We collected only one neonate. This bird is compared to two adults in Table 1. Although it is precarious to base comparisons on so few individuals, the amount of variation among both neonates and adults of other species (e.g. Ricklefs 1979a) is small, and confidence limits on estimates of parameters typically are narrow, particularly compared to differences among species. From

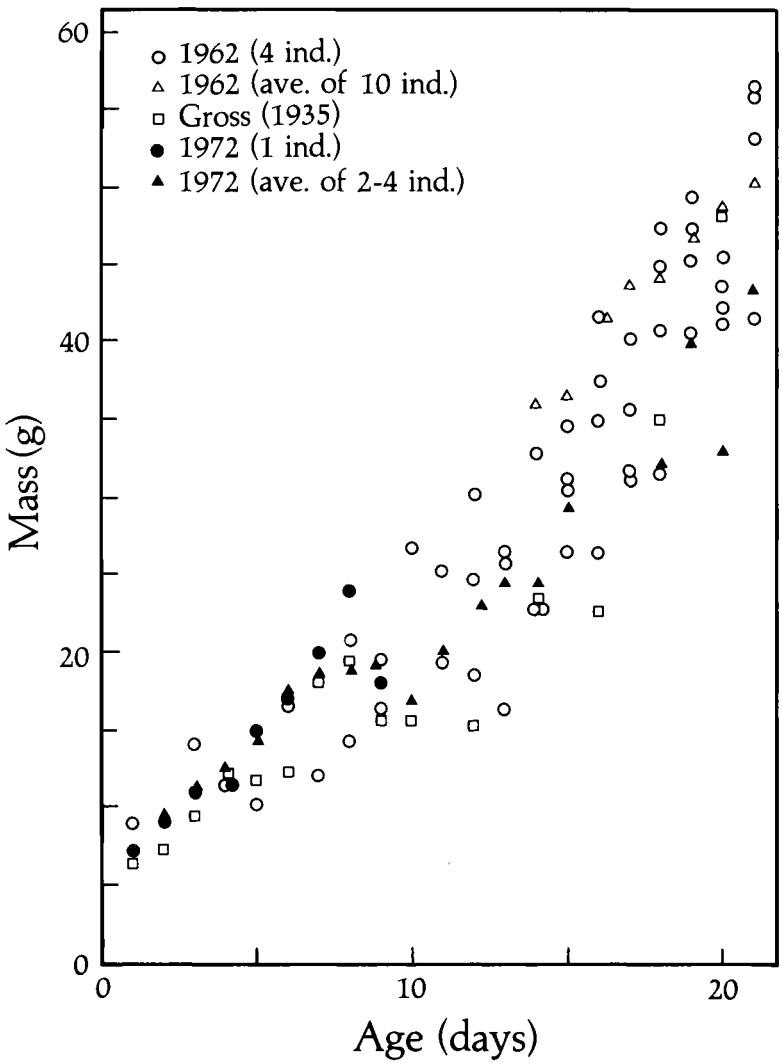

Fig. 3. Relationship between mass and age during the first 3 weeks after hatching, based on Gross (1935) and unpublished data of C. E. Huntington and J. McEnroe.

nest checks, we determined that the neonate was less than 24 h old. It had a small amount of yolk in its gut and its mass (7.05 g) was consistent with the hatching mass expected according to the average size of eggs in the population. Six neonates weighed by J. McEnroe in 1972 had an average mass of 7.3 g. The sex and breeding status of the two adults were not determined. Their masses were 37 and 44 g.

The growth increment (ratio of the mass of a component of the adult to that of the neonate), natural logarithm of the growth increment, and the allometric growth constant (b) of each organ or component are also presented in Table 1. These values parallel the change in proportions of each component between hatching and adulthood. In general, if the growth increment of a component exceeds that for the individual as a whole (ratio = 5.4), its relative proportion increases during devel-

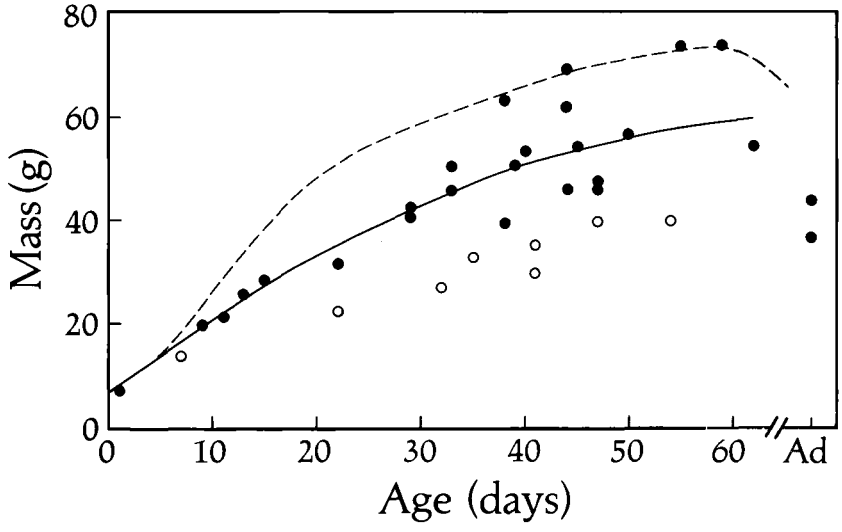

Fig. 4. Relationship between mass and estimated age for the specimens collected in this study. These are compared with the general trend of the average values of Huntington's data from 1962 (dashed line). Eight chicks were kept without food for periods up to a week. These birds (open circles) are excluded from some of the analyses in this study and will be discussed in more detail elsewhere. Solid line drawn by eye to suggest the trend.

opment, and its allometric constant is greater than 1. Some minor discrepancies in these values, e.g. for the heart and liver, appear when allometric constants are based on smaller chicks only, owing to variation among larger chicks, or when the growth is not strictly allometric.

Increase in mass and wing length: aging criteria.—Gross (1935) tabulated masses and measurements of an unspecified number of petrel chicks on Kent Island. Mass increased, with considerable variability about the trend, to a maximum of almost 70 g by 5 weeks of age. Ricklefs (1973) fitted Gross's data by a Gompertz equation having asymptote (A) = 75 g and growth rate (K) = 0.074 days^{-1}. Gross's table of measurements indicated that the lengths of appendages increased little during the first 2 weeks, while mass at least tripled to 23 g. During the third week, the wing and feathers began to grow rapidly.

Figure 1 summarizes the increase in wing length (chord of folded wing, Baldwin et al. 1931) with age, including data for the chick or chicks measured by Gross (1935), 5 chicks of known age measured by C. E. Huntington in 1962, and 4 chicks of known age measured by J. McEnroe in 1972. In addition, we have plotted a composite curve based on 13 5-day growth increments obtained during our study (see Ricklefs and White 1975, 1978).

Figure 2 presents unpublished masses obtained by C. E. Huntington from 19 chicks in 1962. Masses of chicks studied by McEnroe in 1972 were consistently below the 1962 average after the third week of age. Figure 3 summarizes all the available masses for chicks during the first 3 weeks after hatching. Although masses vary greatly according to the history of feeding of each chick and the length of time since its last feeding (e.g. Harper 1976), they allow one to estimate the age of the chick during the first 3 weeks as reliably as do lengths of feathers or appendages.

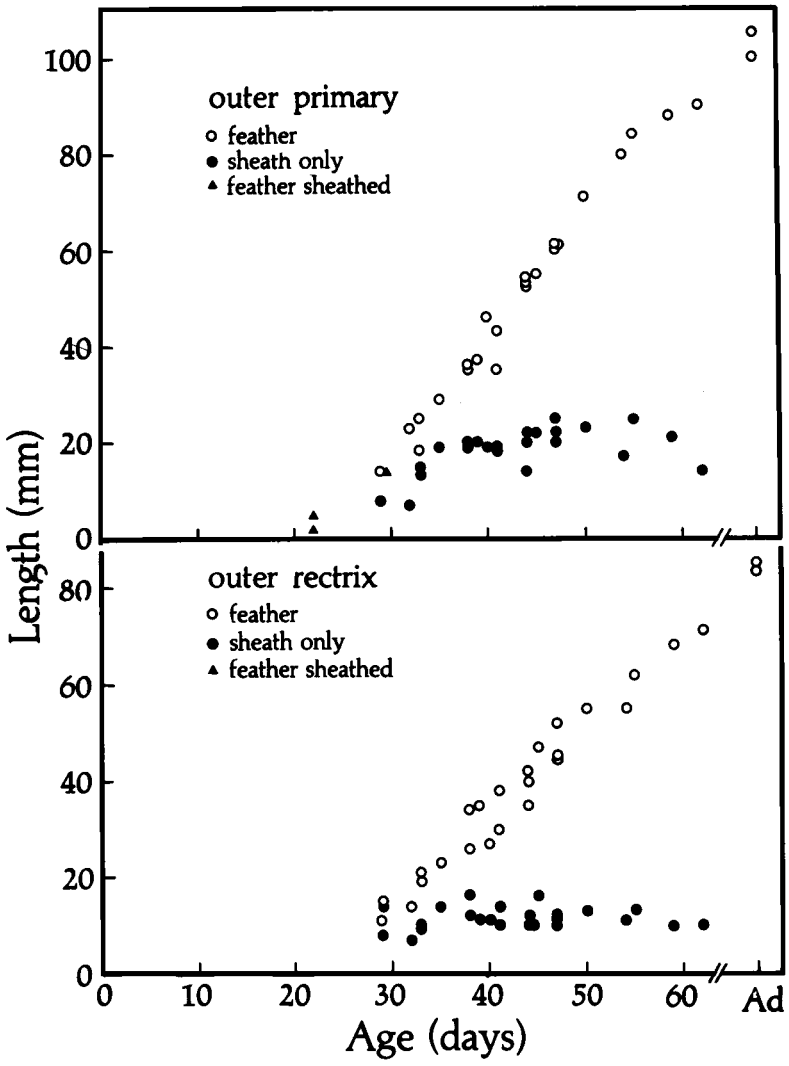

Fig. 5. Relationship between estimated age and the lengths of the outer primary, outer rectrix, and their sheaths.

After the third week, we used only wing length (Fig. 1) to estimate age. We feel that most of our estimates of age are within ±3 days of the true chronological age and that the estimates are unbiased.

In Fig. 4, masses and estimated ages of specimens collected in this study are compared to the growth curve obtained in 1962 (Fig. 2). Although the 1972 chicks generally had less mass than the average for 1962, all had large quantities of fat (Ricklefs et al. 1980). Furthermore, in order to measure their metabolic rates, most of the chicks were kept in the laboratory for a day or more before they were sacrificed. Masses reported here follow whatever loss occurred during captivity. High fat levels in our specimens and the fact that, in 1972, growth increments in the length of the wing were similar to those reported by Gross and Huntington indicate that

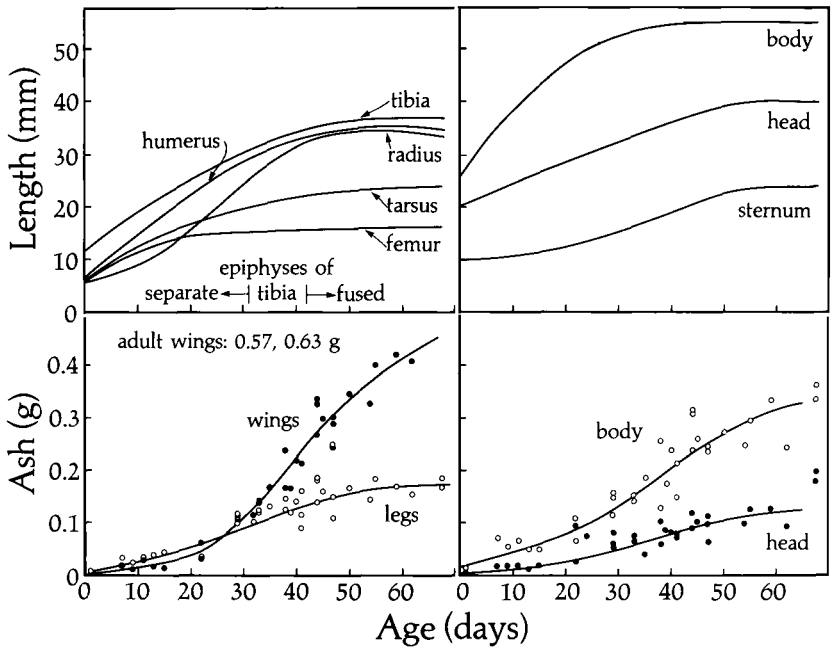

Fig. 6. Relationship between estimated age and the lengths of several bones and ossification of bones. Ash deposited in bone was estimated as total ash − 0.02 × water (see text). Variability of data is similar to that in the lower graphs. Curves were drawn by eye.

development rates of the chicks in our sample were not adversely affected by poor nutrition.

External measurements.—Our data on the lengths of the tarsus, culmen, fifth and outer primaries, and outer rectrix are consistent with Gross's measurements. The tarsus and culmen are approximately one-third and one-half adult length at hatching and complete most of their growth within 4 weeks. The primaries and rectrices begin to grow at about 3 weeks (Fig. 5).

Bone development.—We measured the lengths of bones in the ashed remains of the wings (humerus and radius), legs (femur, tibia, and tarsus), body (sternum and fused vertebral column), and head (tip of beak to posterior edge of skull). Although weakly ossified bones tend to shrink during ashing, the measurements nonetheless present a general picture of skeletal growth (Fig. 6). In the leg, the femur is fully grown by 20 days, whereas the tibia and tarsus continue to grow until between 40 and 50 days, the age at which growth of the humerus and radius ceases. The epiphyses of the tibia were separated in all birds younger than 31 days and fused in all birds older than 42 days. In the legs, mineralization appears to proceed gradually and continuously and is completed before fledging. In the wings, mineralization does not begin until about 3 weeks and achieves only two-thirds adult level by 60 days.

Measurements of the axial skeleton are variable but suggest completion of growth of the fused vertebral column by 20 days and of the head and sternum by 40 days. Mineralization of the body skeleton parallels that of the legs and is nearly completed by fledging. Mineralization of the head follows the same general time course as the

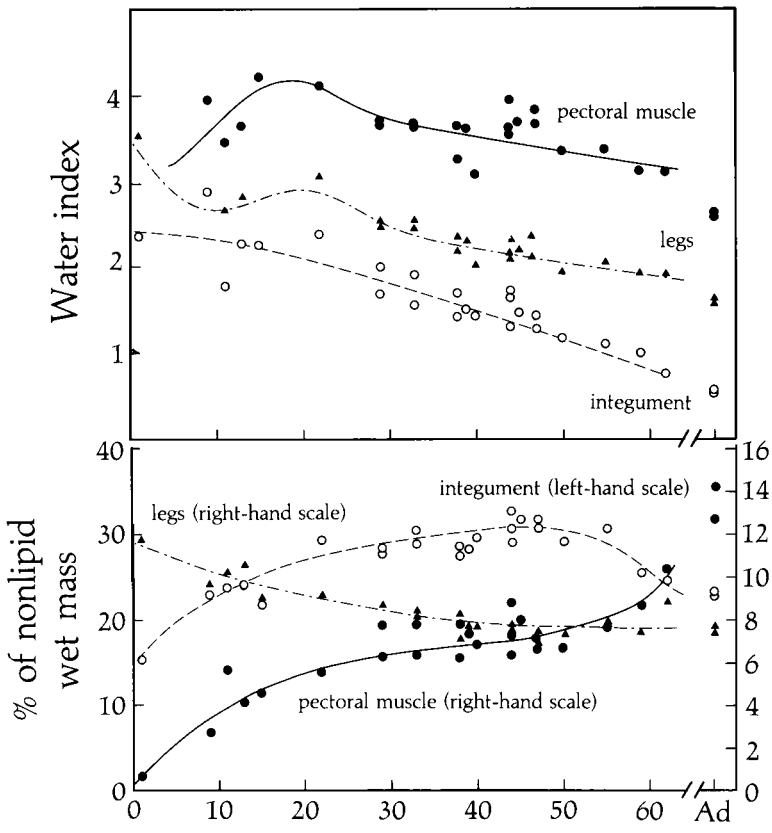

Fig. 7. Relationship between estimated age and the water index and proportion of nonlipid wet mass of the individual in pectoral muscles, legs, and integument. Fasted birds are omitted. Curves drawn by eye.

wings, increasing in rate after the third week and reaching only about two-thirds adult level by fledging.

Organ development.—Changes in water index and relative size of the legs, pectoral muscles, and integument are shown in Fig. 7. The water indices of the leg and integument decrease in a pattern consistent with precocial development. In both components, the water index is relatively low at hatching and decreases to adult levels by 60 days, suggesting more or less complete maturation before fledging (63–70 days).

Growth curves of the integument, pectoral muscles, and leg are shown in Fig. 8. Exponential rates of growth, which are equal to the slope of the relationship of the natural logarithm of mass to age, of all three components are rapid during the first 10 days but slow abruptly thereafter.

Increase in lipid-free body weight.—Increase in the masses of nonlipid wet and nonlipid dry components are shown in Fig. 9. Both curves were fitted by Gompertz equations, which are superimposed on the data. The fitted constants are $A = 40$ g, $t_i = 9$ days, and $K = 0.080$ days^{-1} for nonlipid wet mass and $A = 13.5$ g, $t_i = 14.5$ days, and $K = 0.063$ days^{-1} for nonlipid dry mass. Estimates of K for lipid-

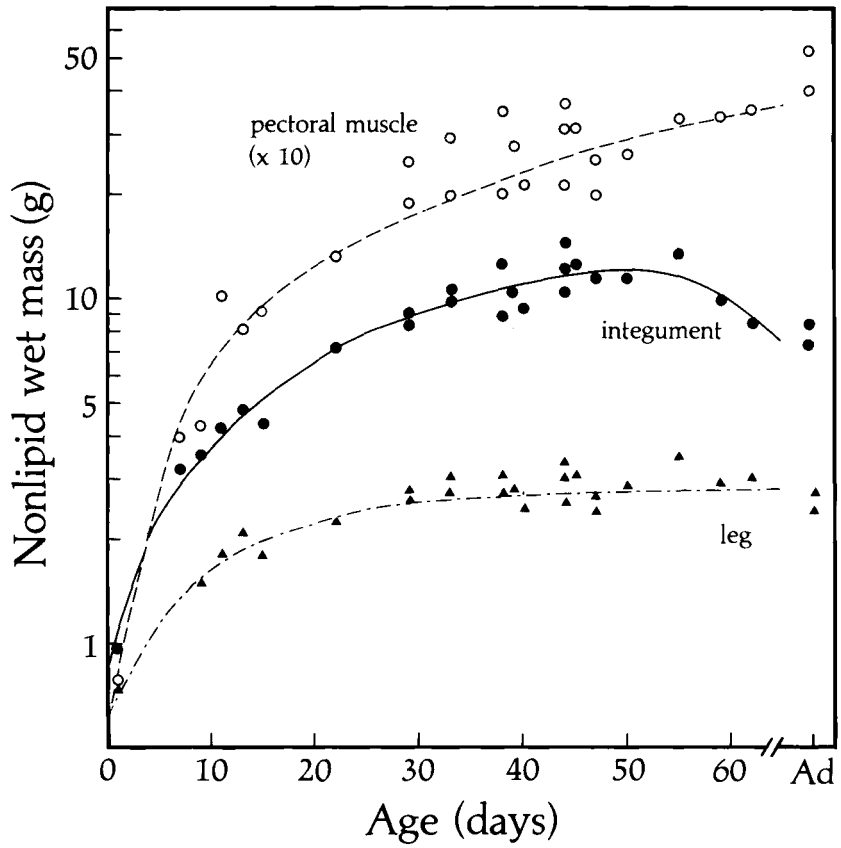

Fig. 8. Relationship between estimated age and the logarithm of nonlipid wet mass of the pectoral muscles, legs, and integument. Fasted birds are omitted. Curves drawn by eye.

free growth curves were similar to the value (K = 0.074) fitted to Gross's weight data, at least compared to variation in values of K among species (Ricklefs 1973).

Discussion

As in most species, changes in body proportion between hatching and adulthood include a decrease in the relative size of the head and increases in the relative sizes of wings and pectoral muscles. Compared to neonates of the European Starling (*Sturnus vulgaris*), Common Tern (*Sterna hirundo*), and Japanese Quail (*Coturnix coturnix*) (Ricklefs 1979a), the petrel neonate differed consistently only in having a slightly smaller head (16% vs. 19–20%). Its integument (15%) was of similar proportion to that of the semi-precocial tern (14%) and precocial quail (14%) and larger than that of the altricial starling (9%); its legs (12%) were of similar proportion to those of the starling (10%) but smaller than those of the tern (16%) and quail (18%). Adult petrels differ from the starling, tern, and quail in having proportionately more integument (23% vs. 12–20%), smaller pectoral muscles (13% vs. 16–20%), and less viscera (stomach, intestine, and liver: 10.5% vs. 13–17%).

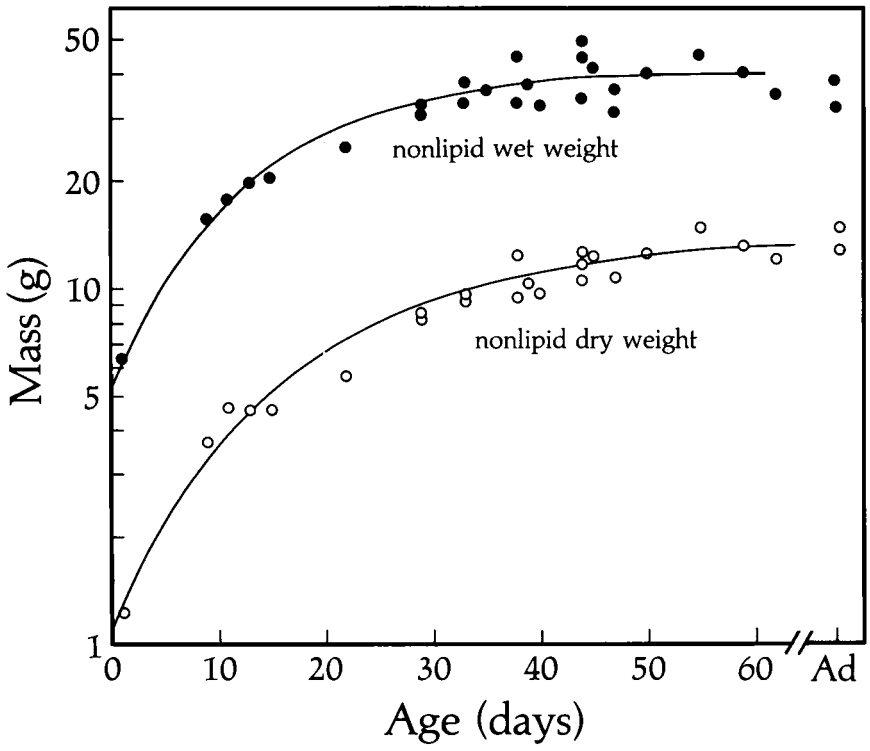

Fig. 9. Relationship between estimated age and the logarithms of total nonlipid wet mass and total nonlipid dry mass. Fasted birds are omitted. The lines are fitted Gompertz equations (see text).

Because the petrel neonate is large relative to the adult [about 16% of adult mass, compared to 7, 13, and 6% for the starling, tern, and quail (Ricklefs 1979a)], the overall postnatal growth increment of the petrel chick is relatively small (5.4 vs. 15, 8, and 20). As in most species, however, the integument, wings, and pectoral muscles (in sum, the flight apparatus) grow more rapidly than the body as a whole, while the head and some visceral organs grow more slowly. The mass of the pectoral muscles increases 59 fold between hatching and adulthood.

The water index of a tissue is inversely related to its functional maturity. Among neonates, this index calculated for the whole chick varies between 6 and 8 for altricial species (Ricklefs 1967b, 1975, 1979a, Brisbin 1969, Dunn 1975, Austin and Ricklefs 1977) and between about 3 and 4 in precocial species (Brisbin and Tally 1973, Clay et al. 1979, Ricklefs 1979a). The water index of the petrel neonate (4.1) places it with precocial species. Among the individual organs, only the water index of the stomach and intestines are within the range for altricial species, but in the adult petrel these organs have high indices as well.

As in most precocial species, the major feathers unsheath soon after they begin to grow, and the sheathed portion of the feather does not lengthen greatly. In the petrel, the feather sheaths are, at most, about 21% of the length of the adult primary and 15% of the length of the rectrix. Comparable values for starling, tern, and quail primaries are 35, 16 and 20%. In the petrel, the growth rates of feathers during the period of rapid linear increase were about 2.5 mm/day for the primary and 1.8 mm/

day for the rectrix. For primaries of the starling, tern, and quail, growth rates were 6.1, 5.1, and 2.5 mm/day. Expressed as a percentage of final length, these five values are 2.4 and 2.1 compared to 7.9, 2.5, and 4.6%/day.

Among species examined to date, the pectoral muscles of the petrel are extraordinary. Their water index during early postnatal development, before they have reached one-tenth of adult size, is approximately 3.5–4.0. At a comparable size, the water indices of pectoral muscles in the Japanese Quail and Common Tern are between 5 and 6 (Ricklefs 1979a). In the tern, the water index of the pectoral muscles does not fall to 4 until the last week before fledging. In the quail, the water index rapidly drops to about 4 during the first 2 weeks, just before the onset of flight (Ricklefs 1979a). If water index is a measure of tissue function, the development of the pectoral muscles in the petrel is similar to that in the quail, even though petrels do not attempt their first flight until 6 weeks later than quail chicks.

The uniqueness of the petrel's pectoral muscles can also be seen in the rate of increase in their relative size. In other species that, like the petrel, do not fly until fully grown, the pectoral muscles are relatively small until the last half of the period between hatching and fledging (Ricklefs 1979a). In the petrel, the pectoral muscles increase to 5% of total nonlipid wet mass of the chick by 10 days (Fig. 7) and have attained half of the adult size by 30 days of age (Fig. 8), fully a month before they are used in flight. Meanwhile, the relative size of the integument increases from 15% of nonlipid wet mass at hatching to about 30% during the latter half of the nestling period. Decrease in the relative proportion of integument to the adult level before fledging results from loss of water from maturing feathers. The relative size of the legs decreases steadily during the nestling period from 12% of the nonlipid wet mass of the neonate to 7.5% of the fledgling.

During the initial phase of rapid development, between days 1 and 10, the legs grow at an average exponential rate of about 10% per day (log of mass at end of interval minus log of mass at beginning, divided by length of interval). In the tern and quail, early growth of the leg averages about 6% per day, in the starling nearly 40% per day. In the last three species, exponential growth rate at a particular age is inversely related to the level of function achieved (Ricklefs 1979b). Both water index and growth rate indicate that the legs of the petrel develop precocially.

The exponential rate of growth of the pectoral muscles of the petrel averages about 24% per day during the first 10 days. In the tern and starling, which do not fly until fully grown, growth rates of the pectoral muscles are on the order of 20% per day or more throughout most of the development period. In the quail, the muscles grow at an average rate of about 19% per day during the first 3 weeks and then more slowly as their function develops (Ricklefs 1979a). In the petrel, between 10 and 40 days, the average growth rate of the pectoral muscles is 5% per day, a level that is consistent with well-developed function, yet the bird does not fly for another 3 or 4 weeks.

Our results indicate, first, that certain aspects of the development of Leach's Storm-Petrel chicks are similar to those of precocial species and, second, that the prolonged developmental period of the Leach's Storm-Petrel is consistent with its precocious mode of development. One need not invoke energy savings to explain slow growth. In addition, growth rate and water level point to the leg muscles and subsequently to the pectoral muscles as the tissues that constrain postnatal growth.

Our metabolic studies (Ricklefs et al. 1980) show that Leach's Storm-Petrel chicks are able to maintain their body temperatures in the nest burrow, where the ambient

temperature varies between 5 and 15°C, virtually from hatching. Chicks are rarely brooded beyond 5 days; small chicks have high metabolic rates and a strong thermogenic response to cold. In birds, thermogenesis is a function primarily of skeletal muscles (Calder and King 1974, West 1965). Neonates of most precocial species have large, well-developed leg muscles, which presumably provide heat as well as mobility. Heat production can be supplemented by the pectoral muscles as they grow and mature, depending upon the age at first flight (Aulie 1976).

In the petrel chick, the legs initially are small, and their proportion of body weight decreases with age. Nevertheless, at prevailing ambient temperatures, the specific metabolic rate of young Leach's Storm-Petrels (5–6 cc $O_2 \cdot g^{-1} \cdot hr^{-1}$) (Ricklefs et al. 1980) exceeds that of the larger neonates of the Common Tern (3–4 cc $O_2 \cdot g^{-1} \cdot h^{-1}$) (Ricklefs and White MS) and Black-headed Gull (*Larus ridibundus*) (3–4 cc $O_2 \cdot g^{-1} \cdot h^{-1}$) (Palokangas and Hissa 1971). At hatching, most of the petrel chick's metabolic heat must be generated by the legs. Within 10 days, however, the contribution of the pectoral muscles probably could equal that of the legs; of the leg component, less than half is skeletal muscle.

We propose the following explanation for slow growth in storm-petrels. First, petrel chicks are thermally independent of their parents after the first week. Second, because of their pelagic, surface-feeding habit, the adults have relatively small legs. The legs of the neonate also are small. Third, to generate the heat required for temperature regulation, the chick must rely on the early attainment of large size and maturation of its legs and pectoral muscles. The inverse relationship between growth rate and function dictates that the subsequent growth of these tissues must be greatly protracted and that age at first flight is delayed accordingly. Ricklefs (1979a, b) has argued that, among precocial species, the growth increment of the leg determines the length of the postnatal development period. In the petrel, that increment (a ratio of 3.5) is sufficiently small to permit more rapid growth of the body as a whole; indeed, the leg attains adult size within 30 days. For comparison, in the Japanese Quail the growth increment of the leg is a ratio of 17.7. It is possible, therefore, that in the petrel the large growth increment of the pectoral muscles (59) and their early maturation limit the pace of development during the latter part of the nestling period.

Hypotheses relating slow growth in petrels to food limitation and nutrient accumulation are explored more fully elsewhere (Ricklefs et al. 1980). The findings reported here are consistent with the inverse relationship between growth rate and precocity suggested for most species by Ricklefs (1973; 1979a,b).

ACKNOWLEDGMENTS

We are indebted to C. E. Huntington for advice, encouragement, logistical support, and permission to use unpublished data, to J. McEnroe for field assistance and unpublished data, and to D. Snyder for field assistance. I. L. Brisbin, M. Coulter, E. H. Dunn, and C. E. Huntington provided helpful comments on the manuscript. The study was supported by NSF Grants GB 31554X and GB 42661 to the senior author.

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DIFFERENTIAL PERCH SITE SELECTION BY COLOR MORPHS OF THE RED-TAILED HAWK (*BUTEO JAMAICENSIS*)

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ABSTRACT.—Ecological relationships among color morphs of the Red-tailed Hawk (*Buteo jamaicensis*) were studied during two successive winters in Benton County, Arkansas. Each mature hawk observed was assigned to one of three predetermined plumage categories (light, intermediate, dark) on the basis of ventral pigmentation. Multivariate analysis of variance showed a significant difference between light and dark morphs in perch site selection. A perch site openness gradient was established using discriminant function analysis. Light hawks occupied open perch sites, while dark hawks more frequently occupied perch sites characterized by dense stem cover. I suggest that the morphs were associated with perch sites that best concealed them from prey. *Received 17 May 1979, accepted 8 April 1980.*

THE Red-tailed Hawk is a polytypic species in which at least one subspecies (*Buteo jamaicensis calurus*) exhibits color polymorphism (Taverner 1936, Bent 1937). Paulson (1973) has suggested that the polymorphism exhibited by many avian predators, including the Red-tailed Hawk, is maintained by apostatic selection. In apostatic selection, the morphs that stand out from the norm would have a selective advantage by virtue of their rarity (Clarke 1962, 1969). Inherent in this hypothesis is the assumption that prey of a polymorphic predator are capable of forming a specific "avoidance image" for the common color morph of that predator. There is yet no conclusive experimental evidence to support this assumption. Furthermore, intuitively it would seem maladaptive for an organism to form such a specific "avoidance image" based on pigmentation alone and to ignore all slightly different, less common color morphs of a predator. Arnason (1978) has pointed out that, although recognition of a predator morph may be learned rather than fixed, providing for the flexibility to deal with changing situations, learning presents a problem to the apostatic selection hypothesis because the prey get eaten. Arnason also pointed out that a prey individual may encounter only one of the color morphs of a territorial predator. Thus, there are at least three major obstacles to applying the apostatic selection hypothesis to predators such as the Red-tailed Hawk.

Many authors, including Levene (1953), Van Valen (1965), Levins and MacArthur (1966), and Hedrick et al. (1976), have suggested that environmental factors may play a role in the maintenance of polymorphism in a population, each of the morphs being best adapted to, and therefore associated with, a slightly different subunit of the environment. There are few reported examples of ecological differences between color morphs of a polymorphic bird species. Johnson and Brush (1972), however, have reported marked ecological differences between presumed color morphs of the Sooty-capped Bush-Tanager (*Chlorospingus pileatus*). Murton (1971) suggested that differences in behavior and ecology existed between color morphs of several Ardeids, but his observations lacked quantitative analysis.

Although color polymorphism in the Red-tailed Hawk has been discussed by several authors (e.g. Taverner 1927, 1936, Bent 1937, Huxley 1955, Paulson 1973), no information regarding the comparative ecology of the color morphs is available.

The large and phenotypically diverse assemblage of Red-tailed Hawks that overwinters in northwestern Arkansas provides an excellent opportunity for study. The purpose of this project was to determine whether significant ecological differences existed among color morphs of the Red-tailed Hawk during their winter residence in northwestern Arkansas.

Morph Variation

I examined study skins from the University of Kansas Museum of Natural History and the University of Arkansas Museum to appraise the potential range in plumage variation among Red-tailed Hawks overwintering in northwestern Arkansas. A graded series of nine variants showing increasingly darker plumage was established, against which all specimens were matched. With experience it was easy to assign specimens to appropriate categories. Subspecific designations were disregarded, and immature birds were eliminated from the study. The following descriptions refer only to those characters used in assigning a specimen to one of the categories; other variation is omitted (numerals I–IX refer to each of the nine variants arranged in order of increasingly darker plumage, and parenthetical numbers indicate how many specimens were assigned to each category).

I. (4) Thin, incomplete brown band across jugulum; gular region white. Breast white, with a few dark specks along sides and flanks. Incomplete brown band extending from flanks across abdomen. Shanks white with scattered dark specks. Overall appearance of underparts white. Example: KU24751 (catalog number of specimen from University of Kansas Museum of Natural History).

II. (15) Plumage pattern similar to variant I, but overall appearance of underparts cream rather than white. Example: KU17131.

III. (6) Throat and breast light rust with widely scattered brown specks along sides and flanks. Abdomen light rust with few specks. Example: KU20610.

IV. (5) Throat lightly speckled with brown. Breast cream with scattered brown specks. Flanks heavily speckled with brown extending across abdomen to form thin, complete band. Shanks cream with scattered brown specks. Example: KU9590.

V. (5) Throat and upper breast heavily speckled with brown on rusty background. Abdomen and shanks heavily speckled with brown on cream background. Example: KU13634.

VI. (4) Solid brown band across jugulum. Gular region and shanks rust with dark specks. Abdomen dark brown. Example: KU4309.

VII. (9) Underparts uniformly black with scattered white specks. Example: KU17129.

VIII. (7) Throat, breast and shanks deep rust; abdomen black. Example: KU18543.

IX. (6) Underparts uniformly black. Example: KU18478.

Not all of the characters used here to categorize the nine variants are easily discerned in the field. There are marked discontinuities, however, between variants III and IV, and between variants VI and VII. Therefore, each hawk observed in the field was classified only as light (I–III above), intermediate (IV–VI above), or dark (VII–IX above).

Study Area and Methods

The study was conducted in a 244-km^2 area near Centerton, Benton County, Arkansas. The region, varying from flat terrain to abrupt ridges, was covered mostly by alternating pastureland and oak-hickory forest, with some old fields, plowed cropland, and winter stubble fields.

During the study, I recorded data from 75 perched hawks (25 per morph group) and 45 soaring hawks (15 per morph group). Observations were made between 14 December 1976 and 25 February 1977 and between 2 November 1977 and 28 January 1978. I attempted to collect the data under a wide range of weather conditions. Although I did not knowingly collect data on any individual hawk more than once, it is probable that some individuals were used more than once during the study. The data were collected as I drove along section roads throughout the study area for an average of 120 km per observation day. Ambient temperature and relative humidity were measured every hour with a sling psychrometer. The remainder of the data were recorded at the time of the hawk sighting. I classified each hawk as light, intermediate, or dark with the aid of a 20× spotting scope. The classification of some soaring hawks was difficult under certain lighting conditions and was accomplished only after lengthy observation. A Dwyer wind meter was used to measure wind velocity. Solar illumination was measured in foot candles with an illuminometer. Percentage cloud cover was obtained with a circular mirror, 15 cm in diameter, marked

TABLE 1. Coefficients of correlation between measured perch site and habitat variables and the first two discriminant functions.

Habitat and perch site variables	DF I	DF II
Percentage forest	0.253	−0.190
Percentage cropland	−0.036	0.735
Percentage pasture	−0.190	0.514
Percentage old field	−0.068	0.005
Percentage stem cover surrounding hawk	0.801	0.272
Height of perch (tree, utility pole, etc.)	0.160	−0.225
Distance between the hawk and the top of the perch	0.711	−0.061

with a 25-unit grid. I held the mirror at chest height and kept it tilted at a 20° angle to the ground to reflect the sky directly above and slightly in front of me. Readings were taken in four orthogonal compass directions. The initial direction was set by the random position of the crosshairs of a sighting tube. Percentage cloud cover equalled the total number of grid units containing cloud reflections. This technique was developed from the suggestions of D. James (pers. comm.).

Each hawk that was perched when first observed was considered the center of a circular 0.081-ha sample area. Four orthogonal transects were established from the center of each area, the first being set by the random position of the crosshairs of a sighting tube. Each transect was 22.5 m long and constituted the radius of the 0.081-ha circle. The habitat category (forest, cropland, pasture, or old field) was recorded at each of 15 randomly generated points along each of the four transects. Thus, there was a total of 60 points used for calculating habitat percentage values for each perched hawk. This sampling procedure is a modification of one described in detail by James and Shugart (1970). A clinometer was used to measure the height of the perch (tree, utility pole, etc.) and the height of the hawk's perch site. The perch site refers to the actual location of the perched hawk. From these measurements I determined the distance between the hawk and the top of the perch. The percentage stem cover surrounding each hawk was estimated with a pane of transparent glass marked with a 100-unit grid. From a kneeling position 20 m from the perch, I held the device at arm's length and placed the hawk's perch site in the center of the grid. Percentage stem cover equalled the number of grid units containing stems. This procedure was repeated from each of the four transects surrounding the perch, and the four resultant percentages were averaged for each hawk.

Habitat values were obtained for each soaring hawk in generally the same manner as for perched hawks. The approximate spot over which the bird was first observed soaring was considered the center of a circular 0.162-ha sample site. Each of the four transects was 45 m long and percentages were calculated from 25 random points along each transect, or a total of 100 points. Soaring altitude was estimated by a technique suggested by D. James (pers. comm.). A transparent pane of glass was marked with four silhouettes of decreasing size, representing Red-tailed Hawks as they would appear at 23-m distance intervals up to 92 m. A taxidermy specimen was used to calibrate the scale. Altitude measured in this way must be considered as only a rough estimate due to the variation in size among individual hawks. Hawks soaring at altitudes greater than 92 m were grouped into one altitude category.

The data were analyzed using an IBM-370 Model 155 digital computer and statistical programs in the computer library at the University of Arkansas. Soaring data and perching data were analyzed separately. In order to meet the normality assumptions of certain statistical procedures used, all of the percentage values were adjusted using the angular transformation discussed by Sokal and Rohlf (1969). Also, 1.0 was added to all measurements of some factors to eliminate null matrices.

Box's test (Sokal and Rohlf 1969) indicated that the variance of the perch site variables was not homogeneous among the three morph groups. Because the validity of some of the statistical procedures used demands at least approximate covariance homogeneity among experimental groups, an attempt was made to stabilize the variance by using an iterative procedure that generates a power transformation for each variable. These procedures were patterned after Box and Cox (1967) and Andrews et al. (1971). Although complete stabilization was not attained, the F statistic for 56 and 14,807 degrees of freedom was reduced from 3.09 with untransformed data to 1.72 with transformed data, which is the best that can be attained with power transformations on these three groups with seven variables each.

Multivariate analysis of variance (Morrison 1967, Cooley and Lohnes 1971) with a step-down procedure (Bargmann 1962) was used to test for a significant difference among the morph groups with respect to either soaring activity or perch site selection and to identify any variables contributing significantly to

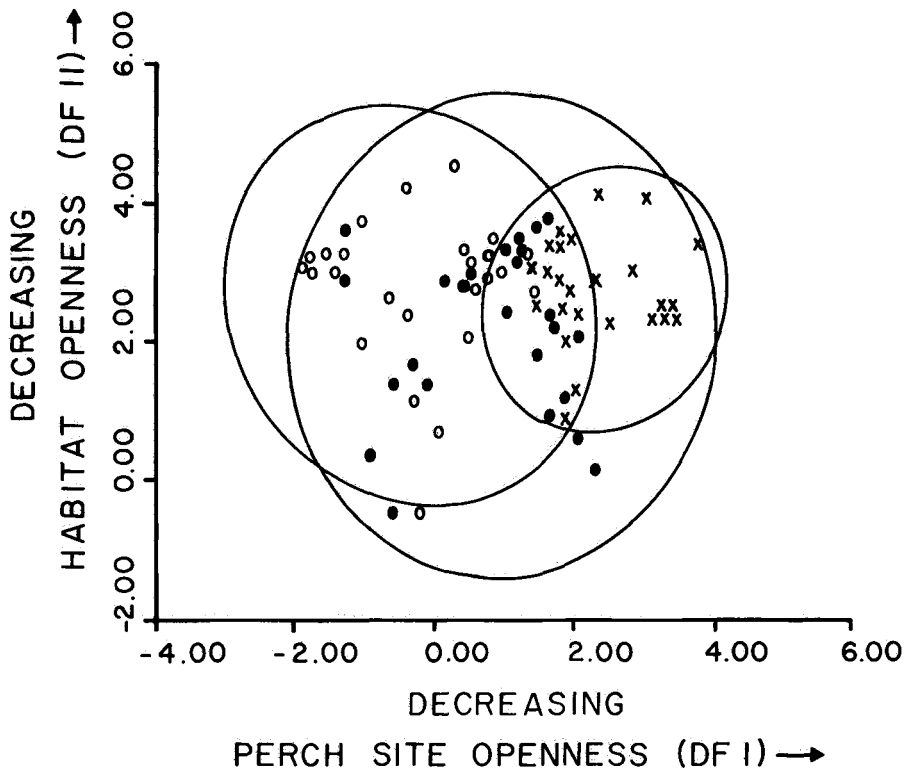

Fig. 1. Ordination of the morph groups' perching niches with 95% confidence ellipses based on discriminant function analysis (○ = light morphs, × = dark morphs, ● = intermediate morphs).

the difference. Discriminant function analysis (Fisher 1936, 1938) was used to maximize any differences among the groups. See Green (1971) for a discussion of discriminant function analysis as applied to ecological data.

Results

Although multivariate analysis of variance showed no significant differences among the three morph groups in soaring activity, it showed a highly significant difference among the groups in perch site selection ($-\text{m} \ln \lambda = 60.727$, $P < 0.001$). The step-down procedure showed that the distance between the hawk and the top of the perch ($P < 0.001$) and the percentage stem cover surrounding the hawk ($P < 0.05$) contributed significantly to the difference. Paired comparisons were made to determine which morph groups exhibited consistent differences in perch site selection. Neither light nor dark morphs differed significantly from intermediate morphs ($P > 0.05$), but there was a highly significant difference between light and dark morphs ($-\text{m} \ln \lambda = 57.46$, $P < 0.001$).

The discriminant function values combine the properties of variation exhibited by all perch site variables adjusted so that the effects of the variation are maximized with respect to separating the morph groups. The percentage stem cover surrounding the hawk and the distance between the hawk and the top of the perch were highly correlated with the first discriminant function, DF I (Table 1). DF I describes a

variation among the morphs with respect to perch site openness. Low values associated with DF I indicate the use of perch sites located near the top of the perch, surrounded by few stems. The DF I mean score for the light group is −0.389, for the intermediate group 0.893, and for the dark group 2.300. The light hawks used perch sites that were relatively open, and dark morphs used perch sites characterized by dense stem cover.

There is very little difference among the morphs with respect to DF II. Percentage pasture and percentage cropland have the highest positive correlations with DF II, while perch height and percentage forest have the highest negative correlations (Table 1). DF II is interpreted to represent habitat openness surrounding the perch. The DF II mean scores for the light, intermediate, and dark morphs are 0.025, 0.021, and 0.026, respectively. Thus, all of the morphs occupied the same habitat (defined by DF II) but selected different perch sites (defined by DF I) within the habitat.

The discriminant functions provide axes for a two-dimensional ordination of the morph groups (Fig. 1). The available perching niche may be defined here as the space, relative to the discriminant function axes, within which all observations recorded during this study lie (see Green 1971). Relative niche breadths (Green 1974) are shown by 95% confidence ellipses drawn about the morph groups. Figure 1 shows that the intermediate morphs, though not using either extreme of the perch site openness gradient, occupied a wider range of perch sites than did the other morphs. The dark morph group exhibited the least variability in perch site selection.

DISCUSSION

The results suggest that light morphs may be disadvantaged if perched in sites characterized by dense stem cover, and dark morphs may be disadvantaged if perched in relatively open sites. Further studies are needed to actually test this hypothesis, however. Possible factors responsible for the differential perch site selection are discussed below.

Thermoregulation.—Hamilton and Heppner (1967) presented evidence that dark plumage decreased energy requirements in cold ambient temperatures (below lower critical) by absorbing more solar energy than light plumage. But if ambient temperature exceeds the upper critical, dark birds exposed to solar radiation may incur an excessive heat load. Heppner (1970) suggested that light-colored birds receive less advantage from the sun in cold weather than do dark birds but do not heat up as quickly as dark birds in hot weather. Therefore, dark hawks might require shady perch sites under the same conditions that light hawks could use more open perch sites. I found no association between weather conditions and perch site selection, however, for any morph group. Walsberg et al. (1978) recently showed that dark birds exposed to solar radiation in the presence of moderate wind velocities could avoid an excessive heat load by ruffling the plumage. Furthermore, there is little variation among the morphs' dorsal pigmentation, and much of the solar radiation would presumably be absorbed directly by the dorsal surface. As more information becomes available, the importance of thermoregulation to differential perch site selection by the morphs can be better evaluated.

Crypsis.—Several authors (e.g. Kettlewell 1956, Murton 1971, Johnson and Brush 1972, Otte and Williams 1972) have associated color polymorphism with crypsis in heterogeneous environments. Color polymorphism in the Red-tailed Hawk is ex-

pressed ventrally, on the surface most exposed to prey. Dense stem cover provides a dark background against which light hawks are more visible than dark hawks to the human observer. Conversely, the absence of cover provides a relatively light background against which dark hawks are more conspicuous. Phillips (1962) showed that by daylight in open situations white plumage allowed the adults of some piscivorous Larids to get closer to potential prey before the prey took avoidance action. Inasmuch as most hunting by Red-tailed Hawks is done from a perch (Fitch et al. 1946), it would seem advantageous for a perched hawk to be concealed from potential prey, assuming that the prey are able to locate and avoid noncryptic hawks and thus act as selective agents. Sufficient information regarding the ability of prey to locate perched hawks is not yet available. The Red-tailed Hawk's diet can be very diverse (Craighead and Craighead 1956), and it would be difficult to determine how great a proportion of the total diet that discriminating prey must comprise in order to exert a significant selective pressure (Paulson 1973). The apparent flexibility in perch site selection exhibited by the intermediate morphs (Fig. 1) indicates that virtually all sites within the available perching niche are equally good for hunting, barring the effects of polymorphism. Future studies are needed to determine the success of representatives of each morph group when hunting from various types of perches.

It is not known whether the differential perch site selection observed in this study is an extension of habitat utilization on the breeding grounds or is unique to these wintering grounds. Because starvation outside of the breeding season may be a critical factor in limiting wild bird populations (Lack 1966), any selective pressures associated with perch site utilization may be particularly strong in winter. Fretwell (1972) pointed out that the feeding behavior of birds may differ greatly from season to season and geographic region to region. *Buteo j. calurus* is evidently the most variable subspecies of the Red-tailed Hawk in plumage pigmentation (Taverner 1936). This race inhabits a strikingly heterogeneous environment across its range, breeding from saguaro-palo verde desert to boreal forest. Color polymorphism may allow *B. j. calurus* to broaden and partition its overall ecological niche, thus relaxing intraspecific competition. A comparison of habitat utilization among color morphs of this subspecies during the breeding season should prove helpful in assessing the role that ecological factors may play in maintaining the polymorphism.

Mayr (1963) and Jones et al. (1977) have pointed out that many types of environmental and genetic factors may act to maintain polymorphism in a population, and that their relative importance varies between populations or loci. Pleiotropy may be involved in the polymorphism exhibited by the Red-tailed Hawk, whereby color determines only a part of the selective value of a genotype. Polymorphism may be tolerated in the population because the phenotypes are selectively neutral. Information regarding the genetic basis of color polymorphism in the genus *Buteo* is vital to an understanding of the processes responsible for the maintenance of plumage variation exhibited by the Red-tailed Hawk.

ACKNOWLEDGMENTS

I especially thank Douglas James for advice and encouragement throughout the study. J. E. Dunn provided helpful suggestions regarding statistical analyses. R. F. Johnston is gratefully acknowledged for providing access to skin collections under his care. J. A. Sealander, L. R. Kraemer, D. Berger, J. P. O'Neill, D. F. Tomback, and J. A. Wiens provided helpful comments on earlier versions of the manuscript. I also wish to express my appreciation to Penny Hatcher. This study was supported in part by the

Arkansas Audubon Society Trust Fund and the Department of Zoology, University of Arkansas, Fayetteville.

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Louis Agassiz Fuertes, Margaret Morse Nice, and Paul A. Stewart Awards

The Wilson Ornithological Society announces the availability of three awards for 1981.

Fuertes Awards are available to all ornithologists although graduate students and young professionals are preferred. Nice Awards are intended for independent researchers without access to funds and facilities available at colleges and universities and thus are restricted to amateurs and students at high school and undergraduate levels. Any type of research may be funded by both Fuertes and Nice Awards. Stewart Awards are available to any applicant for ornithological research, especially studies of bird movements based on banding and analysis of recoveries and returns and investigations in economic ornithology.

One Fuertes Award of $200.00, one Nice Award of $100.00 and one or more Stewart Awards of $200.00 each will be made. Interested applicants should write to **Carl D. Marti, Department of Zoology, Weber State College, Ogden, Utah 84408.** Completed applications must be received by **1 March 1981.** Decisions will be announced at the 1981 Annual Meeting of the Wilson Ornithological Society.

HUMMINGBIRD FORAGING BEHAVIOR AT *MALVAVISCUS ARBOREUS* VAR. *DRUMMONDII*

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ABSTRACT.—Changes in the appearance of *Malvaviscus arboreus* flowers are associated with changes in nectar reward. Nectar volumes found in day-1 flowers were generally larger and less variable than volumes found in day-2 flowers. Observations of nonterritorial Ruby-throated and Black-chinned hummingbirds (*Archilochus colubris* and *A. alexandri*) showed that they distinguished between flowers and preferentially visited the more profitable day-1 flowers. When sucrose solution was added to all day-2 flowers in one *Malvaviscus* patch, the birds stopped discriminating between flowers the first morning of floral enrichment.

These results indicate that the birds can respond to fairly subtle visual cues when determining the appropriate flowers to visit. The ultimate factor in determining which flowers to continue visiting, however, is the nectar reward. The birds learned to respond differently to the same proximate cue when it was advantageous to do so. *Received 13 March 1980, accepted 22 April 1980.*

HUMMINGBIRD foraging behavior can be viewed as a series of hierarchial decisions made among available options (Hainsworth and Wolf 1979, Gass and Montgomerie in press). A bird decides what habitat to forage in, chooses patches within that habitat, and selects flowers within that patch. A decision made at one level may limit the options and utility of decisions made at other levels. Whether or not a bird makes a "wise" decision depends partly on its ability to detect differences in profitability (Gass and Montgomerie in press) and to act upon those differences.

This study examines the ability of hummingbirds to assess differences among *Malvaviscus arboreus* var. *drummondii* flowers of different profitability within a patch and to adjust their foraging behavior accordingly. Three specific questions were asked: How did nectar volumes available to birds vary with flower age? Did birds discriminate between flower ages and prefentially visit the more productive flowers? Could their foraging behavior be modified by adding sucrose solution to the less productive flowers?

METHODS

The study was conducted at the Brackenridge Field Laboratories of the University of Texas at Austin from the end of July through September 1979. *Malvaviscus arboreus* var. *drummondii* is abundant in this 32-ha research reserve and is one of the main food-plants for female and juvenile Ruby-throated and Black-chinned hummingbirds (*Archilochus colubris* and *A. alexandri*) that forage there. It is a shrub-like hummingbird-pollinated perennial found from central Texas eastward into Florida. The showy red flowers last 2 days and undergo distinct changes in appearance during this time. The first day a flower is open, the staminal column bearing anthers and stigma extends above the petals, the petals tightly overlap, anthers are yellow with fresh pollen, and the style branches are erect. By the second morning the petals have partially unfurled with their edges starting to curl. Anthers are no longer yellow, and style branches are starting to droop.

I measured nectar volumes in uncovered flowers to see if amounts of nectar available to birds in day-1 and day-2 flowers differed significantly. Every 2 h, starting at dawn, I removed nectar from 15 flowers of each age chosen randomly from one patch of *Malvaviscus*. All nectar was removed with a 10-μl capillary tube without destroying the flowers or reducing their future nectar production capacity.

I observed hummingbird visits to two patches of *Malvaviscus* used by nonterritorial hummingbirds to determine if birds preferentially visited day-1 flowers. Each time a bird visited a flower, I recorded the flower's age. All flowers were marked with small white tags numbered "1" or "2" so that visited flowers

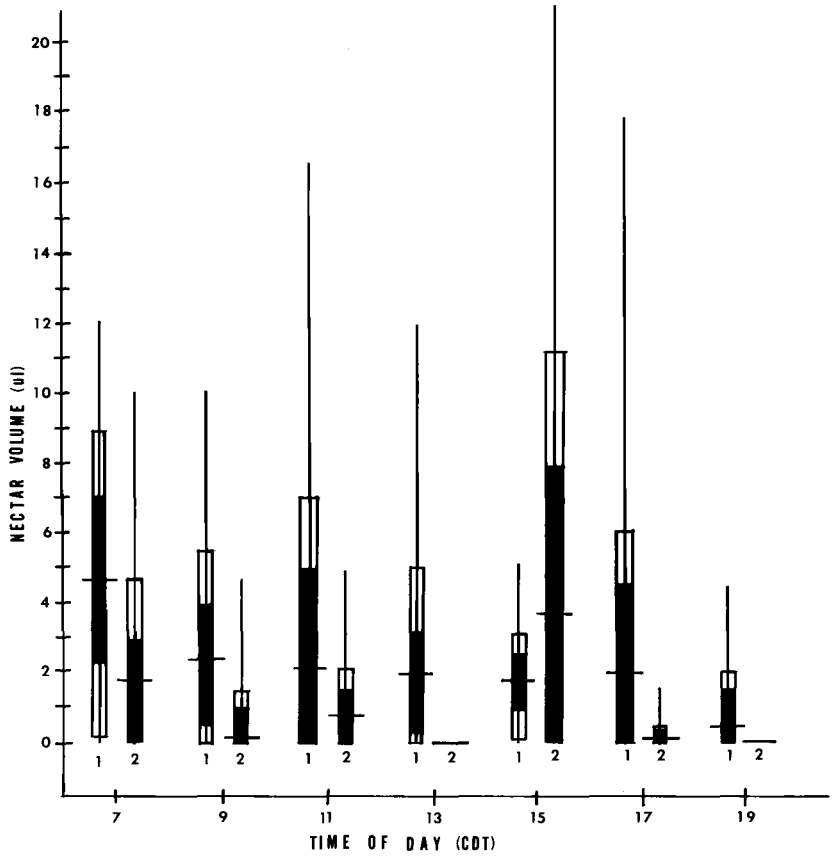

Fig. 1. Nectar volumes of day-1 and day-2 *Malvaviscus* flowers at different times of the day. Mean is indicated by horizontal bar, range by vertical bar, 1 SD on either side of the mean by open rectangle, and 95% confidence interval by black rectangle (after Gill and Wolf 1975).

could be accurately aged from a distance. I assumed that the tags appeared identical to the hummingbirds and would not be used by them as a cue to differentiate between flowers. At the beginning of each observation period all flowers in the patch were counted to determine the number of day-1 and day-2 flowers present. The relative availabilities of day-1 and day-2 flowers remained similiar during the July and September study periods (Table 1, $\chi^2 = 2.1$, $P > 0.30$). Observation periods started at dawn (ca. 0700) and continued for the next 4 h.

Day-2 flowers were artifically enriched at one of the patches to see whether the birds could recognize these new "good" flowers and include them in their foraging bouts. I added 20 μl of 30% by weight sucrose solution to all day-2 flowers at dawn and another 20 μl 2 h later. The amount and concentration of the added solution was equivalent to the average accumulated production in day-1 flowers (George 1980). Observations began immediately after the first sucrose addition at dawn and continued for the next 4 h. After 2 consecutive days of sucrose addition, solution was not added to day-2 flowers, and hummingbird foraging was observed for 4 h, beginning at dawn, to see whether the birds switched back to their previous foraging pattern.

Results

Nectar volumes obtained from day-1 flowers were generally larger and less variable than volumes found in day-2 flowers (Fig. 1). From 0700 to 1100, the average

TABLE 1. Number of hummingbird visits to day-1 and day-2 flowers. Significance of differences determined by a χ^2 test with 1 df.

Date	Number of flowers		Observed visits		χ^2	P
	day-1	day-2	day-1	day-2		
30 July	45	35	48	4	18.0	<0.001
31 July	37	40	55	9	20.5	<0.001
6 September	40	27	59	13	7.3	<0.01

volume in day-1 flowers was 3.0 μl. Nectar volumes in day-2 flowers averaged 0.9 μl in the morning, decreasing to almost zero in the afternoon, with the exception of the sample taken at 1500. Only three out of the 15 flowers sampled contained nectar, but those quantities were large (15, 20, 21 μl). These flowers probably had not been visited their first day, as day-2 flowers do not produce nectar (George 1980).

As day-1 flowers were energetically more rewarding than day-2 flowers and flower appearance changed with age, did birds discriminate between flower ages? If birds probed flowers without respect to their profitability, the expected number of visits to day-1 and day-2 flowers would be in direct proportion to that of the flowers occurring in the patch. Birds visited day-1 flowers, however, more often than expected (Table 1). While day-1 flowers comprised 56%, 48%, and 60% of the flowers in observed patches, they received 92%, 86%, and 87%, respectively, of the visits. The birds preferentially visited day-1 flowers, although they did not totally ignore day-2 flowers.

The birds stopped discriminating between flowers when sucrose solution was added to day-2 flowers (Table 2). By the 3rd h of observation on the first morning of floral enrichment, birds no longer preferentially visited day-1 flowers. The birds did not discriminate between day-1 and day-2 flowers at all during the second morning of enrichment. When the patch was left unaltered after 2 consecutive mornings of enrichment, the birds did not begin to discriminate again until after approximately 3 h of foraging (Table 3).

DISCUSSION

Changes in the appearance of *Malvaviscus* flowers are associated with changes in nectar rewards that hummingbirds can expect to receive. The birds took advan-

TABLE 2. Number of hummingbird visits to day-1 and enriched day-2 flowers on 2 consecutive days. Significance of differences determined by a χ^2 test with 1 df.

Date	Number of flowers		Observation hour	Observed visits		χ^2	P
	day-1	day-2		day-1	day-2		
7 September	34	40	1	36	17	5.2	<0.02
			2	62	23	11.0	<0.001
			3	46	30	2.6	>0.05
			4	43	49	0.003	>0.95
8 September	47	32	1	20	8	0.8	>0.25
			2	24	11	0.5	>0.25
			3	28	20	0.003	>0.95
			4	26	20	0.02	0.90

TABLE 3. Number of hummingbird visits to day-1 and day-2 flowers after 2 consecutive days of enriching day-2 flowers. Flowers were not enriched. Significance of differences determined by a χ^2 test with 1 df.

Date	Number of flowers		Observation hour	Observed visits		χ^2	P
	day-1	day-2		day-1	day-2		
9 September	40	47	1	12	7	1.2	>0.25
			2	13	11	0.2	>0.50
			3	28	18	2.1	>0.10
			4	41	13	11.0	<0.001

tage of this change to increase the amount of nectar obtained per foraging bout by preferentially visiting the more energetically rewarding day-1 flowers.

That hummingbirds and other nectarivorous animals distinguish between flowers of different profitability has been observed several times (Gottsberger 1967, Jones and Buchman 1974, Gill and Wolf 1975, Heinrich 1975, Gass and Montgomerie in press). Because nectar is concealed in flowers, birds probably use visible changes in flowers as cues to flower contents. Most often the cue appears to be a change in flower color (Gottsberger 1971, Gill and Wolf 1975, Schemske pers. comm.), although other changes such as a hole left by a nectar thief (Gass and Montgomerie in press) or predictability of spatial position of unprofitable flowers (Colwell et al. 1973) can be used. My observations suggest that they can learn to use fairly subtle cues to determine the appropiate flowers to visit. I did not detect any color changes in the flowers, although that possibility cannot be excluded. The birds could have detected a change not apparent to me, as hummingbird vision is more sensitive to longer wavelengths than human vision (Stiles 1976) and is also sensitive to near U.V. (Goldsmith 1980).

The ultimate factor used to decide which flowers a bird should continue visiting is the amount of nectar a bird receives. The nectar addition experiment shows that birds can learn to respond differently to the same external cues if their view of the reward associated with that cue changes. The switch to visiting day-2 flowers happened fairly rapidly when the reward found in them changed from a highly variable one to a predictably large one. The birds also appeared to remember the change from morning to morning, as they never distinguished between day-1 and day-2 flowers the second morning of floral enrichment. Even when day-2 flowers were left unaltered, the birds continued to visit them the first 3 h of observation.

Several questions about hummingbird learning ability and its effect on foraging efficiency are raised by these observations. Birds were able to detect changes in reward, because they occasionally probed day-2 flowers under normal conditions. How did the costs of probing day-1 and day-2 flowers and the movement between flowers influence the frequency of day-2 probes given the expected rewards? Did the birds generalize what they had learned at the altered patch to other *Malvaviscus* patches, or were they able to distinguish the altered patch as unique and feed at day-2 flowers only at that patch? How did the size of the reward in the altered day-2 flowers affect the birds' behavior? What would be the minimum reward per flower and minimum number of enriched day-2 flowers needed to produce the switch in foraging described in this paper? Answers to these questions will provide insight into the foraging behavior of hummingbirds and the possible rules they use to make foraging decisions.

ACKNOWLEDGMENTS

I thank L. Gass, R. Montgomerie, L. Wolf, and D. Schemske for their critical comments on previous drafts of this manuscript. Financial support for this study was provided by a Sigma Xi grant-in-aid of research and a Frank M. Chapman Fund grant from the American Museum of Natural History.

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ENERGETICS OF TWO WINTERING RAPTORS

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ABSTRACT.—We present a deterministic model for predicting daily energy expenditure of two raptors—female American Kestrels (*Falco sparverius*) and White-tailed Kites (*Elanus leucurus*)—wintering in coastal northwestern California. Inputs to the model include body mass, air temperature, photoperiod, energy expenditure of flight, and relative portions of the daytime spent in flight and nonflight activities. A simplified version of the model applicable to birds spending less than 20% of the day in flight and inflating daily energy expenditure by 6% or less is also presented. Inputs to the simplified version include body mass, air temperature, energy expenditure of flight, and relative portions of the 24-h day spent in flight and nonflight activities.

Input data were estimated directly and indirectly. The validity of the model was tested by comparing predicted energy expenditure with energy expenditure estimated by observed food consumption of wild birds. The model predicted that individual female kestrels would expend 42.0–61.0 kcal (2.04 to 2.96 W) daily and that individual kites would expend 105.6–118.3 kcal (5.12 to 5.74 W) daily. Daily energy expenditure estimated by food consumption averaged 42.9 and 113.1 kcal (2.08 and 5.49 W) per individual kestrel and kite, respectively. The degree of correspondence between model prediction and field estimation of energy expenditure of kites was considered adequate for model validation. Even though the model predictions bracketed the field estimation of energy expenditure of kestrels, however, the model predictions were considered to be too high because of an erroneous temperature input, and the field estimation was considered to be too low because of an erroneous estimate of the biomass of an important group of prey. Correcting these errors indicated that the daily energy expenditure of kestrels should average 48.7 kcal (2.36 W) per individual. Using the corrected energy expenditure as a standard for female kestrels and the field estimate of energy expenditure as a standard for kites, the predictive accuracy of the versions of the model was evaluated relative to the predictive accuracy of 11 other models. Three of these models, including the two versions presented here, produced estimates that were within 5% of the mean standard value. Eight of the models under-approximated the mean standard value by 10.3–49.5%; the other two over-approximated the mean standard value by 14.8 and 36.9%. *Received 13 August 1979, accepted 21 April 1980.*

EFFORTS to approximate the energetics of free-living birds ideally should include consideration of variations in energy expenditures associated with biological and ecological influences (King 1974). A corollary to this proposition is that the approximations attempted should include information on all the influences involved. Approximations made on wintering birds therefore should include information on variations in energy expenditure associated with variations in air temperature, thermal radiation, wind, and humidity (the "climate space" of birds: Porter and Gates 1969); location and use of environmental resources; social and competitive interactions; and antipredator activities.

This is a report of the derivation and field test of a deterministic model developed to predict energy expenditures of two species of falconiform birds, the American Kestrel (*Falco sparverius*) and the White-tailed Kite (*Elanus leucurus*), wintering

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in coastal northwestern California. The model makes use of the methodology and research of Kendeigh and his coworkers (Kendeigh et al. 1977) on existence metabolism (EM); the research of Lasiewski (1963), LeFebvre (1964), Tucker (1968, 1972), and Gessaman (pers. comm.) on energetics of avian flight; and the research of many avian physiologists on standard and basal metabolism (SM and BM) (recently reviewed by Calder and King 1974 and Kendeigh et al. 1977).

Inputs to the model include: (1) body mass, (2) amounts of time birds are engaged in flight and nonflight activities, (3) air temperature, (4) photoperiod, and (5) the multiple of basal metabolism expressing energy expenditure of flight. Output from the model is "daily energy expenditure" (*DEE sensu* King 1974) or "daily energy budget" (*DEB sensu* Grodzinski et al. 1975, Kendeigh et al. 1977) per bird. The model may be summarized and symbolized by equation 1:

$$DEB = NFA[(EM_{T_a}) - (1 - P)(SM_{T_{na}})] + FA[(BM)(P)(FC)] + (1 - P)(SM_{T_{na}}) \quad (1)$$

where: NFA = duration of diurnal nonflight activities as a proportion of the photoperiod (daylength) ($NFA = 1 - FA$),

FA = duration of flight activities as a proportion of the photoperiod ($FA = 1 - NFA$),

EM_{T_a} = existence metabolism of nonpasserine birds during winter as a function of average daily air temperature (T_a):

$$EM_{T_a} = EM_{0°C} + (T_a)(b) \quad (2)$$

$$\text{where: } b = \frac{EM_{30°C} - EM_{0°C}}{30};$$

$$EM_{30°C} = 1.455\,W^{0.6256} \quad (3)$$

$$EM_{0°C} = 4.235\,W^{0.5316} \quad (4)$$

W = body mass in g

$SM_{T_{na}}$ = standard metabolism of nonpasserine birds during winter at night as a function of average night time air temperature (T_{na}):

$$SM_{T_{na}} = SM_{0°C} - (b)(T_{na}) \quad (5)$$

$$\text{where: } SM_{0°C} = 1.810\,W^{0.5944} \quad (6)$$

$$b = 0.0457\,W^{0.5886} \quad (7)$$

at the lower critical temperature (T_{lc}), $SM = BM$:

$$T_{lc} = 47.17\,W^{-0.1809} \quad (8)$$

BM = basal metabolism

$$BM = 0.4616\,W^{0.7340} \quad (9)$$

P = photoperiod as a proportion of the 24-h day.

FC = flight coefficient; the multiple of BM expressing energy expenditure of flight.

DEB, *BM*, and all expressions of *SM* and *EM* are in kcal·bird^{-1}·day^{-1}. Equation (2) is a linear interpolation to T_a of the allometric equations (3) and (4) of Kendeigh et al. (1977) for predicting *EM* of nonpasserine birds at 0°C and 30°C for 10 ± h photoperiods during winter. Equation (2) is a generalization of an earlier energetics model (Koplin 1972); a modification of the energetics model of Weiner and Glowa-

cinski (1975), derived from allometric equations based on fewer data (Kendeigh 1970); and, except for their use of Kendeigh's (1970) earlier equations, is identical to the energetics model of Wiens and Innis (1973, 1974). Equations (5), (6), (7), and (8) are from Kendeigh et al. (1977) for nonpasserine birds during winter and at night. Equation (9) is Aschoff and Pohl's (1970) allometric equation for resting *BM* of nonpasserine birds.

There are two components to EM_{T_a}: diurnal nonflight activity and nocturnal rest. Flight of kestrels and kites is a diurnal activity; therefore, the energy expenditure of flight should be prorated with the diurnal nonflight component of EM_{T_a}; equation (1) does this. The component $(EM_{T_a}) - (SM_{T_{na}})(1 - P)$ calculates the total energy expenditure of diurnal nonflight activity by deducting the energy expenditure of nocturnal rest, $(SM_{T_{na}})(1 - P)$, from EM_{T_a}. The coefficient *NFA* is a correction factor to simulate the portion of *DEB* attributable to diurnal nonflight activity. The component $FA[(BM)(P)(FC)]$ predicts the portion of DEB attributable to diurnal flight activity. The coefficient *P* prorates *BM*, a daily rate, to the photoperiod portion of the 24-h day; *FA* further prorates *BM* to that portion of the photoperiod spent in flight. *FC* is a multiple of *BM*; the product $(BM)(FC)$ represents the energy expenditure of flight. The portion of *DEB* attributable to nocturnal rest is predicted by the component $(1 - P)(SM_{T_{na}})$. The coefficient $(1 - P)$ is a correction factor prorating $SM_{T_{na}}$, a daily rate, to the portion of the 24-h day that is dark.

For birds spending 20% or less of the photoperiod in flight activities, as was the case for kestrels and kites wintering in coastal northwestern California (Table 2), a simplified version of equation (1) providing predictions exceeding those of equation (1) by 6% or less is:

$$DEB = NFA'(EM_{T_a}) + FA'[(BM)(FC)] \tag{10}$$

where: NFA' = portion of the 24-h day spent in nonflight activities (nocturnal rest plus diurnal nonflight activities); $(NFA' = 1 - FA')$.
FA' = portion of the 24-h day spent in flight; $(FA' = 1 - NFA')$.
DEB, EM_{T_a}, *BM*, and *FC* are as previously defined.

Equation (10) is based on limiting constraints of *FA* and *NFA* in equation (1). Thus, as *FA* goes to 0, *NFA* goes to 1 and equation (1) simplifies to equation (2). Under these conditions the necessity for an explicit estimate of nocurnal rest is superfluous, because, even though unknown, it is implicitly incorporated into equation (2) and therefore does not need to be known. Alternatively, as *FA* goes to 1, *NFA* goes to 0 and equation (1) simplifies to two components, the energy expenditures of flight and nocturnal rest. Under these conditions, an explicit estimate of nocturnal rest is paramount. Consequently, as *FA* goes from 1 to 0 (or as *NFA* goes from 0 to 1) the necessity of an explicit estimate of the energy expenditure of nocturnal rest becomes progressively less important.

Equations (1) and (10) thus account for variations in energy expenditure associated with variations in air temperature and with location and use of environmental resources. To the extent that they are associated with flight activities and/or minimal diurnal nonflight activities, equations (1) and (10) also account for energy expenditures of social and competitive interactions and antipredator activities. Equations (1) and (10) do not account for energy expenditures of growth, reproduction, and molt, nor the influences of wind, thermal radiation, and humidity.

TABLE 1. Comparison of predicted and measured EM_{T_a} for seven species of falconiform birds. Paired t-test (13 df) = 0.11; P = 0.91.

Species	W (Body mass g)	T_a (Temperature °C)	EM_{T_a} (kcal/day)[a]	
			Predicted[b]	Measured
Accipiter striatus	99	15.2	37.1	39.1
A. striatus	108	17.2	37.4	37.6
A. striatus	108	15.5	38.7	42.9
A. striatus	108	13.9	40.0	36.2
A. striatus	107	16.5	37.7	33.0
Falco sparverius	126	8.2	48.4	40.8
F. columbarius	174	9.0	57.0	64.5
F. columbarius	173	12.0	54.0	50.6
F. columbarius	172	12.6	53.2	50.0
F. tinnunculus	194	13.1	56.4	58.9
F. tinnunculus	196	13.2	56.6	53.2
F. mexicanus	497	12.0	97.2	84.0
F. cherrug	1,036	11.8	147.0	184.0
Buteo jamaicensis	1,389	12.6	171.6	162.5

[a] S.I. conversion: 1 kcal/day = 4.85×10^{-2} watt (W).
[b] Equation (2).

METHODS

Use of equation (2) to predict energy expenditure of nonflight activities was tested by a paired statistical comparison of values of EM_{T_a} predicted by the equation with values of EM_{T_a} measured experimentally (Table 1). Pairs of predicted and measured EM_{T_a} were obtained for individual birds with an average body mass (W) at an average air temperature (T_a). Experimental values of EM_{T_a} were obtained by energy balance measurements on birds housed in rooms 3.3 m long by 2.6 m wide and 2.9 m high. With the exception of room size, temperature, and light control, methodology for measuring EM_{T_a} was similar to that used by Kendeigh (1949), i.e. the difference between energy content of food consumed and energy content of egesta of birds maintained at constant body mass for periods of 3 or more days. Birds were fed ground, eviscerated rat (stomach and intestinal tract removed), eviscerated rabbit, or beef heart. Energy content of food and egesta was measured in an adiabatic bomb calorimeter. All experimental measurements were made during the winter; temperatures in the rooms, ventilated to the outside through screened windows, were monitored continuously by thermographs. Experimental T_a was calculated by summing thermograph records at hourly intervals and dividing the sum by the number of hours in each experiment. Natural light filtering through windows in the rooms was the source of light during the experiments. Thus, temperature and light conditions were as close to natural as experimental conditons allowed.

Inputs to equations (1) and (10) were estimated directly and indirectly. *NFA* and *FA* (*NFA'* and *FA'*) were estimated directly by dawn-to-dusk field observations totalling approximately 300 h of individual kestrels and approximately 400 h of individual kites (Table 2). Field observations were made of birds wintering on agricultural lands in the vicinity of Arcata and Eureka, Humboldt County, California. T_a was estimated directly by averaging daily maximum and minimum temperatures occurring between sunset plus 0.5 h and sunrise minus 0.5 h. P was estimated directly by averaging and adding 1 h to the daily amount of time elapsing between sunrise and sunset. Data on temperatures and photoperiod were obtained from the U.S. Weather Bureau in Eureka; the data were averaged over the 92-day period between mid-November and mid-February, which we considered to be the winter season. Body mass (W) was estimated indirectly from the literature for kestrels, and indirectly from the literature and from unpublished data on live birds and in various museums for kites. *FC* was estimated indirectly by comparing the ratio of available data on the energy expenditures of flight to *BM* of nonpasserine birds (Table 3).

The validity of the model was tested by comparing *DEB* predicted by equation (1) with *DEB* estimated on the basis of observed food consumption by free-living birds (Tables 4 and 5). Information on types and amounts of prey eaten by free-living birds was obtained in connection with observations of daily flight and nonflight activities (Table 5 and Appendix).

The predictive accuracy of the two versions of our energetics model relative to the predictive accuracy of other energetics models was evaluated by comparing *DEB* predictions of the models to standard *DEB*

TABLE 2. Flight (*FA*) and nonflight (*NFA*) activities of female American Kestrels and White-tailed Kites wintering on agricultural lands in coastal northwestern California during the average 11-h photoperiod.

Activities	Percent of photoperiod	
	American Kestrels[a]	White-tailed Kites[b]
Perched (*NFA*)		
Searching	74.7	60.1
Inactive	8.6	16.6
Eating	3.6	3.0
Other	6.5	0.8
Subtotal	93.4	80.5
Flying (*FA*)		
Directional	2.5	9.1[c]
Hovering	3.4	8.9
Other	0.7	1.5
Subtotal	6.6	19.5
TOTAL	100.0	100.0

[a] Based on a total of 316.7 h of continuous observation of 7 birds, 4 during the winter of 1972–73 and 3 during the winter of 1973–74.
[b] Based on a total of 441.2 h of continuous observation of four birds during the winter of 1973–74.
[c] Flight to and from the nocturnal roost, which was not found; daily duration estimated to average 1 h.

values (Table 6). Fortunately, our studies provided estimates of all information needed as inputs by the full complement of energetics models evaluated. Information needed in addition to that required for our model included energy-balance data on captive animals (Table 1) and detailed data on time and activity budgets (Table 2). All allometric equations for predicting *BM*, *SM*, and *EM* were expressed in terms of mean body mass (Table 4). *BM* was increased by a factor of 1.091 for kestrels and 1.078 for kites in models predicting *BM* with the allometric equation of Lasiewski and Dawson (1967) for nonpasserine birds. Where possible, only those behavioral and physiological aspects pertinent to kestrels and kites wintering in coastal northwestern California were considered in predictions by other models. That is, only behavioral acts such as flight, eating, preening, etc. and physiological processes such as temperature regulation were included in predictions by other models. Behavioral acts such as hopping, singing, etc. and physiological processes such as reproduction were omitted from predictions by other models.

RESULTS AND DISCUSSION

Fourteen measurements of EM_{T_a} were obtained from seven species of falconiforms ranging in size from a Sharp-shinned Hawk (*Accipiter striatus*) (about 100 g) to a Red-tailed Hawk (*Buteo jamaicensis*) (about 1,400 g) (Table 1). T_a ranged from 8.2°C to 17.2°C during the measurements; hourly temperatures differed from T_a by a maximum of ± 5.0°C. Photoperiod ranged from 10 to 12 h. The null hypothesis that no differences existed between pairs of predicted and measured values of EM_{T_a} was accepted at the 0.05 level of significance. Thus, it was concluded that, under conditions similar to those in the laboratory, linear interpolation of equations (3) and (4) for predicting EM_{T_a} between 0°C and 30°C for wintering falconiforms is a realistic approximation of the birds' total nonflight energy expenditure.

Kestrels and kites averaged 10.3 h and 8.9 h, respectively, in nonflight activities and 0.7 h and 2.1 h, respectively, in flight activities during the daily photoperiod (Table 2). Birds were assumed to be at rest during the dark, which averaged 13 h daily.

FC, the ratio of energy expenditure of flight to *BM*, ranged from 12.0 to 14.5 and averaged 13.7 for five species of nonpasserine birds ranging in mass from 3 g to approximately 400 g (Table 3). Flight energy calculated by the empirical equation

TABLE 3. Relationship between *BM* and flight energy (*FE*) of five species of nonpasserine birds as an estimate of *FC*.

Species	*W* (Body mass g)	*BM* (kcal/h)[a]	*FE* (kcal/h)[a]	*FC* (*FE*: *BMR*)	Reference
Calypte costae	3	0.05	0.60	12.0	Lasiewski (1963)
Melopsittacus undulatus	35	0.26	3.68	14.2	Tucker (1968)
Falco sparverius	126	0.67	9.12	13.6	J. A. Gessaman (pers. comm.)
Larus ridibundus	350	1.42	20.13	14.2	Tucker (1972)
Columba livia	384	1.52	22.00	14.5	LeFebvre (1964)

[a] S.I. conversion: 1 kcal/h = 1.163 W.

of Hart and Berger (1972) is 14.9-fold higher than *BM* for nonpasserine birds. Flight energy calculated by Tucker's (1974) equation 2 for a 119-g bird, the average body mass of female American Kestrels (Table 4), is 14.1-fold higher than *BM* and is 18.3-fold higher than *BM* for a 331-g bird, the average body mass of White-tailed Kites (Table 4). Thus, even though the ratios of flight energy to *BM* in Table 3 average slightly less than those predicted from a larger sample of empirical data (Hart and Berger 1972) or are comparable to or moderately less than those predicted theoretically (Tucker 1974), we prefer the ratio 13.7 for the following reasons. First, Hart and Berger's (1972) empirically derived equation includes data on three species of birds for which measurements were obtained during flights lasting only 7–15 s (Berger et al. 1970: 202); metabolic rates during the first few minutes of flight may be 15-20% higher than later (Tucker 1974: 302). Second, Tucker's (1974) theoretical equation predicts (as seen for kestrels and kites) an increasing ratio of flight energy to *BM* with increasing body mass, predictions conforming poorly with empirical observations, especially by predicting unreasonably high ratios for large birds (King 1974: 32).

It should be noted that a *FC* of 13.7 represents the predicted energy expenditure of birds ". . . flying near the maximal steady-state power output . . ." (King 1974: 32). We assumed that maximal steady-state energy output was the best overall predictor of the types of flights kestrels and kites performed, reasoning that there was probably as much flight activity in which energy expenditure exceeded maximal steady-state output as there was in which energy expenditure was less than required

TABLE 4. Inputs to and *DEB* predicted by equation (1) for female Kestrels and White-tailed Kites wintering on agricultural lands in coastal northwestern California.

		Kestrels	Kites
Body mass (g)	W	119 (86–165)[a]	331 (310–372)[a]
Average air temperature (C)	T_a	8.9	9.1
Average nocturnal air temperature (C)	T_{na}	8.5	8.8
Average photoperiod (% of 24-h day)	P	45.8	45.8
Average duration of darkness (% of 24-h day)	$1 - P$	54.2	54.2
Daily nonflight activities (% of 11-h photoperiod)	*NFA*	93.4	80.5
Daily flight activities (% of 11-h photoperiod)	*FA*	6.6	19.5
Daily energy budget (kcal·bird^{-1}·day^{-1})	*DEB*	50.6 (42.0–61.0)[b]	110.0 (105.6–118.3)[b]

[a] Mean body mass; range in parentheses. Data from Roest (1957), Brown and Amadon (1968), Stendell (1972), and P. M. Bloom (pers. comm.).

[b] *DEB* predicted on basis of mean body mass; range predicted on basis of range in body mass in parentheses. S.I. conversion: 1 kcal/day = 4.85×10^{-2} W.

TABLE 5. *DEB* calculated on the basis of observed food intake for female American Kestrels and White-tailed Kites wintering in coastal northwestern California. See appendix for details on weights and calorific equivalents of prey.[a]

	Kestrels	Kites
Number prey killed/day		
Vertebrates	2.2	3.1
Invertebrates	46.5	—
Biomass of prey killed/day (g)		
Vertebrates	21.6	76.6
Invertebrates	12.6	—
Energy ingested (kcal/day)		
Vertebrates	30.3	137.9
Invertebrates	20.1	—
Energy assimilated (kcal/day)		
Vertebrates	25.6	113.1
Invertebrates	17.3	—
TOTAL energy assimilated = *DEB* (kcal·bird^{-1}·day^{-1})	42.9 (2.08 W)	113.1 (5.49 W)

[a] Kites were observed to consume California voles (*Microtus californicus*) and western harvest mice (*Reithrodontomys megalotis*). Kestrels were observed to consume Lepidoptera larvae and adults, grasshoppers, earthworms, various Coleoptera, California voles, harvest mice, vagrant shrews (*Sorex vagrans*), garter snakes (*Thamnophis sirtalis*), red-legged frogs (*Rana aurora*), and Pacific tree frogs (*Hyla regilla*). Ingested energy corrected to account for the fact that kestrels and kites both usually eviscerated small mammal prey before consumption. Assimilation efficiency assumed to 0.82 for small mammals and 0.86 for other vertebrates and invertebrates, based on efficiencies obtained during feeding experiments.

for maximal steady-state output. Both species averaged 30–50 flights per day. Each flight lasted from a few seconds to about 45 min, and averaged 1–4 min. All flights involved ascending from perches or the ground, many involved hovering, and some involved transporting prey from the ground to elevated perches—types of flight exceeding maximal steady-state energy expenditure (Tucker 1968, 1974). All flights also involved descending from aerial heights or perches, some involved soaring or "kiting," and a few involved long-distance movements between roosts and hunting areas—types of flight requiring less than maximal steady-state energy expenditure (Tucker 1968, 1974; Pennycuick 1971).

Expressed in terms of the range in body mass of the birds, *DEB* approximated by the energetics model (Table 4) bracketed *DEB* estimated by food consumption (Table 5). In terms of mean body mass, however, the model predicted *DEB* 18.0% higher for kestrels and 2.7% lower for kites than *DEB* estimated by food consumption. The discrepancy between *DEB* approximated by the model in terms of mean body mass and *DEB* estimated by food consumption for kites is considered to be inconsequential. Presumably, the discrepancy is attributable to sampling errors in body mass of kites, a total of only four of which were monitored in the field, and/or in weights of prey of kites in the field; a slight energy-expending imbalance among the three elements of the "climate space" unaccounted for in our model; or to some combination of these three phenomena. In any event, the model and existing inputs to the model are considered to provide a realistic approximation of *DEB* for White-tailed Kites living under winter conditions in coastal northwestern California.

The relatively small discrepancy between model prediction and field estimation of *DEB* for kites suggests that the relatively large discrepancy between model prediction and field estimation of *DEB* for kestrels is related to erroneous inputs to the model, a sizable energy-conserving imbalance among the elements of the climate space unaccounted for in our model, erroneous field estimates of food consumption, or to some combination of the three phenomena, but not to any important inade-

quacies of the energetics model. The field estimate of food consumption was based on information from only seven kestrels. Thus, it is possible that body mass of the seven birds averaged less than 119 g, resulting in a realistic but low field estimate of *DEB*. A bias of the magnitude needed to account for the total discrepancy, however, would necessitate body masses of the seven birds involved to cluster at the very lower limit of body mass known for female kestrels, an extremely unlikely possibility. An indication of the prospect of obtaining such an extreme sample mean is provided by the only body masses of local female kestrels we were able to find—two HSU museum specimens (111 g and 116 g) and an injured live bird (130 g)—which averaged exactly 119 g. Nevertheless, it is possible that body mass of the seven birds averaged somewhat less than 119 g, accounting for some of the discrepancy.

A sizable energy-conserving imbalance among elements of the climate space of kestrels in the field is another possibility that may account for the discrepancy between model prediction and field estimation of *DEB*. We consider this possibility unlikely for several reasons. First, and most important, White-tailed Kites and kestrels were exposed to similar climatic conditions; as previously indicated, if there existed a climatically related alteration in *DEB* of kites, it operated to expend, not to conserve, energy. Second, a climatically related conservation of energy would have to have resulted from absorption of solar radiation. During the 184 days of the winters of 1972–73 and 1973–74, there was sunshine an average of only 44% of the time possible, resulting in a mean of 4.8 h of sunshine daily, and there was sunshine during the whole photoperiod on only 19 days (Local Climatic Data, U.S. Weather Bureau, Eureka). Furthermore, even when there was sunshine, the sun was at a low angle; at the latitude of 44°30′N, its warming influence was minimal during the winter. Thus, even though solar radiation may have had a conserving influence on daily energy expenditure of kestrels, we feel that influence could not have accounted for an 18.0% conservation of daily energy expenditure.

We feel that a conservative error in our estimates of T_a and T_{na} accounted for part of the discrepancy between model approximation and field estimates of *DEB* for female kestrels. T_a and T_{na} are based on outside air temperatures; kestrels, however, are known to roost in cavities, crevices, recesses, etc. (Brown and Amadon 1968, personal observation), situations in which air temperatures undoubtedly are warmer than outside. The magnitude of the difference is indicated by studies of incubating kestrels (Gessaman and Findell 1979). Average night-time temperatures in nest boxes of incubating kestrels ranged from 4.5 to 16.0°C and were 4.0–5.0°C warmer than temperatures outside (Gessaman pers. comm.). Daily maximum and minimum air temperatures in California averaged 12.1°C and 5.7°C, respectively, during the two 92-day winters kestrels were studied in the field. If temperature in the nocturnal roosts of the birds averaged 4.5°C warmer than outside, then T_a should be 11.2°C and T_{na} 13.0°C. On the basis of these inputs, the energetics model predicts *DEB* to be 48.7 kcal/day (2.36 W) for a 119-g bird. We consider this approximation to be more realistic for female kestrels than the approximation in Table 4. Nevertheless, the corrected approximation is still 13.5% higher than *DEB* estimated by food consumption (Table 5), indicating the existence of one or more additional errors.

The most likely possibility to account for the remaining discrepancy between model approximation and field estimation of *DEB* for kestrels is a conservative error in our estimate of the weights of prey, especially of unidentified invertebrates (Ap-

TABLE 6. Comparison of accuracy of energetics models for predicting *DEB* for female American Kestrels and White-tailed Kites wintering in coastal northwestern California. Arranged in decreasing order of accuracy.

DEB predicted[a]		*DEB/BM*				
Kestrels	Kites	Kestrels	Kites	Mean	Method of prediction[b]	Source/comment
48.7	113.1	3.16	3.46	3.31	—	Standard values
50.7	110.0	3.29	3.37	3.33	Equation (1)	Present study
46.1	112.0	2.99	3.43	3.21	A	Holmes et al. (1979)
51.4	113.8	3.44	3.49	3.47	Equation (10)	Present study
41.1	106.8	2.67	3.27	2.97	A	Wakely (1978)
56.9	106.6	2.40	3.27	2.84	A	Withers (1977)
52.1	137.5	3.38	4.21	3.80	B	Mosher and Matray (1974)
46.0	85.4	2.99	2.62	2.81	B	West and DeWolfe (1974)
46.4	81.1	3.01	2.48	2.75	Equation (2)	Wiens and Innis (1973, 1974), Wiener and Głowacinski (1975)
38.2	92.1	2.48	2.82	2.65	B	Kushlan (1977)
70.8	145.7	4.60	4.46	4.53	C	King (1974)
23.4	86.5	1.52	2.65	2.09	A	Tarboton (1978)
22.0	67.0	1.43	2.05	1.75	A	Walter (1979)
25.6	54.6	1.66	1.67	1.67	A	Dwyer (1975)

[a] S.I. conversion: 1 kcal/day = 4.85×10^{-2} W.

[b] A, time-activity budget combined with published allometric equations for predicting *BM* and/or *SM*. B, time-activity budget combined with energy-balance studies on captive animals—from Table 1, measured metabolism = $2.2731W^{0.6055}$; W = body mass in g; "measured metabolism" comparable to Mosher and Matray's (1974) "resting metabolic rate," West and DeWolfe's (1977) "caged existence requirements," and Kushlan's (1977) "aviary existence metabolism." C, daily energy expenditure, $DEE = 2.4345W^{0.7052}$; W = body mass in g.

pendix), consumed in the field. Thus, an underestimate in the mean live weight of individual unidentified invertebrates of only 0.08 g (i.e. a live weight of 0.20 g rather than 0.12 g per individual—Appendix), a very likely possibility, could account for the remaining 13.5% discrepancy.

In summary, because of the similarity between model prediction and field estimation of *DEB* for White-tailed Kites and because most of the discrepancy between model prediction and field estimation of *DEB* for female kestrels is likely attributable to an error in our field estimates of weights of an important class of prey consumed, we feel that our energetics model provides a more realistic approximation of *DEB* for kestrels than the estimate based on observed food consumption. Because of errors in temperature inputs to the energetics model, however, we feel the *DEB* in Table 4 for 119-g kestrels is too high. Although we have no means of providing corrected estimates of the temperature inputs other than those previously indicated, we can predict limits. Thus, the value in Table 4 is considered to be the upper limit. The lower limit would occur if kestrels roosted at night under conditions of thermalneutrality.

At thermalneutrality, equation (8) predicts T_{na} for a 119-g nonpasserine to be 19.9°C (at thermalneutrality $T_{na} = T_{lc}$); under these conditions T_a would be 16.0°C and *DEB* 46.0 (2.23 W)/bird. The value we postulated earlier (48.7 kcal [2.36 W]/bird) lies almost midway between these limits, and in the absence of a better prediction is accepted as the most reasonable approximation of *DEB* for female kestrels wintering in coastal northwestern California.

If the *DEB* just approximated for female kestrels is accepted as a standard for birds weighing 119 g and if the *DEB* estimated by food consumption is accepted as a standard for kites weighing 331 g, it is possible to evaluate the predictive accuracy of the two versions of our energetics model relative to the predictive accuracy of other models (Table 6). Accordingly, equations (1) and (10) and the model of Holmes

et al. (1979) are most accurate, predicting values averaging within 5.0% of the mean standard value. The models of Mosher and Matray (1974) and King (1974) over-approximated the mean standard value by 14.8 and 36.9%. The remaining models under-approximated the mean standard value by 10.3–49.5%. Thus, it may be concluded that the two versions of our energetics model approximate the expected energy expenditure of the two falconiforms wintering in coastal northwestern California as accurately as the most accurate of other models evaluated and more accurately than most models evaluated. We wish to emphasize that the foregoing comparisons are offered not as an attempt to affirm or refute the validity of energetics models other than ours, but rather as an indication of the applicability of a group of models to predict energy expenditure of a specific taxon of animals living under a specific set of environmental conditions.

ACKNOWLEDGMENTS

We thank James A. Gessaman for permission to use unpublished information on the energy expenditure of an American Kestrel flown in a wind tunnel. We also thank J. A. Gessaman, Eugene A. LeFebvre, and William R. Dawson for comments on an oral presentation of preliminary results of this study before the joint meeting of the Cooper and Wilson Ornithological Societies in 1975. We are very grateful to J. A. Gessaman and an anonymous reviewer for a much-needed review of this paper. Carl T. Benz, Erick G. Campbell, Theodore Snyder, William W. White, Jeffrey M. Gardetto, Donald Lee, Wallace Prestidge, Lyell Chittenden, Richard K. Willis, Jerome M. Thomas, and Michael A. Ferguson provided valuable assistance in the laboratory. Joel Coenenburg, James F. Miller, Jeffrey B. Froke, Larry K. Norris, John A. Beam, Grant Marcom, and Roger Guinee aided greatly in the field.

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APPENDIX. Average weight, calorific content, and number of prey consumed by female American Kestrels and White-tailed Kites wintering in northwestern California. Weights of small mammals are for eviscerated individuals; parenthetical values are weights of intact individuals.[a]

Prey	Mean live weight (g/individual)	Mean dry weight (g/individual)	Mean calorific content (kcal/g dry wt.)[b]	Mean number consumed/day	
				Kestrels (number prey = 1,533)	Kites (number prey = 168)
Lepidoptera	0.69	0.21	5.83	0.27	—
Orthoptera	1.10	0.39	5.61	0.31	—
Coleoptera	0.67	0.18	5.72	8.80	—
Lumbricidae	0.40	0.07	4.62	6.00	—
Unidentified invertebrates	0.12	0.05	5.72	31.11	—
Microtus californicus	26.6 (34.0)	9.58 (10.80)	5.00	0.34	2.80
Reithodontomys megalotis	7.1 (9.0)	2.62 (2.95)	5.00	0.09	0.30
Sorex vagrans	3.9 (4.9)	1.39 (1.60)	5.00	0.75	—
Fringillidae	20.0	6.00	6.00	0.05	—
Thamnophis sirtalis	11.7	3.98	4.10	0.12	—
Rana aurora	16.5	3.28	4.10	0.21	—
Hyla regilla	4.6	0.60	4.10	0.68	—

[a] Weights of small mammals were measured: *M. californicus*, $n = 177$; *R. megalotis*, $n = 64$; *S. vagrans*, $n = 14$. All other weights except unidentified invertebrates obtained from the literature (Collopy 1975). Weights of unidentified invertebrates visually estimated relative to size of identifiable invertebrates. Calorific data determined by calorimetry or from the literature (Collopy 1975). Daily consumption rates based on observations totaling 316.7 h for kestrels and 441.2 h for kites. Prey selection by kites verified by analysis of 76 pellets, which contained the skulls of 82 voles and 9 harvest mice.

[b] S.I. conversion: 1 kcal = 4.187 kilojoule (kJ).

CROWN COLOR AND DOMINANCE IN THE WHITE-CROWNED SPARROW

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ABSTRACT.—Wintering flocks of Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) consist of black-and-white crowned adults and brown-crowned hatching year birds. White-crowned birds are dominant to brown-crowned birds in free-living unmanipulated flocks. Premature development of the adult crown was effected in juveniles by plucking the crown feathers. Juveniles with induced black-and-white crowns gained high rank when introduced to a strange flock of juveniles and a strange flock consisting of both age classes, indicating that crown color and not age *per se* communicates social status. Disguised (plucked) juveniles reintroduced to their former flock, consisting of all brown-crowned juveniles, did not rise in the peck order. Thus, White-crowned Sparrows may use other cues (besides crown color) to recognize individuals. Previous experience takes precedence over crown color in determining hierarchies. The two-signal system of Gambel's Sparrow is compared with two-signal systems in other avian species, and the adaptive significance of hierarchies in Gambel's Sparrow is discussed. *Received 6 June 1979, accepted 15 April 1980.*

MANY migratory species of birds stay in flocks during migration and on their wintering grounds. Flocking individuals must compete with each other for available resources. The benefits of flock living must outweigh the costs of intraspecific competition, however, or flocking behavior would not be maintained. For example, flocks may: (1) provide many more eyes to detect predators, (2) provide members to deter predation by mobbing behavior, (3) confuse predators by the predator swamping effect, and/or (4) provide members with information about food sources (Bertram 1978).

Intraspecific competition by flock members may result in fighting, which may lead to injury and/or death. Natural selection may reduce actual fighting by the establishment of dominance hierarchies. The latter requires that dominants and subordinates recognize each other. This may be accomplished by morphological characteristics, subtle behavior patterns or postures, or recognizing stereotyped positions and feeding stations of flock members (Shields 1977, Pearson 1979). The correlation of certain plumage characteristics and dominance has been shown in a number of species, such as Chaffinches (*Fringilla coelebs*, Marler 1955a); Evening Grosbeaks (*Hesperiphona vespertina,* Balph et al. 1979); White-throated Sparrows (*Zonotrichia albicollis*, Harrington 1973, Hailman 1975, Ficken et al. 1978); Dark-eyed Juncos (*Junco hyemalis*, Balph et al. 1979, Ketterson 1979a); Harris' Sparrows (*Z. querula*, Rohwer 1975, 1977); and Red-winged Blackbirds (*Agelaius phoeniceus*, Rohwer 1978).

Rohwer (1975: 607) called attention to two forms of plumage variability in winter-flocking species, polymorphic (e.g. Harris' Sparrows or juncos) and dichromatic (e.g. Chaffinches or White-throated Sparrows). Different races of the White-crowned Sparrow (*Zonotrichia leucophrys*) may fall into one or the other category. The sedentary subspecies *Z. l. nuttalli* is polymorphic for crown color circumannually, because yearlings often breed in various stages of incompletely molted crowns (Blanchard 1941, Banks 1964, Ralph and Pearson 1971). Winter flocks of the migratory

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TABLE 1. Correlation of age class (determined by crown color) and success in aggressive encounters in free-living White-crowned Sparrow flocks. Numbers in the table are actual counts of encounters observed.

Location	Age class[a]			
	A > A	A > J	J > A	J > J
UNBAITED FLOCKS				
Los Angeles (Arcadia) Arboretum	4	22	0	8
Occidental College (1976)	14	31	0	31
Palos Verdes	7	22	0	1
Totals	25	75	0	40
BAITED FLOCKS				
Eagle Rock	2	15	8[b]	29
Occidental College (1978)	49	62	2	6
Occidental College (1979)	36	10	0	4
Totals	87	87	10	39

[a] A = adult; J = juvenile; > indicates outcome of encounters with the winner to left of the symbol and loser to the right.
[b] Probably one juvenile attacking the same adult repeatedly.

subspecies *Z. l. gambelii* (= Gambel's Sparrows), the subjects of this paper, are dichromatic for crown color. Adults have black-and-white crowns and hatching year birds have brown crowns.

Balph et al. (1979) have stressed the need for information on the behavior of a variety of winter flocking birds before a generalized model of status signalling can be generated. We studied winter flocks of Gambel's Sparrows in the field and in captivity to answer the following questions: (1) How does status signalling apply to Gambel's Sparrows exhibiting dichromatism of plumage? Are white-crowns dominant over brown-crowns? (2) Is a white-crowned bird dominant over a brown-crowned bird because the white-crown confers dominance to an individual, or is it dominant simply because it is older and more experienced?

METHODS

Gambel's Sparrows winter in large flocks in southern California, arriving about mid-September or early October (Blanchard and Erickson 1949). These flocks consist of individuals of two distinct crown colors. We studied social behavior in free-living *Z. l. gambelii,* looking for a correlation between crown color and dominance. Captives were sexed by laparotomy, color-banded for individual recognition, and housed in outdoor aviaries (2 × 2 × 3 m). Birds were starved for 3–5 h, and peck orders were then determined by counting the number of times each individual displaced other members of a group at a small feeder. Only active displacements involving obvious supplants, aggressive displays, or combat were considered.

Plucking the crowns of juvenile White-crowned Sparrows induces the development of adult-colored crowns several months before the normal onset of prenuptial molt (Emlen 1938, Morton 1962). We plucked the crowns of some juveniles, held them in isolation until adult crowns grew in (6 weeks), and then introduced them to captive groups of other conspecifics familiar or unfamiliar to them. This enabled us to test the respective roles of crown color, age *per se,* and previous experience in determining positions in the dominance hierarchy.

RESULTS

FIELD OBSERVATIONS

Adults invariably dominated juveniles in naturally foraging winter flocks of Gambel's Sparrows (all of 75 encounters recorded at three locations) (Table 1). Juveniles occasionally won encounters with adults when flocks were attracted to baited areas

TABLE 2. Peck order among captive *Zonotrichia leucophrys gambelii* as determined by aggressive encounters.[a]

	Loser							
Winner	A1 M	A2 M	A3 M	J1 M	J2 M	J3 F	A4 F	J4 F
A1	—	23	10	16	15	13	6	9
A2	1	—	15	20	36	13	2	12
A3	3	4	—	19	19	9	17	4
J1		1	1	—	29	19	17	15
J2		1	4	1	—	15	5	6
J3		1	1			—	14	11
A4	1	24			1	1	—	5
J4								—
A1	—	18	18	20	72	31	9	12
A2		—	33	15	64	33		14
A3			—	24	38	10	12	12
J1				—	109	46	47	20
J2					—	30	23	17
J3						—	15	14
A4		38					—	18
J4								—

[a] A = adult; J = juvenile; M = male, F = female. Birds are listed vertically and horizontally in order of dominance rank. Top ranking bird located at the top and left, lowest ranking bird at the bottom and right. Numbers in table are actual counts of wins. Gaps in the table indicate no encounters observed. Each aggressive encounter is tallied to the right of the winner (found in the vertical "winners" column) and below the loser (found in the horizontal "losers" column). The term "stabilization" refers to a sequence of observations when dominance reversals (numbers below the diagonal) are rare or have ceased, usually 2–4 weeks following introduction of unfamiliar birds. Upper part of the table shows the hierarchy before stablization (data from 12 to 24 February are pooled). Lower part of the table shows the stablized peck order (26 February–17 March). Note the dominance triangle involving A2 and A4, i.e. A4 scored 38 wins over A2 but lost to all other birds.

(10 of 87 encounters), but most instances appeared due to one juvenile that repeatedly chased the same adult. Data were collected from six flocks residing at three different localities, indicating a general tendency for adults to dominate juveniles in free-living flocks.

As Gambel's Sparrows are sexually monomorphic, we had no indication of the role of sex within age classes in dominance hierarchies, hence the laboratory studies that follow.

LABORATORY STUDIES

Sex versus age.—In some fringillids males are dominant to females in wintering flocks (Knapton and Krebs 1976, Balph 1977), whereas in others females are dominant over males (Hinde 1955–1956, Thompson 1960, Coutlee 1967). There is some anecdotal evidence that an adult female *Z. l. nuttalli* dominated adult males, which in turn usually dominated other females and juveniles (Stewart and Darling 1972). The dominant female was observed singing repeatedly. In the related Rufous-collared Sparrow (*Z. capensis*), females are dominant to males in the nonbreeding season (Smith 1978). It was desirable, then, to examine the role of sex in dominance hierarchies of *Z. l. gambelii* under controlled laboratory conditions.

Two groups (only one is illustrated) composed of adults and juveniles were sexed by laparotomy and put in aviaries (Table 2). Upon initial introduction of birds into an aviary, instances of combat and dominance reversals were frequent. When these became very infrequent or ceased to occur, the peck order was considered stabilized (Table 2). Hierarchies were for the most part linear. Adults tended to dominate juveniles, supporting field observations, and males tended to dominate females. A peck-triangle between adult female A4 and adult male A2 is evident in Table 2.

TABLE 3. Peck order among six juvenile males.[a]

	Loser					
Winner	*P1	*P2	*P3	C1	C2	C3
*P1	—	3	18	12	18	15
*P2		—	10		4	5
*P3			—	19	16	6
C1		3		—	23	6
C2				2	—	18
C3						—

[a] * = plucked, full black-and-white crown; C1 = 40% black-and-white, 60% brown crown; C2 = 50% black-and-white, 50% brown crown; C3 = all brown crown. Data were taken from 17 March to 2 April.

Peck-triangles have been described for a number of fringillid species (Wessell and Leigh 1941, Tordoff 1954, Marler 1955b, Sabine 1959).

Crown color versus age: plucking experiments.—Are adults dominant over juveniles by virtue of their age and experience alone, independent of crown color, or may the white crown act independently of age as a dominance-conferring signal? To answer this question we set up a group of six juvenile males. Because birds of one sex were involved, the potentially confounding variable of intersexual dominance was avoided. Before introduction into the experimental aviary, these were housed as two separate groups of three each. One group was plucked and developed full adult crowns (P1, P2, P3 in Table 3). Two members of the unmanipulated group (C1, C2) grew some black-and-white crown feathers due to adventitious or prenuptial molting. When placed in an experimental aviary the birds formed a stable hierarchy, with black-and-white crowned birds on top (Table 3). Crown color and high dominance status occurred independently of age class.

A second group was set up consisting of three adult males, one adult female, two juvenile males, and two juvenile females. These birds formed a stable, almost linear hierarchy in which the three adult males ranked highest (Table 2). One adult male (A2) formed a dominance triangle with the adult female (A4). The same female was subordinate to three juveniles. We then induced premature coronal ecdysis in three additional juvenile males and a female by plucking their crowns and isolating them until their adult crowns grew in. These four juveniles with adult crowns and a fourth brown-crowned juvenile (a control) were introduced to the established group described above.

A dominance advantage due to previous residence in a cage has been reported for a number of avian species (Tompkins 1933, Schjelderup-Ebbe 1935, Collias 1944, Guhl and Ortmann 1953, Brown 1975), yet plucked juvenile males P1 and P2 obtained the alpha and third-rank positions upon introduction to an aviary-acclimated flock (Table 4). Plucked female P3 dominated all normal-crowned juveniles but was subordinate to all other adult-crowned birds. Brown-crowned juvenile C1, held earlier with the plucked group as a control, molted after introduction to the flock and developed a full adult crown by May. With the onset of molt, C1 sang and displayed with higher frequency and rose in status to the beta position. This was the only instance of crown-molt occurring during the experiment.

Crown color versus familiarity.—We have established that adult crown color is associated with high dominance status when strange individuals meet an established flock. Are brown-crowned flock members conditioned to accept adult-crowned birds

TABLE 4. Peck order after introduction of plucked juveniles.[a]

	Loser										
Winner	*P1 M	*C1 M	*P2 M	A1 M	A2 M	A3 M	*P3 F	J1 M	J2 M	J3 F	A4 F
*P1	—	6	11	2	7	17	5	4	9	8	2
*C1		—		3	5	1	5	9	2	3	2
*P2			—	4	2	5	5		1	3	2
A1				—	7	8	5	3	1	3	1
A2					—	9	6	1	3	4	1
A3						—	12	8	6	2	1
*P3						1	—	3	3	1	
J1								—	9	3	1
J2									—	1	3
J3										—	2
A4			1		8		2				—

[a] *P = plucked; C = molted. Three plucked juveniles (P1, P2, and P3) with full black-and-white crowns and one unmanipulated juvenile (C1), who later molted and developed the adult crown, were introduced from their aviary into the aviary of the established group in Table 2. The peck order before stabilization (19 March–12 April) is not illustrated. Data after stabilization are presented (18 April–7 May). Bird J4, who appears in Table 2, died on 16 April.

as dominant due to previous attacks from adults, or does the adult crown *per se* confer dominance status on an individual? To answer this question we set up a group of 10 juveniles (five males, five females). For reasons unclear to us, the peck order in this group failed to stabilize completely. Several dominance triangles were evident and reversals were many (Table 5A). We removed what we considered the four lowest ranking individuals, plucked their crowns, and isolated them until adult crowns grew in. These birds were then reintroduced to their former group. One plucked and one unplucked female died. The resultant peck order assumed more order than previously (Table 5B). The triangle between M4 and F4 disappeared. The triangle between F3 and M1 remained. One and two reversals were scored for M5 over M1 and M2, respectively. None of the plucked birds (M5, F3, F4), however, rose appreciably in the flock hierarchy. The advantage gained by previous domination of an individual appears to take precedence over any advantage gained by having a black-and-white crown *per se*.

DISCUSSION

Our field observations of Gambel's Sparrow flocks indicate that black-and-white crowned birds (adults) dominate brown-crowned birds (juveniles). Our laboratory studies reveal that in undisguised flocks males are generally dominant over females within each age class (e.g. Tables 2, 5A). These data are similar to those for other finches (Marler 1955a, Knapton and Krebs 1976, Balph et al. 1979).

Intraspecific competition in wintering Gambel's Sparrow flocks appears to be reduced in a number of ways. (1) Each wintering flock occupies an exclusive home range (Mewaldt 1964). (2) Sex ratios vary geographically (King et al. 1965). Because males tend to dominate females, intersexual competition may be reduced, as the sexes need not occur together in a locality where resources may be in short supply (Ketterson 1979b). (3) Dominance hierarchies are formed, with adults dominating juveniles: because our field observations of unmanipulated flocks at several localities reveal that juveniles do not usually dominate adults (Table 1), Gambel's Sparrow hierarchies must be classified as despotic.

TABLE 5. Fourth group—dominance hierarchy, A. 27 October–25 November. All juvenile (brown) crowns. B. After reintroduction of low-ranking plucked birds, 30 December–12 January.[a]

A.	M1	M2	M3	M4	F1	F2	M5	F3	F4	F5
M1		33	12	16	11	31	16	11	17	5
M2			26	11	8	4	8	11	14	3
M3				14	11	29	13	8	9	6
M4	13		2		15	4	1	9		14
F1	1	4	8			3	4	7	13	4
F2		24	2	16	10		22	10	16	5
M5				16	3			11	15	2
F3	8									
F4				8		1		3		2
F5						1				

B.	M1	M2	M3	M4	F1	*M5	*F3	*F4
M1		26	29		14	13		6
M2			19	17	15	8	13	6
M3				18	10	8	10	2
M4					6	10	12	19
F1						17	21	14
*M5	1	2					12	5
*F3	15							5
*F4								

[a] * = plucked. F2 and F5 died.

Some reversals of juveniles over adults were seen in our baited and captive flocks. Perhaps by our setting out bait, birds that normally avoid each other come together, allowing the observer to record otherwise rarely occurring reversals. Attracting birds to a common food source also increases the chances of temporary reversals due to "mistakes," as suggested by Dilger (1960). Among captives, hunger may be at least partly responsible for temporary reversals, as subordinates may challenge dominants more readily in time of need (Wiley and Hartnett 1979). Some juveniles may be dominant over some adults, such as the adult female being subordinate to the juveniles (Table 2) and what was apparently one juvenile consistently attacking the same adult in one free-living baited flock (Table 1).

Our plucking experiments have demonstrated that crown color enables individuals to achieve high dominance status. Prior experience appears to take precedence over crown color, however, as plucked birds reintroduced to their former flock mates did not move up in the hierarchy. Clearly, birds must recognize individuals by more than one cue. Cues may be behavioral, postural, or simply the positions of individuals relative to each other (Shields 1977, Pearson 1979). Possibly subordinate disguised individuals reintroduced to their former flock mates assume subtle "submissive" postures and are thus recognized by their former dominant flock mates. Alternately, flock mates may recognize each other as individuals, possibly by subtle plumage characteristics (Shields 1977).

The highly conspicuous visual cue, the white crown of the adult sparrow, may serve as a conditioned reinforcer. Perhaps fledglings are attacked by adults about the time of self-sufficiency, forcing them to disperse or join flocks of juveniles that form before migration. These juveniles are conditioned to perceive black-and-white crowned (adult) individuals as aggressive and dominant, avoiding the latter or assuming submissive postures. They are thus accorded low rank in the flock as a result of their learned (conditioned) behavior. Juveniles may thus react to disguised

strangers with subtle submissive signals, encouraging the strangers to attack and achieve dominance status.

The fact that disguised juveniles were dominant to adults (Table 4) is surprising. Rohwer and Rohwer (1978) noted that subordinate Harris' Sparrows dyed to look like dominants did not ascend in rank but were socially persecuted. On the other hand, dyed birds injected with testosterone increased in social status. Our plucking experiments involving two age classes were conducted in mid-April to early May and may not be comparable to data collected earlier in the year. It is conceivable that our plucked birds were also receiving increasing testosterone titres from their gonads due to longer natural photoperiods. They were, in fact, behaving like Rohwer and Rohwer's (1978) disguised and testosterone-injected birds.

Dominance hierarchies in Gambel's Sparrows are maintained by a two-signal system that differs in a number of ways from other two-signal systems studied to date. In the related White-throated Sparrows, bright-crowned birds are also dominant to brown-crowned birds (Harrington 1973, Ficken et al. 1978). Crown dichromatism in Gambel's Sparrows disappears after juveniles molt into adult plumage; however, dichromatism in White-throated Sparrows is permanent and genetically determined (Thornycroft 1975, Ficken et al. 1978). Crown dichromatism serves in maintaining order in winter flocks of Gambel's Sparrows (this study), whereas that in White-throated Sparrows also serves in recognition of morphs in a disassortative mating system (Lowther 1961).

In Gambel's Sparrows dichromatism is age related, whereas in Chaffinches and Evening Grosbeaks it is sex-related. In Gambel's Sparrows dichromatism reduces aggression between age classes, whereas in Chaffinches and Evening Grosbeaks it reduces intersexual aggression (Marler 1955b, Balph et al. 1979). Marler's (1955a) disguised subordinate female Chaffinches in established flocks rose in social status. Disguised low-ranking Gambel's Sparrows in established flocks did not rise in the hierarchy (Table 5B). Marler's data also differ from Rohwer's (1977), whose disguised Harris' Sparrows not only did not rise in status but were socially persecuted.

Studies of other avian species have demonstrated or suggested that high dominance rank provides an increased chance of survival (Murton et al. 1966; Fretwell 1968, 1969; Smith 1976). Rohwer and Rohwer (1978) found that dominant Harris' Sparrows occupied richer winter habitats than subordinates. In intraspecific competiton for food and survival within winter flocks of Gambel's Sparrows, selective pressure would favor the black-and-white crowned birds. Why, then, does natural selection maintain the juvenile brown crown? The benefits of living in a flock must far outweigh the cost of being relegated to a subordinate position. In species in which juveniles pass through a period of surbordinate status during development, low status would better ensure an individual's chance of survival if it were allowed to stay with the group rather than if it wintered by itself. Because subordinates do not challenge the social order, the flock functions with little fighting, and constructive activities are allowed to proceed (Brown 1975).

Adult Gambel's Sparrows are veterans of one or more migratory journeys and return to winter in the same area annually (Mewaldt 1964). Hatching year birds appear to learn the characteristics of their wintering area in their first winter (Ralph and Mewaldt 1975). It has been suggested that the more cryptic brown color may help camouflage inexperienced juvenile White-crowned Sparrows from predators (Ralph and Pearson 1971).

ACKNOWLEDGMENTS

We thank Martha Balph, John Davis, Stephen Emlen, Martin Morton, Lewis Petrinovich, and Sievert Rohwer, who read earlier versions of this paper and made helpful criticisms.

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THE INSULATION IN NESTS OF SELECTED NORTH AMERICAN SONGBIRDS

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ABSTRACT.—The heat flux (Q_n), thermal conductance (h), thermal conductivity coefficients (k), and density (based on light penetration) of 66 nests representing 11 species of North American songbirds are presented. Well-insulated nests have relatively small values of Q_n (0.151 to 0.167 W) and h (3.53 to 3.74 W m^{-2} °C ^{1}). The nest wall is either solid or so dense that it prevents light from penetrating it (0 lux ^{1}). Poorly insulated nests have relatively high values for Q_n (0.364 to 0.373 W) and h (9.95 to 12.35 W m^{-2} $°C^{-1}$), and are exceedingly porous (0.39 to 0.72 lux^{-1}). Nests with moderate insulation have values of Q_n (0.230 to 0.293 W) and h (4.37 to 6.15 W m^{-2} $°C^{-1}$) that are intermediate in size. Some of these nests are moderately porous (0.0016 to 0.0054 lux^{-1}); others are not (0.00002 to 0.0013 lux^{-1}). Many facets of the nest (diameter of the entrance; depth, volume, and surface area of the nest cavity; thickness of the nest wall; density of the nest wall) influence Q_n and h, but generally weakly. The most important of these is nest density. Values of k for nests range between 52 and 239 × 10^{-3} W m^{-1} $°C^{-1}$, but are usually intermediate between those of animal fur and wood. *Received 10 December 1979, accepted 4 June 1980.*

DURING incubation, the temperature of the clutch is between 34 and 38°C (Huggins 1941, Drent 1975). In order to maintain this narrow temperature range, incubating birds must match the heat lost from the clutch with an equivalent input of heat. The quality of the nest, its location, and its orientation with respect to environmental factors therefore figure importantly in reducing the energetic costs of incubation.

Numerous studies illustrate the significance of the nest site. Many avian species orient their nests to obtain the warmth of the morning sun (Dorst 1962, Hadley 1969, Orr 1970, Riehm 1970, Walsberg and King 1978a). Others situate the nest so that it is shaded during the hottest part of the day, or out of the sun entirely (Maclean 1970). Still others place the nest on the leeward side of vegetation to minimize the impact of wind (Hadley 1969, Schaefer 1976). It is well known that hummingbirds station their nests beneath leaves or overhanging limbs and in so doing appreciably reduce radiational heat exchange with the sky and the sun (Calder 1973a, Southwick and Gates 1975). Cactus Wrens (*Campylorhynchus brunneicapillus*) orient the entrance of the nest so that it faces away from cool winds early in the breeding season, but into warm winds late in the breeding season (Ricklefs and Hainsworth 1969).

Some species also vary the location of the nest in characteristic ways during the breeding season (Nice 1937, Walkinshaw 1944, Horvath 1964, Taylor 1965, Holcomb and Twiest 1968, Ricklefs and Hainsworth 1969) for reasons that are largely unknown. However, in at least one species (the Rufous Hummingbird, *Selasphorus rufus*), the changes ameliorate the microclimate around the nest and have an energy-sparing effect on the incubating female (Horvath 1964).

The quality of the nest is also important in reducing the energetic costs of incubation and conserving heat. Zoogeographical differences in the size and composition of nests illustrate this nicely and have been documented especially well among hummingbirds (Pearson 1953, Wagner 1955, Corley Smith 1969), weaver finches (Collias and Collias 1971), and several Canadian songbirds (Horvath 1963).

Yet, for all of the qualitative information available, there is still very little quan-

titative information about nests in the literature. As Drent (1975: 366) observes, "that nests often provide crucial protection from climatic extremes has perhaps seemed so obvious that little critical research has been done in this area." To our knowledge, there are only four publications in which the insulation of the nest is quantified in physical terms. The earliest is that of Palmgren and Palmgren (1939). These investigators attached nests to the surface of a flask containing hot water and measured how rapidly the water cooled. They discovered differences among the nests of 15 species of European passerines that correlated with the distribution of the birds during the breeding season. For example, Bramblings (*Fringilla montifringilla*), which breed in northern Europe, had more highly insulated nests than congeneric Chaffinches (*F. coelebs*), which breed farther south.

The other three studies appeared more recently. In 1977, Whittow and Berger published a note describing the thermal conductance of four nests of the honeycreeper "Amakihi" (*Loxops virens virens*). In 1978, Walsberg and King contributed two papers dealing with nests of Red-winged Blackbirds (*Agelaius phoeniceus*), Willow Flycatchers (*Empidonax trailii*), and Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*).

To this small collection, we now add new data for the nests of nine more North American songbirds and additional data for two of the songbirds studied previously.

Data such as these are of considerable practical value. Nests are often fixed in composition and can therefore be used by avian taxonomists to separate closely related species (Collias 1964). If the physical properties of the nests are also fixed and different, such a tool may be even more powerful. On the other hand, the composition and structure of nests are strikingly variable in many cases. This variation is the raw material on which natural selection operates to increase a species' breeding range and season (White and Kinney 1974). If we can define the limits of this variation in concrete physical terms, we may be able to predict a priori the ease with which a species can extend its range or breeding season under given climatic conditions.

The quality of the nest also influences the behavioral patterns of nesting birds. White and Kinney (1974), for example, have shown that the nest attendance of Village Weaverbirds (*Ploceus cucullatus*) is inversely related to the insulation of the nest. Riehm (1970) has demonstrated that absences of up to 30 min do not adversely affect the clutch of the Long-tailed Tit (*Aegithalos caudatus*) because the nest cavity is so warmly lined with feathers. Quantitative data on nests may enable us to explain what might otherwise appear to be maladaptive behavior on the part of incubating birds.

Finally, the quality of the nest can significantly reduce the energetic costs of incubation. For example, an incubating Broad-tailed Hummingbird (*Selasphorus platycercus*), one-half of whose body is exposed above the nest rim, expends 41–62% more energy thermoregulating than a female only one-quarter exposed (Calder 1973a). It is estimated that an increase in the thickness of the nest of only 0.05 cm reduces the energy requirements of incubating hummingbirds by 13% (Smith et al. 1974). White-crowned Sparrows in the nest expend 10–11% less energy than conspecifics roosting nearby (Walsberg and King 1978b). We need quantitative information about nests so that we can accurately determine the costs of incubation under prescribed conditions. The point is illustrated by the model of nesting energetics developed by Walsberg and King (1978a,b), in which the thermal conductance of the nest is used to calculate its thermal resistivity.

METHODS

Physical relationships.—We express insulation in terms of the nest's heat flux (Q_n, expressed in W), which is measured with a heat flux transducer, and thermal conductance (h, expressed in W m^{-2} $°C^{-1}$), which can be calculated from Q_n, the temperature gradient across the nest wall, and the area of the nest cavity. In addition, we include the thermal conductivity coefficient (k, expressed in W m^{-1} $°C^{-1}$) of the nest. The latter indicates the material to which the nest is comparable in terms of insulation (values of k are available for many materials including metals, glass, soil, wood, water, human tissue, fur, and air). Thermal conductance values are especially useful for comparing heat flow through unit areas of nests of different species under similar ambient conditions, and for modeling nesting energetics.

Thermal conductance can be calculated using the equation $h = Q_n/(A)(T_i - T_o)$, in which Q_n is the heat flow across the nest, A is the area of the nest cavity across which this heat flows, and $(T_i - T_o)$ is the difference between the temperature of the nest cavity and the surface of the nest, respectively.

The thermal conductivity coefficient is more difficult to determine and requires that we make the following simplifying assumptions: (1) the nest cavity is spherical in shape, (2) its walls are uniformly thick, and (3) wall thickness is equal to the thickness of the floor of the nest. These assumptions are subject to more or less error, depending on the nest, but as first approximations they allow us to compute k by rearranging the equation for conductive heat transfer across a sphere (Birkebak 1966):

$$Q_n = (4\pi)(R_iR_o)(T_i - T_o)(\delta)(k)/(R_o - R_i).$$

R_i is the radius of the sphere of which the nest cavity is a part. R_o is the radius of the nest (i.e. R_i + the thickness of the floor of the nest). T_i is the temperature of the floor of the nest cavity. T_o is the temperature of the surface of the nest directly opposite the point where T_i is measured. δ is a constant whose size is related to the portion of the sphere across which heat flow takes place: for a hemisphere, $\delta = ½$; for any other section of the sphere, δ is the surface area of the nest cavity across which heat flow occurs divided by the total surface area of the sphere of which the nest cavity is part.

Experimental apparatus.—To measure Q_n, each nest was suspended from the ceiling of a constant environment chamber (Percival, Boone, Iowa) with 4-ply, 2.54-cm mesh orchard netting (Durex Anti-Bird Mesh, Apex Mills, Inc., New York, N.Y.). The chamber maintained a temperature of 14.9 ± 0.3°C ($\bar{x} \pm CI_{95}$) and was baffled to minimize air flow around the nest. A heat flux transducer (Thermonetics Corp., San Diego, Calif.), with dimensions of 2.86 × 2.86 × 0.16 cm (length × width × thickness, respectively) and a constant of 62.8 W m^{-2} mV^{-1} (calibrated by the manufacturer), was placed on the floor of the nest cavity and connected with a microvoltmeter outside the chamber. The thermal conductivity coefficient of this plate is 0.20 W m^{-1} $°C^{-1}$. Consequently, the maximum heat flux across it was 0.66 W or 0.44% of the minimal heat flux value that we obtained for the nests. It measured Q_n directly. The temperature gradient across the nest was measured with thermisters (model 44004, Yellow Springs Instrument Co., Yellow Springs, Ohio) attached to the center of the nest cavity beneath the heat flux plate and to the external surface of the nest directly opposite. An additional thermister was suspended in the chamber at nest level so that we could monitor chamber temperature for uniformity during each determination of Q_n. All three thermisters were connected with a 4.5-digit multimeter (model 245, Data Precision, Wakefield, Mass.) outside the chamber.

Our source of heat in the nest cavity was a balloon containing 40 to 70 ml water, depending on the nest. This volume did not visibly distort the nest cavity, although it filled it. The balloon was equipped with a thermister and a 1.0 Ω, 5.0 W resistor. The latter was the heater and was connected to a power supply, the voltage of which could be varied by hand. Enough power was supplied to the resistor to bring the water in the balloon to 37°C (approximate incubation temperature; measured by the thermister) and to maintain it there once steady state was established. Spaces between the balloon and the rim of the nest were filled with small packages of loose insulation and a 2.0-cm lid of styrofoam was then placed on top of the nest.

To determine the area of the nest cavity across which heat was conducted from the balloon, we laid strips of paper in the nest and cut them to fit the exposed surface of the balloon. The area of the strips was obtained later using a planimeter.

A pilot study in which we made several independent measurements of heat flux for the nest of an American Robin (*Turdus migratorius*) indicated that the variation between determinations was small. The $\bar{x} \pm CI_{95}$ was 0.207 ± 0.058 W. The coefficient of variation for these determinations was 10.1%.

Nest density.—We quantified the density or weave of the nests in terms of the amount of light that could penetrate them. Each was placed over an opening in the top of a cardboard box. The inside of the

box was otherwise light-tight and painted black. A photometer was mounted on the floor of the box below the opening. An incandescent bulb was then lowered into the nest cavity to a known distance from the photometer.

Light penetration is expressed as the reciprocal of the difference between the light striking the photocell from this distance in the presence (L_{np}) and absence (L_{na}) of the nest. Because a porous nest permits considerable light to enter the box, the difference ($L_{na} - L_{np}$) is small, but the reciprocal (or light penetration) is large. Conversely, a densely woven nest permits little light to enter the box, ($L_{na} - L_{np}$) is large, and the reciprocal is small. Nests with solid linings were arbitrarily assigned a value of 0 lux^{-1} although $1/(L_{na} - L_{np})$ is not 0.

Light penetration is an admittedly crude measure of nest density and involves factors, such as the absorptivity, reflectivity, and transparency of nest material, that are not directly relevant to the structure's insulation. Nonetheless, this measure of density correlates significantly with the heat flux and thermal conductance of the nests and we present it as an initial method of defining nest density in quantitative terms, which may be refined later.

Nests.—We have measured the Q_n (and from that computed k and h) of 66 nests representing 11 species of North American songbirds. The nests were generally in prime condition, having been obtained during incubation or immediately after the young fledged. The species are the Loggerhead Shrike (*Lanius ludovicianus*), American Robin, Field Sparrow (*Spizella pusilla*), Song Sparrow (*Melospiza melodia*), Mountain and Eastern White-crowned Sparrows (*Zonotrichia leucophrys oriantha* and *leucophrys*, respectively), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Grey Catbird (*Dumetella carolinensis*), Red-winged Blackbird (*Agelaius phoeniceus*), Northern (Baltimore) Oriole (*Icterus galbula*), and Yellow Warbler (*Dendroica petechia*). All but one of these species has nests that are open bowls, the exception being the oriole. All except the Eastern White-crowned Sparrow (and occasionally the Mountain White-crowned Sparrow) build nests in vegetation above ground.

Results

The thermal properties of the nests are summarized in Table 1. Nests of Loggerhead Shrikes and American Robins are good insulators, having relatively small values for heat flux and thermal conductance. The nest wall is either solid or so densely woven that it prevents light, and by inference moving air, from penetrating it. At the other extreme are nests of Rose-breasted Grosbeaks and Field Sparrows, which are relatively poor insulators. They have high values for heat flux and thermal conductance and are exceedingly porous. Nests of the remaining species lie between these extremes.

The thermal conductivity coefficients for nests of these 11 songbirds range from 0.052 to 0.239 W m^{-1} $°C^{-1}$. These values lie between the coefficients of animal fur (0.038) and dry soil (0.335). Most of them, however, are between those of animal fur and wood (0.126), which suggests that nests are able to trap air for insulation, but not as effectively as fur.

Many facets of the nest's structure appear to influence its heat flux and thermal conductance. These include the diameter of the nest entrance; the depth, volume, and surface area of the nest cavity; the thickness of the floor and wall of the nest; and nest density, as measured by light penetration. Correlation coefficients between these characteristics and Q_n or h are generally small (significant values of r range between 0.24 and 0.71), suggesting that no single factor is responsible for the quality of the nest. The most influential appears to be nest density, for which r is +0.54 and +0.71 when correlated with Q_n and h, respectively ($P < 0.001$, df = 61). Nests with high insulation values are not penetrated by light. Those of moderate insulation value usually, but not always (see footnote b in Table 1) allow some light to pass through. Nests with little insulation value barely impede the passage of light.

TABLE 1. Insulation of nests of 11 passerine species.[a]

Species	n	Heat flux (Q_n) (W × 10^{-3})	Thermal conductance (h) (W m^{-2} °C^{-1})	Thermal conductivity coefficient (k) (W m^{-1} °C^{-1} × 10^{-3})	Light penetration[b] (lux^{-1} × 10^{-5})
Loggerhead Shrike	6	151.44 ± 31.11 a	3.74 ± 0.94 a	65.69 ± 16.04 a	0 a
American Robin	6	168.18 ± 38.06 ab	3.53 ± 0.53 a	70.34 ± 17.46 a	0 a
Red-winged Blackbird	6	229.56 ± 103.37 ab	4.75 ± 1.34 a	79.96 ± 17.88 a	2 (5) a
Mountain White-crowned Sparrow	13	246.69 ± 35.63 b	4.37 ± 0.70 a	76.62 ± 10.93 a	132 a
Song Sparrow	6	257.49 ± 83.23 bc	6.15 ± 1.26 a	96.46 ± 24.12 a	462 (5) a
Northern Oriole	6	258.20 ± 32.74 bc	5.53 ± 0.76 a	70.92 ± 13.15 a	545 a
Grey Catbird	6	258.87 ± 74.44 bc	4.62 ± 1.09 a	92.99 ± 18.30 a	2 a
Eastern White-crowned Sparrow	6	281.90 ± 81.43 bc	4.38 ± 1.24 a	57.36 ± 13.15 a	160 a
Yellow Warbler	2	293.08	4.45	51.79	440 (1)
Rose-breasted Grosbeak	4	364.25 ± 90.02 c	12.35 ± 7.88 b	238.65 ± 108.56 b	39,021 b
Field Sparrow	5	372.63 ± 83.11 c	9.95 ± 2.97 c	88.26 ± 25.20 a	71,722 c

[a] Values in the table are $\bar{x} \pm CI_{95}$. Sample size appears in parentheses if it differs from the sample size indicated on the left side of the table. In each column, means *not* followed by the same letter differ at the 0.05 level of significance (Student-Newman-Keuls test). Data for the Yellow Warbler were not included in the analyses.

[b] No light penetrated the nests of 5 of the 6 Red-winged Blackbirds and Grey Catbirds or 8 of the 13 nests of Mountain White-crowned Sparrows.

Discussion

If the data of Palmgren and Palmgren (1939) are recalculated as thermal conductance values (which requires that one use the area of their flask as A, initial water temperature as T_i, and ambient temperature as T_o; and translate changes in water temperature into W), the nests of 15 European songbirds can be shown to have thermal conductance values between 3.53 and 6.33 W m^{-2} $°C^{-1}$. It should be noted that these investigators measured the insulation of nests that were cooling, rather than under steady state conditions. This method fails to account for the storage of heat by the wall of the nest. Accordingly, our calculations of thermal conductance are only approximations. Nonetheless, the calculated values are similar to the range exhibited by the Amakihi (2.78 to 5.72, Whittow and Berger 1977) and 12 North American forms (3.02 to 4.77, Walsberg and King 1978a,b; 3.53 to 12.35, Table 1). The uniformity is striking given that the measurements were made by four different methods and are for songbirds in widely scattered geographical areas.

Among these species, thermal conductance has been measured on two separate occasions for Mountain White-crowned Sparrows and Red-winged Blackbirds. The similarity for nests of White-crowned Sparrows [4.12 and 4.37 W m^{-2} $°C^{-1}$ from Walsberg and King (1978a) and Table 1, respectively] is noteworthy given the fact that the nests of Walsberg and King are from Hart Mountain, Lake County, Oregon (42°30′N, 119°45′W; elevation = 1,890 m), whereas our nests are from Tioga Pass, Mono County, California (38°N, 119°W; elevation = 2,743–3,048 m).

The two values for nests of Red-winged Blackbirds [3.02 and 4.37 W m^{-2} $°C^{-1}$ from Walsberg and King (1978b) and Table 1, respectively] are significantly different. Several factors may account for this disparity. Birds studied by Walsberg and King nest in cattail marshes near Pullman, Whitman County, Washington (46°45′N, 117°15′W; elevation = 790 m), whereas our birds nest in weeds, shrubs, and trees bordering reservoirs and lakes in Armonk, Westchester County, New York (41°10′N, 73°40′W; elevation = 118 m). Nest height in Pullman was 51 to 153 cm; in Armonk, 61 to 170 cm. Nests were collected between 20 May and 5 June in Pullman, but between 25 May and 29 September in Armonk. Our nests were collected during incubation and after the young fledged. No information on this point is presented by Walsberg and King (1978b). Any or all of the above factors may contribute to the observed differences among nests in the two studies because (1) the nest cavity of the Red-winged Blackbird is significantly deeper if the nest is 107 cm or more above the ground than it is at lower heights, (2) there is a seasonal change in the nest height of this species, and (3) the young increase the dimensions of the nest during the brooding period (Holcomb and Twiest 1968). It is equally plausible, however, that we have documented real zoogeographical differences between isolated populations of *Agelaius*.

At any rate, the information presented above illustrates some of the factors that influence nest structure and presumably insulation. In some species, we should anticipate considerable variation in nest insulation because the composition or shape of the nest changes during incubation and brooding, either through the activity of the parents (Moynihan 1953, Frith 1956, Krüger 1965, Calder 1973b) or the nestlings (Holcomb and Twiest 1968, Calder 1973b, O'Connor 1975). O'Connor (1975) has pointed out that such changes may be common in species of songbirds with large broods and may be adaptive in that they prevent the young from overheating. If the relationships between nest dimensions and insulation presented above are ap-

plicable to songbirds generally, then alterations in the nest will affect its thermal conductance.

Nest insulation also depends on the materials with which the nest is fabricated [e.g. the correlation coefficient between the thermal conductance and the thermal conductivity coefficient of our nests is +0.80 ($P < 0.001$, df = 64)]. The selection of materials may in turn depend on what is available and on engineering problems associated with nest placement. Nickell (1958, 1965) has made extensive studies of nest materials and documented differences in nest morphology associated with nest site selection. Schaefer (1976) has recently described similar variations in the nests of Northern Orioles. Many Hawaiian songbirds use wool in the nest when it is available (van Riper 1977). Cliff Swallows (*Petrochelidon pyrrhonota*) select mud with a high sand and low silt content for the nest, whereas Barn Swallows (*Hirundo rustica*) mix grass, hair, and feathers into the mud used for their nests (Kilgore and Knudsen 1977).

The insulating qualities of nests may also depend on where they are found in the field. There are several reports of differences in nest morphology as a function of the nest site. For example, ground nests of the Chinese Thrush (*Garrulax canorus*) are flat and pie-shaped, but nests 2.1 to 4.6 m above the ground are deep bowls with compact walls (van Riper 1973). The nests of Black-billed Magpies (*Pica pica*) are domed when they are built at exposed nest sites, but are open bowls when built in thorn bushes (Linsdale 1937).

Nests are also frequently built for purposes other than heat conservation. For example, the need to thwart nest predation may be of overriding importance. The pensile nests of tropical songbirds with their long tubular entrances are clearly built to discourage predators. Other nests of tropical birds are adapted to shed rain (Collias 1964) and perhaps to dry out quickly. The nest of the Adelie Penguin (*Pygoscelis adeliae*), on the other hand, is apparently adapted to prevent the eggs from being flooded during thaws or buried during blizzards (Sladen 1958). Under these circumstances, the relationships between the thermal quality of a nest and its morphology may be of minimal biological importance.

In summary, the nest represents an evolutionary compromise on the part of a bird between the need to provide a thermally uniform microclimate and safety for the young. Some species can vary the structure of the nest to fit the situation at hand, even to the point of altering it on a day-to-day basis. Hummingbirds, partridge, and megapodes belong in this group. Others are apparently unable to change the structure of the nest, perhaps for genetic reasons, and compensate for deficits in its quality by varying its location or by increasing parental attention. Doves (Russell 1969), some hummingbirds (Horvath 1964), and birds that nest in harsh environments (arctic, insular, and desert forms; Collias 1964) commonly fall into this category. Other species lie somewhere between these two extremes, able to vary the nest and nesting behavior to greater or lesser extents. Quantitative information about nest insulation will be useful in sorting out these reproductive strategies.

ACKNOWLEDGMENTS

We thank Fred E. Lohrer of the Archbold Biological Station, Lake Placid, Florida, for providing the nests of the Loggerhead Shrike, and Martin L. Morton of Occidental College, Los Angeles, California, for nests of the Mountain White-crowned Sparrow. Dr. Don Jacobs and Lee Hothem assisted us with the design and other technical aspects of the project. This study was subsidized by Wilson Funds from the College of Wooster.

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DISPLAY RATE AND SPEED OF NEST RELIEF IN ANTARCTIC PYGOSCELID PENGUINS

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ABSTRACT.—The three species of the genus *Pygoscelis, P. adeliae* (Adélie Penguin), *P. antarctica* (Chinstrap Penguin), and *P. papua* (Gentoo Penguin) perform an elaborate Nest Relief Ceremony (NRC) upon one mate's return to the nest. The NRC consists of a number of displays, each of which is performed one or several times. The most conspicuous displays during NRC are the Loud Mutual Display (LMD) and Quiet Mutual Display (QMD) in *P. adeliae* and *P. antarctica,* and their morphologically different functional equivalents in *P. papua,* the "donkey call" (LMD) and "bow-gape-hiss" (BGH). The displays whose repetition rate is negatively correlated with the time elapsed between arrival of the mate and actual changeover are the LMD in *P. adeliae,* "circling" in *P. antarctica,* and BGH in *P. papua.* *Received 17 December 1979, accepted 6 June 1980.*

NEST relief ceremonies (NRC) have been described for many avian species, notably aquatic birds such as herons, pelicans, penguins (Armstrong 1947, Smith 1977), or albatrosses (Lefebvre 1977), or in doves (Heer 1975). Such "formalized interactions" (Smith 1977) often depend on ambivalence, i.e. behavior involving conflict (Hinde 1970). In waterfowl, species with shared incubation have a nest relief ceremony that is most elaborate in the colonially breeding Black Swan (*Cygnus atratus*) (Kear 1970). Three functions ascribed to NRCs in general are appeasement (Lorenz 1938), mate and nest-site recognition, and facilitating nest relief in the mate, the latter described as "stimulating the sentinel to vacate his (or her) post and to make way for the other" (Armstrong 1947).

The genus *Pygoscelis* comprises the Adélie Penguin (*P. adeliae*), the Chinstrap Penguin (*P. antarctica*), and the Gentoo Penguin, (*P. papua*). The Adélie Penguin is distributed circumpolarly in continental Antarctica and breeds most southerly. The Gentoo Penguin is the most northerly species and occurs on subantarctic islands from the Falkland Islands (52°S, 60°W) to Macquarie Island (55°S, 160°E). The Chinstrap Penguin is most restricted in its longitudinal distribution, breeding on the Antarctic Peninsula and islands in the South Atlantic Ocean. The three species overlap in the area of the Antarctic Peninsula (55°–65°S), but segregate by species in pure colonies where they share the same rookeries.

The displays of the Adélie Penguin have been described (Sladen 1958, Sapin-Jaloustre 1960, Spurr 1975) and their motivation analyzed (Ainley 1975), while the displays of the Gentoo (Bagshawe 1938, van Zinderen Bakker 1971) and Chinstrap (Sladen 1955) penguins have been described in only a qualitative fashion. Individual recognition by vocalizations has been demonstrated for the Adélie Penguin (Penney 1968).

The more closely related Adélie and Chinstrap penguins show the same displays in slightly different forms during nest relief. These are the "loud mutual display" (LMD), in which both birds stand and wave their necks back and forth while uttering a loud cackling with open bill; the "quiet mutual display" (QMD), in which both birds wave their necks back and forth and utter a soft humming sound with closed bill (see Fig. 1); and "circling," in which one bird walks around the rim of the nest while nodding with its head. The bird may circle from one step to a full round

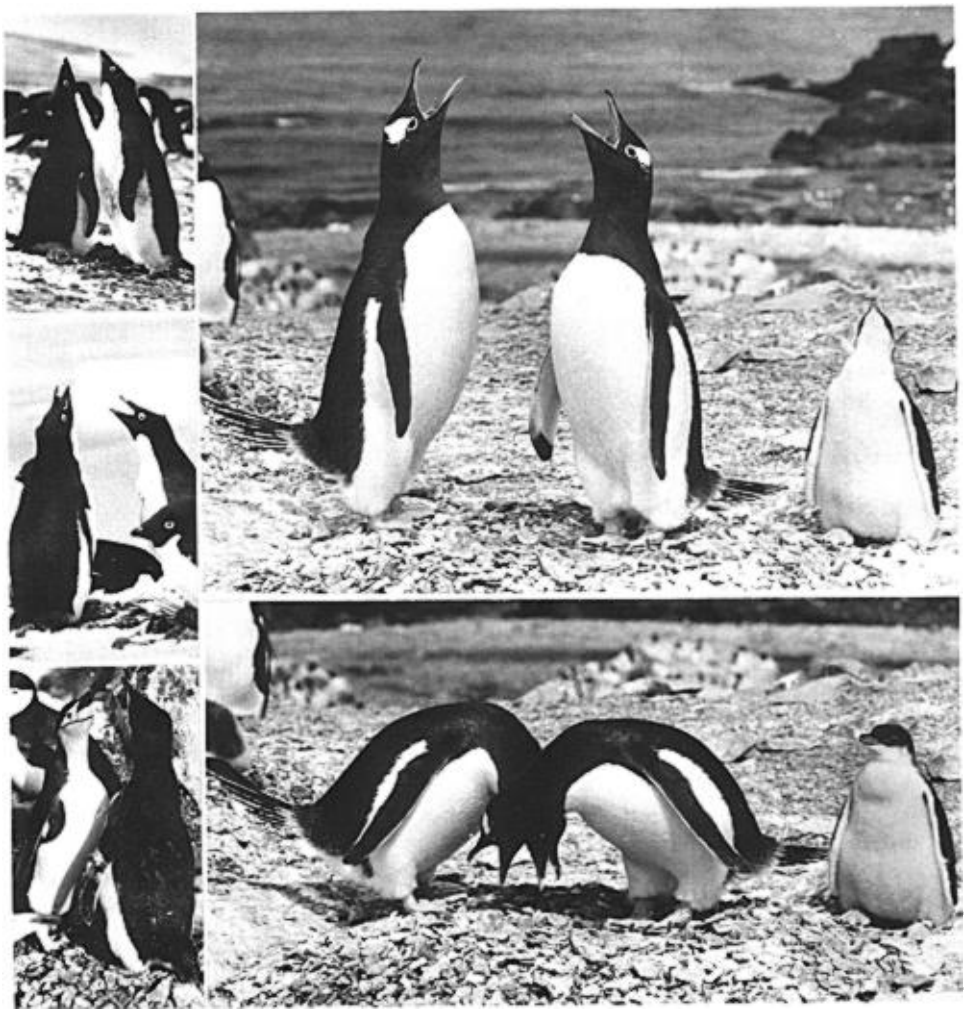

Fig. 1. Clockwise from upper right: Loud Mutual Display (LMD) in Gentoo Penguin (note the participating chick), Bow-Gape-Hiss (BGH) in Gentoo, LMD in Chinstrap Penguin, LMD in Adélie Penguin, and Quiet Mutual Display (QMD) in Adélie Penguin.

around the nest. The Gentoo Penguin's version of the LMD lacks the lateral neck movements, and the sound uttered resembles the braying of a donkey. The second main display of the Gentoo is the "bow-gape-hiss" (BGH), in which the bird bends down to the nest, opens it bill showing the bright red lining, and hisses (Fig. 1). This movement is derived from nest-building behavior, as the Gentoo may deposit a pebble on the nest and then open its bill and hiss.

The functions ascribed to the LMD in the Adélie Penguin are personal recognition (Penney 1968), sexual appeasement and reducing the probability of attack (Spurr 1975), and expression of hesitance to locomote (Ainley 1975). Sladen (1958) suggested three possible functions of the Adélie's LMD: "incipient threat and an appeasement ceremony (i.e. basically aggressive)," "a greeting ceremony," or "a confirmation."

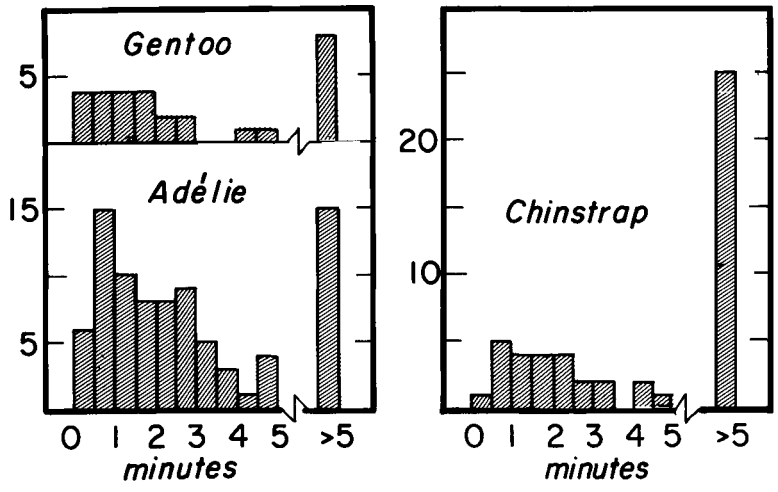

Fig. 2. Frequency distributions of Relief Times (in min) in the three penguin species. Number of observations is given on the ordinate.

These three behavioral contexts overlap, and any display can have more than one function. Roberts (1940) postulated an appeasement function for the Gentoo's BGH.

Here we report correlations between the rates of these displays and the lag until nest relief occurs (Relief Time). The displays used to indicate readiness to switch roles at the nest differ among the three species.

Methods

We recorded 100 NRCs of Adélie Penguins tending chicks ("guard stage") between 24 December 1970 and 6 January 1971 at Cape Crozier in the Ross Sea (77°31'S, 169°23'E), and 31 NRCs during incubation (4–6 December 1971) on Torgersen Island, off the Antarctic Peninsula (64°46'S, 64°05'W). Fifty NRCs were recorded for the Chinstrap Penguin on Nelson Island in the South Shetlands (62°19'S, 50°15'W) between 2 January and 15 January 1972. We recorded 50 NRCs for the Gentoo Penguin between 29 December 1971 and 7 January 1972. Both species bred at the same site, and were observed during the guard stage. Each pair was observed only once.

We recorded NRCs for 5 min from the time a returning bird approached its nest and mate. All behavior patterns performed by the arriving bird, by the bird on the nest, and by both individuals jointly were recorded on prepared data sheets. After each 5-min observation, one or (when the first bird was difficult to sex) both birds of the pair were caught with a net and sexed by means of a cloacoscope. The exact time that a bird had spent on the nest before being relieved was not known. Adélie Penguins relieve one another about three times during the 37 days of incubation and about once a day after the chicks have hatched (Sladen 1958, Penney 1968).

Results

The frequency distributions of the three species' relief times are shown in Fig. 2. Relief time averages 2.63 min in the Adélie Penguin and the arriving bird starts the LMD regardless of its sex. They average 7.9 LMDs (range 1–18) before nest relief during incubation and 6.7 during the guard stage (2–15). The QMD is less frequent: 0.29 (0–4) during incubation and 0.61 (0–8) during guard stage. The number of LMDs per minute is negatively correlated with the nest relief time: 5 LMDs per min precede nest reliefs that take place 1–3 min after arrival of the mate, while 1 display per min is usually followed by a nest relief after 5 min or longer (Fig. 3A).

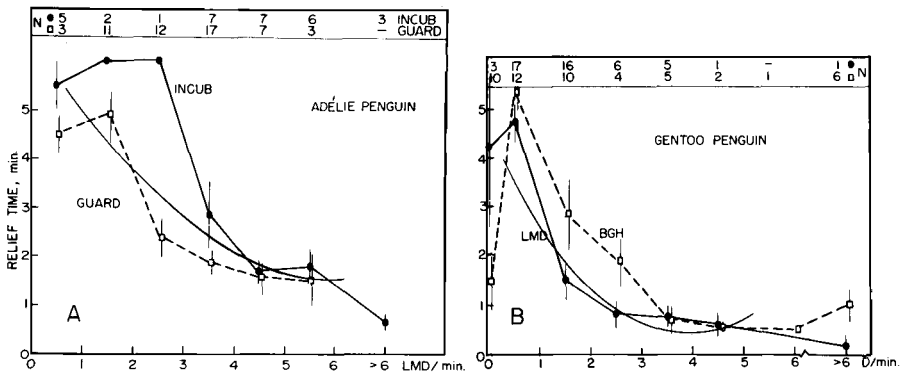

Fig. 3. A. Rate of loud mutual display (LMD/min) between arrival of mate and relief in relation to relief time in Adélie Penguins. Dots = incubation period (Torgersen Island); squares = guard stage (Cape Crozier); N = number of nest reliefs analyzed. Vertical lines indicate standard error of mean. The solid curve indicates the values expected from a multiple regression analysis (see text). B. Rate of loud mutual displays (LMD/min) and bow-gape-hiss (BGH/min) (D/min = displays per min) in relation to relief time in Gentoo Penguins. All data from guard stage at Nelson Island; N = number of reliefs analyzed; solid curve as in A.

The number of LMDs during the first 30 s after arrival of the mate is predictive of the relief time (Fig. 4A). During incubation at Torgersen Island (T), the bivariate correlation coefficient $r_T = -0.461$ ($P = 0.005$), and during guard stage at Cape Crozier (C), $r_C = -0.390$ ($P < 0.005$). The difference between r_T and r_C is not significant. In the Adélie Penguin the rates of QMD, circling, nestbuilding, or preening are not correlated with relief time. Nest building occurred only 4 times during 50 reliefs, and preening 3 times. Stepwise multiple regression analysis for relief time (RT, variable 1), LMD (2), and QMD (3) during the entire time until relief yields the partial correlation coefficients $r_{12.3} = -0.645$, $r_{13.2} = 0.357$, and $r_{23.1} = 0.001$. None of these values is significant at $P < 0.05$. This shows that more precise information is exchanged during the initial 30 s than during the remainder of the relief time (multiple $R = 0.788$; $R^2 = 0.544$). The regression equation RT = 4.742 − 0.660 LMD + 1.865 QMD reflects the trend shown in Fig. 3A. Because only the regression coefficient for LMD is significant ($P < 0.02$), the equation RT = 6.515 − 1.676 LMD + 0.148 LMD^2 fits the data better (shown in Fig. 3A).

Chinstrap Penguins relieve each other after 3.63 min on the average (if times longer than 5 min are arbitrarily counted as 5.5 min). They average only 1.38 LMDs (range 0–4) per NRC. The LMDs occur at the beginning when the birds meet, can be started by either sex, and the nest bird and arriving bird display equally often. The QMD is more frequent than in the Adélies ($\bar{x} = 4.88$, range 0–17) and is more often started by the bird at the nest ($P < 0.001$) than by the arrival. Only females show the QMD in response to the mate's feeding the young ($n = 17$; $P < 0.005$). Circling is the Chinstrap's only display whose rate is correlated with relief time. A high frequency of circling during the first minute is followed by a fast relief ($r = -0.410$, $P < 0.005$). The intensity of circling, measured in angular degrees, shows no correlation with relief time. The arriving bird circled before relief in 28 of 29 cases. The nest bird circled in 24% of all cases, before and after relief. Not correlated with relief time were the number of LMDs ($r = -0.034$, NS) and the frequency of bowing ($r = -0.067$, NS) during the first 30 s (Fig. 4B).

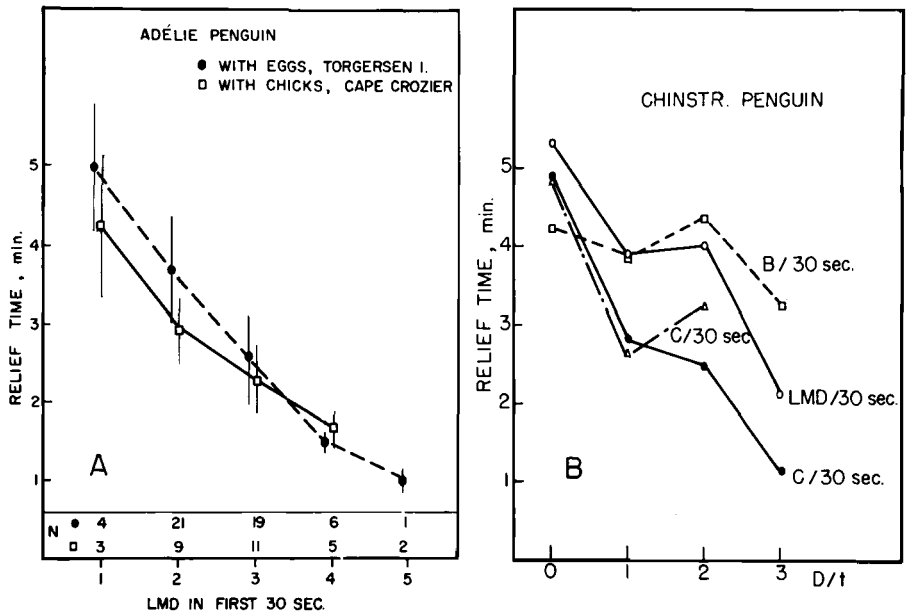

Fig. 4. A. Number of LMDs in first 30 s after arrival of mate in relation to relief time in Adélie Penguins. Dots = incubation period, Torgersen Island; squares = guard stage, Cape Crozier. B. Frequency of LMD, bowing (B), and circling (C) during the first 30 s and C during first min in relation to relief time in Chinstrap Penguins. The abscissa gives displays per time unit (D/t) of 30 or 60 s.

Stepwise multiple correlation was performed for Chinstrap Penguin relief times (1), QMDs (2), and Circlings (3) during the first 30 s and LMD (4) during the first 60 s. The partial correlation coefficients are: $r_{13.24} = -0.3150$; $r_{14.23} = -0.2940$; $r_{23.14} = -0.2887$; $r_{34.12} = -0.0623$; and $r_{12.34} = 0.0122$. The better correlation of relief time with LMD and circling is also shown in Fig. 4B. The corresponding bivariate correlation coefficients are very similar: $r_{13} = -0.3263$; $r_{14} = -0.2863$; $r_{23} = -0.3077$; $r_{34} = -0.0267$; and $r_{12} = 0.104$. The regression equation for the Chinstrap is: RT = 5.253 − 0.890 LMD − 0.575 C (the regression coefficient for QMD was not significantly different from zero); $R^2 = 0.184$.

Relief time averages 2.4 min in the Gentoo Penguin. The nest bird starts the LMD most often ($P < 0.01$) regardless of the sex of the bird, and it occurs usually only once or twice when the mates meet ($\bar{x} = 1.92$, range 0–8). The BGH is more frequent ($\bar{x} = 3.22$, range 0–13) than the LMD and is started most often by the arriving bird ($P < 0.001$). A short nest relief ceremony results when the arriving bird gives a rapid sequence of BGH displays. Changeover occurs within 1 min or less after 4–5 displays per min; an arrival-relief interval of 2 min to over 5 min is correlated with 0.5 displays per min (Fig. 3B). If the bird at the nest joins in the BGH of the arriving bird, time from arrival to nest exchange is shortened: relief time was shorter than 200 s in 78% of the cases in which over 50% of the arrival's BGH led to mutual BGH (44% of those in which under 50% led to mutual BGH). ($P = 0.025$). Rates of other behaviors were not correlated with relief time. The partial correlation coefficient for LMD (1) and BGH (2) is $r_{12.3} = 0.452$, that for BGH (2) and Relief Time (3) $r_{23.1} = -0.412$, and that for LMD (1) and Relief Time (3) $r_{13.2} = -0.134$. The regression equation RT = 5.1 − 3.051 LMD + 0.615 LMD^2 − 0.034 LM^3 describes the relationships for 1–5 displays per min (Fig. 3B).

When returning to their nests after having been captured and sexed, males showed better orientational ability. Males headed straight for the nest in 13 of 15 cases, while females did so in only 1 out of 8 cases ($P < 0.005$). Females often headed for the sea or approached strange nests where they were attacked and became more "confused."

DISCUSSION

To our knowledge this is the first demonstration of a correlation between the rate of an avian display and the time of nest relief. Three communicatory implications can be distinguished. First, the arriving bird indicates its readiness to relieve the mate by its display intensity, measured as rate of repetition. Second, the nest bird in turn may indicate its readiness to leave the nest by its displays, either spontaneously, as in doves (Heer 1975), or in response to the arriving bird's behavior, resulting in mutual displays. Third, in addition to announcing its already existing readiness, each bird may stimulate the behavior of the other and accelerate the relief by synchronization of the pair. We have demonstrated the first two effects, but the stimulatory function of the displays must be analyzed by experimental techniques.

The need for a precisely synchronized nest relief that minimizes the time of exposure of eggs or chicks is particularly great in Antarctic penguins for two reasons: exposed eggs or chicks may be chilled, and they may be preyed upon by South Polar Skuas (*Catharacta maccormicki*) within a few seconds. By comparison, other birds leave their eggs exposed for considerably longer times. For example, successfully breeding female Pink-footed Geese (*Anser brachyrhynchus*) in Iceland were absent from the nest 3.8% of the time on the average, broken down into several episodes daily (Inglis 1977). This is about 1,000 times longer than the estimated 3 s that the Adélie Penguin's eggs are exposed during a nest relief. Smith (1969) stressed that the response to a message has to meet the needs of both the recipient and the communicator. In the case of nest relief, communication between the mates serves to protect their investment in a third party, their eggs or chicks.

ACKNOWLEDGMENTS

This work was supported by two grants from the National Science Foundation (Division of Polar Programs). We thank the personnel of Holmes and Narver and the crew of R/V Hero for support in the field, James R. Ellenwood for assistance at the computer, Judith McIntyre for critically reading the manuscript, and Sarah Lennington for valuable suggestions.

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Recognizing the need to support the **publication of major taxonomic revisions and monographs,** the National Science Foundation has announced the availability of funding during Fiscal Year 1981 for such purposes. Proposals will be considered for support of publication of manuscripts that have been accepted for publication by an established scientific series or publisher of recognized standing in scholarly circles. Requests must be accompanied by at least preliminary estimates from the editor of production costs and anticipated income, along with a statement by the editor detailing the review process that the manuscript has already received. Initial priority will be given to the publication of revisions and monographs resulting substantially from past NSF research grants. Additional information may be obtained from **James C. Tyler, Program Director, Biological Research Resources Program, National Science Foundation, Washington, D.C. 20550.**

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A.O.U. Announcements

Fellows and Elective Members are reminded that nominations for Elective Member may be submitted to the Secretary on the prescribed form up until five months prior to the opening of the next Stated Meeting. The deadline for 1981 is **24 March.** Nominations for Fellow of the A.O.U. also must be received by that date. Nominations for Vice-President and Elective Councilors (3) may be made in writing to the Secretary at any time prior to the Annual Meeting.

The 99th Stated Meeting of the A.O.U. will be held at the **University of Alberta, Edmonton, Alberta, Canada** during the week of **August 24–27, 1981.**

The American Ornithologists' Union solicits applications for research grants from its **Josselyn Van Tyne** and **Alexander Wetmore Memorial Funds.** The Van Tyne awards will consider any aspect of avian biology; the Wetmore awards are limited to taxonomy/systematics. Grants are usually in amounts of a few hundred dollars. Preference is given to students and other persons without other sources of funds. Application forms may be obtained from **Dr. A. S. Gaunt, A.O.U. Committee on Research Awards, Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210.** Applications must be completed before **18 March 1981.**

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman.

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Louis Agassiz Fuertes, Margaret Morse Nice, and Paul A. Stewart Awards

The Wilson Ornithological Society announces the availability of three awards for 1981.

Fuertes Awards are available to all ornithologists although graduate students and young professionals are preferred. Nice Awards are intended for independent researchers without access to funds and facilities available at colleges and universities and thus are restricted to amateurs and students at high school and undergraduate levels. Any type of research may be funded by both Fuertes and Nice Awards. Stewart Awards are available to any applicant for ornithological research, especially studies of bird movements based on banding and analysis of recoveries and returns and investigations in economic ornithology.

One Fuertes Award of $200.00, one Nice Award of $100.00 and one or more Stewart Awards of $200.00 each will be made. Interested applicants should write to **Carl D. Marti, Department of Zoology, Weber State College, Ogden, Utah 84408.** Completed applications must be received by **1 March 1981.** Decisions will be announced at the 1981 Annual Meeting of the Wilson Ornithological Society.

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