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The Auk is fortunate to benefit from the services of many individuals who act as reviewers of manuscripts that are submitted. Their efforts are considerable, and their care and constructiveness continue to impress me as an editor and as a sometime author. The individuals listed below helped make publication of a journal with high scientific and scholarly standards possible; my thanks to all of them.

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FLIGHT ENERGETICS OF FREE-LIVING
SOOTY TERNS

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ABSTRACT.—The CO_2 production of free-ranging Sooty Terns (*Sterna fuscata*) was measured using doubly labeled water (HTO-18). Metabolic rate during flight was determined to be 4.8 times standard metabolic rate (*SMR*). This value is much lower than estimates of flight metabolism predicted from previously published equations. Observations of these birds at sea indicate that flapping flight predominated at the windspeeds (0–5 m/s) that prevailed during our measurement periods, so factors other than gliding must account for the comparatively low flight metabolism we measured. Sooty Tern flight metabolism is similar to that of some other birds, such as swallows and swifts, that also have high aspect ratios and low wing loadings. *Received 27 April 1983, accepted 12 October 1983.*

THE reliability of estimates of energy flow through biotic communities depends upon the extent to which the model used conforms to reality and the accuracy of the input parameters. In a sensitivity analysis of 44 model-specific and species-specific parameters of his bioenergetic model of a seabird colony, Furness (1978) identified several inputs that had the greatest effect on the precision of the model. Among these for Arctic Terns (*Sterna paradisaea*) were the hours of activity per day, the intercept and exponent of Lasiewski and Dawson's (1967) *SMR* equation, and the energy requirements of flapping and gliding flight. For birds, such as terns, that spend a large proportion of their foraging time in flight, the accuracy of estimates of daily energy expenditure depends on knowing the total time spent in various flight activities (i.e. flapping, gliding, and hovering) and the metabolic cost of those activities.

One goal of this study was to determine the energetic cost of free, natural flight in a species of bird. A second goal was to assess the reliability of several models that may be used for predicting the total metabolic rate of birds during flight by comparing model estimates with empirical measurements. Doubly labeled water (HTO-18) was used to measure CO_2 production in free-ranging Sooty Terns (*Sterna fuscata*) in the northwestern Hawaiian Islands during the incubation stage of breeding. We estimated the metabolic rate of flying birds from time-budget and field metabolic-rate (*FMR*) results. Sooty Terns are particularly amenable to this type of

experiment, because they do not rest on the water (Gould 1974) and can be assumed to be in constant flight when not at the breeding colony. The flight behavior of Sooty Terns was observed at sea, and morphological measurements were made in order to compare the power input predicted by aerodynamic models and measurements of gull flight in wind tunnels with field measurements.

MATERIALS AND METHODS

Incubating pairs of adult Sooty Terns were studied during April and May 1981 on Tern Island, French Frigate Shoals (approximately 24°N latitude and 166°W longitude). Pair members were captured with a dip net, marked with colored leg bands and dye, and observed for several days to determine the duration and frequency of their incubation-foraging cycle. Incubation spans at Tern Island commonly last 2–3 days. Birds that were just beginning or just ending their turn at incubation were captured, weighed, injected intramuscularly with 0.60 ml of water containing 0.15 millicurie tritium and 95 atom percent oxygen-18, and held for 1 h while the isotopes mixed thoroughly in body fluids (time previously determined in the laboratory). Then, a small blood sample (ca. 0.10 ml) was taken from a brachial vein, and the birds were released. Incubating birds were recaptured about 48 h later, just before their mates relieved them on the nest. Foraging birds were recaptured as soon as possible after their arrival (15–80 h after release). The amount of time foraging birds actually spent in flight was estimated by periodically (every 2–4 h) surveying the nesting area and recording the presence or absence of marked birds. We assumed that the birds flew continuously while away from the island. This procedure yielded flight times that were accurate to

within ±9%. Sooty Terns with chicks or eggs do not "loaf" or form "clubs" and are virtually never seen on land except at or near the nest site. Watson and Lashley (1915) found that Sooty Terns do not have plumage suitable for swimming and become waterlogged after 10 min of contact with the ocean surface.

At recapture, a second blood sample was taken and body mass was recorded before the bird was released onto the nest. While adults were being handled, the nests were covered to prevent egg overheating and predation by Ruddy Turnstones (*Arenaria interpres*). Eighteen terns were injected, and all were recaptured. Four of these birds, however, had been away much longer than the others, and too much of the isotope given to them had been washed out before recapture to yield reliable metabolic rate data. A normal proportion of injected birds went on to fledge their chicks.

Blood samples were vacuum-distilled to obtain pure water, which was analyzed for tritium content by liquid scintillation spectrometry and for oxygen-18 content by proton activation analysis (Wood et al. 1975, Nagy and Costa 1980). Body-water volumes at the time of injection were determined from oxygen-18 dilution space (Nagy 1980). Water contents of recaptured birds were estimated from their body masses and their initial water contents, assuming fractional water contents remained constant. Rates of CO_2 production were calculated by means of equation 2 in Nagy (1980). Field metabolic rates (*FMRs*) were converted from CO_2 production values to units of energy (joules) by means of the factor 24.7 J/ml CO_2. This factor was based on diet analyses (53.5% by volume of squid, 46.5% fish) of Sooty Terns in the northwestern Hawaiian Chain (Harrison et al. 1983), along with measurements of the composition of fresh squid (80.2% water, 16.4% protein, 0.9% fat, 1.5% carbohydrate, and 1.0% ash; Watt and Merrill 1963) and fresh anchovy (72.7% water, 19.7% protein, 5.2% fat, <0.5% carbohydrate, 2.0% ash; Fishing Industry Research Unit, University of Cape Town, South Africa, Annual Report, 1980), and energy and CO_2 yields of protein, fat, and carbohydrates (Schmidt-Nielsen 1975). The published standard metabolic rate of Sooty Terns was converted from oxygen consumption to joules by means of the factor 19.7 J/ml O_2 consumed (fat metabolism).

We estimated flight metabolism of Sooty Terns with predictive equations using measurements of body mass, wing area and span, and flight velocity (see Results section for details). The behavior of flying Sooty Terns at sea between French Frigate Shoals and Pearl and Hermes Reef was observed from the 'R/V Feresa' over an 8-day period. The behavior of an individual bird was recorded continuously while it was in visual range of the vessel. The average duration of visual contact was 45 s per bird. Wind speeds at sea were also recorded. Wing area and span were measured from tracings of Sooty Tern wings. Live

Sooty Terns were restrained with their backs to paper and wings fully extended. Span and area measurements include body width. These were used to calculate aspect ratio and, along with body mass values, wing loading.

Results are reported as means ± standard deviations. The regression line in Fig. 1 was calculated using the least squares method. Statistical comparisons were done using Student's *t*-test.

The increment of metabolic heat production by a flying bird above that of a resting animal is termed "cost of flight," and the total metabolic rate of a flying bird (including resting costs) is called "metabolic rate during flight" in this paper.

RESULTS

Body Mass.—The mean body mass of nine incubating terns (188 ± 17 g) was slightly greater than that of five foraging birds (184 ± 11 g), but the difference was not significant ($P > 0.2$). The overall mean body mass of the 14 terns was 187 ± 15 g. Foraging birds gained body mass at a mean rate of 2.6 ± 3.5%/day, while incubating terns lost 5.2 ± 1.7% of body mass/day ($P < 0.01$).

Energy Metabolism.—Metabolic rates of the nine incubating ("on nest") birds averaged 1.27 ± 0.38 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$, which is equivalent to 0.751 ± 0.224 $kJ \cdot g^{-1} \cdot day^{-1}$. The five "off nest" terns had significantly higher ($P < 0.01$) *FMRs*, averaging 2.98 ± 0.79 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$, or 1.850 ± 0.534 $kJ \cdot g^{-1} \cdot day^{-1}$. The average *FMR* of "off nest" birds is not equivalent to energy expenditure while flying, because these terns spent some of the time actually flying and some of the time standing in the nesting area. To estimate the *FMR* of a flying Sooty Tern, we regressed *FMRs* against the number of hours per 24-h period off the nest that individual birds were actually flying (Fig. 1). The regression line is described by the equation:

$$kJ \cdot g^{-1} \cdot day^{-1} = 0.748 + 0.061 \text{ h flying/day}$$

($r = 0.92$, $F_{(1,12)} = 62.1$, $P \ll 0.001$, SE of slope = 0.008, SE of predicted 24-h flying value = 0.270). The slope of the line has the units $kJ \cdot g^{-1} \cdot (h \text{ flying})^{-1}$. Thus, an estimate of the incremental cost of flight for a Sooty Tern is 0.061 $kJ \cdot g^{-1} \cdot (h \text{ flying})^{-1}$, which is equivalent to 1.46 $kJ \cdot g^{-1} \cdot (day \text{ flying})^{-1}$. Adding a maintenance cost of 0.748 $kJ \cdot g^{-1} \cdot day^{-1}$ (the intercept of the regression line) yields an estimate of the total metabolic intensity of a flying tern: 2.21 $kJ \cdot g^{-1} \cdot day^{-1}$. This procedure involves the assumption
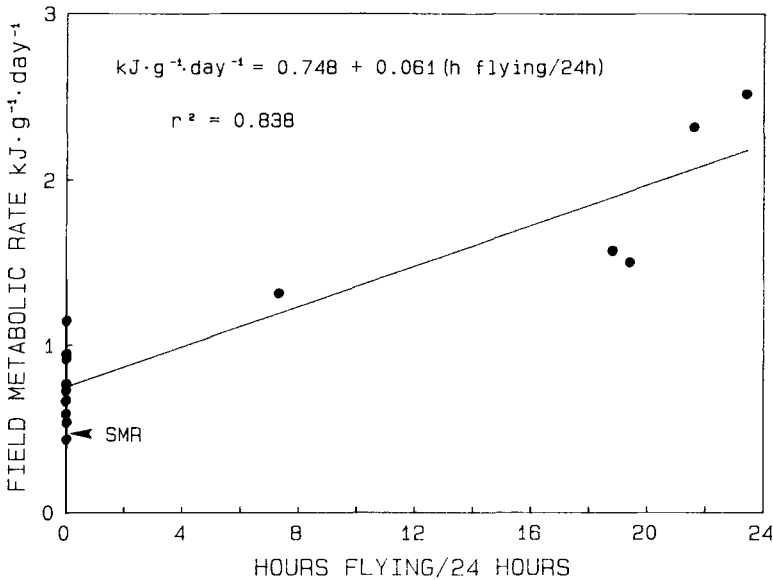
Fig. 1. Relationship between field metabolic rate of Sooty Terns and hours spent flying per 24-h period during the breeding season. The line is the least-squares regression, and the arrow indicates standard metabolic rate (0.463 kJ·g^{-1}·day^{-1}).

that flying terns had the same metabolic expenses for maintenance as did nonflying terns. Nonflight metabolism includes standard metabolism (energy expenditure of birds that are postabsorptive, thermally nonstressed, and completely at rest) plus costs of food digestion and assimilation, thermoregulation, alertness and muscle tension, comfort movements, and other activities of minor energetic cost. Because birds probably incur most of these energetic costs while flying as well as while incubating, we feel this assumption is reasonable.

Standard metabolic rate (*SMR*) of Sooty Terns is 0.98 ml O$_2$·g^{-1}·h^{-1} (MacMillen et al. 1977), which is equivalent to 0.463 kJ·g^{-1}·day^{-1}. Thus, nonflight metabolism (*FMR* of a nonflying tern, the intercept in Fig. 1) was 1.62 × *SMR*, and metabolic rate during flight was 4.77 × *SMR*. The cost of flight (above nonflight metabolism) was 3.15 × *SMR*.

Flight behavior.—Terns flying over water used a flapping mode of flight about 95% of the time in relatively calm air (Table 1). At higher wind speeds, the birds glided more often but still flapped about three-quarters of the time. These observations included terns that were apparently in transit between feeding and nesting areas, as well as birds that were foraging.

Aerodynamic properties.—The 11 terns used for morphological measurements had masses averaging 194 ± 15 g, wing spans averaging 0.84 ± 0.023 m, and a mean wing area of 626 ± 44.2 cm^2. Wing loading, calculated from these measurements, was 0.311 ± 0.028 g/cm^2. Aspect ratio [(wing span^2/wing area) as defined by Pennycuick (1975: 33)] of the same birds averaged 11.3 ± 0.593.

Predicted flight costs.—Metabolic rate during flight was predicted using equations derived from aerodynamic theory for species whose flight costs have also been measured by doubly labeled water. These equations require an input of parameters such as flight speed, wing span, mass, and wing area.

Tucker's (1973) equation #49 was used to predict metabolic rate during level flapping flight. The necessary species-specific variables were mass (*m*, in kg), wing span (*b*, in m), flight speed (*V*, in m/s), and basal metabolic rate (*BMR*, in watts). For Sooty Terns the following values were used: *m* = 0.187, *b* = 0.84, *V* = 10.4 (estimated from data of Schnell and Hellack, 1979), and *BMR* = 1.023 (MacMillen et al. 1977). For House Martins (*Delichon urbica*) *m* = 0.019 (Bryant and Westerterp 1980), *b* = 0.292 (Magnan 1922), *V* = 11.18 (Meinertzhagen 1955), and

$BMR = 0.258$ (Hails 1979); for Barn Swallows (*Hirundo rustica*) $m = 0.018$ (Magnan 1922), $b = 0.33$ (Magnan 1922), $V = 7.598$ (Schnell 1965), and $BMR = 0.305$ (Aschoff and Pohl 1970); for pigeons (*Columba livia*) $m = 0.4$ (Pennycuick 1968), $b = 0.66$ (Pennycuick 1968), $V = 16.09$ (LeFebvre 1964), and $BMR = 1.818$ (Aschoff and Pohl 1970).

Greenewalt's (1975) equation #23 for total power yields the power required to overcome induced drag and parasitic drag. Variables required for this equation are W (mass in g), S (projected wing area in cm^2), b (wingspan in cm), V (velocity in km/h), and SMR ($J \cdot g^{-1} \cdot h^{-1}$). In order to compare the results of this equation with those of Tucker's and with our doubly labeled water data, we multiplied the result by 4 to account for 25% muscular efficiency (Greenewalt 1975) and added nonflight metabolism. For Sooty Terns we measured nonflying or maintenance metabolism to be $1.62 \times SMR$. For pigeons we calculated it to be $1.71 \times SMR$ (data from LeFebvre 1964). For House Martins and Barn Swallows we used the average of these two figures, $1.66 \times SMR$.

For Sooty Terns the following values were used in Greenewalt's (1975) equation: $W = 187$, $S = 625.5$, $b = 83.99$, $V = 37.44$ (from Schnell and Hellack 1979), and $SMR = 19.3$ (MacMillen et al. 1977); for House Martins $W = 18.8$ (Bryant and Westerterp 1980), $S = 92$ (Magnan 1922), $b = 29.2$ (Magnan 1922), $V = 40.25$ (Meinertzhagen 1955), and $SMR = 49.4$ (Hails 1979); for Barn Swallows $W = 18.35$ (Magnan 1922), $S = 135$ (Magnan 1922), $b = 33$ (Magnan 1922), $V = 27.35$ (Schnell 1965), and $SMR = 59.8$ (Aschoff and Pohl 1970); for pigeons $W = 400$ (Pennycuick 1968), $S = 630$ (Pennycuick 1968), $b = 66$ (Pennycuick 1968), $V = 57.93$ (LeFebvre 1964), and $SMR = 16.4$ (Aschoff and Pohl 1970).

Pennycuick's (1975) equation #25 yields total mechanical power required to fly horizontally as a function of forward speed. We corrected the value obtained from this equation for muscular efficiency (23%; Pennycuick 1975) to obtain total power input. Variables required for this equation are m (mass in kg), W (weight in newtons), b (wingspan in m), v (velocity in m/s), and SMR in watts.

For Sooty Terns we used $m = 0.187$, $W = 1.83$, $b = 0.84$, $v = 10.4$ (estimated from data of Schnell and Hellack 1979), , and $BMR = 1.023$ (MacMillen et al. 1977); for House Martins $m = 0.019$ (Bryant and Westerterp 1980), $W = 0.184$,

TABLE 1.   Flight behavior of Sooty Terns at sea (n = number of birds observed).

	Percentage of total flying time	
	Wind velocity 0–5 m/s ($n = 61$)	Wind velocity 5–10 m/s ($n = 6$)
Flapping	94.3	75.4
Gliding	5.5	24.6
Hovering	0.2	0

$b = 0.292$ (Magnan 1922), $v = 11.18$ (Meinertzhagen 1955), and $BMR = 0.258$ (Hails 1979); for Barn Swallows we used $m = 0.018$ (Magnan 1922), $W = 0.180$, $b = 0.33$ (Magnan 1922), $v = 7.598$ (Schnell 1965), and $BMR = 0.305$ (Aschoff and Pohl 1970); for pigeons $m = 0.400$ (Pennycuick 1968), $W = 3.92$, $b = 0.66$ (Pennycuick 1968), $v = 16.09$ (LeFebvre 1964), and $BMR = 1.82$ (Aschoff and Pohl 1970). We used 1.22 kg/m^3 to represent the density of air.

Estimates of total power in Greenewalt's equation #23 and power input in Tucker's equation #49 and Pennycuick's equation #25 were not calculated for the Purple Martin, because wingspan measurements (b) were not available. Tucker (1973) provided an equation (derived from Greenewalt 1962) for estimating wingspan from mass, but, because aspect ratio may affect the cost of flight (see below), it would be counterproductive to use an "average" wingspan for a bird of a given mass.

DISCUSSION

One approach to predicting the cost of flight has been the formulation of equations based on aerodynamic theory that require the input of measured parameters (Pennycuick 1969, 1975; Tucker 1973; Greenewalt 1975; Rayner 1979). Metabolic rates during flight, measured with isotopes for all four species considered here (Table 2), are generally lower than those predicted by Tucker's equation #49. Validation studies indicate that double labeled water measurements are accurate to within ± 8% in a variety of vertebrates (Nagy 1980). The 95% confidence interval for the slope of the regression in Fig. 1 (the incremental cost of flight for Sooty Terns) is ± 28% (0.044–0.078). All of the differences for Sooty Terns in Table 2 are much larger than 28%. Some portion of the differences shown in Table 2 may be attributed to the fact

TABLE 2. Comparison of doubly labeled water (DLW) method with three other methods for estimating total metabolic rates ($J \cdot g^{-1} \cdot h^{-1}$) during free flight in birds.

Method	Sooty Tern (187 g)	House Martin (18.8 g)	Barn Swallow (18.35 g)	Purple Martin (50.5 g)	Pigeon (400 g)
Doubly labeled water					
$J \cdot g^{-1} \cdot h^{-1}$	92.1	167–239[a]	247[a]	289[b]	230[c]
Multiple of SMR	4.77	3.39–4.83	4.16	6.37	14.06
Tucker (1973)					
$J \cdot g^{-1} \cdot h^{-1}$	228	546	320	—	429
(% difference from DLW method)	(+147)	(+128–227)	(+30)	—	(+87)
Greenewalt (1975)[d]					
$J \cdot g^{-1} \cdot h^{-1}$	178	352	262	—	270
(% difference from DLW method)	(+93)	(+47–111)	(+6)	—	(+17)
Pennycuick (1975)					
$J \cdot g^{-1} \cdot h^{-1}$	175	304	197	—	410
(% difference from DLW method)	(+90)	(+27–82)	(−20)	—	(+78)
12 x SMR[e]					
$J \cdot g^{-1} \cdot h^{-1}$	232	593	718	545	196
(% difference from DLW method)	(+151)	(+148–255)	(+191)	(+89)	(−15)

[a] Hails (1979).
[b] Utter and LeFebvre (1970).
[c] LeFebvre (1964).
[d] Corrected to include nonflight metabolism (see text).
[e] Raveling and LeFebvre (1967); King (1974: 32).

that free-living birds have opportunities to take advantage of atmospheric movements to reduce the power requirements of flight. The failure to correct for the proportion of time spent gliding also contributes to the overestimate for the House Martin and Barn Swallow. House Martins in flight only flap 37.7% of the time (Bryant and Westerterp 1980).

Greenewalt's equation #23, modified for comparison, gives estimates of metabolic rate during flight that are higher than those measured using doubly labeled water (DLW) in the Sooty Tern and House Martin, but are relatively close to isotopic water results from the Barn Swallow and pigeon. The close agreement between Greenewalt's equation and LeFebvre's data for the pigeon may occur because Greenewalt used LeFebvre's data to estimate values for induced drag and parasitic drag. Agreement between DLW measurements and the results of equation #23 can be improved by using predicted flight velocities for minimum power output (V_{mp}; Greenewalt 1975: 42), which are lower than the measured flight velocities we used to predict the values shown in Table 2. With V_{mp} values, the differences between equation #23 and DLW decline to between +13 and +51%. For purposes of estimating the bioen-

ergetics of birds in the field, we feel it is best to use measured values in predictive models whenever these measurements are available. In cases where flight velocities are unknown, however, V_{mp} may be a useful substitute. Greenewalt (pers. comm.) suggested that his equations are most useful on a comparative, rather than an absolute, basis.

It has become a standard procedure in the formulation of time-energy budgets of birds to adopt some multiple of basal metabolic rate as the cost of flight. This multiple is often an average value derived from empirical measurements made on a variety of species. Nisbet (1967) questioned the validity of this approach, stating that the cost of flight in birds depends on their aerodynamic properties. In his extensive treatment of flight in birds, Greenewalt (1975) found no basis for predicting a constant ratio of metabolic rate during flight to that at rest.

Metabolic rate during flight in Sooty Terns, estimated with isotopes of oxygen and hydrogen, is not closely predicted (1) by the commonly used multiples of SMR obtained from several species (Raveling and LeFebvre 1967, King 1974: 32) or (2) by the multiples of SMR obtained in wind-tunnel studies of members of

the same family. Using Tucker's (1972) factor of 13 × *SMR* for metabolic rate during flapping flight in the Laughing Gull (*Larus atricilla*) and 3.1 × *SMR* for gliding flight in Herring Gulls (*Larus argentatus*), derived from the measurements of Baudinette and Schmidt-Neilsen (1974) and measurements of *SMR* in Herring Gulls (Lustick et al. 1978), we calculated a rate of 241.3 $J \cdot g^{-1} \cdot h^{-1}$ for Sooty Terns flying at low windspeeds (0–5 m/s). The isotopically measured value at those windspeeds (92.1 $J \cdot g^{-1} \cdot h^{-1}$) was only 38% of this estimate.

The results of this study and Lyuleeva's (1970, cited in Hails 1979) estimate of flight costs in the Common Swift (*Apus apus*) do not support the suggestion made by Utter and LeFebvre (1970) that passerines may have some physiological advantage in flight proficiency over nonpasserines. Values for metabolism during flight relative to *SMR* of the Sooty Tern (a nonpasserine) fall in the same range (3.4–6.4) as those of martins and Barn Swallows (passerines) that have been measured (summarized by Hails 1979). Aerial feeding, low wingloading (values of 0.116–0.232), and high aspect ratio (values of 8.07–13.5) are characteristic of each of these groups. In contrast, pigeons exhibit wingloading values of 0.343–0.515 and aspect ratios of 6.30–8.19 (data summarized in Greenewalt 1962), and their metabolic rate during flight is 14 × *SMR*.

Sooty Terns are an extremely aerial species. During 3 yr of study of the distribution and behavior of Sooty Terns, the Pacific Ocean Biological Survey Program made 51,095 observations of bird behavior at sea. Only 0.16% of these were of birds sitting on the water (Gould 1974). At French Frigate Shoals, the terns are absent from the colony from September to January or February, presumably in continuous flight during this 4–5-month period. This would be a remarkable metabolic feat if flight costs for Sooty Terns were as high as, for example, pigeons (14 × *SMR*; Table 2). It appears that the morphology of Sooty Terns is largely responsible for their surprisingly low flight costs.

A standard multiple of *SMR* to estimate the cost of flight in all birds would greatly simplify making estimates of daily energy expenditure from time-activity budgets. There is no obvious reason, however, why birds of different habits and structure should have the same power requirements for flight, considering all the morphological compromises that might be made for

habitat type and terrestrial or aquatic locomotion. Our results indicate that behavior while aloft and the aerodynamic properties of different birds can have a large influence on their energetic costs of flight.

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DIETARY SELECTIVITY IN RELATION TO AVAILABILITY AND QUALITY OF FOOD FOR GOSLINGS OF CACKLING GEESE

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ABSTRACT.—Food selection by and diet of Cackling Goose (*Branta canadensis minima*) goslings were studied in relation to the quality and availability of food during brood rearing, 1977–1979. Arrowgrass (*Triglochin palustris*) was the most important food in the diet of goslings before wing-molt of adults and sometimes during molt. *Carex mackenziei* was the most common sedge in the diet but was less important than arrowgrass. Leaves of other species were relatively unimportant during premolt. Arrowgrass declined, while *Carex* seeds and crowberries (*Empetrum nigrum*) increased, in the diet as brood rearing progressed. Arrowgrass was highly preferred, whereas other sedges and grasses (except *C. mackenziei*) were avoided in areas for which both availability and consumption were measured. Preference for arrowgrass was related to its higher protein and energy content and lower cell-wall content compared to other forage species. Thus, geese benefitted nutritionally from selecting their preferred diet. Seeds and berries contained high levels of lipids and carbohydrates relative to green leaves. Less arrowgrass was consumed in a year when brood densities were higher than in the other 2 years of the study. Arrowgrass availability declined as brood rearing progressed in another year. Thus, Cackling Geese may have been reducing the availability of their most nutritious food, at least at high brood densities. Food quality in breeding areas may be influencing population dynamics of geese despite the high overall availability of green plants. *Received 16 May 1983, accepted 7 November 1983.*

GEESE are primarily herbivorous during the breeding season (Owen 1980: 127). Plant foods are generally lower in protein and energy content and are usually less digestible than animal foods. For geese, the relatively poor nutritional quality of green vegetation is exacerbated by their simple gastrointestinal tracts. Adult geese must replenish fat and protein reserves, which are at annual lows during hatching or early molt (Hanson 1962, Ankney and MacInnes 1978, Raveling 1979), and goslings must grow under these nutritional constraints. Nutrition during the brood-rearing period may affect such life history parameters as overwinter survival or future reproductive success. Poor food quality, in conjunction with the importance of nutrition following nesting, should have resulted in selection for foraging behavior that maximizes nutrient intake.

There have been few studies of the summer foraging ecology of geese that nest in the Arctic of North America other than general or food-habits investigations (Barry 1967, Mickelson 1975, Eisenhauer and Kirkpatrick 1977). Lieff (1973) reported associations between preferred foraging areas and the presence of particular plant species for both Lesser Snow Geese (*Chen caerulescens caerulescens*) and Canada Geese (*Branta canadensis*), and both he and Harwood (1975) demonstrated preferences for fertilized vegetation by grazing geese. None of these studies related the nutrient content of particular plant species to their importance in the diet, however. In view of the potential importance of summer foraging behavior, we undertook a study of this aspect of the ecology of Cackling Geese (*B. c. minima*) in order to describe their diet in relation to the availability and nutrient content of foods. The study was conducted from the first week of June through mid-August 1977–1979.

STUDY AREA

Our study area was located within the Clarence Rhode National Wildlife Range (now Yukon Delta National Wildlife Refuge) on the Yukon-Kuskokwim Delta, Alaska in the vicinity of the U.S. Fish and Wildlife Service field station at Old Chevak (61°N, 165°W). The primary study plot was a 40.4-ha area surrounding a cabin and observation tower between the Onumtuk slough and Kashunuk River (see Mickelson 1975 for further description).

We classified two main types of habitat on the study area: upland and lowland. Upland habitat consisted of relatively well-drained areas about 1.3–1.7 m above mean high-tide levels that were dominated by lichens, moss (*Sphagnum* spp.), *Empetrum nigrum, Rubus chamaemorus, Salix fuscescens,* and *Ledum palustre.* Areas about 0.5 m above mean high-tide levels were defined as lowland. About 50% of the lowland area consisted of small ponds (i.e. <0.8 ha in area). We recognized two subtypes of terrestrial lowland habitat, mudflat and meadow. Mudflats, adjacent to ponds, comprised 5% of terrestrial lowland habitat and were characterized by bare mud or small, nearly pure patches of either *Puccinellia phryganodes* or *Carex subspathacea,* which were less than 5 cm tall. Nearly pure stands of *C. mackenziei* and *Hippuris tetraphylla* also occurred adjacent to ponds and mudflat areas. Meadows consisted of vegetation up to 20 cm in height, dominated by *C. rariflora, C. ramenskii, Calamagrostis deschampsioides,* and *Dupontia fisheri.* Scattered individuals of *C. mackenziei* occurred in both mudflats and meadows. *Triglochin palustris* (arrowgrass) occurred in small numbers in both lowland subhabitats and in stands of *C. mackenziei.*

METHODS

Plant species density.—Densities of plant species in meadows commonly used by wild geese were estimated by counting all individual shoots within a 14.5 cm² wire square, randomly placed 11 times along each of three 30-m-long transects (definition of individual shoot as in Chapin et al. 1980). Sampling locations along the transect line were selected before the first sampling date and were used for subsequent dates. Approximately the same transects were sampled three times during both 1978 and 1979, and the total numbers of individuals of each plant species at each sampling location (33 locations in each year) were recorded. We then calculated the mean percentage of total leaves contributed by each species. On mudflats, the wire square was tossed arbitrarily 62 times, and all arrowgrass individuals in the square were counted. The density of all other mudflat species combined was determined by counting all individuals within samples clipped from 15 0.1-m² quadrats during 1979.

Diet.—Goslings were removed from nests at hatching, imprinted on humans, and allowed to graze on the principal study area in both 1978 and 1979. The diet of these goslings was augmented with commercial poultry starter for their first 10 days. Imprinted goslings were periodically sacrificed after being allowed to feed in areas of known plant-species density. These feeding trials allowed a comparison between the abundance of plant species and their presence in the gosling diet. In addition, wild geese were collected by shooting on a 12.7-km² area adjacent to the principal study area during 1977, 1978, and 1979.

After all collections, esophageal contents were removed immediately, rinsed with 80% ethyl alcohol, and placed into vials. Within 3 h, esophageal samples were rinsed with water and returned to vials. Samples were refrigerated following rinsing and frozen within 24 h. Esophageal samples were sorted by plant species at the University of California, Davis, and freeze-dried to constant weight. Contributions of foods to the diet are reported as a percentage of dry weight.

Collection and chemical analysis of plant samples.— Mixed-species samples from mudflats and meadows, along with pure samples of *C. mackenziei* and *C. subspathacea,* were collected for chemical analyses by clipping from 0.1-m² quadrats randomly placed within previously delineated 3 × 5-m plots during 1978 and 1979. These previously delineated plots were located in areas where grazing geese had been observed. Mixed-mudflat samples (nearly entirely *P. phryganodes*) included only erect shoots and leaves. Samples were clipped to litter level. Litter and standing dead material were removed in the laboratory and mixed-mudflat and *C. subspathacea* samples were washed to remove excess mud. Individual arrowgrass plants were removed from mixed-meadow samples collected in 1978 to provide a pure sample of meadow arrowgrass for that year. All other arrowgrass samples were hand-collected.

All sampled plant species were represented in 1978 samples, whereas only *C. mackenziei,* mixed-mudflat, and arrowgrass were sampled in 1979. Plant samples were clipped on 25 June, on 3 and 4, 19, and 29 to 31 July, and on 7 August 1978, with the exception of early July mixed-mudflat samples, which were collected on 11 July 1978. All 1979 clipped samples were collected on 24 June, on 7, 17, and 28 July, and on 9 August. Samples of *T. palustris* were collected from mudflats and meadows on 10 dates through the summer of 1979. The amount of material was insufficient for separate analyses representing each date, however. Therefore five composite aliquots were formed for both mudflat and meadow *T. palustris* by combining material collected on the following pairs of dates: 24 and 30 June; 4 and 7, 17 and 21, 28 and 31 July; and 9 and 12 August. *Carex* seeds were collected only during August 1979, while *Empetrum nigrum* berries were collected on 7 and 29 July and 7 August 1978 and 9 August 1979.

Samples were frozen within 24 h. In Davis, samples were thawed, blotted lightly with paper towels, weighed, freeze-dried to constant weight, and then ground in a Wiley Mill to pass a 40-mesh sieve. Nitrogen was determined by the macro-Kjeldahl method (Horwitz 1975). Crude protein was estimated by multiplying 6.25 times Kjeldahl nitrogen. Crude fat was determined by extracting samples for 12 h with anhydrous ether in a Goldfisch apparatus. Samples

were ashed by combustion of ether-extracted samples for 4 h at 500°C. Acid and neutral detergent-insoluble fractions (ADI and cell wall, respectively) were estimated by the Van Soest method (Goering and Van Soest 1970). Neutral detergent-insoluble material was saved, and the nitrogen content of this fraction was estimated by Kjeldahl analysis. Amino acid concentrations were determined on a Durham 500 amino-acid analyzer following 24 h hydrolysis in 6 N HCL (Spackman et al. 1958). Cysteine concentrations were determined using the same technique, except that samples were oxidized in performic acid for 24 h before hydrolysis (Hirs 1967).

Digestibility of protein in cell walls was calculated by assuming that the nonprotein fraction of cell walls was an indigestible marker (Drent et al. 1978). The percentage of protein in the cell-wall fraction of the diet was estimated by calculating a weighted average of the percentage of protein in the cell-wall fractions of the arrowgrass and nonarrowgrass portions of the diet, with the weights consisting of the proportional contributions of arrowgrass and non-arrowgrass foods to total cell wall in the diet. The protein content of cell walls in the feces was determined by Kjeldahl analysis of the fecal cell-wall fractions.

Statistical analyses.—Distribution of dietary data (percentage contribution to diet by a food) was nonnormal and in some cases approached a bimodal distribution (see Fig. 1). For this reason we used Kruskal-Wallace or Mann-Whitney U-tests to compare the percentage contribution of a particular food to the diet of groups of goslings. Spearman rank correlation was used to analyze seasonal trends in diet and the correlation between cell-wall and protein content of plants. The dietary preference of imprinted goslings feeding in meadows was determined by means of a Mann-Whitney U-test to compare the percentage of leaves of a given type in esophagi versus that in the environment. We did not statistically evaluate the preference of imprinted goslings feeding on mudflats, because the use of different size quadrats for estimating densities of arrowgrasses and nonarrowgrasses precluded an estimation of among-sample variation of the percentage of arrowgrasses on mudflats. We analyzed the chemical constituents of plants by means of a 2-way ANOVA (species × sampling dates, for protein and water) or 1-way ANOVA (other constituents) followed by a protected Least Significant Difference comparison between means (Carmer and Swanson 1973) in cases with a significant F value.

RESULTS

DIET

We divided the brood rearing period into three time periods for presentation of dietary data: preceding the molt of adult remiges (pre-

molt), coincident with the adult flightless period (molt), and coincident with fledging of young (fledging). The dividing points between premolt and molt collection periods were 14 July in 1979, 15 July in 1978, and 28 July in 1977. Molt and fledging periods were separated by 2 August in 1978, the only year in which collections were made during fledging. These periods correspond approximately to the following gosling ages: premolt, 1–23 days; molt, 24–41 days; fledging more than 42 days. Contributions of foods to the diet are expressed in aggregate percentages.

Imprinted and wild goslings differed significantly ($P < 0.05$) in diet in only 3 of 16 possible pairwise comparisons (4 food categories × 2 yr × 2 time periods within years, Fig. 1). These differences were due to the single collection during the 1979 molt period of three wild goslings from the same brood, which contained a significantly lower percentage of *T. palustris* and *C. mackenziei* and a significantly higher percentage of *Carex* seeds and *Empetrum* berries than did the tame goslings collected during the same period. There were no foods for which differences between the two groups in the consumption of a food were consistent between years. Because of the lack of differences between wild and tame goslings except for the one collection, we combined results from the two groups for subsequent analyses. (See Appendix for a complete summary of the diet of goslings.)

Because of initial difficulties in identification of plant species, some *C. subspathacea* was included with arrowgrass in the analysis of esophageal contents from goslings collected during 1977. Of the original arrowgrass sample from these goslings (a sample comprised of arrowgrass from all 1977 goslings that contained arrowgrass), 13% was available for reanalysis. *Carex subspathacea* comprised 4% of the dry weight of this material. This error did not have a substantial effect on either the presentation of, or the conclusions drawn from, our data.

Seasonal variation.—Arrowgrass predominated in the premolt diet of goslings, contributing 92% of the diet during this period in 1977, 44% in 1978, and 98% in 1979 (Fig. 1). Other foods were unimportant during premolt in 1977 and 1979, but *C. mackenziei* comprised 28% and other leaves (other *Carex* spp. leaves, grasses, and forbs) 19% of the 1978 premolt diet.
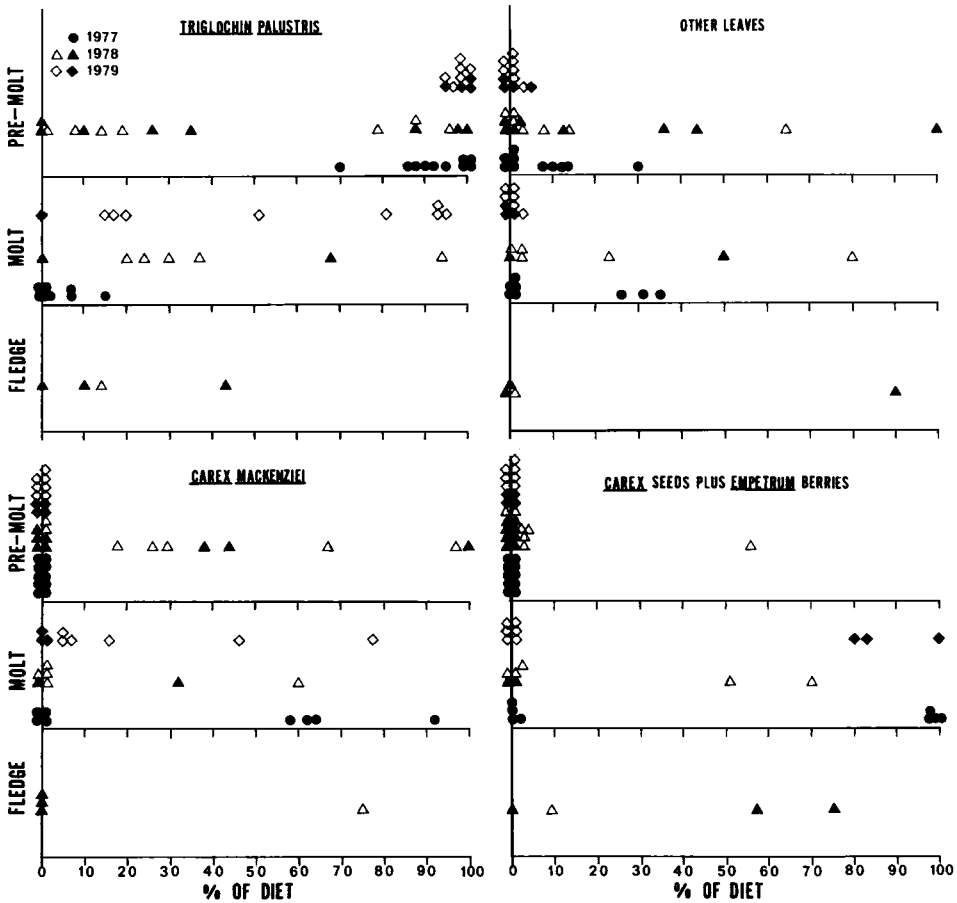
Arrowgrass declined in dietary importance

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Fig. 1. Diet of Cackling Goose goslings during brood rearing 1977–1979. Each point within a food type corresponds to one individual, and each individual is represented in all four food types. Points are arrayed along the horizontal axis, representing percentage of diet (dry weight). Points representing goslings collected during the molt, premolt and fledging periods (see Results) are plotted separately within each food type. Points representing goslings collected in different years are separated vertically within plots for each of the three time periods. Open symbols represent tame goslings; solid symbols represent wild goslings.

during brood rearing in 1977 ($r_s = -0.71$, $P < 0.005$) and 1979 ($r_s = -0.77$, $P < 0.001$), while a slight nonsignificant negative trend was observed in 1978, the year of lowest premolt feeding on arrowgrass ($r_s = -0.19$, $0.2 < P < 0.4$, Fig. 1). Carex seeds and Empetrum berries tended to increase in the diet as brood rearing progressed in 1978 and 1979 ($r_s = 0.30$, $0.1 < P < 0.2$ and $r_s = 0.32$, $0.1 < P < 0.2$, respectively), and we observed a significant increase in 1977 ($r_s = 0.72$, $P < 0.001$).

Seasonal variation in the diet resulted in a reduction in the contribution of arrowgrass to 4% of the diet during molt in 1977, 39% in 1978,

and 52% in 1979 (Fig. 1), with a further reduction to 17% of the fledging diet in 1978. Carex mackenziei was the most important sedge in the diet during molt, comprising between 13% (1978) and 35% (1977) of the diet (18% in 1979). Seeds and berries increased from less than 10% of the premolt diet during all 3 yr to 49% of the molt diet in 1977, 18% in 1978, and 29% in 1979, and to 35% of the 1978 fledging diet. Other leaves combined comprised between 1% (1979) and 23% (1978) of the diet during molt (12% in 1977).

Among-year variation.—Goslings from the premolt period in 1978 contained significantly
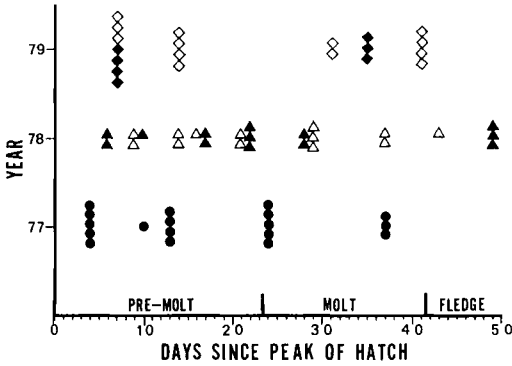
Fig. 2. Timing of collection of Cackling Goose goslings. Peak hatch was 4 July 1977, 21 June 1978, and 20 June 1979. Points from goslings collected within the same year are arrayed along the horizontal axis, while points from different years are segregated vertically. Each point represents one gosling. Open symbols represent tame goslings; solid symbols represent wild goslings.

less arrowgrass ($P < 0.002$) and significantly more *C. mackenziei* ($P < 0.001$) than did goslings from the same period in 1977 and 1979 (Fig. 1). Arrowgrass comprised a slightly (but nonsignificantly) larger fraction of the molt diet in 1979 than in 1978 and was a significantly larger fraction of the molt diet during these 2 yr than during 1977 ($P < 0.002$).

More goslings were collected later in the premolt period during 1978 than during 1977 and 1979 ($P < 0.01$, Fig. 2). This was probably not the cause of the among-year differences in premolt diet, however, for two reasons: (1) goslings from the first 14 days of the premolt period (in which all 3 yr were represented) still contained less arrowgrass in 1978 than in 1977 and 1979 ($P < 0.01$), and (2) goslings collected 15–16 days into the premolt period in 1978 (later than collections in 1977 and 1979) contained between 87% and 97% arrowgrass, among the highest levels recorded for 1978.

Preference.—Imprinted goslings were highly selective of arrowgrass leaves in meadows (Fig. 3, Mann-Whitney *U*-test, $P < 0.0002$), consuming them approximately five times more frequently than they occurred in the environment. Arrowgrass was selected at a similar relative rate on mudflats, although we could not evaluate this statistically, because we had no measure of variability in the availability of

arrowgrass on mudflats. Other sedges and grasses comprised a much smaller fraction of the diet than of available individuals.

CHEMICAL COMPOSITION OF VEGETATION

Concentrations of all constituents varied among species ($P < 0.001$, Tables 1, 2). Crude protein ($P < 0.0005$) and water content ($P < 0.01$) varied among sampling dates. Temporal variations in protein and water concentration were parallel among species (Kendall's Test of Concordance $P < 0.01$); the same proportion of each species' samples were collected on a given sampling date. We thus combined data across sampling dates for purposes of presentation. We will report on temporal variation in vegetation constituents in a separate paper.

Results dealing with the water content of vegetation must be interpreted with caution. Samples were collected under variable, but usually wet, conditions. Mixed-mudflat and *C. subspathacea* samples were washed to remove mud associated with these samples. As a result, the apparent water content of these samples was inflated and these data were not analyzed statistically.

Gross nutrients.—Crude protein content was highly variable among species and was highest (30%) in arrowgrass from mudflats (Table 1). Crude protein in arrowgrass from meadows and in *C. subspathacea* averaged 19%, whereas all other types of green vegetation and *Carex* seeds contained between 13.3% and 15% protein. *Empetrum nigrum* berries contained substantially less protein (5%) than did other foods.

Crude fat concentrations were 2–3 times greater in seeds and berries (7.8–9.7%) than in green plants (3.2–4.4%, Table 1). The ash content of seeds and berries (2.4–3.9%) was considerably lower than that of vegetative parts of green plants (6.1–13%, Table 1).

Cell wall.—Arrowgrass contained substantially less cell wall than other green plants, and there was lower cell-wall content in arrowgrass from mudflats than arrowgrass from meadows (Table 2). *Carex subspathacea, C. mackenziei,* and mixed-mudflat vegetation did not differ from one another in percentage cell wall. Cell walls constituted the largest proportion (58.3%) of dry weight (among green plants) in mixed-meadow vegetation.

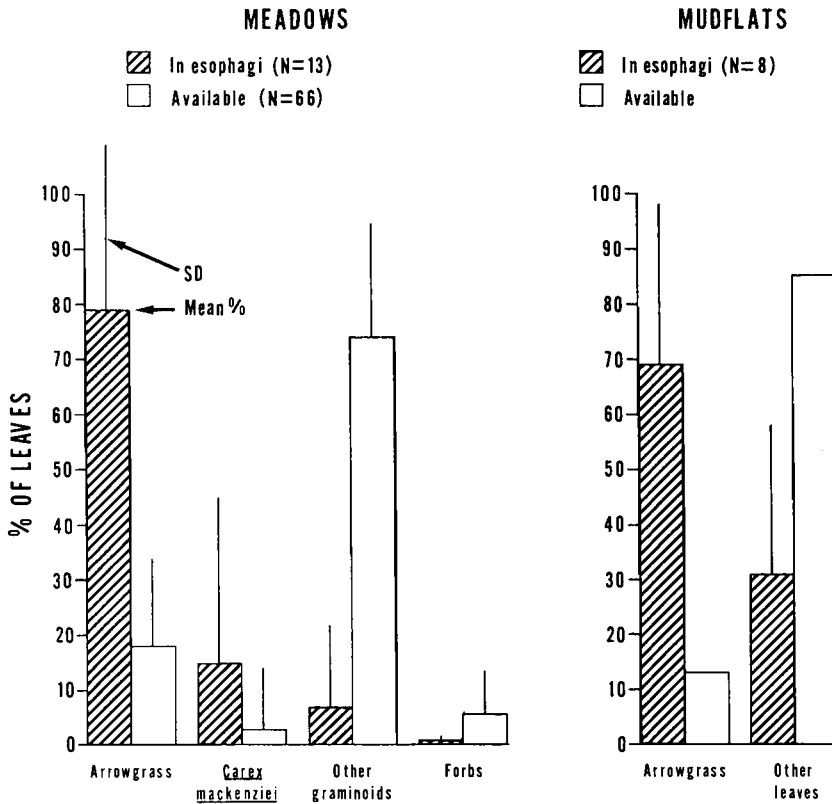Mean levels of ADI (consisting of cellulose, lignin, and some ash) varied between 21.1% and

Fig. 3. Dietary selectivity by imprinted goslings in 1978 and 1979. Species composition of leaves in esophagi was determined by counting all leaves in esophagi of goslings that had fed in the vicinity of meadow vegetation transects (13 goslings) or on mudflats (8 goslings). We did not present variability in percentage of leaves available on mudflats, because numbers of arrowgrass leaves were estimated from quadrats of a size different from those for other leaves (see Methods).

29.2% of plant dry weights (Table 2). *Carex mackenziei* and *C. subspathacea* contained significantly less ADI than mixed-meadow vegetation, whereas mixed-mudflat vegetation contained intermediate levels of ADI. Other samples were not compared statistically due to insufficient sample sizes.

Significant differences among species in the percentage of cell wall comprised of protein were not detected (1-way ANOVA, $P > 0.05$, Table 2). When averaged across all species, cell walls contained 0.72% nitrogen, or 4.5% crude protein. This is a slight underestimate, because cell-wall fractions were contaminated with cellite from the NDF procedure. The percentage of cell wall was inversely correlated with total crude protein ($r_s = -0.32$, $P < 0.01$). In conjunction with the constant protein fraction in

cell walls, this resulted in a larger fraction of total protein being associated with cell walls in plants that contained less total protein. Cell-wall protein constituted 2–4% of total crude protein in arrowgrasses but 22% of crude protein in mixed-meadow vegetation.

Available protein and carbohydrate.—Protein associated with cell walls is relatively unavailable to nonruminants (Van Soest and Moore 1965). Cackling Geese digested approximately 38% of cell-wall protein (Sedinger and Raveling unpubl. data). Hence, the association of protein with cell walls significantly reduced the protein available for digestion. Available protein was further reduced below crude protein, because the 6.25 multiplier used to calculate crude protein failed to account for nonamino-acid nitrogen in plants (McDonald et al. 1973).

TABLE 1. Nutrient content of foods used by Cackling Geese ($\bar{x} \pm$ SE).

Plant species/ type	H_2O (%)	Crude protein[a] (%)	Crude fat[a] (%)	Ash[a] (%)
Arrowgrass (from mudflats)	86.5 ± 1.5 (A)[b] (n^c = 5)	30.1 ± 1.7 (A) (n = 5)	3.8[NT] (n = 1)	13.0[NT] (n = 1)
Arrowgrass (from meadows)	84.9 ± 0.7 (A) (n = 5)	19.5 ± 1.5 (B) (n = 10)	3.9[NT] (n = 1)	12.5[NT] (n = 1)
Carex subspathacea	79.6 ± 1.7[NT] (n = 5)	19.0 ± 1.6 (B, C) (n = 5)	4.4 ± 0.4 (A) (n = 5)	9.2 ± 1.0 (A) (n = 5)
C. mackenziei	78.3 ± 1.1 (B) (n = 15)	14.0 ± 0.7 (D, E) (n = 15)	3.2 ± 0.2 (A) (n = 13)	9.2 ± 0.4 (A) (n = 13)
Mudflat-mixed	82.2 ± 0.6[NT] (n = 20)	15.2 ± 0.6 (C, D) (n = 20)	3.2 ± 0.2 (A) (n = 17)	7.9 ± 0.7 (A) (n = 15)
Meadow-mixed	70.1 ± 1.0 (C) (n = 15)	13.3 ± 0.6 (E) (n = 15)	3.2 ± 0.1 (A) (n = 15)	6.1 ± 0.1 (B) (n = 15)
C. rariflora seeds	66.1[NT] (n = 1)	14.9[NT] (n = 1)	7.8[NT] (n = 1)	3.9[NT] (n = 1)
Empetrum nigrum berries	80.9 ± 1.8 (A, B) (n = 4)	5.0 ± 0.4 (F) (n = 4)	9.7[NT] (8.7–10.6)[d] (n = 2)	2.4[NT] (2.2–2.6) (n = 2)

[a] Percentage of dry weight.
[b] Entries within a column, not sharing a common capital letter were significantly different (α = 0.05). NT indicates entry was not tested (because of small samples or bias in water content data; see text).
[c] n = number of samples from distinct sampling dates and/or areas.
[d] Parentheses indicate range for crude fat and ash of *E. nigrum* berries.

TABLE 2. Cell-wall content (% dry weight) of food plants used by Cackling Geese ($\bar{x} \pm$ SE).

Plant species/type	Neutral detergent insoluble (% cell wall)	Acid detergent insoluble (%)	Cell-wall nitrogen[a] (%)
Arrowgrass (mudflat)	23.7 ± 1.2 (A)[b] (n^d = 4)	23.7[NT] (n = 1)	0.4 (0.3–0.4)[c] (n = 2)
Arrowgrass (meadow)	29.1 ± 0.8 (B) (n = 5)	28.0 (24.0–32.0)[NT] (n = 2)	0.5 ± 0.1 (n = 4)
Carex subspathacea	47.6 ± 1.6 (C) (n = 5)	23.1 ± 0.9 (A, B) (n = 5)	0.8 (0.7–1.0) (n = 2)
C. mackenziei	50.4 ± 0.8 (C) (n= 15)	21.1 ± 0.8 (A) (n = 15)	0.8 ± 0.1 (n = 5)
Mudflat-mixed	49.5 ± 1.9 (C) (n = 20)	25.8 ± 1.0 (B, C) (n = 20)	0.9 ± 0.2 (n = 3)
Meadow-mixed	58.3 ± 1.0 (D) (n = 15)	27.1 ± 0.4 (C) (n= 15)	0.8 ± 0.1 (n = 4)
C. rariflora seeds	60.4[NT] (n = 1)	22.7[NT] (n= 1)	—
Empetrum nigrum berries	36.8[NT] (n = 1)	29.2[NT] (n= 1)	—

[a] No significant, among-species variation (1-way ANOVA, P > 0.05).
[b] Entries within a column not sharing a common capital letter were significantly different (α = 0.05). NT indicates entry was not tested.
[c] Values in parentheses are the range for entries when n = 2.
[d] n = number of samples from distinct sampling dates and/or areas.

TABLE 3. Available protein and carbohydrate content of foods used by Cackling Geese (% dry weight).

Plant species/type	Available protein[a] (%)	Soluble carbohydrate[b] (%)
Arrowgrass (from mudflats)	24.3	35.4
Arrowgrass (from meadows)	15.0	39.8
Carex subspathacea	13.7	25.9
C. mackenziei	9.4	28.7
Mudflat-mixed	10.4	29.8
Meadow-mixed	8.5	24.5
C. rariflora seeds	11.3	17.6
Empetrum nigrum berries	3.3	48.4

[a] Calculated from: % available protein = $5.44 \cdot$ % N $- 1.47 - 0.62 \cdot$ % protein in cell walls. For seeds and berries % available protein = $5.44 \cdot$ % N $- 0.62 \cdot$ % protein in cell walls (because seeds and berries contained little nonprotein nitrogen).

[b] Percentage soluble carbohydrate = 100% $-$ % cell wall $-$ % non-cell-wall protein $-$ % crude fat $-$ % ash. % non-cell-wall protein = $5.44 \cdot$ % N $- 1.47 - $ % protein in cell walls (except seeds and berries; see a).

We estimated the true relationship between nitrogen and protein by regressing the sum of the percentages of amino-acid concentrations (Sedinger in press) against the percentage of nitrogen, using nine samples of green vegetation. The accurate relationship between protein and nitrogen was:

$$\begin{aligned} \text{percentage of} \\ \text{true protein} = -1.47 + 5.44 \\ \text{(percentage of} \\ \text{nitrogen).} \end{aligned}$$

Accounting for cell-wall protein and the conversion from Kjeldahl nitrogen to protein resulted in estimates of protein available for digestion of between 19% (arrowgrass) and 36% (mixed-meadow) below crude protein values (Table 3).

Soluble carbohydrate comprised 48% of *Empetrum nigrum* berries (Table 3), whereas arrowgrass contained the largest fraction of soluble carbohydrate among green plants (35.4–39.8%). Other green plants contained between 24.5% (mixed-meadow) and 29.8% (mixed-mudflat) soluble carbohydrate.

DISCUSSION

Diet.—Arrowgrass dominated the summer diet of young Cackling Geese before they fledged despite its low abundance relative to other graminoid species. Such selectivity resulted both from preferential foraging in mudflats (Sedinger and Raveling unpubl.), where arrowgrasses were more available, and from discrimination among available food plants at particular feeding sites (Fig. 3). The preference for arrowgrass displayed by Cackling Geese means that actual food availability was much lower than one might qualitatively assume from the large extent of sedge meadows on the Yukon-Kuskokwim Delta.

The preference for arrowgrass was associated with its content of protein, water, ash, and soluble carbohydrate being higher than, and its cell-wall content being lower than, that of other graminoids. The relationship between available nutrients and food preference was highlighted by a preference for foraging in mudflats (Sedinger and Raveling unpubl.), where arrowgrass contained more protein and less cell wall than it did in meadows. The choice among grasses and sedges was less clearly related to nutrient content. *Carex subspathacea* contained the highest protein and lowest cell-wall content among grasses and sedges; yet, it was not an important component of the diet. *Carex mackenziei* was consumed at 2–3 times the rate of other grasses and sedges combined; yet, it did not contain higher protein or lower cell-wall content than these other species. *Carex mackenziei* contained less ADI than either mudflat or meadow vegetation. Less cellulose and lignin in cell walls of *C. mackenziei* may have allowed greater mechanical breakdown of plant cell walls, thus rendering nutrients in this species more available and making it a preferred food. Acid and neutral detergent fiber contents of diets were both negatively correlated with growth rates of meadow voles (*Microtus pennsylvanicus*), herbivores with simple gastrointestinal tracts, indicating that cellulose and/or lignin interfered with utilization of nutrients (Russo et al. 1981).

The lack of correspondence between nutrient content and contribution to the diet of foods other than arrowgrass may have been partially due to differences between the chemical composition of vegetation actually consumed by geese and vegetation samples collected for chemical analysis. Arrowgrass from esophageal contents of geese contained an average of 28% and *C. mackenziei* leaves 51% more protein than did hand-collected or clipped leaves of the same species (Sedinger and Rav-

eling unpubl. data). An unknown fraction of this "extra" protein was due to contamination by saliva (Moss 1972), but higher protein levels in esophageal samples were probably at least partially due to selection by geese of higher-quality feeding areas or higher-quality plants or plant parts. Geese have the ability to select plants with higher protein content (Lieff et al. 1970, Harwood 1975, Owen et al. 1977). Geese also select younger and probably more nutritious leaves from within plants (Prins et al. 1980), and McLandress and Raveling (1981a, b) demonstrated that geese grazed in a manner that maximized nutrient intake. If Cackling Geese were capable of detecting patches of vegetation of higher nutrient content, then species that were more variable in nutrient content (e.g. *C. mackenziei*) could have been preferred due to the presence of some plants or plant parts with high nutrient content, even though there were no between-species differences in mean nutrient content in our samples or in the species as a whole.

Carex subspathacea and *P. phryganodes* had low growth forms in which arrowgrass was readily available. Hence, on mudflats, geese were able to maintain a high rate of intake while feeding exclusively on arrowgrass. Arrowgrass was probably less available in stands of *C. mackenziei* due to the longer growth form of the latter species. This could have resulted in *C. mackenziei* being grazed along with arrowgrass in order to increase the rate of intake over what would have been possible if only arrowgrass were being eaten. Thus, *C. subspathacea* and *P. phryganodes* were probably consumed less frequently than expected, because their growth forms allowed a high enough rate of intake of arrowgrass alone, whereas *C. mackenziei* was consumed more frequently than expected from its nutrient content, because its growth form precluded a high enough rate of intake when feeding on arrowgrass alone.

The minimal contribution of invertebrates to the diet (Appendix; Mickelson 1973) is of interest, because such foods provide a concentrated source of protein of high biological value (Krapu and Swanson 1975) known to be important in the early diet of other waterfowl (Sugden 1973). Goslings of Cackling Geese readily consumed insects under enclosed conditions (pers. obs.). A relatively small return from consuming single insects at a time in meadows may select against the consumption

of insects except under conditions (e.g. cold weather, M. R. McLandress pers. comm.) in which insects are highly vulnerable and thus available in large numbers. The grazing behavior of geese may also contribute, because search images required for correct selection of preferred food plants may preclude feeding on insects except when superabundant and available.

Nutritional considerations.—Discrimination among potential foods resulted in a clear nutritional benefit to Cackling Geese. If the ability of geese to select more nutritious individuals from within a species is disregarded and only the nutritional advantage of selection among species is considered, the protein content of the actual diet was 37% higher in meadows and 43% higher in mudflats than random selection would have provided. Dietary protein was directly related to the growth rate of domestic and Mallard (*Anas platyrhynchos*) ducklings (Dean 1972, Street 1978). Adult muscle size may be maximized by sufficient dietary protein during early development (Moss et al. 1964, Swatland 1977). Canada Goose goslings grew faster when raised on fertilized vegetation than on unfertilized vegetation (Lieff 1973) and goslings of Bar-headed Geese (*Answer indicus*) grew faster on an artificial diet than they did in the wild (Wurdinger 1975), indicating that diet in the wild was inadequate for maximum rate of growth.

A preference for arrowgrass also increased energy content in the diet because of its higher soluble carbohydrate levels compared to grasses or sedges. Low energy levels in the diet of chicks less than 10 days old may result in both fewer and smaller adipose cells (March and Hansen 1977). Hence, the dietary selectivity displayed by Cackling Geese probably maximized growth rate, final adult body size, and ability to store both fat and protein. These factors could significantly influence their reproductive capacity as adults (Ankney and Mac-Innes 1978, Raveling 1979). Faster growth may also have reduced susceptibility to predation, and, as Scott et al. (1955) demonstrated, mortality due to cold and wet weather may be reduced by improvement of the diet in gallinaceous birds. Furthermore, Cole (1979) found that larger Lesser Snow Goose goslings survived better than smaller ones in cool summers.

Seasonal and annual variation in diet.—Cackling

Geese ingested less arrowgrass and more energy-rich *Carex* seeds and *Empetrum* berries as summer progressed. This change in diet was possibly in response to an increased requirement for energy to allow premigratory fat deposition and to a decreased growth demand. Reduced arrowgrass consumption, however, began while goslings were still growing rapidly and presumably still requiring a high-protein diet. Esophagi of four imprinted goslings collected on 31 July 1979, approximately 1 week before fledging, contained between 81% and 95% arrowgrass, indicating that this food was readily consumed when available, even during the late brood-rearing period. Biomass of arrowgrass declined in mid-July 1979 (Sedinger and Raveling unpub. data) on mudflats, indicating that declining consumption of arrowgrass was at least partially due to reduced availability of that species.

Arrowgrass comprised a smaller fraction of both the premolt and molt diets during 1978 than during 1979 (Fig. 1), although the difference was significant only during premolt ($P < 0.002$). This was associated with higher densities of geese on our principal study plot during 1978 than during 1979 [an average of 23 Cackling Goose families during 1978 vs. 12 families during 1979 and an average of 1 family of either Brant or Emperor Geese (*Chen canagica*) in each year]. This inverse correlation between goose density and the presence of arrowgrass in the diet, in conjunction with declining arrowgrass biomass through the brood-rearing period, indicates that Cackling Geese were reducing the availability of their preferred food, especially when densities of geese were high. Reduced consumption of arrowgrasses due to reduced availability would reduce protein and energy intake by geese.

Population and distribution considerations.—To the extent that nutrition influences survival and future reproduction, availability of vegetation of sufficient quality may, in conjunction with habitat features providing for safety from predation, determine preferred nesting habitat. Nesting geese are not uniformly distributed throughout arctic areas, and their distribution may be related to the presence of brood-rearing areas with the "proper" plant species composition. Lieff (1973) suggested that different nesting and brood-rearing areas at McConnell River, N.W.T., Canada produced different "quality" goslings, which may have been re-

lated to differences in food quality. In view of the ongoing commercial development of arctic areas, it is important to determine the contribution of particular plant species to the maintenance of goose populations and to determine the relationship between these plant species and preferred goose breeding areas.

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APPENDIX. Food of Cackling Goose goslings on the Yukon-Kuskokwim Delta. Results from 64 goslings containing a total of 14.6 g in esophagi (dry weight).

Food species	Frequency of occurrence	Dry weight (%)
Triglochin palustris	88	68
Carex mackenziei leaves	38	18
C. ramenskii leaves	20	1
C. rariflora leaves	5	Trace[a]
C. subspathacea leaves	2	Trace
C. glareosa leaves	6	Trace
Carex (unident.) leaves	5	Trace
Puccinellia phryganodes leaves	6	1
Graminae (unident.) leaves	14	Trace
Hippuris tetraphylla leaves	11	Trace
Potentilla egedii leaves	8	Trace
Empetrum nigrum leaves	6	Trace
Stellaria crassifolia leaves	11	Trace
Ranunculus hyperborea leaves	5	Trace
Chrysanthamum arcticum leaves	2	Trace
Salix ovalifolia leaves	2	Trace
Carex seeds	28	8
E. nigrum seeds	6	1
E. nigrum berries	3	1
Moss (unident.)	2	Trace
Litter	14	Trace
Insects	16	Trace

[a] Trace = <1%.

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RELIABILITY OF SINGING BIRD SURVEYS: CHANGES IN OBSERVER EFFICIENCY WITH AVIAN DENSITY

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ABSTRACT.—Field trials in which paired observers were used and indoor simulations in which recorded bird songs were used indicated that, as the number of singing birds audible from a listening station increased from 1 to 4, the fraction of them recorded by observers declined by up to 50%. This reduction in efficiency violates one of the basic assumptions of any index—that the proportion of animals detected remains constant—and could cause surveyors who rely primarily on auditory cues to underestimate changes in population density by up to 25% for common species and 33% for abundant species. The change in efficiency, which is best regarded as measurement error, cannot be detected by a statistical examination of the data and thus may pass undetected in many field studies. It seems unlikely that any general procedure for "correcting" the error would be reliable. The results indicate that singing bird surveys of common species should be supplemented by other methods if accurate estimates of changes in density are needed.

A general conclusion of the study is that whenever animals "compete" for a place in the survey, for example by filling up traps or suppressing one another's songs, then the index tends to underestimate a change in density. If efficiency increases with density, then the survey tends to overestimate a change in density. If the sign of the bias can be determined, the survey can be used to provide a minimum or maximum estimate of a change in density even if the magnitude of the bias cannot be estimated. *Received 11 July 1983, accepted 9 January 1984.*

Two approaches are available to estimate a difference in avian densities from transect or point-count data. The counts may be translated into density estimates, or the difference in counts may be used as a direct estimate of the difference in densities. Density estimation is not reliable in many habitats, because the critical assumption that observers record all birds near them is not valid (Mayfield 1981). In addition, many of the density-estimation methods require accurate estimates of the distance to each bird, which may be difficult to obtain. Index methods require that the same proportion of birds in each population be detected. Many observers feel that this is a more reasonable assumption than that all birds near the observer are detected. They therefore recommend the index method when a change in density, rather than density itself, is to be estimated (Dawson 1981). Historically, far more data have been analyzed by means of index methods than by means of density estimation, and indices continue to be used in numerous regional and national surveys (grouse: Rodgers 1981; quail: Robel et al. 1969; pheasant: Carney and Petrides 1957; turkey: Scott and Boeker 1972; woodcock:

Duke 1966; doves: Sayre et al. 1978; other gamebirds: Sanderson 1977; Breeding Bird Survey, many terrestrial species: Bystrak 1981).

Although index methods are widely used, some observers have expressed concern over the assumption that surveyors record the same proportion of each population (Caughley 1977, Sayre et al. 1980, Dawson 1981). Surveys are usually designed so that factors such as time of day and season, weather conditions, observer skill, and habitat parameters are either standardized or have similar distributions in each population. A more difficult problem is posed by factors that respond directly to density. If, for example, song output per bird varies with density, then there is no way to design the survey so that the average song output is the same in each population. This issue, while potentially quite serious, has received little detailed study. Walankiewicz (1977) and Frochot et al. (1977) concluded, on the basis of indirect evidence, that observers missed a higher proportion of birds when density was high. Dawson (1981) and Järvinen and Väisänen (1976) examined the issue briefly but could not reach definite conclusions. Bystrak (1981) mentioned

"overloading" as a possible problem for some uses of Breeding Bird Survey data. Scott and Ramsey (1981) compared counts of one and three target species when observers listened only for the target species and when they listened for all species. When listening for all species, they recorded 25–50% fewer individuals of the target species, suggesting a pronounced saturation effect. None of these studies provided estimates of how much observer efficiency might change with density.

These reports pertain mainly to interspecific effects: the increased likelihood of missing a bird when numerous other species are present. Intraspecific factors may also cause problems. DeSante (1981) reported, in a study of the variable circular-plot method (Reynolds et al. 1980), that at high density some birds were missed and at low density they were over-counted. This caused the variable circular-plot estimates to be inversely correlated with actual density (determined through intensive surveys), and the same would be true if the simple index results had been used. DeSante attributed the errors in part to greater movement by birds (and thus double counting) in larger territories. Other factors that may also be important are that, when several individuals of a species are audible from a listening station, a near bird may mask a far one, two individuals may be close together and therefore difficult to separate, and after the observer records one or two individuals of a species his attention may turn to other species he thought he heard or thought he ought to have heard based on the habitat. Field experience suggested to us that the problem of reduced observer efficiency when many conspecifics are present might be of significance. We undertook this project to determine whether or not observer efficiency does decrease as the number of singing conspecifics increases and, if it does, to determine how seriously this compromises the singing bird index.

METHODS

Two methods were used to measure how efficiency—the average proportion of singing birds recorded by the observer—changes with the number singing. In the first method we accompanied observers conducting surveys of breeding birds. During the first 4–5 h of daylight, observers counted all birds heard during 3 min spent at each of 50 roadside stations. The survey resembled the Breeding Bird Survey (Bystrak 1981), but the birds detected only by visual

cues were excluded from the analysis. While the surveyors listened for all species, we each listened for only one species. The observers were unaware of which species we listened for. We calculated the average number of birds they recorded when we recorded one individual, two individuals, etc., and we used our results as a standard with which to estimate their efficiency at different actual densities. During 2 yr of fieldwork in east-central Ohio, we accompanied 11 observers on 16 routes and recorded more than 3,000 individual birds.

The field methods gave us considerable realism, but we could not control extraneous variables such as traffic noise, dispersion of the birds, and habitat characteristics. In addition, there was no objective measure of how accurate our counts were. We therefore designed an indoor simulation of the dawn chorus using tape-recorded bird songs. This experiment provided the needed control and an independent check on the field-study results.

In preparation for the indoor trials, two seasons were first spent studying the vocal behavior of birds in the study area. The fieldwork described above provided estimates of the number of species, and individuals of each species, that typically sing during a 3-min listening period. We also monitored song duration of individual birds at randomly selected roadside locations. During 840 15-min periods in June of 1980 and 1981, we recorded the amount of song for each individual of species selected in advance. The results were used to construct species-specific frequency distributions of song duration during 3-min intervals (Table 1). Song duration was defined as the total time in 15-s intervals during which the bird sang at least once. If in a 3-min interval the bird sang once in the first 15-s interval and once in the final 15-s interval, duration of the song would be recorded as 30-s. We used the results of this fieldwork to insure that the distribution of durations in our simulations was realistic.

The simulation consisted of 43 3-min listening periods during which recorded songs were played from loudspeakers surrounding the surveyors. Each listening period had 12 species and 20 or 21 individuals singing at typical rates. Approximately two-thirds of the species and individuals were placed in two-thirds of the circle labelled "scrubgrowth"; the remainder were placed in the "forest" segment. Volume (simulating distance) and duration varied within the listening period but had identical distributions between periods. Conspecifics were spaced out as evenly as possible over no more than one-third of the circle.

We use the term "treatment group" to designate the set of periods having the same density of a particular species. Within each species, the distributions of song volume and duration were similar in each treatment group. For example, the average duration of song by American Robins (*Turdus migratorius*) in periods with one robin present was the same as in

TABLE 1. Frequency of song durations during 3-min periods in which the individual sang at least once. Presence or absence of song in each 15-s interval was recorded.

Species	Number of periods	Number 15-s intervals with song					
		1–2	3–4	5–6	7–8	9–10	10–11
Mourning Dove (*Zenaida macroura*)	91	0.35	0.24	0.19	0.05	0.08	0.09
Great Crested Flycatcher (*Myiarchus crinitus*)	55	0.42	0.15	0.07	0.07	0.11	0.18
American Crow (*Corvus brachyrhynchos*)	35	0.48	0.23	0.03	0.03	0.06	0.17
House Wren (*Troglodytes aedon*)	95	0.12	0.20	0.16	0.12	0.15	0.26
Gray Catbird (*Dumetella carolinensis*)	376	0.26	0.18	0.14	0.07	0.11	0.24
Brown Thrasher (*Toxostoma rufum*)	18	0.33	0.11	0.11	0.17	0.06	0.22
American Robin (*Turdus migratorius*)	108	0.16	0.14	0.11	0.07	0.17	0.35
Wood Thrush (*Hylocichla mustelina*)	42	0.29	0.05	0.14	0.02	0.05	0.45
Red-eyed Vireo (*Vireo olivaceus*)	130	0.12	0.13	0.11	0.08	0.12	0.45
Common Yellowthroat (*Geothlypis trichas*)	304	0.16	0.13	0.09	0.08	0.08	0.46
Northern Cardinal (*Cardinalis cardinalis*)	140	0.26	0.21	0.14	0.13	0.11	0.15
Indigo Bunting (*Passerina cyanea*)	377	0.09	0.09	0.09	0.07	0.09	0.57
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	28	0.25	0.21	0.11	0.07	0.14	0.21
Field Sparrow (*Spizella pusilla*)	167	0.21	0.10	0.13	0.10	0.09	0.38
Song Sparrow (*Melospiza melodia*)	360	0.24	0.12	0.16	0.11	0.09	0.28

periods with two robins present. A total of 39 species occurred during the 43 periods; the experiments were designed to study 16 of them. Each of these 16 species had 10 periods with one individual present and 8 periods with 2 individuals present. Among 7 species, densities of 3 (5 periods) and 4 (4 periods) also occurred.

A total of 20 experienced birdwatchers from Maryland, all of whom had run Breeding Bird Surveys, participated in the trials, which were held in a large high school cafeteria. Participants arrived for the simulation at 1700 and were acquainted with the layout of the experiment before they began the 4–4.5-h trial. They were not informed of the purpose of the study or of any of the parameters, such as number of species per listening period. They stood in a 1.5-m-diameter circle surrounded by 27 loudspeakers equally spaced around a circle of 20-m radius. Each loudspeaker was attached to a separate cassette player located in a control booth adjacent to the circle. Four people worked in this booth playing the cassettes at predetermined times during each 3-min listening period. Each cassette contained songs of a single species. There were no call notes, and no other birds were audible on the tapes. The surveyors used a separate sheet for each listening period to avoid recording errors; they were asked not to discuss their results until after the entire trial. Two to five people participated per night. The simulations were identical each night.

RESULTS

The fieldwork and indoor simulations both indicated, for all species studied, that efficiency declined steadily and markedly with increas-ing density (Fig. 1, Table 2). In only one case was there an increase in efficiency with an increase in density [Field Sparrows (*Spizella pusilla*) in the field trials between densities 1 and 2]. For all species combined, the field-trial estimates declined 32% from 0.72 at density = 1 to 0.49 at density = 4. Comparable figures from the indoor simulations were 1.1 to 0.56, a 49% decline. In the indoor simulations, the decline in efficiency was greatest between the first two density classes, but this trend was absent or weak in the field-trial data.

Although the trends shown by the two methods are similar, some differences can be seen. The greatest difference is that efficiencies from the indoor trials were higher than those from the field study, perhaps because the participants requested that we set the volumes higher than we had intended to. Indoor efficiencies also decreased somewhat faster than outdoor ones, probably because the individuals of each species were closer together in the indoor simulation, on average, than is usually true in the field.

During the fieldwork, our observers frequently recorded individuals of a species we were monitoring when we had not detected the species. We suspected, but could not prove, that these were misidentifications. This impression was confirmed by the tape recorder sessions. All observers occasionally recorded species not present during the listening period. The average number of "phantom species" re-
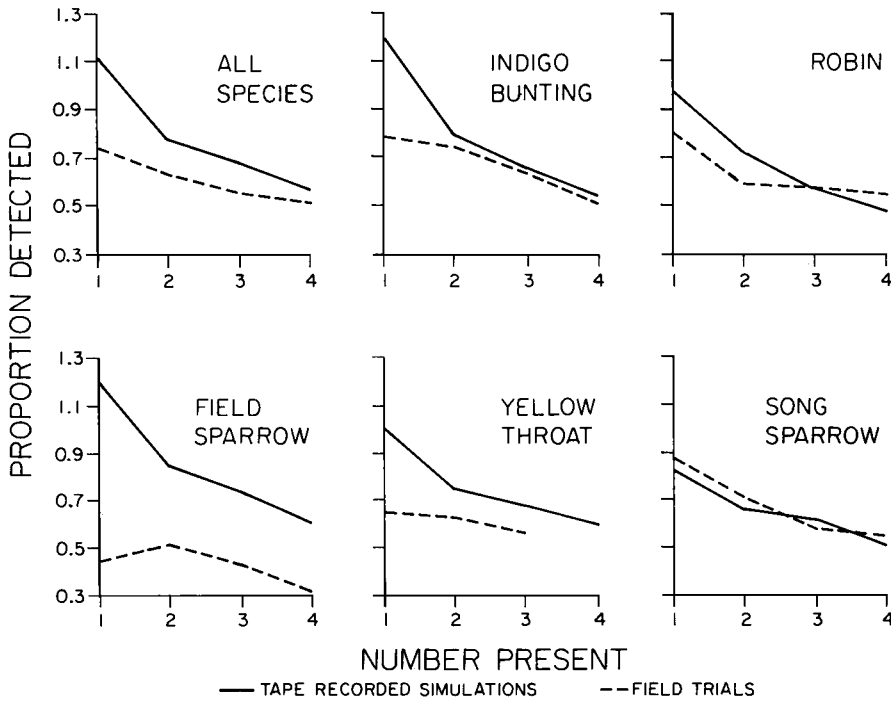
Fig. 1. Relationship between number of birds present and average proportion detected in field and indoor trials. For standard errors, see Table 2.

corded was 0.67 per listening period. The averages for individual observers varied from 0.19 to 2.02; 80% of the observers had averages between 0.37 and 0.95 inclusive. A related statistic is that, for 8 of the 16 species studied in detail, when only 1 individual was present, 2 were recorded more often than 0, producing "efficiencies" exceeding 1.0 (Fig. 1, Table 2).

TABLE 2. Relationship between number of birds present and average proportion detected (efficiency) in field trials (excludes species in Fig. 1) and standard errors for field and indoor trials.

	Number present			
	1	2	3	4
A. Point estimates of efficiency				
Mourning Dove	1.02	0.72	0.68	0.56
American Crow	1.08	0.93	0.72	0.62
Eastern Wood-Pewee (*Contopus virens*)	1.30	0.87	0.74	0.62
Red-eyed Vireo	1.12	0.82	0.62	0.53
Gray Catbird	0.64	0.55	—	—
Brown Thrasher	0.78	0.57	—	—
Wood Thrush	0.94	0.72	—	—
Great Crested Flycatcher	0.84	0.67	—	—
House Wren	0.84	0.72	—	—
Rufous-sided Towhee	0.73	0.63	—	—
Northern Cardinal	0.95	0.74	—	—
B. Pooled standard errors[a]				
Field trials with 1–4 present	0.069	0.051	0.041	0.035
Indoor simulations with 1–2 present	0.046	0.035	—	—

[a] Calculated by considering the results from all species as a single data set.

The finding that even highly competent observers regularly misidentify species or overestimate their numbers may be of interest to field workers, but it should not cause undue concern about the singing-bird index. If an observer always recorded twice as many birds as were present, the index would estimate change in density with perfect accuracy. The same is true of the observer who always records 10% of those present.

The change in efficiency with density was similar among species. In the indoor simulations, less common species (max. density = 2) had lower average efficiencies. Their proportional change in efficiency (the component of bias we were studying) was not consistently different from that of the more common species.

These results demonstrate clearly that efficiency does change with density, and they provide an estimate of the magnitude of the change. The next step is to determine how much this variation affects the ability of the survey to measure changes in population density. To do this, let

$$\bar{N}_1 = \sum_1^4 df_{1d} = \text{average number present/station in year 1, and}$$

$$\bar{n}_1 = \sum_1^4 df_{1d}e_{1d} = \text{average number recorded/station in year 1,}$$

where f_{1d} = proportion of stations in year 1 with d birds present, and e_d = average proportion recorded when d birds are present (efficiency). If similar terms are defined for year 2, then

$$\text{actual change} = \frac{\bar{N}_2}{\bar{N}_1} - 1,$$

$$\text{estimated change} = \frac{\bar{n}_2}{\bar{n}_1} - 1,$$

and the bias in the survey estimate of change in population density may be expressed as

$$\text{relative bias} = \frac{\text{estimated change}}{\text{actual change}} - 1$$

$$= \frac{\dfrac{\sum df_{2d}e_d}{\sum df_{1d}e_d} - 1}{\dfrac{\sum df_{2d}}{\sum df_{1d}} - 1} - 1. \qquad (1)$$

Bias arises from variation in the e_d. It is identical to zero if all $e_d = e$. The sign of relative bias indicates the direction of the error; relative

bias = -0.11 means that the survey, on average, would underestimate the true change by 11%.

Some difficulty may be caused by our use of the phrase "number of birds present," because this number depends on how much area is included, and it is not immediately clear what size area is appropriate. If we assume that the listening stations are placed randomly with respect to birds in the population we wish to make inferences about (an assumption required for any statistical use of the data), then, in calculating relative bias, the size of the area around the listening station is of no consequence as long as it only includes birds in the population of interest. Conceptually, it is easiest to imagine that the area includes all the birds that even the best observer may record. How much additional area is included does not matter, because the relative bias is determined by the proportional change in efficiency, $(\bar{n}_1/\bar{N}_1)/(\bar{n}_2/\bar{N}_2)$. Changing the size of the area used to calculate $\bar{N}_1$ and $\bar{N}_2$ simply changes these numbers by a constant multiplier; it has no effect on the proportional change in efficiency.

The basic question addressed in this study is how closely $\bar{n}_2/\bar{n}_1$ estimates $\bar{N}_2/\bar{N}_1$. The field and indoor trials provide estimates of e_d, but to estimate relative bias the change in frequency of each density class between years must also be determined. This point can be made clear by an example. If the zero-density class increased during a population decline and all other frequencies decreased by the same proportional amount, $f_{2d}/f_{1d} = a$ for all d, then substituting $f_{2d} = f_{1d} a$ in equation (1) yields zero, indicating that the relative bias would be zero regardless of how much efficiency changed with density. This example is not realistic, because it is unlikely that the frequency of each density class would decline by the same proportional amount, but it shows that the change in frequency cannot simply be ignored in the calculations.

We investigated two models specifying how the frequency of each density class changes as the result of a population decline. Both models assume that density is the only change between years. Under this assumption, the frequencies in year 2 are

$$f_{2d} = \sum_{N=d}^4 f_{1N}b_{d/N}, \ d = 0, \ldots, 4, \qquad (2)$$

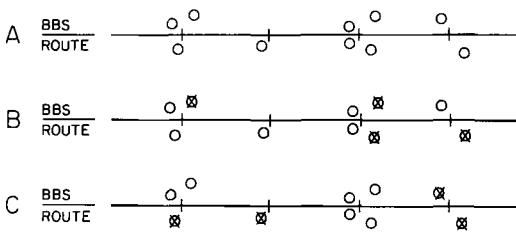where $f_{1N} = f$ (stations in year 1 with N birds

Fig. 2. Two models of how a population decline affects the distribution of bird densities at survey stations. A. Distribution of birds if no decline had occurred. B. Losses distributed randomly (constant-loss model). C. Losses concentrated at stations that would have had fewer individuals present (variable-loss model).

present), and $b_{d/N}$ = proportion of the stations with N birds in year 1 that have d birds in year 2. In the first model, vacancies (at locations that were occupied in Year 1) are assumed to be randomly distributed among the density classes. If we define

$$p = \bar{N}_2/\bar{N}_1,$$

then $b_{d|N}$ is the binomial probability

$$b_{d|N} = \binom{N}{d} p^d (1 - p)^{N-d}. \tag{3}$$

This is referred to as the constant-loss model (Fig. 2). The second model recognizes that there may be a correlation between habitat quality and number of birds present in Year 1 at a station. In this case, vacancies in Year 2 might be concentrated at stations that had high or low density in Year 1. Thus, the probabilities of a vacancy $(1 - p)$ would vary with density class, so we substitute p_N, $N = 1, \ldots 4$, in equation (3). Given an overall change in density, p, and the initial density class frequencies, f_{1N}, the p_N may be calculated by specifying one frequency as a dummy variable, say $p_4 = k$, and then defining the other probabilities in terms of k: $p_3 = 0.9k$, $p_2 = 0.5k$, $p_1 = 0.3k$, for example. This would indicate that vacancies were concentrated at stations having lower density in Year 1. The unknown, k, can then be calculated by iterative methods from which the p_N can be determined. They are substituted for p in equation (3). We refer to this as the variable-loss model (Fig. 2).

The results of the simulations are that the

TABLE 3. Sensitivity of relative bias to initial frequencies and change in efficiency.[a]

A. Initial distributions and efficiencies

Parameter	Type	Density			
		1	2	3	4
Initial	A	0.80	0.20	—	—
frequency	B	0.60	0.30	0.10	—
	C	0.40	0.30	0.20	0.10
	D	0.20	0.30	0.40	0.10
Efficiency	Field study	0.72	0.63	0.55	0.49
	Lab study	1.10	0.78	0.67	0.56

B. Relative bias (actual decline = 0.10)

Distribution type	Evaluation	Survey result		Estimated decline	Relative bias
		Before	After		
A	Field study	0.828	0.748	0.097	−0.030
	Lab study	1.192	1.084	0.091	−0.094
B	Field study	0.975	0.887	0.090	−0.097
	Lab study	1.329	1.220	0.082	−0.180
C	Field study	1.130	1.034	0.085	−0.150
	Lab study	1.477	1.366	0.075	−0.248
D	Field study	1.378	1.270	0.078	−0.216
	Lab study	1.716	1.601	0.067	−0.330

[a] Random-loss model (see text).

relative bias increased as the proportion of stations with more than one bird present increased (Table 3). The proportion of stations without any birds present has no effect on relative bias, as seems intuitively reasonable. Furthermore, if all stations with any birds had exactly one bird present, then relative bias would be zero, because the samples in each year would be based on only one efficiency. As the proportion of stations with only one individual present dropped to 60%, 45%, and 20%, relative bias rose steadily, reaching 33% in the worst case investigated.

Relative bias was higher for the efficiencies obtained in the laboratory study, because there was a greater change in the lab efficiencies than in those from the field. With frequency type A (Table 3), there was a three-fold difference in the estimates of relative bias, depending upon whether the efficiencies obtained in the lab or field were used. With frequency type D, this difference dropped to about one-third. Thus, when relative bias is large enough to be of con-

TABLE 4. Relative bias with three different population declines.[a]

Change in efficiency	Decline in population density		
	0.02	0.10	0.25
Field study	−0.156	−0.150	−0.126
Lab study	−0.256	−0.248	−0.216

[a] Initial frequency distribution: type C, Table 4.

cern to investigators (Types C, D), it makes little difference whether one uses the laboratory or field efficiencies to calculate the bias. This indicates that the exact value of the true efficiencies may be of little consequence.

The magnitude of relative bias is also insensitive to the magnitude of the population decline over the range of values we investigated (Table 4). Changing the size of the decline by more than an order of magnitude caused only a small change in the size of relative bias with either the laboratory or the field efficiencies. All of these results were obtained using the random-loss model.

The results produced by the variable-loss model were nearly identical, tending to be slightly smaller when high-density stations suffered lower than average losses (because in that case a larger proportion of stations changed from 1 present to 0 present). Because there is probably no way to be sure what loss model is most realistic, it is fortunate that the results are little affected by this parameter.

DISCUSSION

The magnitude of the population decline was underestimated in all cases. This would also be true if density increased, for underestimates are caused by the inverse relationship between efficiency and density. In many cases, it may be possible to guess the direction of change in efficiency. It is therefore worth stressing that if efficiency varies directly with density, then change will be overestimated, whereas if, as is probably true of many indices, the relationship is inverse, the change will be underestimated. Anytime animals "compete" for a place in the survey, for example by filling up a trap or suppressing one another's song, the survey will tend to underestimate changes in density. Conversely, if efficiency increases with increasing density, then the survey will tend to overestimate change. This trend appears to occur some-

times at hawk migration stations (Sattler and Bart in prep.). Efficiency increases with increasing numbers of raptors passing the lookout, perhaps because the observer becomes more attentive then and because high-flying birds pass in clusters. If the observer sees any one of the birds, he is likely to see them all. These examples suggest that sometimes it may be possible to predict the direction of the bias caused by changing efficiency so that the estimated change in density can be viewed as a minimum or maximum.

It can be argued that the relative bias uncovered in this study has little effect on the survey's ability to detect change in density, even though estimating its exact magnitude may be difficult. With a relative bias of −0.15 to −0.25, the survey results would be expected to decrease 7.5–8.5% if a 10% decline occurred in a common species, clearly showing that a decline had occurred. There would be some loss of statistical power, because the expected difference is up to 25% smaller than it would be in the absence of relative bias, and thus the significance of the observed difference would be lower than if relative bias were zero. But, the argument goes, extensive programs such as the Breeding Bird Survey often have very large samples. Hypothesis tests are therefore likely to establish the significance of observed declines despite the loss of power caused by relative bias—at least if the true decline is large enough to be of any biological importance.

There is considerable merit in this argument. The problem of relative bias *is* most serious for investigators trying to measure the magnitude of a change in density rather than simply establish its occurrence. A few rejoinders should be made to the points above, however. First, many investigators do not have the large samples typical of a national monitoring program. Suppose, for example, that a random sample of 1,000 3-min listening stations is taken in each of two years during which a true decline of 10% occurs. If the SD is 0.65, then standard power calculations show that the survey has a 99.8% chance of detecting the decline (with $\alpha = 0.05$) if the relative bias is zero, and this probability is 95.5% even with relative bias equal to 25%. Thus, the presence of relative bias has little impact in this case. With a sample of 300, however, the power is 77% with no relative bias, a respectable figure, but drops to 51% with a relative bias of 25%. Many investigators prob-

ably would feel that a study with a power of only 51% is not worth doing. Another approach is to contrast situations with and without relative bias. Relative bias might be reduced to nearly zero, for example, if observers avoided the dawn chorus or counted only a few species. If we wish the power to be the same in both cases, then how much larger a sample must be taken in the case with relative bias not equal to zero? The answer is $(1 + b)^{-2}$, where b is relative bias. With a relative bias of -0.25, the sample must be 78% larger than if the relative bias were 0.0. Thus, with the sample sizes typical of small studies, relative bias has a substantial impact on power. If the relative bias is assumed to be absent, then the power may be considerably overestimated, and the increase in sample size needed to compensate for the effects of relative bias may be considerable.

The second point, which must be mentioned in response to doubts about the importance of relative bias, is that even if a very large sample is taken, relative bias may still cause trouble. If two areas are being compared and a statistically significant change in sample results occurs, then two interpretations are possible: that there is a difference in density or that there is a difference in detectability. Suppose, for example, that the frequencies of stations with 1 and 2 birds actually present are 40% and 10% at one location, and 30% and 15% at the other (no difference in density). The application of the efficiencies obtained in the indoor trials indicates that a 5% difference in sample results would be expected. The bias is caused by the second location having a higher frequency of stations with lower efficiency. Even if a single location is being studied, the average efficiency may change in response to long-term changes in habitat. The United States Fish and Wildlife Service Mourning Dove [*Zenaida macroura*] Coo Count routes (Baskett et al. 1978) have shown such a trend in some areas in recent years, and wildlife managers are currently trying to decide whether a real decline has occurred or whether an artifact such as the one described here has caused the change (D. Dolton pers. comm.).

Which of the density distributions (Types A–D, Table 3) are most realistic? Type D, the most dense, would apply to few species, as more than 50% of stations with the species present had three or four individuals. Such densities are unlikely to occur in surveys like the Breeding Bird Survey where the routes are laid out randomly and thus pass through many different habitat patches. In such cases, many stations have only a small amount of favorable habitat for a given species within hearing range. This is evident in the BBS data. For example, among all BBS routes surveyed in Ohio and West Virginia in 1979–1981, Common Yellowthroats (*Geothlypis trichas*) occurred singly at about 80% of the stations (with the species present), whereas Indigo Buntings (*Passerina cyanea*) and Red-eyed Vireos (*Vireo olivaceous*) occurred singly at 50–60% of the stations (Bart unpubl. data). At these frequencies, the relative bias will be less than 15% in most cases. On the other hand, in a study with transects intentionally placed in homogeneous habitat, as occurs in many research projects, higher densities such as Types C or D may well occur. In the area of Ohio that we studied while estimating song frequencies, several species, including most of the ones we evaluated in the field study, most closely approximated the Type C distribution. A study solely in scrubgrowth or woods might well encounter species having Type D distributions. Thus, the problem uncovered in this study is unlikely to be serious in extensive surveys using randomly laid-out routes but may well be significant when routes are located primarily in homogeneous habitat.

Diurnal timing of the surveys may also be important in determining the magnitude of relative bias. During the first hour of daylight, most birds sing more actively, and some, especially robins, sing far more actively than they do later in the morning. This proliferation of song makes it difficult to separate individuals from one another and probably intensifies the decline of efficiency with density. Thus, when relative bias is a concern, surveyors should consider avoiding the early morning period. This will often decrease the number of birds detected, of course, but the effect on precision may be surprisingly small (Bart and Herrick 1984).

An unexpected finding of the study was that the contribution to relative bias from stations with two birds present is at least as great as the contribution from stations with four birds present. The bias is caused by a proportional change in efficiency, e_{d+1}/e_d, $d = 1, 2, 3$, most of which varied from 0.85 to 0.90. The indoor trials, however, yielded a great change in efficiency between one and two birds present. As an ex-
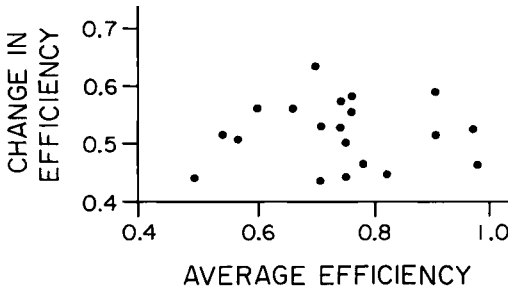
Fig. 3. Relationship between average efficiency and change in efficiency during indoor trials. Each dot represents the results for one observer. Change in efficiency = efficiency with 4 present/efficiency with 1 present.

TABLE 5. Comparison of species lists when observers were counting only species and when they were counting species and individuals. In all cases, 12 species were actually present.

	Number species recorded when counting	
Listening period	Species only	Species and individuals
1	11.04	11.39
2	10.61	10.26
3	10.04	10.04
4	10.04	10.43
5	10.74	10.74
6	10.52	10.43
7	10.83	10.56
Average	10.55	10.55
SE	0.14	0.16

ample of how important this is, if stations all had two birds present and the indoor efficiencies applied, then (with a 10% decline) relative bias would be −37%, higher than in any of our other examples. Thus, it is not always safe to assume, as was, for example, by Bystrak (1981), that relative bias will be negligible simply because densities do not exceed three or four.

The indoor simulations provided one of the first data sets in which it was known what birds were present, and conditions were sufficiently standardized to enable clear trends to emerge in the survey results. This makes it possible to examine several other issues related to the use of singing-bird survey data.

Efficiency vs. relative bias.—One question that may interest field workers is: Are observers with high overall efficiency most successful in estimating a change in population density? Although intuition might suggest that the answer is yes, there was no detectable relationship between observer efficiency (over the range of efficiencies in our sample) and relative bias calculated from their data (Fig. 3). This may be explained by an observation we have often made in the field. Keen observers frequently seem to concentrate on detecting rare species at the expense of getting more individuals of the common species. The senior author participated in both the field trials and the indoor trials, and his change in efficiency was about average. It thus appears that the problem of changing efficiency is difficult to overcome even if the observer is aware of the danger.

Presence/absence data.—It has sometimes been suggested that if observers only recorded species and did not try to count individuals,

their data might be more accurate. Such a plan would raise formidable analysis problems, at least in trying to estimate a change in density, and might be opposed on that ground alone. Another question, which our tape-recorder trials provided a means of answering, is whether or not species lists are significantly more accurate when observers are not counting individuals. To answer this question we interspersed the listening periods with seven "species only" periods during which observers were instructed not to count individuals. Each species-only period was an exact replica of one of the regular periods and was separated from it by 10 other periods. In three cases the species-only period came first; in 4 cases the regular period came first. These steps were taken to eliminate any effects of learning or fatigue. The results (Table 5) provide no support for the hypothesis that species lists will be more accurate if only species are being surveyed. It seems likely that with more than 12 species present— as often happens in the field—it would be at least slightly easier to detect species if individuals were not counted. Our results suggest that the average difference for all stations is unlikely to be large, however.

Fatigue.—Many breeding-bird surveyors have remarked that 50 3-min periods makes a very long morning, and this has caused concern that towards the end of the experiment data collection might be less diligent. Our experiment provides no support for this suggestion either; efficiency did not vary systematically during the trials. Average efficiencies for the periods

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TABLE 6. Ratio of maximum number recorded by members of a party to number actually present as a function of party size.[a]

Party size	Mourning Dove	American Robin	Common Yellow-throat	Field Sparrow	Song Sparrow	Great Crested Fly-catcher	Rufous-sided Towhee	Average	SD
1	0.797	0.734	0.819	0.802	0.683	0.813	0.715	0.77	0.05
2	0.823	0.935	0.995	0.990	0.868	0.941	0.906	0.92	0.06
3	0.926	1.110	1.219	1.169	1.076	1.062	1.062	1.09	0.09
4	1.043	1.158	1.392	1.365	1.137	1.260	1.240	1.23	0.13
5	1.058	1.186	1.339	1.317	1.140	1.260	1.257	1.22	0.10
6	1.070	1.216	1.421	1.319	1.185	1.264	1.326	1.26	0.11

[a] Entries are the means from 8 randomly selected groups of observers, 43 listening periods per observer.

(excluding the 7 species-only periods), divided into 6 groups of 7 or 8 periods each, were: 0.79, 0.75, 0.76, 0.76, 0.75, and 0.75, suggesting a possible decline in efficiency early in the trials but no decline in the later ones. There was considerable peer pressure in our experiments, which may have counteracted the effects of fatigue.

Effects of party size.—Preston (1979) suggested that the change in the maximum number of birds recorded as party size increases might be used to estimate the number of birds actually present. His model rests heavily on the assumption that all birds are equally detectable, a condition we feel is unlikely to be met in practice, but it does raise the issue of whether useful information is contained in the change in numbers reported by different individuals recording simultaneously. Without attempting to answer the question directly, we wish to point out that observers may be recording birds not actually present more commonly than is often supposed. This has a serious impact on any attempt to use the maximum number of birds recorded as party size increases. In our indoor simulation, averaging across all species, parties of three or more tended to overestimate the number of birds present when the maximum number any person recorded was used as the party estimate (Table 6). In all cases, combining the records from a party of four and using the maximum estimate as the "best" estimate led to overestimating the number present, in some cases by as much as 40%. Thus, modeling efforts that imply that there is no overcounting are probably too unrealistic.

CONCLUSION

It would be satisfying to end the study with suggestions for adjusting data to reduce rela-

tive bias. Unfortunately, this does not seem possible. Changes in observer efficiency undoubtedly depend heavily upon the number and kind of other species singing, on other noises present, on habitat, and on other features. This study suggests that the change in observer efficiency with density is unlikely to cause errors exceeding 25% for common species or 33% for abundant species, and in many cases the error is surely much smaller. As noted above, relative bias would be 0.0 for a species that never occurs more than singly at a station. Thus, no single recommendation for adjusting estimates would be appropriate for all situations.

Relative bias may be caused by several other factors than the one analyzed here. Average song duration, and the proportion of birds that sing at all, may change with density. Another possibility, often overlooked, is that the survey may be far more sensitive to a change in reproductive success than to a change in density. For example, unmated Mourning Doves sing 10 or more times as much as mated ones (Sayre et al. 1978). Thus, a decline in mating success or an increase in female mortality could lead to an *increase* in survey results. This problem can be avoided if it is possible to insure that the birds in each population being compared are, on average, at the same stage of reproduction. In practice, however, it may be impossible to determine the reproductive stage of the individuals being surveyed.

There is also a difficult problem with interactions among some species. For example, robins often mask other species during the first 30–45 min of daylight. If they declined in density, the number of them reported might not change much, because more distant individuals would be detected, but the reported numbers

of less conspicuous species might increase, because they would be more detectable. This may account for Robbins' (1981) report that Northern Orioles (*Icterus galbula*) are recorded only one-half as often during the Breeding Bird Survey's first hour when robins, which have a similar song and are far more abundant, are in full chorus, than in each of the subsequent 3-h.

The general situation might be summarized by the error function,

$$\text{relative bias} = f(e_1, e_2, e_3, e_4, \ldots),$$

where e_1 = change in recorder efficiency with density, e_2 = change in proportion of birds singing with density, e_3 = change in amount of song per bird and consequent change in detectability, and e_4 = change in detectability caused by change in extraneous noises. Clearly, the total bias could be quite large, especially if the factors tend to have the same sign.

For all these reasons, it seems best not to assume that singing-bird surveys yield highly accurate estimates of a change in abundance. They are certainly capable of detecting major changes in range or density (the major purpose of large programs like the Breeding Bird Survey), and they may indicate smaller changes. Nonetheless, in the absence of more information on relative bias than now exists, it seems unwise to carry out standard statistical analyses, such as interval estimation of differences in density, without noting that the relative bias is unknown and may, for abundant species, be as large as 33%.

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COMPONENTS OF VARIANCE IN MEASUREMENTS OF NESTLING EUROPEAN STARLINGS (*STURNUS VULGARIS*) IN SOUTHEASTERN PENNSYLVANIA

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ABSTRACT.—I report the results of experiments designed to distinguish factors affecting within-population variability in measurements of nestling European Starlings (*Sturnus vulgaris*). Individuals were switched among pairs of nests at the beginning of the incubation period and at the beginning of the nestling period. Variables were analyzed in a replicated (nested), three-way factorial analysis of variance to distinguish the contributions of factors associated with (1) the genotype of the embryo or composition of the egg, (2) the incubation period, and (3) the nestling period. In addition, I analyzed the correlations among growth variables within the sample as a whole and among main effects in the experimental design to search for patterns of genotypic and phenotypic interrelationship. I also related growth variables of nestlings to the size and composition of sibling eggs and to the length of the incubation period.

The present experiment did not reveal any genetic or egg-quality component to within-population variation in rate of mass increase and mass asymptote achieved, length of the tarsus of fully grown nestlings, or rates of growth of the wing and outer primary feather. Similarly, the nest in which the individual was incubated had no effect on postnatal growth. The nest in which the individual was reared significantly contributed between 19 and 29% of the sums of squares in rate of mass increase, length of the tarsus, rate of increase in length of the wing, and the maximum length of the sheathed portion of the outer primary feather. Rearing nest did not have a significant effect on the mass plateau of the chick. These results, particularly the absence of some effects, are difficult to interpret, because a large proportion of the variation in several variables occurred between pairs of switched nests. These differences undoubtedly included some of the variation that might have been attributable to effects within experiments.

Growth variables were weakly correlated over the entire sample, revealing little pattern of variation in postnatal growth. Over certain of the effects in the experimental design, however, particular groups of variables were strongly correlated, indicating interrelated responses of some of the growth parameters to environmental and, perhaps, genetic factors.

The size of the egg had a small effect only on the mass plateau and the length of the tarsus of the chick. The composition of a sibling egg influenced only the maximum length of the sheath of the outer primary feather.

The present study was somewhat weakened by small sample size and an inexplicable between-experiment effect that reduced its power to distinguish among effects of interest. The experimental design has the potential, however, to disentangle many classes of factors associated with genotype and parental care that contribute to within-population variation in phenotypic measurements. *Received 16 May 1983, accepted 5 December 1983.*

WITHIN-POPULATION variation in growth parameters of passerines birds on the order of 5–15% of their mean values has been reported for the fitted constants of growth equations and for masses and measurements at particular ages (e.g. Ricklefs 1976, O'Connor 1977, Ricklefs and Peters 1979, Ross 1980, Zach 1982, Zach and Mayoh 1982). Such variation can arise from (1) general factors affecting the whole population, such as weather; (2) factors varying within the population related to variation among pairs of breeders; and (3) factors whose effects vary among offspring reared by particular parents. The second type of factor includes variables related to the quality of parental care, whether it is associated with genotypic differences among adults, related to age, or expressive of developmentally acquired characteristics. These components may reside in the genotype of the embryo, in the composition of the egg (hence

reflecting the female parent), and in influences exerted during the incubation, nestling, and postfledging periods of parental care. The third type of factor, whose variation is expressed within pairs of breeders, may be associated with intrinsic differences in the quality of the young arising from genotypic differences, the effects of competition and other interactions among siblings, and other largely unaccountable factors—the so-called "error" term in analysis of variance.

Although the role of extrinsic factors in producing within-population variation has received some attention recently (e.g. year, season, and habitat effects: Ricklefs and Peters 1979, Ross 1980), relatively little is known about how differences in quality of parental care contribute to intrapopulation variation in the characteristics of offspring. Within-population variation ultimately is related to variation in the action of external factors on individuals, either as the result of selection acting on genetic variation or through the developmental flexibility of individuals. Genotypic variation is transmitted from generation to generation by the rules of heredity. Nongenetic variation also may be transmitted through the response of offspring to nongenetic variation in the quality of adults as parents. The rules of such nongenetic inheritance are, for the most part, unexplored.

In altricial birds, much of the variation in measurements of nestlings is expressed among natural broods, reflecting the contributions of genotype and parental care. For example, among first broods of European Starlings (*Sturnus vulgaris*) in southeastern Pennsylvania, 73% of the variation in the mass asymptotes of nestlings and 51% of the variation in the rate of achievement of the asymptote occurred among broods in one study (Ricklefs and Peters 1979). The separate contributions of genotype and various aspects of parental care to this variation, however, can be determined only by experimental manipulation.

The genetic component of variation is most readily determined from the correlation of traits between parents and offspring and by the covariation among half-siblings (Falconer 1960). Both types of data are difficult to collect in the field, the first because offspring are difficult to recover as adults, at which time their measurements can be compared to those of their parents, and the second because the required mating schemes are either not present in natural

populations or are difficult to control when they are present, as in polygynous species. Parent-offspring correlations have been measured in certain species in which offspring remain close to their natal sites and are easily recovered. Several of these studies have revealed high heritabilities for several size traits (e.g. mass, lengths of appendages) of fully grown birds (e.g. Boag and Grant 1978, Smith and Zach 1979, Van Noordwijk et al. 1980, Garnett 1981). Because nestlings were not assigned to parents at random within the population in these studies, it was not possible to separate the effects of nestling genotype from attributes of parents related to both their measurements and their qualities as parents. To circumvent this problem, Smith and Dhondt (1980) switched eggs and hatchlings among broods; their results confirmed that factors associated with the clutch (i.e. the natural genetic parents), and not the foster nest, were responsible for the observed correlations of traits within families.

Where it is impractical to calculate parent-offspring correlations and half-sib correlations, one may obtain an upper limit to genetic heritability by estimating the covariance among full sibs. This value is equal to the sum of ½ the additive genetic variance, ¼ the dominance variance, and the variance due to common environment, e.g. the nest in which the chicks are reared. When the common environment effect is eliminated by switching offspring at random among nests, the variance among genetic full sibs provides a reasonable upper limit to additive genetic variation, hence heritability.

Ricklefs and Peters (1981) performed a series of switching experiments with the European Starling in order to determine the contributions of genotype and parental care to variation in growth parameters of the nestlings. In one set of experiments, individuals were switched among nests at hatching; both natural and foster parents contributed significantly to variation in the rate constant of logistic equations fitted to body masses and to variation in the asymptote of the equation. In another experiment, in which individuals were switched among nests at the beginning of the incubation period, only the foster nest exerted a significant effect on growth parameters. The two experiments together suggested that postnatal growth was affected by aspects of parental care during both the incubation and nestling periods but not by the genotype of the nestling or the composi-

TABLE 1. Pattern of switching individuals among pairs of nests (X and 0) within each experiment.

	Individual							
	1	2	3	4	5	6	7	8
Nest in which egg laid	X	X	X	X	0	0	0	0
Nest in which egg incubated	X	X	0	0	X	X	0	0
Nest in which chick reared	X	0	X	0	X	0	X	0

tion of the egg. The second experiment was sufficiently sensitive to detect a heritability of about 12%.

The designs employed by Ricklefs and Peters (1981) were not fully adequate, in that variation could not be simultaneously separated into components associated with the egg and the incubation and nestling periods. For this reason, the experiments had relatively little power to detect effects with small contributions to variation.

The present study reports a new design that overcomes some of the weaknesses of previous experiments. It involves a double switching of individuals between pairs of nests, first at the beginning of the incubation period and second, with a partly overlapping set of individuals, at the beginning of the nestling period. Various measurements of nestling size and growth rate are analyzed in a three-way factorial analysis of variance replicated over (nested within) pairs of nests involved in each switching experiment. This design allows one to distinguish clutch, incubation, and chick-rearing factors as main effects. In addition, I have calculated correlations among growth variables, in the sample as a whole and over the main effects in the model, and between growth variables on the one hand and the size and composition of eggs and the length of the incubation period on the other.

METHODS

General.—The study was conducted during 1982 at a colony of free-living starlings attracted to nest boxes at the Waterloo Mills Field Station of the University of Pennsylvania, near Devon in southeastern Pennsylvania. The colony is similar to that described by Ricklefs and Peters (1979). Experiments were limited to nests initiated during a 1-week period at the end of April and beginning of May. Nests were checked each day during the laying period. Eggs were removed from nests within 1 day of laying and stored at room temperature until clutches were complete

and switches between nests could be accomplished (see Ricklefs and Smeraski 1983). Each pair of nests selected for switching was chosen at random from nests in which clutches were initiated over a given 3-day period. Only the first 4 eggs in the laying sequence (of generally 5 or 6 eggs) were used in each experiment. Two of the 4 eggs in each nest of the pair were switched before replacing the eggs in the nests to be incubated (plaster eggs were substituted during the laying period). The switched clutches were replaced in the nests within a few minutes of each other. Hence, within each experimental pair, incubation of every egg was begun at the same time. Fifth and sixth eggs were removed from clutches for analysis of chemical composition (see below).

Switching.—Each pair of nests was referred to as an experiment designated by a capital letter (A, B, C, . . .). Switches between nests always involved the same numbered eggs in the sequence to avoid clerical confusion, but the pattern of switching was varied among experiments. The pattern of switching, illustrated for a single experiment in Table 1, was designed so that the effects of clutch, incubation nest, and rearing nest could be distinguished in a nested three-way factorial analysis of variance explained in detail below.

Measurements.—Lengths (L) and breadths (B) of eggs were measured to the nearest 0.01 cm with vernier calipers. The fresh mass (M) of each egg (g) was estimated from an empirically determined equation: $M = 0.035 + 0.530 LB^2$ (Ricklefs 1984). Fifth and sixth eggs in a clutch were separated into shell, albumen, and yolk components. These were air-dried at 60°C; yolks were soaked in two baths of a 5:1 mixture of petroleum ether and chloroform to remove lipids (see Ricklefs and Smeraski 1983). The following calculated variables were used in this analysis: egg mass, yolk mass, yolk fraction (yolk mass/total mass), and the lipid fraction of the dry matter of the yolk. Based on a principal components analysis of egg composition, Ricklefs (1984) determined that egg mass, yolk fraction, and lipid fraction were the major orthogonal components of variation in the composition of starling eggs.

Incubation periods and the time of day at which eggs hatched were determined to within 2 h in most cases by periodically checking each nest during the 12th and, if necessary, 13th days of incubation (Ricklefs and Smeraski 1983). Incubation periods are re-
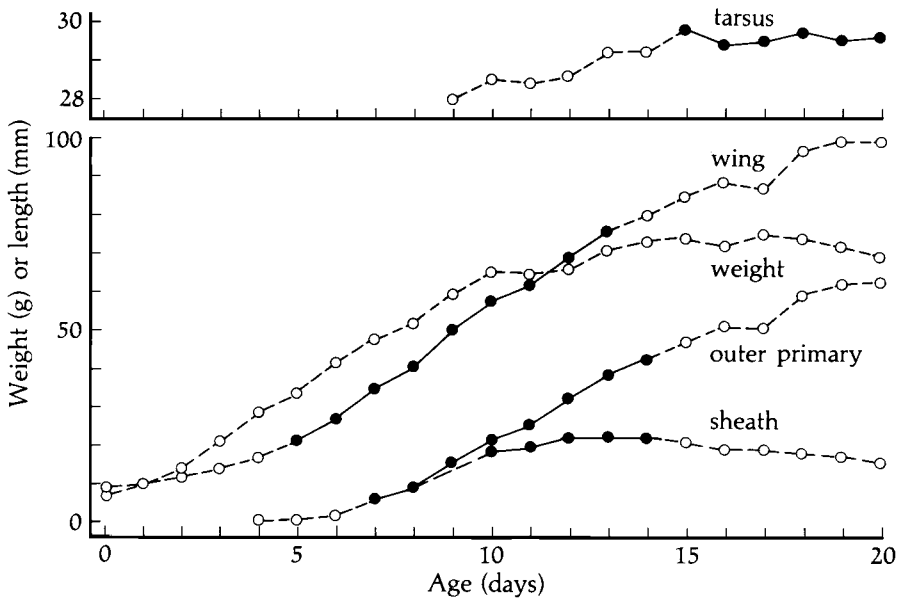
Fig. 1.   Increase in mass and lengths of appendages of nestling European Starlings. Solid lines and symbols represent data used to calculate indices of growth and size used in this study.

ported as hours deviation from 12 days (288 h). In most of the experiments, incubation was begun during the mid- to late afternoon. Eggs that hatched during the night (between 20 h of one day and 6 h of the next) were considered as having hatched at 6 h on the second day. Only experiments in which all the hatchlings could be matched with certainty to eggs were included in this analysis.

At intervals of 1, most commonly 2, or 3 days, I weighed the nestlings to the nearest 0.5 g with Pesola spring scales (100-g capacity) and measured the lengths (mm) of the wing (bend of the wrist to the tip of the manus or the longest primary feather), outer primary, outer primary sheath, and the tarsus, using flexible plastic rulers. Masses of nestlings were fitted by logistic equations having the form

$$M(t) = A\{1 + \exp[-K(t - I)]\}^{-1},$$

where $M(t)$ is the mass (g) at age t days, A is the asymptote (g) of the growth curve, K is a constant (days^{-1}) describing the rate at which the asymptote is achieved, and I is the age (days) at the inflection point of the growth curve [$M(I) = 0.5A$] (Ricklefs 1967). Equations were fitted to data by a nonlinear least-squares method (SAS procedure NLIN, Helwig and Council 1979). Maximum mass of the nestling (MAX) was also included as a variable. Measurements of appendages were averaged over all nestlings in the experiments and plotted as a function of age (Fig. 1) to determine suitable derived variables

for comparisons among treatments. The tarsus is too fully grown by hatching to estimate its rate of increase in length accurately, and so only its final length (TAR) was characterized by calculating the average of values obtained for each chick at age 15 days or later. The maximum length of the sheath of the outer primary feather (SH) was similarly estimated by calculating the average of values obtained between 10 and 14 days. Neither the wing nor the primary attains its full length by the end of the nestling period (about 21 days); hence, it is difficult to interpret asymptotic equations fit to the data, even though this technique has been used by Zach (1982) and Zach and Mayoh (1982). Instead, I fitted straight lines through approximately linear portions of the curves, 5–13 days for the wing (WN) and 7–14 days for the outer primary feather (PR) (see Fig. 1). These lines, having the general form $Y = a + bX$, were estimated by a least-squares procedure (SAS procedure REG). I selected the slope of the regression (b, acronyms WNS, PRS) and the intercept of the line on the X (age) axis ($-a/b$, acronyms WNI, PRI) as variables for comparison.

Data.—Several experiments had to be eliminated from consideration, because one or more eggs failed to hatch or nestlings could not be matched to eggs with certainty. Seven experiments (herein A–G: 14 nests, 56 chicks) were successful, with the exception of single eggs that did not hatch in each of experiments E, F, and G. These were replaced with nestlings from other nests, but the positions of these

TABLE 2. Outline of analysis of variance table for main effects.

Effect	Acronym	df[a]	Expected mean square
Expt	E	6	$V(error) + 4V[C(E)] + 4V[I(E)] + 4V[N(E)] + 8V(E)$
Clutch(Expt)	C(E)	7	$V(error) + 4V[C(E)]$
Incubation nest(Expt)	I(E)	7	$V(error) + 4V[I(E)]$
Rearing nest(Expt)	N(E)	7	$V(error) + 4V[N(E)]$
Error(Expt)		25	$V(error)$
Total		52	

[a] Degrees of freedom, discounting the error(expt) and total by 3 to take into account missing values.

chicks in the experimental design were treated as missing values. To balance the design fully, values for these individuals were replaced with the mean for both nests in the experiment. Sokal and Rohlf (1981: 364) recommend a more involved correction for missing values, but the additional calculations, when applied to a few cases, did not alter the statistical results of analyses in which the mean was substituted for missing values. Error and total degrees of freedom in the ANOVA were reduced by the number of missing values.

Analysis of variance.—The data were treated as a three-way factorial ANOVA nested within experiments. The experiments and each of the treatments within experiments are random effects; hence, this is a model II ANOVA. There are 7 degrees of freedom (df) within each experiment (E), three distributed among the main effects [clutch (C), incubation nest (I), and rearing nest (N)], three among three two-way interactions (C*I, C*N, and I*N), and one to the three-way interaction (C*I*N). Because there are no replications within cells, all two-way interactions were tested over the three-way interaction (Sokal and Rohlf 1981: 383). In those experiments with missing values, there were too few degrees of freedom to test the significance of the two-way interactions. Therefore, these were tested only in experiments A–D, with a total of 4 df for the numerator of F and 4 for the denominator. Because there were no a priori reasons to expect two-way interactions and because calculated interactions were very small (see Results), however, their sums of squares and degrees of freedom were added to those for the three-way interaction to yield an error term with 4 df (3 df with missing values) within each experiment (Sokal and Rohlf 1981: 285). The main effects in the model were then analyzed as outlined in Table 2. All two-way interactions were assumed to be zero in constructing this table. Sums of squares and degrees of freedom were added over experiments; therefore, each of the three main effects was tested by the ratio $F = MS(effect)/MS(error)$ with 7 and 25 df. The effect of experiments was determined by subtracting the sums of squares within experiments from the total, leaving 6 df. Because the mean square (MS) attributable to experiments contains terms with both error and main-effect vari-

ances, the statistical significance of differences between experiments cannot be tested by a simple F-ratio (Scheffe 1959). Instead, one may substitute

$$F'' = \frac{[MS(E) + 3MS(error)]}{\{MS[C(E)] + MS[I(E)] + MS[N(E)]\}}$$

(Winer 1971). Representing this equation as $F'' = (u + 3v)/(w + x + y)$, the numerator degrees of freedom may be estimated by

$$df(num) = \frac{(u + 3v)^2}{\dfrac{u^2}{df(u)} + \dfrac{3v^2}{df(v)}}$$

and the demonimator degrees of freedom by

$$df(denom) = \frac{(w + x + y)^2}{\dfrac{w^2}{df(w)} + \dfrac{x^2}{df(x)} + \dfrac{y^2}{df(y)}}$$

(Satterthwaite 1946). The ANOVAs were calculated with the SAS procedure GLM; variance components for each of the main effects and among experiments were calculated by the SAS procedure VARCOMP.

Correlations among variables.—Correlation coefficients (r) among any two variables (X and Y) were calculated from the appropriate sums of squares and crossproducts (SS) by the expression $r = SS(XY)/[SS(X)SS(Y)]^{-2}$. Sums of squares of the main effects were calculated according to Snedecor and Cochran (1967: 425). In order to examine further the relationships among variables, I performed a principal components analysis (PCA) based on the correlation matrix calculated within the sample from all the experiments taken together, using the FACTOR procedure of SAS.

Postnatal growth variables were related to egg size (EGG), egg composition, length of the incubation period (INC), and time of hatching (T). Egg size, incubation period, and time of hatching were known for all the nestlings in experiments A–G. The effects of these variables (X's) on growth measurements (Y's) were tested by models of the form $Y = E + I(E) + N(E) + X + error$ for egg size, and $Y = E + C(E) + N(E) + X + error$ for INC and T. That is, variation due to differences in experiments, rearing nests, and either clutches or incubation nests within experiments was

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TABLE 3. F-ratios (4,4 df) for two-way interaction terms in the analysis of variance model.[a]

Interactions	Variable					
	A	K	TAR	WNS	PRS	SH
Clutch *Incnest(Expt)	2.61	1.03	0.75	0.30	2.34	0.84
Clutch *Nest(Expt)	2.26	0.60	0.56	1.31	0.41	0.31
Incnest *Nest(Expt)	1.29	0.48	0.24	0.63	3.56	1.92

[a] None of the F-values was significant at the 0.05 level.

removed to reduce the error sum of squares. Effects of either clutch or incubation nest within experiments were not removed for each variable, because they included much of the variation in the predictor variables (see Results).

The composition of eggs was estimated from one egg per clutch. Most of the variation in egg composition within the population is related to differences between clutches (Ricklefs 1984), and so one egg provides a good estimate of the composition of others within the clutch. Because eggs were not analyzed from several of the nests in experiments A–G, analysis of the effects of egg composition on postnatal measurements was extended to other nests involved in incomplete switching experiments. Within each rearing nest (N), I averaged measurements for chicks from the same clutch; hence, all variation within nests could then be attributable to clutch and error. The effects of egg composition were analyzed according to the general model $Y = N + X_1 + X_2 + \cdots + error$ in a stepwise regression in which X's were the egg-composition variables. The effects of rearing nest were factored out as a separate component to reduce the error term. The relationship of growth variables to incubation period and hatch time were analyzed in a similar fashion, except that values were averaged

for individuals within nests sharing the same incubation nest. Further details of the analysis are presented in relevant parts of the Results section.

RESULTS

Analysis of variance.—Two-way interactions among the effects of clutch (C), incubation nest (I), and rearing nest (N) are presented in Table 3. Main effects [E, C(E), I(E), N(E)] were included in the model but are not presented in the table. None of the variables exhibited significant two-way interactions between the main effects C, I, and N. The largest F-ratios were for the rate of elongation of the outer primary, for which the I*N(E) term had a value of 3.56 (P = 0.2). The response profile for this variable (Fig. 2) shows that the interaction between I and N was due primarily to a single experiment (C). In the subsequent treatment of all variables, I assume that there are no significant two-way interactions and combine these interactions with the error term.

The nested three-way factorial analysis of

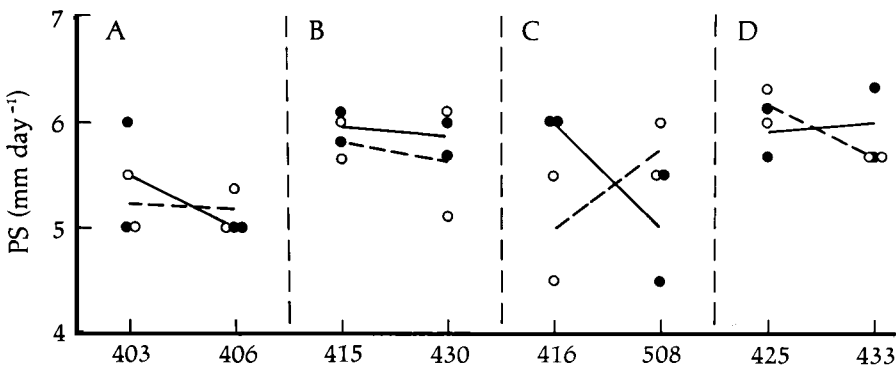Fig. 2. Profile analysis of the effects on PS of nest(expt), distinguished among experiments along the horizontal axis, and incnest(expt), distinguished by differences in symbols and lines within experiments. Solid symbols refer to the nests at the left within each experiment.
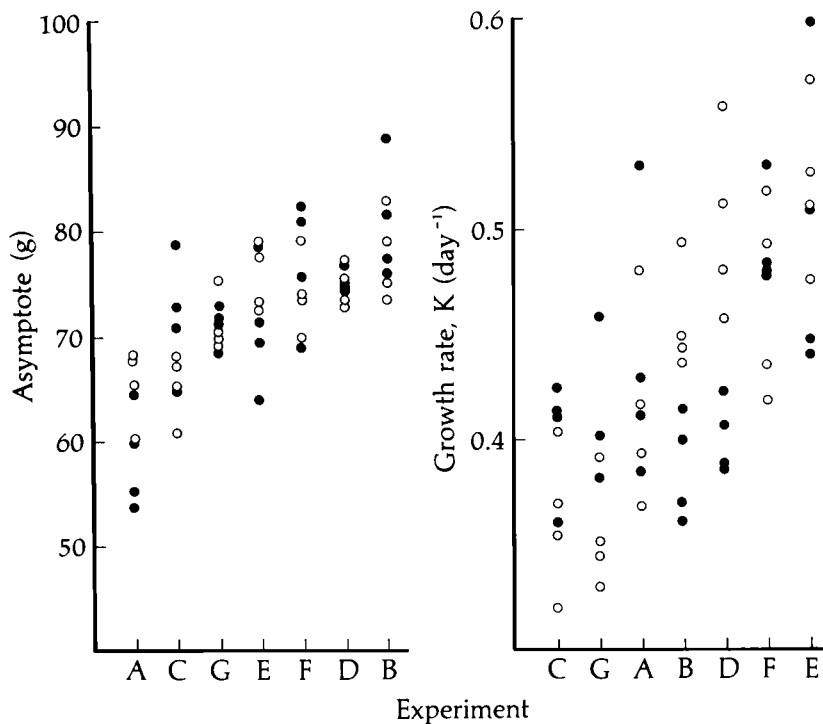
Fig. 3. Profile analysis of the effect of experiment on the asymptote (*A*) and growth rate (*K*). Solid and open symbols within experiments distinguish nests within which nestlings were reared.

variance is presented in Table 4. Coefficients of variation (CV) over the sample from all the experiments taken together varied from a low of 2.0% for (*TAR*) to 14.7% for the rate constant (*K*) of the logistic equation. Most of the other CV's were close to 10%. Clutch (*C*) was a significant main effect only for the size of the egg, which generally is uniform within natural clutches in most species of birds. This effect accounted for 68% of the total sum of squares (*SS*) within the sample. For other variables, *C* accounted for less than 10% of the total *SS* and was not a significant effect. The incubation nest (*I*) was a significant effect only for the length of the incubation period and time of hatching, confirming an earlier analysis focussing only on incubation variables (Ricklefs and Smeraski 1983).

Rearing nest was a significant effect for *K*, *TAR*, rate of elongation of the wing (*WNS*), and the length of the outer primary sheath (*SH*), each accounting for between 19 and 29% of the total *SS*. For the asymptote of the mass growth curve (*A*), nest was a marginally significant ef-

fect [$F(7,28) = 2.02$, $P = 0.08$] but accounted for only 11% of the total *SS*.

Differences between experiments accounted for a large and significant ($P < 0.05$) proportion of the variation (35–60% total *SS*) in *A*, *K*, *MAX*, and the intercept of the linearized wing growth curve (*WNI*) (Fig. 3). This result was surprising, because nests were assigned to experiments at random. One would, however, expect the experiment effect to account for a large portion of the total *SS* in the model, because it incorporates variances attributable to effects within experiments (Table 2).

Correlation structure and principal components.—Correlations among postnatal measurements are presented in Table 5. Most of the large correlation coefficients, on the order of 0.50 or greater, involve one or both of the intercepts of the wing and primary growth curves and the age at inflection of the logistic growth curve for body mass. Because of the manner in which intercepts were calculated, one would expect positive correlations between the slope of the regression and the intercept on the

TABLE 4. Descriptive statistics and analysis of variance for measurements of nestlings and characteristics of eggs and incubation.[a]

	Variables						
	A	K	I	MAX	TAR	WNS	WNI
Mean	72.07	0.436	5.23	74.03	29.61	6.85	1.84
Standard deviation	6.77	0.064	0.63	6.48	0.59	0.61	1.03
Coefficient of variation (%)	9.4	14.7	12.0	8.8	2.0	8.9	—
Sums of squares							
Total	2,523	0.225	21.7	2,313	19.46	20.2	57.9
Percentage of total							
Expt	60.4**	49.1*	33.1	58.5**	24.2	46.0	34.7
Clutch(Expt)	3.6	2.2	10.3	2.6	4.7	3.8	5.4
Incnest(Expt)	4.2	4.2	10.8	5.2	9.8	3.5	5.2
Nest(Expt)	10.7	19.2*	12.2	14.1	29.1*	27.7*	11.6
Error	21.1	25.2	34.0	19.5	32.1	19.0	43.1
Standard deviations (square roots of variances)							
Total	6.77	0.064	0.63	6.48	0.59	0.61	1.03
Among Expts	5.31	0.042	ns	4.81	ns	ns	0.64
Within Expts	4.52	0.048	—	4.43	—	—	0.88
Among Nests(Expt)	2.20	0.032	ns	ns	0.38	0.41	ns
Error	4.36	0.045	0.51	4.02	0.47	0.37	0.94

[a] *$0.01 < P < 0.05$; **$P < 0.01$; ns, effect not significant in ANOVA.

X(age)-axis, and therefore these correlations may have no biological significance. The same may be said of the strong negative correlation between the growth rate constant (K) and the age at inflection (I) (-0.71). Passing over the obvious correlation between A and MAX, there remains only one other value exceeding 0.50, a negative correlation between K and WNS.

The rather weak correlation structure among variables in this study is reconfirmed by a principal components analysis (PCA), presented in Table 6. Ten variables were entered in the PCA, based on the correlation matrix in Table 5; 5–6 components were required to account for 90% of the variance, and the first (I) accounted for only 34%. Correlations of the components with the original variables revealed that component I was associated primarily with A (0.80), I (-0.75), and WNI (-0.89). Although I and WNI are positively correlated, neither is related to A in Table 5. Component II was associated with A (0.79), MAX (0.73), and PRS (0.64); III distin-

TABLE 5. Matrix of product moment correlation coefficients ($\times 100$) among measurements of nestling starlings (df = 51).[a]

Variables	A	K	I	MAX	TAR	WNS	WNI	PRS	PRI	SH
A	100	10	03	95**	45**	09	−37**	30*	−23	−05
K		100	−71	26	21	−35**	−60**	−11	−39**	45**
I			100	−10	−06	40**	70**	04	35**	−41**
MAX				100	41**	09	−41**	30	−26	05
TAR					100	07	−20	31*	−00	15
WNS						100	61**	13	−10	−07
WNI							100	−06	45**	−28
PRS								100	55**	−14
PRI									100	−31*
SH										100

[a] * $0.01 < P < 0.05$; ** $P < 0.01$.

TABLE 4. Continued.

		Variables			
PRS	PRI	SH	EGG	INC	T
5.72	6.33	21.2	7.07	7.05	10.9
0.73	0.87	1.7	0.66	13.59	3.6
12.7	—	8.1	9.4	—	—
29.0	41.9	163	24.1	10,152	705
20.5	22.5	32.8*	21.4	68.0	16.8
5.5	7.8	2.8	67.7**	1.8	11.8
21.4	16.3	5.3	3.3	26.0**	34.5**
10.0	10.9	26.4*	0.8	0.5	10.3
42.6	42.5	32.6	6.8	3.7	26.6
0.73	0.87	1.72	0.66	13.6	3.6
ns	ns	ns	ns	ns	ns
—	—	—	—	—	—
ns	ns	1.03	ns	ns	ns
0.66	0.80	1.38	0.24	3.65	2.6

guishes WNS (0.60) and PRS (−0.60), although the two are not strongly correlated among themselves (0.14), and PRI (−0.73); IV and VI are strongly associated with SH (0.63, 0.50); and

V with TAR (0.56). ANOVAs for each principal component revealed that experiment was the only significant effect for I and II, and nest was the only significant effect for III, IV, and V; no effect was significant for VI. These results are consistent with the ANOVAs for each of the original variables, except that nest is not a significant effect for component I; this component is strongly associated with the variable K, for which nest was a significant effect (Table 4).

Correlations over effects.—For the variables A, K, TAR, WNS, PRS, and SH, I calculated intercorrelations both within and among effects. For the sample from all the experiments taken together, within experiments, and within effects (error), none of the correlation coefficients exceeded 0.50 and most were very low (Table 7). I take this result to mean that these variables are not intrinsically correlated by measurement, as are A and MAX for example, or by calculation, as are WS and WI.

The strong correlations revealed over experiments are difficult to interpret, because they incorporate all the correlations over effects within experiments. Furthermore, because the degrees of freedom over experiments were so small (4), none of the coefficients was statistically significant ($P < 0.05$). Variation in mea-

TABLE 6. Principal components analysis of measurements of nestling starlings.[a]

	Factor					
	I	II	III	IV	V	VI
Eigenvalue	3.41	2.37	1.44	1.04	0.63	0.52
Proportion of variance	0.34	0.24	0.14	0.10	0.06	0.05
Cumulative proportion	0.34	0.58	0.72	0.83	0.89	0.94
Factor pattern[b]						
A	48**	79**	18	−26	01	15
K	80**	−26	−07	20	−05	−25
I	−75**	38*	22	−12	27	24
MAX	57**	73**	17	−17	−11	13
TAR	37*	54**	−07	42**	56**	−25
WNS	−41**	40**	60**	40**	−32*	−22
WNI	−89**	07	23	26	03	−03
PRS	−03	64**	−60**	26	−35**	−02
PRI	−56**	21	−73**	15	03	13
MS	49**	−29	17	63**	−00	50**
Analysis of variance (F'')						
Expt	4.26**	3.20*	1.00	1.02	1.32	2.20
Clutch(Expt)	0.81	0.39	0.59	0.69	0.54	0.25
Incnest(Expt)	0.55	1.92	1.98	0.42	0.96	0.33
Nest(Expt)	1.21	1.60	3.39**	4.33**	4.18**	1.40

[a] * $0.01 < P < 0.05$; ** $P < 0.01$.
[b] Correlations (×100) of each original variable with each principal component (df = 41).

TABLE 7.   Correlations ($\times 100$) among measurements over effects.[a]

		Effect						
Degrees of freedom	Total (51)	Expt (4)	Within expt (39)	C(E) (14)	I(E) (14)	N(E) (14)	Error (11)
A vs. *K*	10	32	−17	−30	−74**	−03	−13
TAR	45**	72	31	−14	66**	32	31
WNS	09	07	10	13	33	34	−14
PRS	30*	51	22	−28	12	40	25
SH	−05	−32	18	14	−15	35	14
K vs. *TAR*	21	03	32	13	−65**	60*	33
WNS	−35**	−53	−18	−77**	19	06	−42
PRS	−11	−05	−15	−49	−06	13	−27
SH	45**	74	27	33	35	59*	00
TAR vs. *WNS*	07	08	07	−27	−08	36	−17
PRS	31*	73	19	44	63**	−21	19
SH	15	−23	30	15	−56*	62**	24
WNS vs. *PRS*	14	43	01	62**	−14	−21	08
SH	−07	−60	27	−20	40	48	08
PRS vs. *SH*	−14	−16	−13	−23	−86**	32	−15

[a] * $0.01 < P < 0.05$; ** $P < 0.01$.

surements over experiments was nonetheless closely linked among *K*, *SH*, and *WNS*, and among *PRS*, *TAR*, and *A*. The correlation between *PRS* and *A* disappeared when correlations between *PRS* and *TAR* and between *TAR* and *A* were removed by partial correlation analysis (Sokal and Rohlf 1981: 656). The same was true of the correlation between *K* and *WNS*. Therefore, the only unique correlations involved the relationships of *PRS* and *A* to *TAR* and of *K* and *WNS* to *SH*.

Even though clutches and incubation nests accounted for very little of the total *SS* in the study, small differences distributed over these effects were highly correlated among several of the variables. Over clutches, variation in *WNS* and *PRS* were positively related ($r = 0.62$), even though the two variables were largely unrelated in other comparisons. I interpret this result to mean that clutch does exert a small but significant effect on some combination of variables, which cannot be detected by the analysis of each variable separately. The strong negative correlation of *K* and *WNS* over clutches (-0.77) is reflected less strongly over experiments (-0.53) and within the error (-0.42) and the study as a whole (-0.35). Incubation nests appear to exert similar effects on combinations of the variables, notably *PRS* and *SH* (-0.86) and *A* and *K* (-0.74). This is the only situation

in which there is a strong relationship between *A* and *K*. Several variables (*TAR*, *K*, and *SH*), for all of which nest was a significant effect, were also intercorrelated over nests.

Relationship of growth to other variables.—For all the individuals within the seven experiments, I recorded the size of the egg (*EGG*), incubation period (*INC*), and time of hatch (*T*). None of these was significantly related to growth variables *A*, *K*, *MAX*, *TAR*, *WNS*, *PRS*, and *SH* in separate analyses of covariance (ANCOVA).

Egg composition was estimated for only one or two eggs per clutch, and data were not available for several of the clutches used in experiments A–G. Hence, the relationship of growth variation to egg composition, as well as to *EGG*, *INC*, and *T*, was examined over all of the nests in the study. In analyses involving *EGG*, *INC*, and *T*, only *PRS* [$F(1,74) = 3.05$, $P = 0.085$] and *SH* [$F(1,75) = 6.10$, $P = 0.016$] were related to *T* [*PRS* $= -0.221 + 0.0215$ (0.0123 SE) *T* and *SH* $= 0.744 - 0.0722$ (0.0292 SE) *T*].

An analysis of the relationships of growth variables to egg composition revealed that adjusted values of both *A* [$F(1,45) = 7.72$, $P = 0.008$, $R^2 = 0.15$] and *TAR* [$F(1,45) = 4.70$, $P = 0.036$, $R^2 = 0.10$] increased in direct relation to egg mass [*A* $= -14.57 + 2.06$ (0.74 SE) *EGGMASS* and *TAR* $= -2.17 + 0.32$ (0.15 SE) *EGGMASS*].

Hence, an increase of 1 SD in *EGGMASS* (0.66 g) corresponds to increases of 1.4 g (0.20 SD) in *A* and 0.21 mm (0.36 SD) in *TAR*. In addition, *SH* was related to egg composition by the following equation: $SH = 2.18 + 3.59$ (1.30 SE) *YOLK* [$F(1,44) = 7.58, P = 0.009$] $- 38.09$ (10.55 SE) *YOLK FRACTION* [$F(1,44) = 13.03, P = 0.001$, total $R^2 = 0.23$]. None of the other relationships was significant.

DISCUSSION

Main effects.—The major results of this experiment may be summarized as follows. First, neither clutch nor incubation nest influenced any of the postnatal growth variables. Second, rearing nest was a significant effect, accounting for between 19 and 29% of the total sums of squares and 38–51% of the within-experiments sums of squares, for growth rate (*K*), rate of wing elongation (*WNS*), and the lengths of the tarsus (*TAR*) and sheath of the outer primary feather (*SH*). Third, significant proportions of the variation in asymptote (*A*), *K*, and, by correlation with *K*, intercept of the wing length regression (*WNI*) were distributed over the experiments.

The absence of a clutch effect indicates that genotype and maternal effects expressed through the composition of the egg did not affect the posthatching growth of the nestlings. In other studies, parent-offspring regressions have revealed high heritabilities in several characters, including measurements of the beak and tarsus as well as mass, in some populations (Boag and Grant 1978, Van Noordwijk et al. 1980, Garnett 1981). High heritabilities for measurements of both adults and growing chicks have also been reported in the poultry literature (Kinney 1969). Although some of the parent-offspring correlation revealed in natural populations may have been due to environment-genotype interactions (i.e. adults that nourish themselves well also feed their offspring well), Smith and Dhondt (1980) eliminated this problem by switching eggs and young of Song Sparrows (*Melospiza melodia*) to foster nests and obtained similar results. Measurements of offspring at 9 weeks of age were related only to their genetic parents and bore no resemblance to foster parents. Because regressions of offspring upon male and female parents did not differ, there were also no detectable maternal effects expressed through the

composition of the egg. These results differ substantially from the findings of this study to the extent that midparent-offspring correlation and variance among full sibs estimate the same quantities (V_A/V_P in the first case and $V_A/2 + V_D/4 + V_{Ec}$ in the second). One way of reconciling the different results of these studies is to postulate that measurements of nestlings are influenced by the quality of parental care during the growth period, while the final sizes of the various appendages, achieved for the most part after fledging, are determined by genotypic factors.

The results of the present experiment also differ in several respects from the findings of Ricklefs and Peters (1981). These studies are compared in Table 8. In Experiment I of Ricklefs and Peters, nestlings were switched among nests at hatching, and effects were determined in a two-way factorial analysis of variance, much like the replicated three-way design of the present experiment. The total variance in *A* and *K* in the two sets of experiments was similar. In Experiment I, however, the clutch/incubation nest term was a significant effect for both *A* and *K*. In experiment II of Ricklefs and Peters, in which the total variance was considerably less than that in Experiment I and the present study, there was a strong incubation nest/rearing nest effect, but no clutch effect. In this respect, Experiment II was consistent with the present study. Experiments I and II led Ricklefs and Peters to conclude by subtraction that clutch was not a significant effect, whereas incubation nest was. The analysis of variance employed in the present study is able to distinguish these effects unambiguously but indicates that neither is significant. Three possibilities present themselves. First, the design of Experiment II, in which the offspring from each clutch were switched among a large number of foster nests, did not permit a two-way ANOVA and therefore had limited power to detect significant effects. In that experiment, the clutch effects accounted for 19% of the total *SS* in *K* and 39% of the total *SS* in *A*. Effects of this magnitude may have been significant if a factorial design had been used. Certainly, clutch explained a greater proportion of the *SS* of these variables than in the present study (2.2 and 3.6%, respectively), but the nonsignificance of the result for clutch is unaltered when *A* and *K* are adjusted with respect to the mean value for the incubation/rearing nest in order to re-

TABLE 8. Means, standard deviations of asymptotes (A), and growth rates (K) of starling nestlings among and within effects.

	Asymptote (A)[a]					Growth rate (K)[a]				
	A[b]	B	C	D	E	A	B	C	D	E
Means	78.7	79.9	75.9	76.1	72.1	364	358	442	446	436
Standard deviations										
Total	8.0	8.0	4.2	3.6	6.8	45	41	42	61	64
Within experiments		5.2	—	3.6	4.5		35	—	61	48
Clutches				ns	ns				ns	ns
		1.9					28			
Incubation nests			2.3		ns			28		ns
				1.8					54	
Rearing nests		2.8			2.2		18			32
Error	4.8	4.2	3.6	3.1	4.4	37	28	33	33	45

[a] Asymptote (A), g; growth rate (K), days^{-1} × 1,000.
[b] Columns are as follows: A = natural early broods 1970–1972 ($n = 214$), Ricklefs and Peters (1979); B = experimentally manipulated nests 1970–1972, experiment I ($n = 86$) of Ricklefs and Peters (1981); C = natural early broods of 1976 ($n = 43$) (Ricklefs and Peters 1981); D = manipulated nests 1976, experiment II ($n = 37$) of Ricklefs and Peters (1981); E = this study ($n = 56$).

duce the error mean square. A second possibility is that clutch effects in the present experiment may have been subsumed by the significant between-experiment effects (49 and 60% of the total SS) just by chance. Third, the experiments involved such small samples of nests that significant genetic variation may have been included in one year and not another, just by chance. Moreover, mean values of A and K (Table 8) suggest differences in environmental conditions that may have influenced the expression of genetic differences between sibships.

The significant experiment effect revealed in the present study suggests either that nests were distributed nonrandomly among experiments or that I was unlucky. Much of the SS in A of the experiments was associated with a single pair of nests (Expt A), and much of the SS in K was associated with two pairs of nests (Expts. C ang G) (see Fig. 3). In neither case was this variation related to laying or hatching dates, the length of the incubation period, or time of hatching, although the length of the incubation period itself had a large between experiments SS (68% of the total). Further resolution of these effects must await a larger data base. One may conclude from the present study, however, that neither genotype nor factors associated with egg composition or expressed during the incubation period influence measurements of nestlings. Parental effects during the nestling period, probably associated with

brooding or feeding the young, significantly influenced rates of increase in body mass (K) and winglength (WNS) and the maximum lengths of the tarsus (TAR) and the sheath of the outer primary (SH).

Correlations among variables.—Within the sample of all experiments taken together, correlations among variables were generally weak, and large correlation coefficients were related primarily to age-scaling factors rather than to rates of increase and final sizes achieved. The size to which the nestling grows (A) bore little relation to any other variable. As growth rate (K) increased, the inflection point of the growth curve (I) occurred earlier and the wing and outer primary began to grow at an earlier age, but rates of elongation of the wing and outer primary were not related. Hence, except for its inception, growth of the feathers and wings is unrelated to rate of increase in body mass. Large values of K apparently are associated with faster early development, inasmuch as wing and feather growth commence at an earlier age.

A principal components analysis corroborated the general independence of growth measurements, singling out K on component I, A on II, a contrast between WNS and PRS on III, SH on IV and VI, and TAR on V. I and II exhibited significant variation over experiments, while III through V exhibited significant variation over nests within experiments. Hence, factors responsible for between-experiments variation appeared to act upon different

aspects of growth and development than those underlying the rearing-nest effect. In studies with larger data bases, principal components may provide less ambiguous and uncorrelated measurements of postnatal development than do the original variables.

Correlations over effects.—Even in the small study reported here, there were strong correlations among variables over certain of the effects, even when the effects did not contribute significantly to variation in the measurements individually. The correlations varied among the different effects, and it is not possible to attach particular biological significance to any of them without additional analyses. These correlations do, however, suggest certain functional relationships between measurements of growth that could form the basis of more detailed studied on patterns of intraspecific variation. They also indicate that the influence of certain effects in the model employed here may be most readily detectable when several variables are considered in combination. Correlations among variables over clutches are indicative of either genetic covariance between measurements or correlated effects of egg characteristics on postnatal growth. Correlations over incubation nests are indicative of effects on embryos that carry over developmentally into the nestling period.

The fact that correlations can be detected over effects where none are detected within the error term or in the sample as a whole suggests that the influence of effects is so complex that correlations cancel out as effects are added, or that the influence of effects is small compared to other sources of covariation, and that whatever factors contribute to the error term act independently on the several measurements of growth.

Relationships with other variables.—Among the nests in experiments A–G, none of the measurements of nestlings was correlated with the size of the egg from which the nestling hatched, contrary to the findings of several other studies. In the larger data set, adjusted values of both A and TAR were positively related to the mass of the egg (coefficient of determination $[R^2] = 0.15$ and 0.10, respectively). In several studies of passerines, the mass of the neonate was positively correlated with the size or mass of the egg (Schifferli 1973, Howe 1976, Nolan and Thompson 1978). Several authors also have claimed that the mass of the egg is correlated with the subsequent development of the nest-

ling. For example, Howe (1976) found that, among nestlings of the same sex that hatched within 4 h of each other in the same nest, differences in egg mass of 0.3 g (ca. 5% of the mean) minimum were translated into differences in the masses of the nestlings of about 4 g (18%) at 4 days of age and 6 g (about 10%) at 12 days of age. Howe's data are somewhat difficult to interpret, however, because one cannot distinguish variation in A and K and because only 50% of the nestlings could be matched to eggs with certainty. Another 40% were matched on the ". . . basis of differences in egg masses and sibling masses of newly hatched young within the nest . . . ." This procedure may have artificially created some of the correlation observed. Within clutches of starlings, the masses of eggs have a standard deviation of about 0.38 g, or about 5% of the 7.2 g average (Ricklefs 1984). This is on the same order as the differences within clutches of Common Grackles (*Quiscalus quiscula*) studied by Howe (1976). Differences of 2 SD's in egg mass in this study were associated with an approximately 3-g (4%) difference in A.

Schifferli (1973) compared growth in body mass of nestlings of the Great Tit (*Parus major*) that hatched from large and small eggs. To my eye, the growth curves for the two sets of individuals are virtually superimposable, with nestlings from large eggs keeping slightly ahead of the others on the age scale. This suggests that nestlings hatch from large eggs a little farther along a growth curve common to chicks regardless of the size of the egg. Under these circumstances, one might expect larger eggs to lead to a somewhat longer incubation period, but Schifferli did not report on this. In the European Starling, incubation period is unrelated to the mass of the egg (Ricklefs and Smeraski 1983). O'Connor (1975) also reported differences in postnatal growth according to the size of the egg, but, because his measure of egg size was the mass of the hatchling at the time it was first discovered, hatching time confounded the results. I cannot find any compelling evidence that the size of the egg influences growth rates of nestling passerines, although there may be a positive correlation with final size achieved.

The composition of the egg did not exhibit any relationship to postnatal measurements, with the exception that 23% of the sums of squares of SH was related positively to the mass

of the yolk and negatively to the relative size of the yolk. The regression coefficients indicate that *SH* increases by 3.6 mm per g of yolk and decreases −0.38 mm per yolk percentage of egg size. The biological significance of these relationships will be made clear only with further experimentation on a larger scale.

Among nests in experiments A–G none of the posthatching variables was related to incubation period (*INC*) or to hatching time (*T*). Much of the variation in the length of the incubation period was distributed between experiments, perhaps by coincidence; hence, this analysis had reduced ability to detect relationships between incubation period and subsequent growth. In the larger analysis, in which all nests in the study were included, the rate of outer primary feather elongation (*PRS*) was positively but weakly related, and the length of the sheath (*SH*) more strongly and negatively related to hatching time. By extrapolation of the linear regression, the 12-h difference between 6 and 18 h corresponded to differences in *PRS* of 0.26 mm/day (0.35 SD units) and in *SH* of −0.87 mm (−0.51 SD units). These relationships suggest some developmental conditioning of the young nestling in response to factors associated with hatching time that carries over into the latter part of the nestling period.

GENERAL CONCLUSIONS

This experiment on factors contributing to variation in postnatal measurements of the European Starling suggests the following general conclusions. First, no genetic effect could be detected. The sums of squares attributable to the clutch effect were generally less than 10% of the total sums of squares, setting an upper limit to heritability in this study. Second, there was a fairly substantial effect of the nest in which the chick was reared, suggesting a direct influence of parental care on the postnatal development of the offspring. Third, correlations between growth variables were weak overall but were strong over some of the effects and in different combinations for each effect. This suggests that there may be complicated patterns of influence by the major effects on combinations of the growth variables. Fourth, I could detect little influence of egg size on postnatal development, nor could I find compelling

evidence for such a relationship in the literature.

The experimental design used in this study appears capable of separating most parental effects upon postnatal development of nestling passerines and identifying most of the correlations between growth variables. Larger samples than the 14 nests presented in this study will be required for a full description of these relationships, and further experimentation will be required to determine fully the biological significance of the relationships revealed. It seems feasible, however, to determine the role of parental care and genetic inheritance in generating and maintaining variation within populations by this approach.

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GROWTH ENERGETICS OF NESTLING NORTHERN GANNETS (*SULA BASSANUS*)

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ABSTRACT.—We describe the energetics of postnatal growth and development of wild and
captive Northern Gannet chicks. For 14 chicks 0–9 weeks old, a 24-week immature, and a
breeding female, we determined water, lipid, and nonlipid content. During the 13-week
nestling period, mass increased over 40-fold. Accumulation of lipid caused the energy den-
sity of chicks to increase steadily through 9 weeks. Lipid eventually accounted for about
60% of energy in tissues. Two captive chicks grew at rates comparable to wild young and
consumed, on average, about 24 kg of fish containing 190,000 kJ during the nestling period.
The energy density of chick guano was 13.3 ± 0.8 kJ/g. Estimated metabolizable energy
(ME) rose rapidly from 952 kJ during week 1 to 19,318 kJ during week 6, after which ME
fluctuated between about 9,000 and 16,400 kJ/week. During week 1, the growth increment
(GI) was 801 kJ; GI increased sharply to 9,667 kJ during week 4 and peaked at 12,711 kJ in
week 7. Net growth efficiency was 49% to 8 weeks of age and 33% to fledging at 13 weeks.
The food requirement of the gannet population of Newfoundland is estimated. *Received 2
August 1982, resubmitted 28 January 1983, accepted 1 September 1983.*

CONSIDERATIONS of how parents and chicks
are coupled by time, energy, and nutrition are
crucial to an understanding of the evolution
and ecological diversification of develop-
mental and parental-care patterns among sea-
birds. Much more needs to be known about
how growth energetics are related to parental
investment and feeding ecology, particularly
among large species that raise altricial young
(see Dunn 1975a, b, 1980; Cooper 1978). In this
paper developmental changes in the energy
composition and requirements of Northern
Gannet (*Sula bassanus*) chicks are analyzed as a
step toward a better understanding of life-his-
tory patterns in marine birds.

Northern Gannets are large, long-lived, fish-
eating seabirds that feed primarily inshore.
They begin breeding at 5–7 yr and pair mo-
nogamously (Nelson 1978a, b). Each year the
female lays one small egg (3.6% adult mass),
which has little yolk (15.5% egg mass, Ricklefs
and Montevecchi 1979). Hatching and fledging
success are high, often greater than 80 and 90%,

respectively (Nelson 1978a, b). Altricial young
are cared for intensively by both parents at the
nest for 13 weeks, after which chicks go to sea
and parental care ends (Montevecchi and Por-
ter 1980). Post-fledging mortality in the first
year may be at least 60% (Nelson 1978a).

In this study we examined the water, lipid,
and nonlipid contents and energy densities of
different-aged nestlings. The food consump-
tion of captive chicks was monitored over the
nestling period, and the organic composition
and energy contents of different foods were de-
termined. Data were integrated to construct a
nestling energy budget. We also estimated the
gannets' harvest of their major foods (macker-
el, herring, capelin, squid) in Newfoundland
waters.

METHODS

In 1978–1979, four Northern Gannet chicks were
removed from nests within 10 days of hatching on
Baccalieu Island (48°07′N, 52°47′W), Newfoundland
and were raised in captivity. For 4 weeks they were
fed primarily capelin (*Mallotus villosus*), thereafter
mackerel (*Scomber scombrus*); these fish are the most
common items fed to chicks of these ages on Bacca-
lieu Island (Montevecchi and Porter 1980). As in na-
ture, neonates were fed frequent (up to 6 times per
day), small meals, and older chicks were fed large

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pieces of mackerel once or twice daily. Our food consumption data are based on two chicks who were taken in 1979 and whose food intakes were precisely monitored.

Protein levels in food samples were measured by the Kjeldahl method. Lipids were extracted with diethyl ether, and their levels were determined by subtracting lipid-free mass from pre-extracted mass. Amino-acid compositions of foods were analyzed with a Beckman Amino Acid Analyzer (Model No. 121M) with AA-10 resin and manobore flow systems following a 24-h HCl hydrolysate at 110°C.

Body composition of 14 chicks (10 killed at the nest and 4 that died after brief periods in captivity but whose masses were within the ranges of noncaptive chicks of the same ages), a hand-reared 24-week immature, and a breeding female collected on Baccalieu Island in 1977 and frozen for later analyses was determined. Thawed birds were dissected into several components, which were air-dried at 68–70°C to constant mass. Lipids were extracted for 24 h in each of three fresh baths of a 5:1 mixture of petroleum ether: chloroform. From primary measurements (wet, dry, and lipid-free dry masses) we calculated water = wet − dry mass, lipid = dry − lipid-free dry mass, and lipid-free wet mass = wet mass − lipid. The energy equivalent of tissue was calculated by applying the conversion factors: 38 kJ/g lipid and 20 kJ/g lipid-free dry matter (Ricklefs 1974).
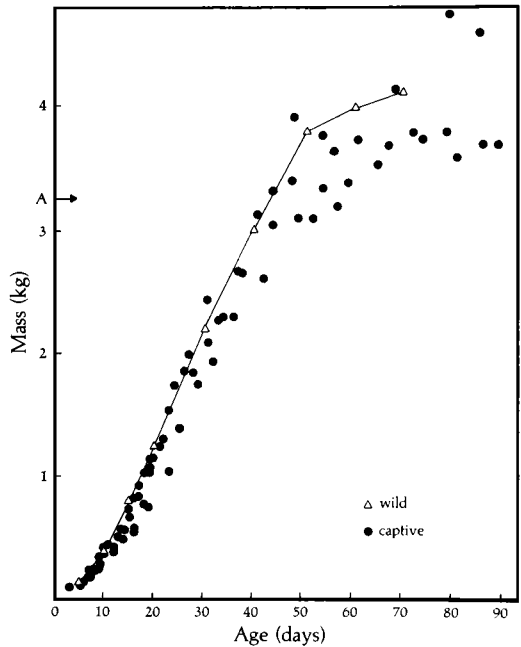

Fig. 1. Masses of wild (from Nelson 1964) and four hand-raised Northern Gannet chicks as a function of age. Average adult mass (A) is indicated on ordinate.

RESULTS

Chicks averaged (± SD) 79.3 ± 11.2 g (n = 12) at hatching, about 70% of the fresh egg mass (114.1 ± 9.4 g; Ricklefs and Montevecchi 1979) and about 2.5% of adult mass (3,236.4 ± 41.9 g, n = 40). Young chicks increased their masses very rapidly, more than 10-fold in 3 weeks (Fig. 1). By 7 weeks, chicks were as heavy as adults, and by 10 weeks, they weighed about 4 kg, about 25% more than an adult (Fig. 1). Up to 60 days, our captive chicks did not differ significantly in mass from Nelson's (1964) sample of wild chicks at Bass Rock, Scotland. Weekly mass increments were relatively constant to about 50 days, after which further gain slowed and became quite variable. Using the Gompertz equation (Ricklefs 1968a), we found that the Northern Gannets' growth constant (K), calculated for Nelson's (1964) data, was 0.063 day^{-1}, similar to those of altricial landbirds of similar size (Ricklefs 1973). The K-value calculated for captive chicks in this study was 0.073 day^{-1}, but a lower asymptote was achieved. After masses peaked around 10 weeks, captive and wild chicks exhibited slight mass recessions be-

fore fledging age, when most weigh more than 3,500 g (Montevecchi unpubl. data, cf. Kirkham and Montevecchi 1982: adult mean = about 3,250 g). Captives near fledging age had similar masses to fledglings that had recently departed from the colony (Montevecchi unpubl. data).

Increases in water, lipid, and lipid-free dry matter during the first 60 days of postnatal development are illustrated in Fig. 2, and the total energy equivalent of these components is illustrated in Fig. 3. Four chicks aged 50–63 days contained an average of 965 g of lipid-free dry matter, equivalent to 19,300 kJ, and 729 g of lipid, equivalent to 27,702 kJ. Lipid therefore accounted for about 60% of the energy in the nestling's tissues around the time of peak mass. The energy densities of chicks increased with age, due largely to progressive accumulation of lipid, at least to 9 weeks (Fig. 4). The linear relationship, determined by a least squares fit of the data, may be expressed as energy density (kJ/g) = 3.35 + 0.16 age (days). The energy densities of two fully grown birds were similar to those of chicks at peak mass, about 13 kJ/g.
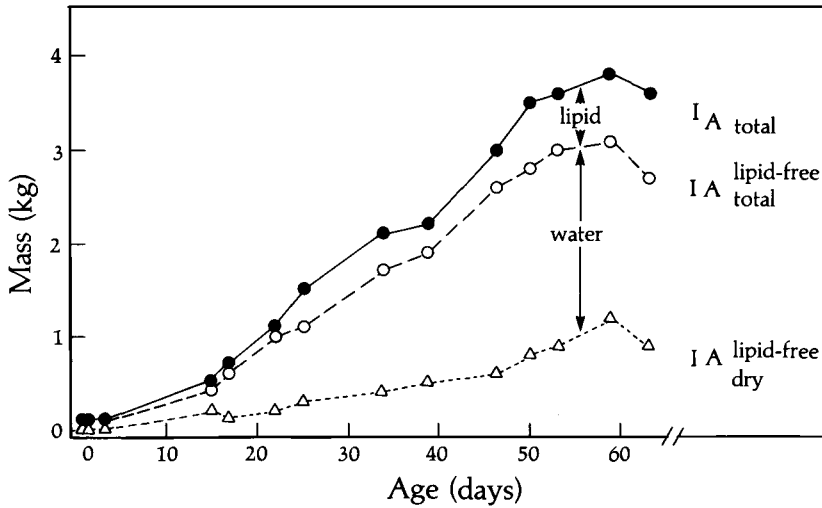
The organic composition and energy equiv-

Fig. 2. Changes in lipid, lipid-free dry material, and water content of body tissues of Northern Gannet chicks as functions of age. Contents of a 24-week immature (I) and breeding female (A) are indicated.

alents of items most frequently fed chicks are presented in Table 1. Owing to high lipid content, mackerel is the most energy rich of the foods. Other foods have substantially lower lipid levels and higher protein indices (100 × g protein/kJ).

The amino acid composition of capelin, mackerel, squid (*Ilex illecebrosus*), and herring (*Clupea harengus*) were analyzed. The levels (nanomoles/mg of dry weight, including lipid) of all amino acids and ninhydrin positive substances, except hydroxyproline and hydroxylysine, were found to be higher in capelin, an important food for neonates, than in mackerel, the food most commonly fed older chicks. Capelin also contained substantially higher levels of most amino acids than did either squid or herring, foods also fed primarily to older chicks by parents (see Montevecchi and Porter 1980). Squid had relatively high amounts of cysteic acid/phosphoserine and taurine. The differences among these species generally reflect the varying ratios of protein to fat. Essential amino
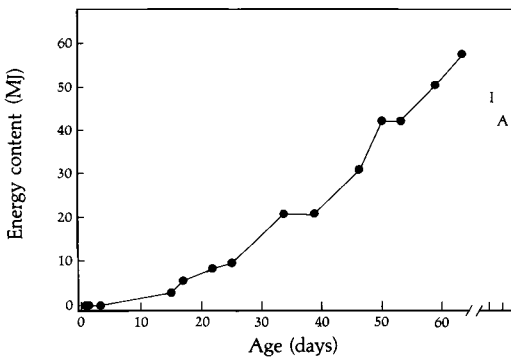

Fig. 3. Changes in energy content of Northern Gannet chicks as a function of age. Contents of a 24-week immature (I) and breeding female (A) are indicated.
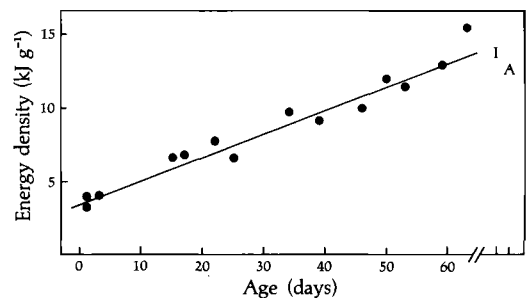

Fig. 4. Energy density (kJ/g) of Northern Gannet chicks as a function of age. Those of a 24-week immature (I) and breeding female (A) are indicated.

TABLE 1. Energy values and organic composition of foods most frequently fed to Northern Gannet chicks in Newfoundland.

Food	Energy[a] (kJ/g)	Percentage wet mass				Protein index[b]	Lipid index[c]
		H$_2$O	Protein	Lipid	Ash		
Mackerel (*Scomber scombrus*)	10.3	62.3	16.2	18.6	2.0	1.6	1.8
Capelin (*Mallotus villosus*)	4.2	78.4	14.9	3.3	2.0	3.6	0.8
Squid (*Ilex illecebrosus*)	4.3	78.2	15.9	3.0	1.8	3.7	0.7
Sand Lance (*Ammodytes hexapterus*)	7.3	63.5	19.5	8.9	7.3	2.7	1.2
Atlantic Saury (*Scomberesox saurus*)	6.8	70.1	19.6	7.6	1.5	2.8	1.1
Herring[d] (*Clupea harengus*)	9.2	62.9	20.0	13.6	—	2.2	1.5

[a] Wet mass, protein = 20 kJ/g, fat = 38 kJ/g.
[b] Percentage protein/energy.
[c] Percentage lipid/energy.
[d] Based on cleaned fish (Adams 1975); probable overestimates.

acids (Lloyd et al. 1978) varied by no more than a factor of two among prey types. Avian protein needs during growth are not well understood, and it is difficult at present to assess the nutritional significance of the different protein levels.

Over the 13-week nestling period, captive chicks consumed, on average, 24,174 g of food containing about 190,550 kJ. The guano samples, collected from captives of about 6 weeks of age and combusted in a bomb calorimeter, averaged ($\pm$ SD) 13.3 $\pm$ 0.8 kJ/g, which did not differ significantly (*t*-test) from the average energy density (12.8 $\pm$ 1.2 kJ/g; n = 10; range = 12.1–15.2 kJ/g; calculated from Cooper 1978) of the guano of two hand-reared Cape Gannet (*Sula capensis*) chicks. Systematic records of chicks' excretion were not kept, and Cooper's (1978) assimilation efficiency of 76.1% was used to estimate metabolizable energy (ME). The assumption that the efficiencies of these two congeneric species are similar is supported on many counts: (1) taxonomic affinity of *bassanus* and *capensis* (Nelson 1978a, b), (2) diet similarity of the two species (Nelson 1978a, b), (3) similar energy densities of chick's guano, and (4) the narrow range of assimilation efficiencies of fish-eating seabirds in general (e.g. Dunn 1975a, 1980).

Assuming 76.1% assimilation efficiency, we estimated that about 45,550 kJ were excreted, leaving 145,000 kJ of ME for growth, maintenance, temperature regulation, and activity. The chick's average weekly energy intake (and estimated ME) increased rapidly up to 6 weeks of age, after which intake appeared to decrease slightly and then level off (Fig. 5).

The energy accumulated in a developing an-imal's tissues per unit of energy either consumed or assimilated is an index of growth efficiency (Kleiber 1961). Dividing the net increase in carcass energy content between the date of hatching and 13 weeks (47,835 kJ) by total energy intake (190,550 kJ) and total ME (145,000 kJ) yields estimates of gross and net growth efficiencies of 25.1 and 33.0%, respectively, over the nestling period. During the first 8 weeks, the period of most rapid growth, gross and net growth efficiencies were 37.0 and 48.6%. These efficiencies are on the same order as those reported for most passerines (22–29%, Drent and Daan 1980) and for many other fish-eating seabirds (e.g. Koelink 1972, Brisbin cited in Westerterp 1973, Ricklefs 1983).

DISCUSSION

Gannet chicks grow rapidly, achieving a 40-fold increase in mass in the first 2 months of life (see also Montevecchi and Porter 1980, Kirkham and Montevecchi 1982). Similar growth rates have been reported for Northern Gannets in Scotland (Nelson 1964) and for Cape Gannets (Cooper 1978). Other species of sulids, the tropical, pelagic boobies in particular, grow much more slowly (Nelson 1978a, b). In comparison with other nonsulid Pelecaniformes, Northern Gannets gain weight at a rate similar to that of Brown Pelicans (*Pelecanus occidentalis*, K = 0.071, Ricklefs 1973) but slower than that of the smaller Double-crested Cormorants (*Phalacrocorax auritus*, K = 0.208, Dunn 1975b).

Lipid increase accounted for 60% of the energy accumulated by Northern Gannets during growth. Rising lipid and decreasing water levels resulted in a linear increase in energy density
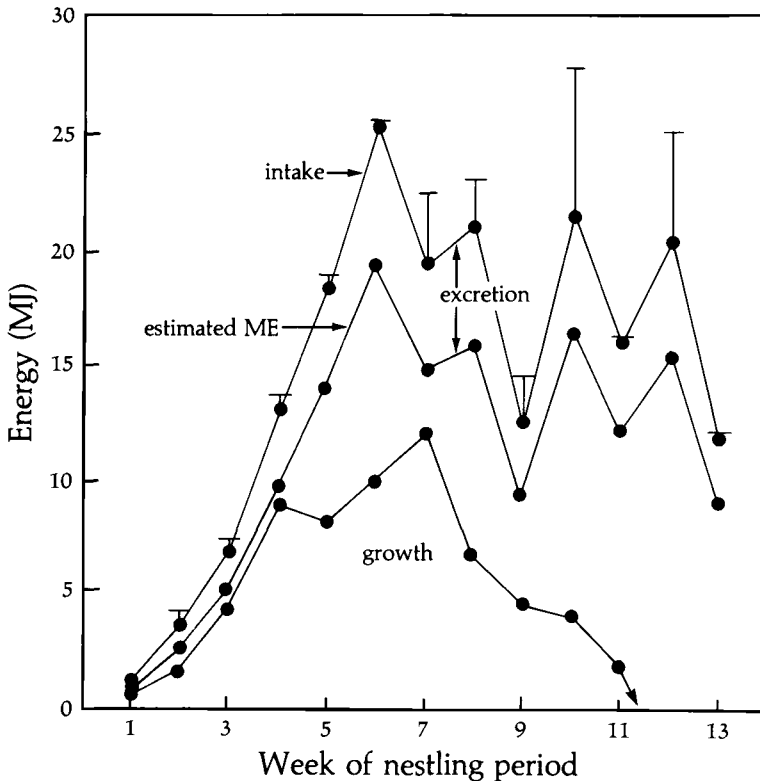
Fig. 5. Average (± SD) total energy intake of two captive Northern Gannet chicks and estimated metabolizable energy (ME) based on an assimilation efficiency of 76.1% (from Cooper 1978; see text for explanation).

with age, at least to 9 weeks (Fig. 4). Dunn (1975b) found a similar trend in Double-crested Cormorants and, after reviewing other studies, suggested that the energy densities of altricial chicks generally increase from about 3 kJ/g at hatching to 8 kJ/g at fledging. The energy densities of gannet neonates (3.4 kJ/g) are similar to that proposed by Dunn for other altricial neonates, but large lipid deposits in older chicks yielded densities (up to 14 kJ/g) that greatly exceeded those of other altricial fledglings.

Estimates of energy accumulated in tissues were obtained by converting lipid and non-lipid dry material to kJ (Fig. 3). Maintenance energy (activity and temperature regulation) was estimated as the difference between ME (Fig. 5) and growth energy and is compared to an estimate of BMR of gannet chicks, based on the Lasiewski and Dawson's (1967) equation for adult birds, in Table 2.

Growth requirements increased rapidly to a plateau between 6,000 and 12,000 kJ/week during weeks 4 through 8. Maintenance requirements showed wide weekly fluctuations, which we could not incorporate into our calculations of growth energy, that were probably due to changes in the chick's lipid content. Approximately 44% of the nestling's ME is allocated for growth (including the cost of biosynthesis); perhaps 33% is accumulated in tissues before fledging.

From 3 weeks, nestlings store increasing amounts of lipid, which accounts for most of the growth energy requirement. Parents tended to feed older chicks richer food (mackerel) than they fed to younger chicks which are more commonly fed capelin, a food with a higher protein to lipid ratio (see Montevecchi and Porter 1980). Subcutaneous fat reserves may be adaptive in the event of poor parental foraging

TABLE 2. Energy budget of a nestling Northern Gannet (see text).

Age (weeks)	Mass[a] (g)	Energy density[b] (kJ/g)	Accumulated energy (kJ)	Growth increment[c] (kJ/week)	Maintenance[d] (ME − GI) (kJ/week)	Maintenance[e] (equation) (kJ/week)
Hatch	79	3.35	265	—	—	—
1	194	4.47	867	801	151	701
2	409	5.59	2,286	1,888	737	1,202
3	834	6.71	5,596	4,402	793	2,013
4	1,643	7.83	12,865	9,667	113	3,286
5	2,122	8.95	18,992	8,149	5,674	3,954
6	2,632	10.07	26,504	9,991	9,327	4,620
7	3,189	11.19	35,685	12,211	2,532	5,307
8	3,282	12.31	40.401	6,273	9,733	5,419
9	3,425	13.0	44,525	4,124	5,302	5,588
10	3,732	13.0	48,516	3,991	12,411	5,947
11	3,877	13.0	50,401	1,885	10,245	6,113
12	3,702	13.0	48,126	−2,275	17,870	5,912
13	3,700	13.0	48,100	−26	9,021	5,910

[a] $\bar{x}$ weekly mass of two hand-raised chicks.

[b] From Fig. 4, energy density (kJ/g) = 3.35 + 0.16 age (days) up to 8 weeks, 13.0 thereafter.

[c] Assumes 75% production efficiency: 1.33 × weekly increment of accumulated energy.

[d] Metabolizable energy (ME) − growth increment (GI).

[e] BMR from Lasiewski and Dawson (1967) equation h: (kcal/day) = 78.3 M (kg)$^{0.723}$ multiplied by 7 to convert daily to weekly estimates and by 4.187 to convert kcals to Joules.

conditions (O'Connor 1978). Older gannet chicks show no overt deleterious effects from starvation lasting up to 2 weeks (Nelson 1978a, b; see also Schreiber 1976). With a maintenance requirement of no more than 6,000 kJ/week and a maximum lipid accumulation of 26,000 kJ (700 g), nestlings could easily survive extended periods without food. Lipid reserves must also sustain independent fledglings during their flightless period at sea.

Chicks lose weight during the third (and last) month of the nestling period, though they fledge with substantial fat reserves at masses in excess of those of adults (see Nelson 1978a, b). Accumulation of mass by nestlings in excess of adult levels, followed by prefledging recession, is common among marine birds with no postfledging care and among aerial foraging birds, such as hirundines (Harris 1966; Lack 1968; Ricklefs 1968a, b; Schreiber 1976; Ricklefs et al. 1980; cf. Sealy 1973, Dunn 1975b). Such mass recession is associated with decreased parental feeding rates, lowered feeding motivation among older chicks, and increased activity, mostly wing flapping (Montevecchi and Porter 1980; see also Ricklefs 1968b; Cooper 1978, 1979; Nelson 1978a).

Estimates of metabolizable energy requirements during the nestling period total 145,000 kJ (Table 2). On the basis of Lasiewski and Dawson's (1967) equation, adult resting metabolism equals 767 kJ/day or 5,369 kJ/week. The peak energy requirement of a chick, about 15,000 kJ/week, equals about 300% adult BMR, or about 150% per parent. Because females provide about 60% of the chick's food energy (Montevecchi and Porter 1980), the sexes make differential parental feeding investments: about 180% BMR/female and about 120% BMR/male. Males forage about 9 h/day and females about 6 h/day throughout the nesting season, based on periods of absence from the nest (Montevecchi and Porter 1980). Assuming a flight cost of 500% BMR (Cooper 1978, Hails 1979, Kirkham 1980), another 188% BMR would be added to the male's daily expenditure, 125% BMR to the female's, bringing the parental foraging and feeding energy totals of both sexes to virtual identity at 308% and 305% BMR, respectively. These hypothetical estimates are similar to those recently derived for Leach's Storm-Petrel (*Oceanodroma leucorhoa*, Ricklefs et al. 1980) and Lesser Sheathbills (*Chionis minor*, A. E. Burger pers. comm). Drent and Daan (1980) have estimated that the energy expenditure of breeding adults is about 400% BMR during sustained foraging.

The gannets' main foods (mackerel, capelin,

TABLE 3. Estimates of (A) the energy intake of the Northern Gannet population in Newfoundland and (B) their takes of different food items during the breeding season.

A				
Age class	Number of birds	Energy intake (kJ/ day)	Number of days	Total energy (kJ)
Breeding adults	18,688[a]	2,500[d]	210	9.81×10^9
Fledglings	6,728[b]	(190,500)		1.28×10^9
Nonbreeders	1,682[c]	2,000[e]	150[f]	0.51×10^9
Totals	27,098			11.60×10^9

B			
Food item[g]	Percentage utilization[h]	Total energy take (kJ)	Tonnes[i]
Mackerel	46	5.34×10^9	518.5
Capelin	23	2.67×10^9	635.7
Squid	19	2.20×10^9	511.6
Herring	12	1.39×10^9	151.1

[a] Based on Montevecchi et al. (1980) and unpublished data.
[b] Assumes 80% hatching and 90% fledging success.
[c] Estimated at 9% of breeding population.
[d] 320% of estimated BMR.
[e] 250% of estimated BMR.
[f] Estimate of 5-month colony occupation for nonbreeders (Montevecchi unpubl. data).
[g] Gannets in Newfoundland also take other fish (see text).
[h] Derived from Kirkham et al. (MS).
[i] Total energy take/energy densities from Table 1.

squid, herring) in Newfoundland are commercially valuable, and it is useful to estimate the food needs of the population during the breeding season. In Newfoundland waters, gannets also take Atlantic saury (*Scomberesox saurus*), sand lance (*Ammodytes hexapterus*), cod (*Gadus morhua*), and salmon (*Salmo calar*), although, with the exception of saury, always in very small numbers (Kirkham et al. ms). The breeding population (about 9,344 pairs) in Newfoundland occupies three colonies for about 7 months (210 days, April–October), during which time they produce about 6,700 chicks (see Table 3). A substantial population of nonbreeders also occupies colony areas for about 5 months. These data are combined in Table 3 with energy intake estimates to yield an overall intake of 11.60×10^9 kJ of food. In Table 3, es-

timates of the population harvests of mackerel (518.5 t), capelin (635.7 t), squid (511.6 t), and herring (151.3 t) are derived. Whether these speculated levels of exploitation are in competition with local fisheries efforts (see Sanger 1972, Wiens and Scott 1975, Furness 1978) remains to be determined.

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FLIGHT SPEED AND DIRECTIONAL RESPONSES TO WIND BY MIGRATING CANADA GEESE

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ABSTRACT.—We monitored headings, flight speeds, and time of flight of nine transmitter-tagged giant Canada geese (*Branta canadensis maxima*) during 10 different autumn migration flights during which data on wind directions and speeds were also available. Destination of these individuals was known because of previous observations of the same birds. This enabled us to evaluate their headings with respect to wind drift. As the magnitude of the following component of the wind increased, air speeds of migrating geese declined while ground speeds were not significantly changed. Therefore, the cost of transport over the ground, and probably metabolic rate, were minimized. Headings of migrant geese varied systematically and significantly with wind direction, but track directions did not deviate significantly from the goal direction. Thus, the geese compensated for wind drift. Visual reference to landmarks may have been the cue used to correct for drift, as weather conditions were such that geese could see the ground. *Received 1 March 1983, accepted 5 December 1983.*

THE ability of migrating birds to detect and adjust to winds is variable; migrants either maintain a constant air speed (Blokpoel 1974; Alerstam 1978a, b) or vary it in relation to wind conditions (Bellrose 1967, Bruderer and Steidinger 1972, Pennycuick 1975, Able 1977, Larkin 1980, Larkin and Thompson 1980, Bellrose and Crompton 1981, Block and Bruderer 1982). Relying on assumed migration routes and destinations based on the knowledge of a species' distribution, researchers have documented apparent compensation (partial or complete) or the lack of it for lateral displacement caused by cross winds (Drury and Nisbet 1964; Lack 1969; Parslow 1969; Bergman and Donner 1971; Evans 1972; Gauthreaux 1972; Williams et al. 1972, 1977; Alerstam 1975a, b, 1976; Richardson 1976; Bingman et al. 1982). In our study, the destination of individual, migrating Canada Geese (*Branta canadensis*) tagged with transmitters was known because of previous observations of the same marked birds. This allowed us to monitor headings of experienced migrants with respect to wind drift because of our precise knowledge of their migratory destination.

METHODS

We collected data during the autumn 1973 and 1974 migrations of individuals from a population that nests

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between Lakes Manitoba and Winnipeg in Manitoba and migrates (865 km) to Silver Lake, Rochester, Minnesota (Raveling 1976a, b, 1978). Migration flight paths and speeds of transmitter-tagged geese were monitored with the use of a ground vehicle, airplane, ground observers, and a base station, as described by Cochran et al. (1967). The transmitter design was similar to that described by Raveling (1969), except that a whip antenna was used to maximize signal-reception range. As a result, a package containing either the transmitter or both the transmitter and batteries was positioned on the back of the bird. The total weight of transmitters (including harness) varied between 50 and 75 g (1–3% of adult body weight), depending on size and number of batteries used. Before each migration season, 17–29 geese were outfitted with transmitters. Geese used in this study had been previously marked between 1968 and 1970 with individually identifiable, plastic neck-bands at the Marshy Point Goose Sanctuary (50°32'N, 98°7'W), located on the southeast shore of Lake Manitoba about 105 km northwest of Winnipeg, Manitoba, and identified as having regularly migrated to Rochester, Minnesota (43°55'N, 92°30'W; Raveling 1978). The direct-line following direction (direction from which birds were coming) for migration between Marshy Point and Rochester is 325°.

Migrations of transmitter-tagged geese occurred between 14 October and 18 November. Data on headings, times, and winds for the present analysis were obtained for nine birds during 10 migration flights. Three geese flew nonstop, whereas six geese (including one bird for which the migration was tracked in both 1973 and 1974) interrupted their migration in western or northwestern Minnesota. While tracking the migration flight, we observed a flock containing a transmitter-tagged goose on seven occasions. We

TABLE 1. Wind characteristics and flight speeds of Canada Geese during autumn migration.[a]

			Wind characteristics[b]				Flight speed[b]	
Level	Direction[c]	Speed (km/h)	Magnitude of following/opposing component[d] (km/h)	Cross component[d] (km/h)	Angle of incidence[e]		Ground (km/h)	Air (km/h)
Surface	315° ± 5° (270°–10°)	23 ± 1 (11–40)	17 ± 3 (0–37)	13 ± 2 (0–28)	40° ± 5° (0°–90°)		83 ± 4 (49–110)	65 ± 4 (32–101)
Geostrophic	355° ± 5° (308°–48°)	50 ± 3 (24–87)	18 ± 4 (−16–56)	40 ± 5 (2–80)	60° ± 5° (5°–89°)		83 ± 4 (49–110)	60 ± 5 (16–100)

[a] Values presented are the mean ± SE with the range in parentheses.

[b] Sample sizes for surface-wind direction and speed correspond to the number of weather stations supplying appropriate information during 10 migration flights ($n = 44$). Sample sizes ($n = 20$) for flight speeds and for following component, cross component, and angle of incidence correspond to the total number of surface-wind determinations made during 10 migration flights (measurements were made on one occasion each for 6 migration flights and on 2, 2, 4, and 6 occasions during the other 4 flights). Sample sizes were reduced by one for each geostrophic wind category due to an inappropriate heading that could have resulted from an error in estimation of wind during one migration flight ($P < 0.01$ that the aberrant heading is part of the population of calculated headings, Snedecor and Cochran 1967: 157).

[c] Direction from which wind was blowing.

[d] Wind direction and speed were resolved trigonometrically along axes parallel and perpendicular to the headings of the goose to yield following/opposing and cross components. Headings were the direction toward which the bird oriented; track directions were those flown relative to the ground (Lack and Williamson 1959). The heading direction and speed were determined by subtracting the wind direction and speed vector from the track direction and speed vector.

[e] Angle between wind direction and a bird's heading.

visually estimated these flocks to be flying 100–600 m above the ground ($\bar{x} = 330$ m).

We obtained weather and wind conditions from weather stations located along the migration route: Winnipeg, Manitoba; Grand Forks and Fargo, North Dakota; and Thief River Falls, Detroit Lakes, Alexandria, St. Cloud, Minneapolis, Redwood Falls, and Rochester, Minnesota. Surface-wind data were available for all migrations. Upper level wind may vary from surface wind. A measurement of upper wind (600 m) was available on only eight occasions during the migration season (only two of which corresponded to a time when a transmitter-tagged goose was migrating). Therefore, we used both surface wind data (as have others, e.g. Alerstam 1978a) and estimates of the geostrophic wind (prevailing between 500–1,500 m, Godske et al. 1957) to assess the effects of wind on migration speeds and directions.

RESULTS AND DISCUSSION

There were no significant differences between nonstop and interrupted migration flights for surface and estimated geostrophic wind characteristics or for the birds' ground and air speeds ($t < 0.57$, $P > 0.50$ for all comparisons); therefore, the data for all migrating

geese monitored were combined (Table 1). Regardless of whether surface or estimated geostrophic wind data were used, regression analyses (Bartlett's 3-group test, Sokal and Rohlf 1969) indicated that, as the magnitude of the following component increased, air speeds of migrating Canada Geese declined, whereas ground speeds were not significantly altered (Fig. 1).

A migrating bird may minimize energy use by: (a) maintaining the minimum metabolic rate for flight, (b) minimizing the cost of transport through the air (flying at a constant air speed), or (c) minimizing the cost of transport over the ground (air speed varies with wind speed and the bird's heading) (Schnell and Hellack 1979). Assuming a goose has 20% mechanical efficiency (Tucker 1973) and flies at 330 m, the following equation, modified from Tucker [1974, equation (2)] estimates power requirements during flight:

$$P_i = 1.11[5(73.42m^2b^{-2}V^{-1} + 6.6 \times 10^{-3}m^{0.66}V^{2.5}) \times (1 + 1.81m^{-0.167}V^{-0.5}) + 3.7m^{0.723}],$$

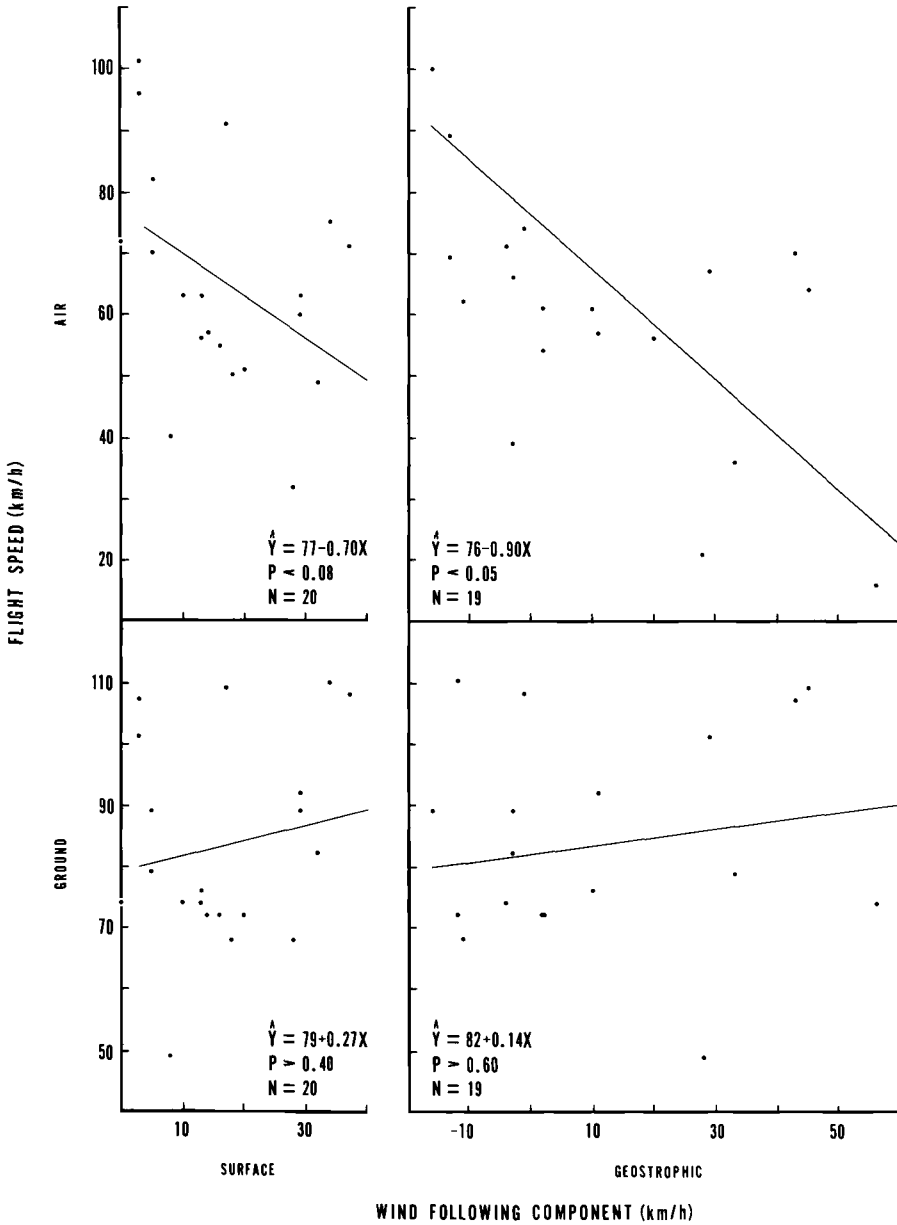where P_i is power input in watts, m is body

Fig. 1.   Influence of wind speed on flight speed of migrating Canada Geese.

mass in kilograms, b is wing span in meters, and V is air speed in meters per second. Wing span was estimated from the formula $b = 1.1m^{0.33}$ [Tucker 1974, equation (4)]. This power estimate was then divided by weight (in newtons) to obtain metabolic rate and weight (in newtons), which multiplied by ground speed of the bird in meters per second yielded cost of trans-

port over the ground (Tucker 1974). Predicted air speeds for the minimum metabolic rate for flight and the minimum energy cost of transport over the ground were then calculated (Table 2).

The decrease in air speed as the following wind increased (Fig. 1) indicated that the birds did not minimize the cost of transport through

TABLE 2.   Predicted air speeds for minimum metabolic rate for flight and minimum energy cost of transport over the ground.

Wind level	Predicted air speed (km/h) for minimum cost of transport[a] ($\bar{x} \pm SE$)	Compared to observed air speed[b]		Predicted air speed (km/h) for minimum metabolic rate ($\bar{x} \pm SE$)	Compared to observed air speed[b]	
		t	P		t	P
Surface[c]	69 ± 1	1.13	>0.20	52 ± 0[d]	3.20	<0.005
Geostrophic[c]	72 ± 1	2.89	<0.01	52 ± 0[d]	1.54	>0.20

[a] Calculated using monthly average body weight in kg (4.01, 4.14, 4.82, 4.92, and 5.02) corresponding to the month and year of migration departure and sex of the goose.
[b] Contained in Table 1.
[c] The range in speed for surface wind was 0–37 km/h and −16–56 km/h for geostrophic wind.
[d] Values are the same because metabolic rate is independent of wind conditions.

the air (see b above). They did appear to minimize the cost of transport over the ground (see c above), because there was no significant difference between predicted and measured air speeds for surface-wind conditions (Table 2).

Similarly, there was no significant difference between predicted and measured air speeds required to minimize metabolic rate (see a above) for flights in geostrophic wind conditions (Table 2). Because the wind conditions in which
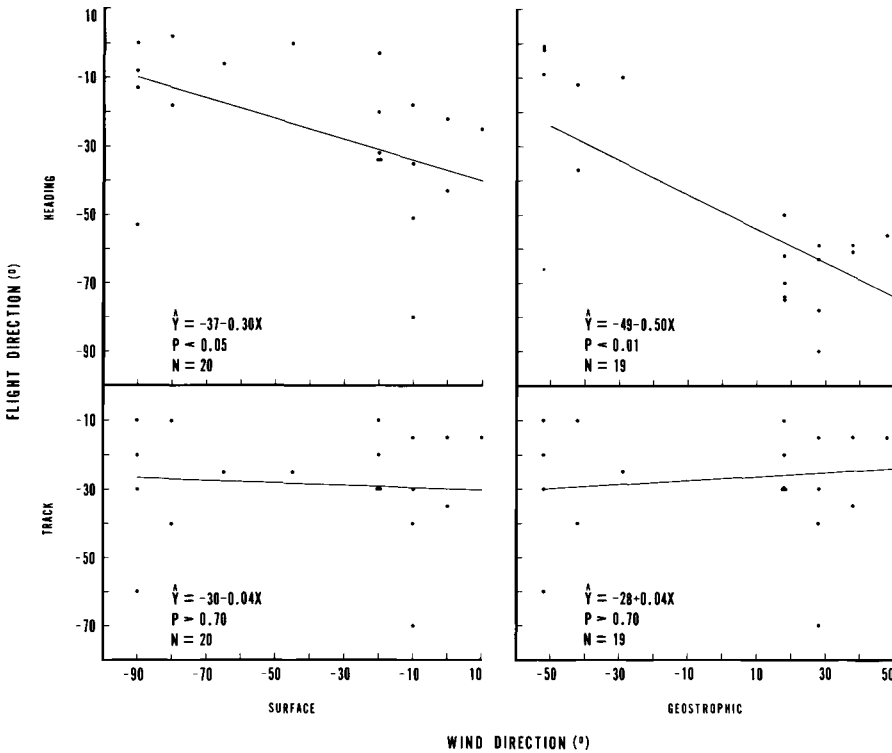
Fig. 2.   Influence of wind direction (direction from which wind was blowing) on flight direction (direction from which bird was flying) of migrating Canada Geese. Directions are measured relative to north (360°). Directions west of north are negative; those east of north are positive.
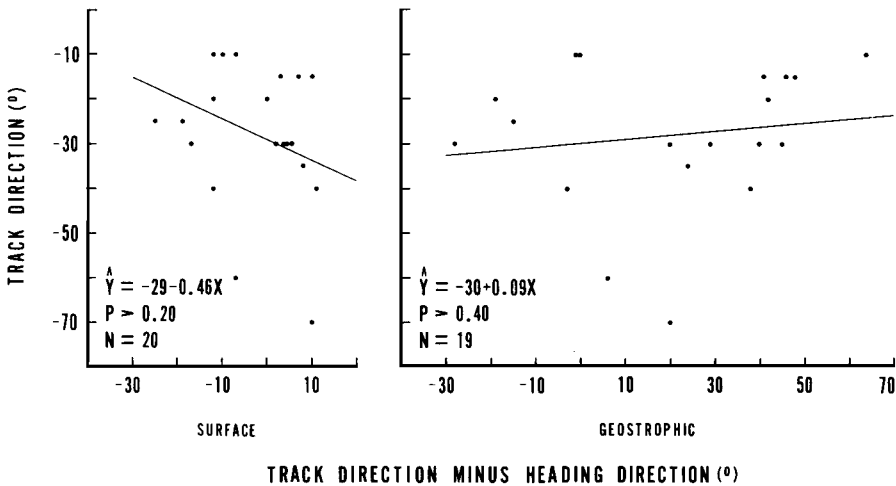
Fig. 3. Influence of the angle between track and heading directions on the track direction of migrating Canada Geese for surface and geostrophic wind conditions. Track directions (direction from which bird was flying) are measured relative to north (360°). Directions west of north are negative; those east of north are positive.

the bird was flying were not accurately known, actual air speeds may represent a compromise between these two types of optimization (see also Schnell and Hellack 1979). With a goal in mind, a bird may conserve energy in response to strong winds by flying longer at a slower speed. In moderate or light winds, flying faster and at a speed that maximizes the distance traveled per unit of time will minimize the migration time.

While headings varied systematically and significantly, track directions did not vary significantly with wind direction (Fig. 2). Regressions of the track direction on the angle between the heading and track directions were performed to determine the magnitude of compensation for wind drift. With drift compensation, the regression coefficient will be 0. A value of 1 indicates complete drift from a constant heading. These analyses indicated that the birds compensated for wind drift during all migration flights, whether nonstop or interrupted, and therefore only the combined data are presented (Fig. 3). As weather conditions allowed these geese to see the ground during all flights reported on here, visual reference to landmarks may have been the cue used to detect their departure from their goal track.

In autumn, this population of Canada Geese tends to migrate between wildlife refuges, which provide protection from hunters, and to minimize the number of migration stopover locations (Raveling 1978). Migrations documented during this study tended to be characterized by direct flight paths, nonstop flights when departure time and weather conditions permitted, and the resumption of interrupted migrations as soon as weather conditions permitted (Wege and Raveling 1983). Flight paths of individual geese whose migration origin and destination were known revealed that the direct nature of autumn migrations was accomplished with the use of minimal energy (reducing air speed with increasing following wind) and by the correction for drift from the goal track.

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Report of Meeting of the Committee on Classification and Nomenclature
Louisville, Kentucky, 24–26 February 1984

The Committee on Classification and Nomenclature takes the opportunity of reporting on its annual winter meeting to note several taxonomic changes that have an immediate effect, and to solicit information from the ornithological community.

The scientific name of the Crissal Thrasher (p. 573, A.O.U. Check-list, 6th edition) is now *Toxostoma crissale* Henry, which replaces *T. dorsale,* suppressed by the International Commission on Zoological Nomenclature (1983, Opinion No. 1249). The names of the tribe Gallinagoini (p. 204) and Subfamily Cyclarhinae (p. 600) become Gallinaginini and Cyclarhininae, respectively, because incorrect roots have been used in the past for formation of these names. American Black Oystercatcher (p. 173) reverts to Black Oystercatcher; an extralimital (African) species with the same color modifier and group name is now considered to have a different, nonconflicting English name (Blackish Oystercatcher), and the additional modifier "American" is no longer necessary. Fernandina's Woodpecker (p. 396) is changed to Fernandina's Flicker to promote uniformity with closely related species; Bare-eyed Thrush (p. 561) becomes Bare-eyed Robin, to avoid confusion with the English name of an extralimital thrush. Note also the correction of "Turquoise-browned Motmot" (p. 371, typographical error) to "Turquoise-browed Motmot."

The preferred citation for the 6th edition (p. ii) is incomplete for bibliographic purposes; it should also list as publisher "American Ornithologists' Union, Washington, D.C." (Allen Press, Lawrence, Kansas, is the printer).

Recently published papers proposing taxonomic changes (e.g. recognition of *Pluvialis fulva;* recognition of *Sphyrapicus nuchalis;* merging of *Phaeornis* in *Myadestes* and splitting of *"Phaeornis" obscurus* into several species; splitting of *Microcerculus marginatus* into several species) as well as other taxonomic issues will be deliberated at Committee meetings in August 1984 and February 1985, with decisions to be published in the next supplement to the A.O.U. Check-list (scheduled for July 1985). Additional data affecting these decisions, as well as other data that are pertinent to potential taxonomic changes, are solicited by the Committee (please send to **Burt L. Monroe, Jr., Chairman, Department of Biology, University of Louisville, Louisville, Kentucky 40292**).

Preparation of a companion volume to the 6th edition dealing with geographic variation and subspecies is well underway, with a schedule for publication in about 5 years. The Committee is seeking data on geographic variation (especially data that may not be published in the near future) and volunteers for review of accounts of various taxonomic groups.

It has been pointed out that ornithology seems to be the only discipline in which English names of species are capitalized. The Committee strongly supports continuation of this policy. The advantages in the designation of a bird species by capitalization greatly outweigh the disadvantages, particularly with the large number of descriptive modifiers that form part of the English names. Confusion is easily avoided; e.g. the phrases "a White Tern" and "a white tern" have distinctly discrete meanings. The use of lower case initial letters in English names in other disciplines seems to be a matter of tradition, but we encourage capitalization for English names of species not only in birds but in other groups as well.

As of the end of the February 1984 meeting, Committee membership consists of Chairman Monroe, Secretary Richard C. Banks, John W. Fitzpatrick, Thomas R. Howell, Ned K. Johnson, Henri Ouellet, James V. Remsen, Jr., and Robert W. Storer.

A COMPLEX CALL OF THE BLACK-CAPPED CHICKADEE (*PARUS ATRICAPILLUS*). I. MICROGEOGRAPHIC VARIATION

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ABSTRACT.—We studied the syllabic structure of the Gargle, a complex vocalization of the Black-capped Chickadee that is often associated with agression, at three main sites in southeastern Wisconsin, at one site over an 11-yr period. Sites as close as 5.7 km showed major differences in syllables, and birds at some sites differed somewhat in the number of syllables per call. Each individual probably uses all the syllables (16–23 different ones) occurring at a particular site. The syllables occurring at the end of the vocalization were shared among different demes, while the introductory syllables were usually different. Syllables showed relatively little change with time. Dialects apparently correspond to demes in this species.

The syllables are arranged in many combinations and permutations to generate a large variety of Gargle types, most of which are very rare. A few Gargle types are more common ("universals") and are usually confined to a particular site. Such a complex dialect pattern is unusual in a call. *Received 27 April 1983, accepted 5 December 1983.*

SONG dialects have been much studied, and the picture that emerges is one of considerable variability among species (for review, see Mundinger 1982). No general rules apply to all species about the nature of the dialect variation, size of dialect groups, stability of dialects with time, or the correspondence of dialect groups to demes. Certainly, detailed studies are needed of a variety of avian species. Although song dialects occur and have been studied in many species, few researchers have dealt with nonsong vocalizations, i.e. those not involved with the dual role of territorial advertisement and pair formation. The exceptions are Thielke's study of Chaffinch vocalizations (*Fringilla coelebs*), Bertram's (1970) work with mynahs (*Gracula religiosa*), and Adkisson's (1981) work with Pine Grosbeaks (*Pinicola enucleator*).

We investigated the microgeographic distribution of the Gargle, a vocalization of the Black-capped Chickadee (*Parus atricapillus*), at five sites in southeastern Wisconsin, at one site for an 11-yr period. We were concerned with the following questions. (1) What is the syllabic composition of this call in different areas? (2) Does this pattern correspond to dialects? (3) Is there any evidence that dialects correspond to demes? (4) How is information about the identity of the individual, population, and species coded? (5) What is the pattern of transmission from generation to generation? Elsewhere, we examine individual repertoires, the functional significance of Gargles, and the possible selection pressures affecting Gargle dialects (Ficken et al. in prep.).

Black-capped Chickadees are highly social, relying strongly on vocal signals (Ficken et al. 1978). Two vocalizations are especially complex: the commonly uttered Chick-a-dee, which has flock-specific characteristics (Mammen and Nowicki 1981), and the Gargle, a sputtery, explosive-sounding vocalization, which occurs year round, primarily in agonistic situations (Ficken et al. 1978). Gargles have several song-like properties: they have much greater syllabic complexity than the whistled "Fee Bee" (usually considered the "song" in this species) and are given primarily by males (Ficken 1981). Gargles often occur when males from adjacent territories engage in boundary conflicts, but they are not used in territorial advertisement. These calls also often precede copulation (Ficken et al. 1978). In the nonbreeding season, Gargles are usually associated with agonistic encounters, often when one bird directly faces or supplants another. In these contexts Gargles are a potent threat display, affecting access to food at feeders (Wipf 1981). Gargles are most often given singly, but, if the opponent does not leave immediately, a few additional ones may be given.

An understanding of the social behavior and population ecology of the chickadee is necessary for an interpretation of their vocalizations.

The following is a brief summary of certain relevant aspects of the life history of the non-migratory populations we studied in southern Wisconsin. Chickadees live in small flocks comprised of 4–8 individuals, including adults and juveniles of both sexes, for most of the year (late July to April). A flock is not necessarily permanent in composition, as some birds may leave or join. Certain individuals, however, tend to remain in association (Odum 1942). Pair formation occurs within the winter flock (Ficken et al. 1981).

In spring (March–April), the flock gradually disrupts, pairs spending more and more time each day on their territories near or on the winter flock range (Odum 1942; pers. obs.). The young fledge in mid-June, stay with their parents for several weeks after fledging, and then disperse, mainly in early July, moving 0.24–11 km (median 1.1 km) from their birth places in our study area in Wisconsin (Weise and Meyer 1979). Following dispersal, young chickadees join flocks in their new area and are very likely to remain there permanently (Weise and Meyer 1979). Thus, the flocks formed in late summer consist of the resident adults of the area and juveniles that have dispersed to that area. Many chickadees live to be 2–5 yr old, and some very few survive 7–10 yr.

MATERIALS AND METHODS

We recorded vocalizations at five feeders in Ozaukee County, Wisconsin. Three are at the University of Wisconsin-Milwaukee Field Station, a site described by Weise and Meyer (1979). Two of these feeders (F9 and A8) are at the edge of Cedarburg Bog, where the predominant vegetation is white cedar (*Thuja occidentalis*) and tamarack (*Larix laricina*). The third (D7) is in a small swamp-hardwood forest at the edge of a large beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) forest. The Field Station and adjacent areas of Cedarburg Bog that we studied comprise 440 ha, which support 250–325 chickadees. Each year about 200 chickadees frequent the six feeders in the area, which are stocked with sunflower seeds and suet from mid-November through April. We selected three feeders that were among those most distant from one another and supported a moderate number of birds. The birds using each feeder came daily from distances of up to 1 km or more. Each feeder had two perches 15 cm apart at the entrance. Although two chickadees frequently perched on the feeder at once, only one at a time would enter to feed. Agonistic interactions were frequent. Recordings were made from November to April each year.

TABLE 1. Number of recordings of Gargles by year and site.

Year	Field Station			River-edge	Graf-ton
	D7	F9	A8		
1970–1974	251	0	0	0	0
1974–1975	140	0	0	0	0
1975–1976	91	0	0	0	55
1976–1977	16	0	176	91	248
1977–1978	296	439	139	22	0
1978–1979	473	580	109	104	18
1979–1980	845	0	0	281	36
1980–1981	183	0	0	4	107
Total for site	2,295	1,019	424	502	464

The Grafton site was a backyard feeder in a suburban area, a narrow wooded strip along the Milwaukee River. The fifth feeder was at the Riveredge Nature Center, a wooded area of about 120 ha. The Field Station feeders usually served several flocks each, and some flocks used two different feeders. Only rarely, however, was there an interchange of individuals among the three feeders we selected. At Riveredge and Grafton birds were not color-banded, and we have no information on flock size or movements, except that there were four or more birds. The chickadees at the Field Station were individually color-banded.

Riveredge is 5.7 km northwest of the Field Station; Grafton is 9.8 km southeast. Grafton and Riveredge are 15 km apart. All Field Station feeders are within 650 m of each other.

The sample sizes of vocalizations obtained from each feeder each year are listed in Table 1. The years 1970 to 1974 were combined, as these recordings were made as part of another study (Ficken et al. 1978). This sample, however, is useful for comparisons with recordings made at later dates at the same feeder. Intensive recordings were made from fall 1975 to January 1981. We recorded at feeders because of the ease of reading color bands and the ability to obtain good-quality recordings by placing the microphone close to the feeder.

We recorded calls at 9.5 c.p.s. with a Nagra III 4.2 L tape recorder and Sennheiser omnidirectional microphone. Occasionally, we used an Uher 4000 tape recorder and Electrovoice 644 Soundspot microphone. The microphone was placed within 1 m of the feeder.

We analyzed the vocalizations with a Kay 6061B Sona-Graph on an intermediate band-width setting (150 Hz). We refer to the discontinuous individual components of a Gargle as syllables and have assigned a letter or letter-number combination to each different syllable. In the preliminary analysis we

measured the frequency and duration of syllables and compared unknown syllables with these. Later, we determined syllable identity by comparing unknowns with tracings of syllables from sonograms, as it became apparent that syllables were quite stereotyped. Identification of syllables was based on their shape on sonograms and their frequency (Hz) and temporal characteristics. Although variation in frequency (pitch) occurs, syllables are usually very discrete. Rarely was syllable identity questionable, and then usually because the recording was poor; such syllables were not used in this analysis. The data were prepared for analysis using the Univac 1100 computer.

RESULTS

We examined Gargles at two levels of organization: component syllables and the syllabic combinations constituting the call (the Gargle type). It might have been possible to devise a scheme for lumping call types with similar syllabic composition and ordering of syllables, but, because of the complex arrangements of syllables in the calls and our lack of knowledge of the functional significance of the various syllables and syllable combinations, we treated every unique syllable combination as a different call type, e.g. EVRFSQ is a different type from EVFSQ.

Syllabic composition of gargles.—Sonograms of the more common syllables at the various sites are presented in Fig. 1. Many are frequency sweeps, often covering wide frequency ranges very rapidly. Only three syllables (I, Z, and the very infrequent M) are short pure tones. Three syllables are buzzes or trills (P1, P2, and Q). Usually, all the syllables in a single call are different. (Fig. 2 presents some representative calls.)

Number of syllables in calls.—As calls vary in the number of syllables, possible a principal difference among populations is the number as well as the kind of syllables.

The number of syllables in a call varied from 2 to 13 (Fig. 3). The following are the means and standard deviations of number of syllables per call at the various feeders: D7: 5.9 $\pm$ 3.84; A8: 6.1 $\pm$ 1.82; F9: 6.04 $\pm$ 3.06; Grafton: 5.69 $\pm$ 1.68; Riveredge: 7.25 $\pm$ 1.89. The overall distribution of number of syllables per call is not a normal one. For example, calls with 2 and 3 syllables are rare at all feeders (5% of total), whereas 4-syllable calls are much more frequent (about 20% of all calls, except at River-

edge). Riveredge (and to a lesser degree Grafton) birds tend to give more calls of 10–13 syllables than do the Field Station birds. The incidence of 10- and 11- syllable calls at Riveredge is significantly different from the Field Station sample ($\chi^2_1 = 9.56$, $P < 0.01$). The calls of all Field Station birds tend to peak at 4 syllables and at 6–8 syllables, then to decline rapidly at 9–10 syllables. Among Grafton birds there is the same trend toward 2- to 4-syllable calls, but they differ in having a sharp peak at 5 syllables and then a rapid decline; they also have a higher proportion of calls with 9–13 syllables than do the Field Station birds. Riveredge birds have a lower proportion of 4-syllable calls than the others do and a higher proportion of 10- and 11-syllable calls.

Considerable variation in syllable number occurred from year to year at the same feeder, and only at F9 feeder was there no statistical difference between years ($\chi^2_6 = 12.1$, $P > 0.05$).

We combined data from all Field Station feeders and compared syllable number with the other sites. The Field Station was significantly different from Riveredge ($\chi^2_8 = 516$, $P < 0.001$). Grafton and Riveredge were also significantly different ($\chi^2_{12} = 154$, $P < 0.001$) in syllable number. There were also significant differences among the three feeders at the Field Station ($\chi^2_{12} = 154$, $P < 0.001$).

Individual repertoires of syllables.—We tested the hypothesis that all individuals produce the full syllable repertoire of their particular population by surveying the repertoires of four individuals at D7 feeder for which there were sample sizes of over 100 calls (Table 2). The individuals differed significantly in the frequency of usage of syllables ($\chi^2_{48} = 480$, $P < 0.001$). All birds shared the more common syllables, however (excluding the rare I, U, and R4, the latter given by only one individual).

Syllables at different sites.—We tested the hypothesis that the syllabic composition of calls is different at different sites. Because all three Field Station sites are very close together, we expected that syllable sharing would occur among them, that Riveredge would differ somewhat from the Field Station, and that Grafton, because of its distance, would be very different from both the Field Station and Riveredge.

The feeders differed in the syllables present (Table 3). We calculated a coincidence index (Dice 1945): $2h/(a + b)$, where h = total number
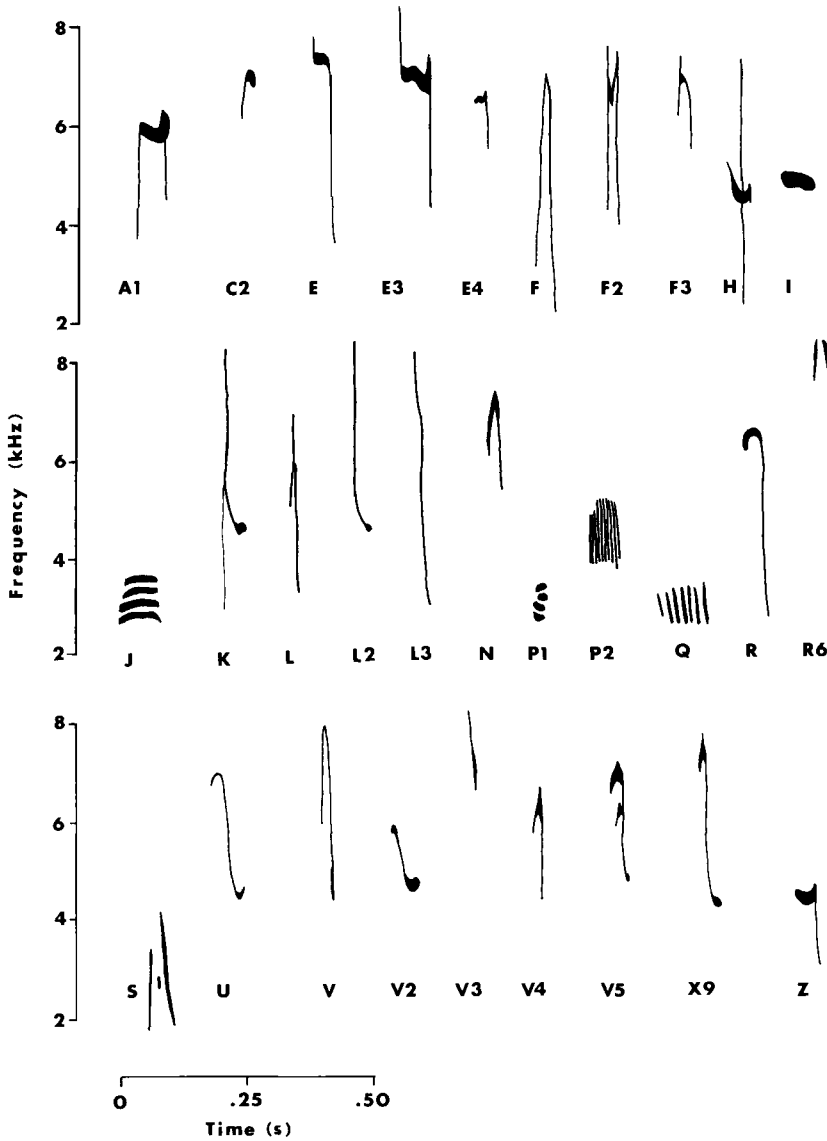
Fig. 1.   Syllables of Gargles at the five study sites. (A few very rare syllables were omitted.)

of shared syllables, a = total number of sylla-
bles at one feeder, and b = total number of syl-
lables at the other feeder. Syllables at the three
Field Station feeders were very similar, but
these sites showed a lower degree of similarity
with Grafton and Riveredge; and the lowest
degree of similarity occurred in the two feeders
that are the most distant from each other—
Grafton and Riveredge (Table 4).

One syllable (C2) was unique to the three

Field Station feeders, while Riveredge had 8
syllables not shared with any other study site,
and Grafton had 5. These unique syllables were
usually at the beginning of the call. For ex-
ample, these site-specific syllables were in-
volved in 142 Gargle types; they were the first
syllable in 109, the second in 18, and the third
or more in only 15.

Birds at the three Field Station sites and at
Grafton used 16–17 different syllables. The
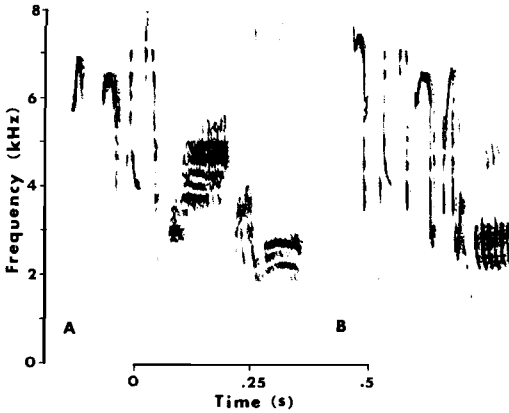
Fig. 2. Two common Gargle types at the Field Station. A. Syllabic combination C2RKVP1P2SJ. B. Syllabic combination EKVRFSQ.

number (23) was unexpectedly higher at Riveredge, however. To understand this phenomenon, it would be important to know the number of birds using each feeder and the immigration rates from other sites.

One interesting finding was that those syllables that are usually near the end of a Gargle, if they occur at all (P1, P2, S, Q, and J), were found in all the populations studied. All populations also shared 5 other syllables (E, F, K, L, and V), but 18 other syllables were not found universally. Clearly, microgeographic variation occurred in the distribution of many syllables, although those syllables typically near the end of the call were found at all sites.

As differences occurred in the frequency of usage of syllables at the same site in different years, it is not surprising that there were also
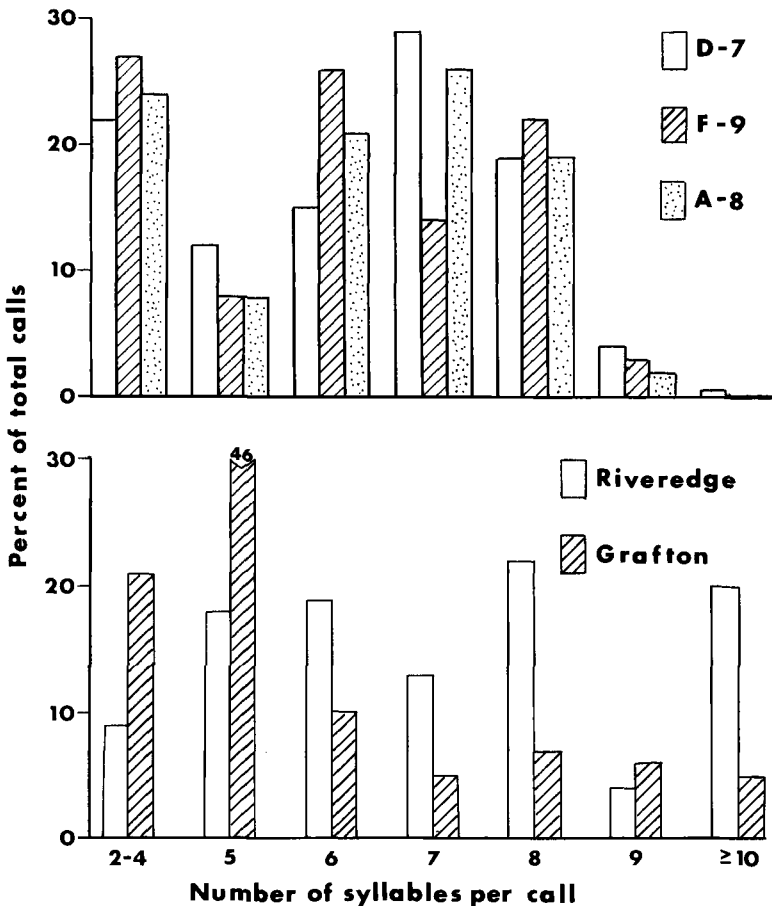
Fig. 3. Distribution of number of syllables in a call at all study sites.

TABLE 2. Frequency of occurrence of syllables for four individuals at D7 feeder.

Syllable type	Individual[a]			
	AOCJ (n = 133)	AOYR (n = 122)	PCAO (n = 134)	AOPB (n = 146)
C2	47	1	24	3
E	38	111	68	90
F	77	107	74	108
H	33	6	14	18
I	0	0	1	8
J	73	9	22	13
K	90	112	83	98
L	34	6	15	27
N	30	3	5	4
P1	65	10	22	14
P2	66	10	49	35
Q	35	96	67	97
R	92	119	100	118
R4	0	0	0	4
S	110	110	99	94
U	0	0	2	6
V	93	116	99	114

[a] n = total number of calls for that individual.

significant differences in the frequency of usage of syllables that comprised more than 1% of the total among the three Field Station sites ($\chi^2_{30} = 477$, $P < 0.001$).

Rank order of frequency of occurrence of syllables.—Although considerable variation occurred in the frequency of usage of particular syllables at the same site from year to year, we postulated that the rank order of frequency of occurrence of syllables would be the same at the same feeder in different years, as well as at different feeders. In other words, the most common syllables at one feeder would also be the most common ones at other sites, and the rare ones would be rare at all sites.

First, we compared rank order using Spearman's rho for different years at the same site. All the seven periods at D7 feeder compared individually with one another were significantly correlated ($P < 0.01$), except for 1975–1976 versus 1979–1980 and 1980–1981, and 1970–1974 versus 1974–1975 ($P > 0.05$). Thus, at D7 the rank order of syllables of some of the earlier years was not correlated with some of the later years. At F9 feeder data for 1977–1978 were compared with 1978–1979 ($\rho s = 0.83$, $P < 0.01$); the same trend occurred at A8 in a comparison of 3 yr ($P < 0.01$). Grafton exhibited a similar pattern for the 2 yr tested ($\rho s = 0.57$, $P < 0.05$), as did Riveredge ($\rho s = 0.84$, $P < 0.001$).

TABLE 3. Occurence of syllables at the various sites (syllables that were more than 1% of total syllables for that site).

Syllable	Sites				
	D7	F9	A8	River-edge	Graf-ton
A1	0	0	0	0	+
C2	+	+	+	0	0
E	+	+	+	+	+
E3	0	0	0	0	+
E4	0	0	0	0	+
F	+	+	+	+	+
F2	0	0	0	0	+
F3	0	0	+	0	+
H	+	+	+	+	0
I	+	+	+	+	0
J	+	+	+	+	+
K	+	+	+	+	+
L	+	+	+	+	+
L2	0	0	0	0	+
L3	0	0	0	+	0
N	+	+	+	+	0
P1	+	+	+	+	+
P2	+	+	+	+	+
Q	+	+	+	+	+
R	+	+	+	+	0
R6	0	0	0	+	0
S	+	+	+	+	+
U	+	+	+	+	0
V	+	+	+	+	+
V2	0	0	0	+	0
V3	0	0	0	+	0
V4	0	0	0	+	0
V5	0	0	0	+	0
X9	0	0	0	+	0
Z	0	0	0	+	0
Total number of syllables	16	17	16	23	16

We tested the hypothesis that, despite the differences in syllables among sites, there would be a correlation for shared syllables in rank order of the syllables. All the Field Station sites were significantly correlated in rank order ($P < 0.01$). Grafton and Riveredge were significantly

TABLE 4. Coincidence indices of syllables at all sites.

Site	D7	F9	A8	River-edge	Graf-ton
D7		1.0	0.97	0.67	0.63
F9			0.97	0.72	0.63
A8				0.75	0.67
Riveredge					0.51
Grafton					

TABLE 5. Number of different Gargle types in which a particular syllable was used at D7 feeder. (Total number of Gargle types = 182. In the rare cases when a syllable was used more than once in a Gargle type, it was scored only once. * = syllable also present at Riveredge and Grafton.)

Syllable	Number of Gargle types in which it occurred
F*	118
S*	114
V*	105
K*	97
R	76
E*	72
P2*	71
Q*	64
P1*	59
L*	57
J*	47
H*	32
C2	19
N	11
I	11
U	5
C	2
V3	2
M	2
A	1
Y	1
R3	1
R4	1

Fig. 4. Frequency distribution of Gargle types at D7 feeder.

corded after that time. Syllables L and H were absent in the earliest period (1970–1974) but were common thereafter.

There were similar trends at the other feeders: some rare syllables were not present in all years, but the common ones persisted. The most common syllables at D7 were also found at Riveredge and Grafton; this was not true of the rarer syllables. As might be expected, the more common syllables, involved in a large number of call types, persisted over 11 yr at D7.

Relatively little change occurred over a span of 11 yr except for the introduction of two syllables. There was no trend for very rare syllables to become well established over the years, nor did any of the more common syllables become extinct, although there was substantial variation in the frequency of occurrence of many syllables from year to year at the same site.

Distribution of gargle types.—A system based on 2–13 syllables that can be combined in many different ways generates an incredible variety of call types. While our sample probably includes all syllables uttered at the feeders during the years studied, except perhaps for the very rare ones, the situation with Gargle types is much more complex. Most Gargle types are very rare (Fig. 4). Of a sample of 182 Gargle types at D7 feeder, 104 of these comprised less than 0.1% each of the total Gargles given. Many Gargle types occurred only once in our sample. Because Riveredge and Grafton have a number of syllables differing from those at the Field Station, the Gargle types there would be expected to be largely different.

correlated (ρs = 0.83, P < 0.01), but Grafton was not significantly correlated with D7 at the Field Station in either of the 2 yr (P > 0.05). Riveredge and the Field Station were significantly correlated (ρs = 0.7, P < 0.01).

A general pattern of rather stable rank ordering of the frequency of occurrence of syllables among the various sites occurs. As the earlier and later samples at the Field Station were often not significantly correlated, however, there may be some shifts in rank order with time, and rank order may be different at more distant sites (i.e. Grafton and Field Station).

Distribution of syllables over time.—The syllables at D7 feeder were assessed over an 11-yr period, and most syllables were present in all years. Exceptions were some of the rarer syllables (C2, N, and U), present in some years but not others. These three syllables were unusual, however, in that each was associated with only a few Gargle types (Table 5). The syllable M was rare in 1970–1974 and was never re-

TABLE 6. Coincidence indices for Gargle types at the various sites (* = total number of Gargles).

Site	D7	F9	A8	River-edge	Graf-ton
D7 (1,635*)		0.76	0.62	0.38	0.01
F9 (813)			0.68	0.36	0
A8 (349)				0.33	0
Riveredge (414)					0
Grafton (453)					

TABLE 8. Frequency of occurrence of the two most common Gargle types at Field Station sites.

Site	Gargle type[a]	
	EKVRFSQ	VRP2Q
D7	525	208
	(19.7)	(7.8)
A8	48	83
	(12.2)	(21.0)
F9	84	196
	(9.2)	(21.6)
Riveredge	0	2
	0	(4)
Grafton	0	0

[a] Percentage of total Gargles in parentheses.

Each male probably has at least 15 Gargle types (Ficken et al. in prep.). Coincidence indices of Gargle types were calculated to examine sharing of Gargles at all feeders (Table 6). The amount of sharing of Gargle types among the three Field Station feeders was relatively high (0.62–0.76); the similarity with Riveredge was lower, and Grafton shared almost no Gargles with the Field Station. Thus, although birds at different sites may share some of the same syllables, different sites may have few or no Gargles in common due to the large number of syllable combinations possible.

The distribution of the 12 most common Gargle types at D7 was examined over 11 yr. The frequency of occurrence of the various Gargle types in different periods at D7 was significantly different ($\chi^2_{55} = 881$, $P < 0.001$) (Table 7). Thus, there are year-to-year differences, even in the most common Gargles, in the frequency with which they occur at the same site.

Although most Gargle types are very rare, a few at each feeder are much more common. Table 8 indicates that two Gargle types occurred at a high incidence at all three Field

Station feeders, the two comprising about a third of all Gargles given. These we term the Field Station "universals." Although all the syllables of the universals are present at Riveredge, Field Station universals made up less than 0.1% of the total Gargles at Riveredge. One of the two most common Gargle types at Riveredge did not occur at all at the Field Station. The frequency of usage of the two universals at D7 feeder over the 11-yr period differed significantly ($\chi^2_6 = 64$, $P < 0.001$).

We hypothesized that endings of Gargles (defined as the last two syllables, regardless of the number of syllables in the vocalization) might be more conservative than the beginning (defined as the first two syllables of the Gargle). These numbers of syllables were chosen, as the average number of syllables in the vocalization is about six. Although there are a variety of endings, most are very rare. SQ and

TABLE 7. Occurrence of the 12 most common Gargle types at D7 feeder in different years.

Gargle type	1970–1974	1974–1977	1977–1978	1978–1979	1979–1980	1980–1981
C2RKVP1P2SJ	18	15	14	42	53	0
RKIFSQ	6	16	13	18	24	1
EKVFP1P2SQ	2	7	7	31	29	0
EKVFSQ	0	4	4	22	43	0
EKVR	0	3	11	10	31	4
LEKVFSQ	0	0	0	27	18	5
LHRF	0	2	1	1	16	6
LHRFP1P2SJ	0	43	0	7	65	5
LHRFSJ	0	0	51	7	1	0
KIFSQ	34	16	0	2	0	0
EKVRFSQ	30	30	75	130	184	38
VRP2Q	58	13	14	29	85	6

SJ are the most common ones at all sites, accounting for 56% of the endings at D7, 70% at A8, 55% at F9, 37% at Grafton, and 62% at Riveredge. Grafton differed somewhat from the other sites in having another common ending (FS). Statistically significant differences are evident among sites in the frequencies of occurrence of the two most common endings ($\chi^2_4 = 11.2$, $P < 0.05$). One interesting feature is that these common endings occur at all feeders, although other syllables in the vocalizations may be very different, varying microgeographically. We also tested the hypothesis that the frequency of the syllables ending Gargles would not be significantly different at the three Field Station feeders, and this hypothesis was rejected $\chi^2_8 = 68$, $P < 0.001$). Thus, although these syllables are universal at the sites studied, the frequency of usage of the syllables differs from site to site.

The most common beginnings were EK and LH at D7 and A8 feeders; at F9 EK and ER were the most common, with LH being the next most common. Gargles beginning with F2K predominated at Grafton, followed by E4K and KF; at Riveredge V3L and LH were the most common beginnings. At these latter two feeders, Gargles most often began with syllables that were rare or absent at the other feeders.

When very rare syllables occurred (comprising less that 10 observations each), they were usually the first syllable (10 cases) or, more rarely, the second (3 cases) ($n = 15$), supporting the idea that it is the ending rather than the beginning syllables that are more widespread. In summary, although most Gargle types were rare, the two most common ones were shared at all Field Station sites and may be considered specific to that population. Even more distant sites shared endings, however.

DISCUSSION

Microgeographic patterns of variation.—Dialects are generally considered to occur if conspecifics in a particular geographic area share vocalizations that are different from vocal patterns in different geographic areas (Thielcke 1969, Krebs and Kroodsma 1980, and Mundinger 1982, review avian dialects). A dialect pattern is evident in Black-capped Chickadees at the level of syllables and at the level of syllabic combinations (Gargle types). Furthermore, the

pattern is microgeographic, as marked differences occur in areas as close as 5.7 km. The three Field Station sites, separated by only a few hundred meters (but including birds with breeding sites up to 3 km distant), were very similar, particularly in the call syllables. Similar microgeographic distributions occur in other species. For example, Mundinger (1975) found that dialects in House Finches (*Carpodacus mexicanus*) were confined to a few square kilometers, and Payne (1973) noted that in Village Indigobirds (*Vidua chalybeata*) neighbors shared most song types, but birds 6.5 km away shared no song types.

All chickadees seem to possess the full repertoire of syllables of their population, although a few very rare syllables may be specific to certain individuals. Birds at different sites may differ in their syllables, but most sites have about the same number of syllables, indicating that there may be an optimal repertoire size of syllables. Another feature common to all sites is that the rank order of shared syllables is usually similar, indicating that the same basic "vocal rule" holds for the occurrence of syllables at the various sites. At certain sites calls tend to have more syllables than at others.

Much variation in vocal dialects occurs among different species. Some, such as the White-crowned Sparrow (*Zonotrichia leucophrys*), have only one song type that varies geographically (Marler and Tamura 1962). In the Indigo Bunting (*Passerina cyanea*), unlike the chickadee, most song figures (these correspond to our syllables) occur in only a few individuals (Thompson 1970). The chickadee dialect pattern is similar to that of the Northern Cardinal (*Cardinalis cardinalis*) (Lemon 1966), in that most birds in a locale share the same syllables; although some syllables are widespread, others have a more restricted distribution. Most of the song types of territorial neighbors are similar in Cardinals, and in the chickadee there is some sharing of call types in birds of the same locale.

Our data indicate that it is necessary to examine vocalizations and their variation at two levels: that of syllables and that of the combination of these in various call "types." In chickadee Gargles, the distribution of syllables is independent of that of the call types, in that some syllables have a wider distribution than do the call types. For example, even though Riveredge birds had the component syllables

of the two most common Gargle types at the Field Station, one of these types was very rare at Riveredge and the other apparently absent.

Coding of information in the call.—Rare syllables were more common at the beginning of the call than at the end, and more differences occurred among localities in the beginning syllables than in the ending ones. In fact, the most common endings were found even in our two most distant localities, Grafton and Riveredge. Two recordings of a Black-capped Chickadee from the Great Smoky Mountains (Cornell University collection) had three beginning syllables not found in our Wisconsin sample, but the terminal syllables were also common endings in southeastern Wisconsin. We therefore suggest that the terminal syllables of Gargles may be species-specific features, while the beginning ones may specify the particular population.

Relationship of dialects to demes.—A central question concerning avian dialects is whether or not these vocalizations act as barriers to gene flow (Nottebohm 1969). Several workers have suggested that dialects may reduce gene flow between demes (Baker 1974, Baker and Mewaldt 1978), while others doubt that this is the case (Petrinovich et al. 1981). Clearly, more data on a variety of species are necessary to resolve the question.

Do dialects correspond to demes in Black-capped Chickadees? As the Field Station supports some 200–300 chickadees during the breeding season and, although movements occur within the area, there is not much immigration or emigration apart from juvenile dispersal, the Field Station chickadees might be considered to constitute a deme. A minimum estimate of median dispersal distance is 1.1 km (Weise and Meyer 1979). Howitz's (1981) estimates of 1.34–2.39 km for a Minnesota population are consistent with these data. Riveredge Nature Center (5.6 km from the Field Station) probably constitutes another deme. There are four other bird-trapping stations where chickadees are banded within 6 km of the Field Station. Yet, of over 2,000 birds trapped at the Field Station since 1970, only three have been retraps from the other stations. Two Field Station birds have been retrapped at the other stations. This part of southeastern Wisconsin is a mosaic of woodlands, most very small except for the Field Station area. The Field Station is separated from areas such as Riveredge and Grafton

by habitats unsuitable for breeding, especially agricultural fields. Grafton and Riveredge are both well beyond the median dispersal ranges of Field Station birds, and Grafton and Riveredge are even more distant from one another. Thus, we can probably conclude that different demes of chickadees have somewhat different syllables and, of course, different combinations of these in their call types.

Dialects would be expected in the vocalizations of species, such as Black-capped Chickadees, that are largely sedentary, disperse as juveniles over relatively short distances, and have discontinuous habitats. Dialects in Cardinals are maintained because of high site fidelity, low annual mortality, and a relatively short dispersal distance (Lemon 1975).

Dialects over time.—Detailed studies of how song patterns in the same area change over time have been done for only a few species (e.g. Lemon 1975, Cardinal; Baptista 1975, White-crowned Sparrow; Jenkins, 1977, Saddleback, *Creadion carunculatus*; Slater and Ince 1979, Chaffinch; and Payne et al. 1981, Indigo Bunting). Avian patterns of cultural transmission are reviewed by Slater and Ince (1979) and Payne et al. (1981). In Indigo Buntings a few song types persisted over 15 yr, suggesting that local songs may remain similar for several generations, although some year-to-year changes occurred in the frequency of occurrence of syllables (Thompson 1970). Baptista (1975) found a marked change in songs of White-crowned Sparrows in 2 yr. Jenkins (1977) noted that the distribution of song-dialect patterns was stable over a 4-yr period but found some changes in note structure and the combinations of parts of songs. Ince et al. (1980) studied changes in Chaffinch song over a 20-yr period that involved 8–10 generations of Chaffinches. He found that some syllables stayed the same while others changed, and a reassortment of syllables occurred between song types. Lemon (1975) postulated that changes will occur over time because of the processes of cultural transmission involving copying errors, improvisations by individual birds, and immigration of birds with different cultural experiences. As chickadees average only 2–3 yr of survival, we probably sampled at least three generations of chickadees.

The most common syllables persisted over a long term at a Field Station site studied over 11 yr. Rare syllables, usually occurring in the

Gargle types of only a single individual, seemed to disappear rather than to become incorporated into the population's repertoire. Because of insufficient data, we could not follow the transmission of Gargle types as well as that of syllables. The most common Gargle types persisted over our sampling period at the Field Station, however. Ince et al. (1980) noted that the more common song types of Chaffinches persisted for a longer time than did the rarer ones, probably because a bird had more individuals from which it could learn the common than the rarer songs.

Some of the more unusual features of chickadee vocal dialects.—Dialects occur in chickadee vocalizations at the levels of the syllable and of the more common Gargle types. What is noteworthy of the chickadee, as compared with most other avian species, is its use of an array of different syllables that occur in a great variety of combinations. Each individual uses about 15 syllables, which it combines in various ways to generate a large number of call types. Such complexity of dialect pattern is unusual in avian calls, which, if there is a dialect pattern at all, usually have a macrogeographic rather than a microgeographic pattern (Mundinger 1982).

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The **XIX International Ornithological Congress** will take place in Ottawa, Canada, from **22 to 29 June 1986.** Prof. Dr. Klaus Immelmann (West Germany) is President and Dr. Henri Ouellet (Canada) is Secretary General. The program is being planned by an international Scientific Programme Committee chaired by Professor J. Bruce Falls (Canada). The program will include plenary lectures, symposia, contributed papers (spoken and posters), and films. There will be a mid-congress free day. Pre- and post-congress excursions and workshops are planned in various interesting ornithological regions of Canada. Information and requests for application forms should be addressed to: **Dr. Henri Ouellet, Secretary General, XIX Congressus Internationalis Ornithologicus, National Museum of Natural Sciences, Ottawa, Ontario, Canada K1A 0M8.**

The **Third International Congress of Systematic and Evolutionary Biology** will be held on 4–10 July 1985 at the University of Sussex, near Brighton, England. Symposia are being organized on a wide variety of evolutionary, systematic, and ecological topics, and additional sessions will be available for contributed papers, films, and poster presentations. For additional information contact **Professor Barry Cox, ICSEB Congress Office, 130 Queen's Road, Brighton, Sussex BN1 3WE, United Kingdom.**

The Hawk Mountain Sanctuary Association is accepting applications for its eighth annual **award for raptor research.** To apply for the $500 award, students should submit a description of their research program, a curriculum vita, and two letters of recommendation by **30 September 1984, to James J. Brett, Curator, Hawk Mountain Sanctuary, Rt. 2, Kempton, Pennsylvania 19529.** The Association's Board of Directors will make a final decision late in 1984. Only students enrolled in a degree-granting institution are eligible. Both undergraduate and graduate students are invited to apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to conservation of North American raptor populations.

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REVIEWERS FOR *THE AUK,* 1982-1983

The Auk is fortunate to benefit from the services of many individuals who act as reviewers of manuscripts that are submitted. Their efforts are considerable, and their care and constructiveness continue to impress me as an editor and as a sometime author. The individuals listed below helped make publication of a journal with high scientific and scholarly standards possible; my thanks to all of them.

Individuals who have contributed reviews of two or more manuscripts are indicated by an asterisk.

Kenneth P. Able, Alan D. Afton*, Marianne G. Ainley, S. D. Albon, John Alcock, Thomas Alerstam, Dean Amadon, Daniel W. Anderson, Stanley H. Anderson, Per Angelstam, C. Davison Ankney*, Einar Arnason, Conny Askenmo, William R. Atchley, John C. Avise*, G. Baeyens, Myron Charles Baker*, Russell P. Balda*, David Balph, Martha Balph*, Richard C. Banks, Luis Felipe Baptista*, George Barrowclough*, Range Bayer*, Jim Bednarz*, Michael Beecher*, Steven R. Beissinger, Frank C. Bellrose, Jr.*, Gregory Bentz, Marvin H. Bernstein, P. Berthold, Louis Best, Herbert Biebach, Keith Bildstein, Verner P. Bingman, Charles R. Blem, Lawrence J. Blus, David A. Boag, Walter Bock*, P. Dee Boersma, Eric G. Bolen, William R. P. Bourne*, Mark S. Boyce, Eliot Brenowitz, I. Lehr Brisbin*, James H. Brown, Jerram L. Brown, Patrick W. Brown, Richard G. B. Brown*, Alan H. Brush*, D. M. Bryant*, M. G. Bulmer, Guy L. Bush, William Buttemer, Thomas J. Cade, Peter Calow*, R. Wayne Campbell, Cynthia Carey*, Joseph A. Chapman, Meifang Cheng, Roger Clapp, Anne B. Clark, Charles T. Collins*, Scott Collins, Robert K. Colwell*, Richard N. Conner, Edward F. Connor, Peter G. Connors, John Cooper, Kendall W. Corbin, J. C. Coulson, Joel Cra-

craft*, Adrian J. F. K. Craig, Marie Crock, John Croxall, Thomas W. Custer, D. G. Dawson, William R. Dawson, Allan Degen, David DeSante*, Diane De Steven*, Jared M. Diamond, Robert W. Dickerman, Keith Dixon, R. D. Drobney*, William H. Drury, David C. Duffy, Erica H. Dunn, G. M. Dunnet, Thomas J. Dwyer, David H. Ellis, Hugh I. Ellis, J. Emmerton, James Enderson, Roger M. Evans*, Paul W. Ewald*, D. S. Farner, J. Alan Feduccia, Kent Fiala*, Millicent Ficken*, Scott Findlay, James S. Findley*, Hans Fisher, Richard E. Fitzner, John W. Fitzpatrick*, Jon Fjeldså, Glenn Ford, Norman L. Ford, Dennis M. Forsythe, Mercedes S. Foster, Robert W. Furness, Kimball Garrett*, A. J. Gaston, Sidney A. Gauthreaux*, James A. Gessaman, Kenneth M. Giesen, Frank B. Gill*, Robert E. Gill, J. M. Gillespie, Timothy H. Goldsmith, Görgen Göransson, John D. Goss-Custard*, Bradley M. Gottfried, James L. Gould, Patricia A. Gowaty, Crawford H. Greenewalt, T. C. Grubb, Jr.*, James L. Gulledge*, Eberhard Gwinner, Svein Haftorn, Yrjö Haila, Jack P. Hailman*, F. Reed Hainsworth*, Ruud van Halewijn, William J. Hamilton, III, Ilkka Hanski, Dennis Heinemann, Carlos M. Herrera, Joseph J. Hickey*, William Hodos, Wayne Hoffman*, Olav Hogstad, Göran Högstedt, Richard T. Holmes*, Robert D. Holt, John L. Hoogland*, Peter Houde, Alastair Houston, Henry F. Howe*, Marshall Howe*, Thomas R. Howell*, John P. Hubbard*, George L. Hunt, Jr., Steve Hunter, R. Hutto*, George Innis*, Jerome A. Jackson*, Fabian M. Jaksić, Douglas James, Frances C. James*, Daniel H. Janzen*, Olli Järvinen*, Joseph R. Jehl, Jr.*, Donald A. Jenni, Paul A. Johnsgard, Douglas H. Johnson*, Ned K. Johnson*, P. J. Jones, Nancy Joste, John A. Kadlec, M. Philip Kahl, Alan C. Kamil, James R. Karr, James O. Keith,

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The American Ornithologists' Union will offer several **Marcia Brady Tucker Travel Awards** to help defray expenses of outstanding students wishing to present posters or lectures at the society's annual meeting at Lawrence, Kansas (5–10 August 1984). To apply, send the following materials to **Michael J. Hamas, Department of Biology, Central Michigan University, Mt. Pleasant, Michigan 48859** by **10 May 1984**: (i) expanded abstract of the paper (max. 3 pp. typed, double-spaced; to include methods, major results, and scientific significance), (ii) curriculum vita, (iii) anticipated budget of expenses (to include travel expenses, registration fee, and room and board), and (iv) a letter of support from the academic advisor supervising your research (which should be mailed under separate cover). Please note that seven (7) copies of *all* materials must accompany each application. Applications for MBT Travel Awards do not guarantee a place on the Scientific Program. Students must make arrangements for that as per the instructions given with the Call for Papers announcement.

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