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Foraging Radii and Energetics of Least Auklets (*Aethia pusilla*) Breeding on Three Bering Sea Islands

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Abstract

*We studied the relationship between the foraging radius and energy economy of least auklets (*Aethia pusilla*) breeding in colonies on three islands in the Bering Sea (St. Lawrence, St. Matthew, and St. George Islands). The distance to which auklets commuted on foraging trips varied by more than an order of magnitude (5–56 km), but mean field metabolic rate (FMR) did not vary significantly among birds from the three islands. These observations indicate that allocation to various compartments of time and energy budgets is flexible and suggest that least auklets may have a preferred level of daily energy expenditure that is similar across colonies. We modeled the partitioning of energy to various activities and hypothesize that the added cost of commuting incurred by auklets from St. Lawrence Island (foraging radius, 56 km) was offset by reduced energy costs while foraging at sea. Data on bird diets and prey abundances indicated that auklets from St. Lawrence Island fed on larger, more energy-rich copepods than did auklets from St. Matthew Island (foraging radius, 5 km) but that depth-averaged prey density did not differ significantly between the birds' principal foraging areas. However, previous studies have indicated that zooplankton abundance is vertically compressed into near-surface layers in stratified waters off St. Lawrence Island, which suggests that variation in foraging efficiency may have resulted in part from differences in the accessibility of food rather than its absolute abundance in the water column. Our findings demonstrate why long-dis-*

tance commuting between colony and feeding areas need not significantly affect total daily adult energy expenditures, even in heavily wing-loaded species such as auklets. Interpretation of the energetic ecology of auklets and other seabirds can strongly benefit from information regarding foraging distributions, diets, and prey accessibility.

Introduction

Breeding seabirds commute to sea on foraging trips that vary greatly in distance and duration. Foraging radii observed in different species span more than four orders of magnitude, from <200 m to >2,000 km (Brown 1976; Kuletz 1983; Pennycuick, Croxall, and Prince 1984; Weimerskirch et al. 1988; Wilson, Nagy, and Obst 1989; Fasola and Bogliani 1990; Flint 1991; Wanless, Harris, and Morris 1991; Weimerskirch et al. 1993; Jouventin et al. 1994). In some species, individuals feed at widely varying distances on different days and even on consecutive foraging bouts (see, e.g., Anderson and Ricklefs 1987; Wanless, Harris, and Morris 1990). Whereas theoretical models can be used to predict the maximal foraging radius of a species (Andersson 1978; Pennycuick et al. 1984; Flint 1991), they provide little insight into the ecological causes or energetic consequences of intraspecific variation in commute distance. Because of the high cost of flight, these consequences are expected to be substantial, yet few empirical studies have attempted to examine the relationships between foraging radius and energy expenditure.

We studied the energetic ecology of least auklets (*Aethia pusilla*) breeding on different islands in the Bering Sea. These smallest members of the alcid family are planktivorous divers that specialize on copepods during the summer breeding season (Bédard 1969; Springer and Roseneau 1985; Hunt and Harrison 1990). Auklets have a specialized flight morphology associated with their subsurface foraging mode and use muscle-powered (nongliding) flight exclusively while commuting between colonies and pelagic foraging sites. Their short wings, which are adapted for underwater propulsion, result in high wing-disc loading and poor fuel economy in flight (Pennycuick 1987). Although long-range foraging by auklets is therefore unexpected, radically different spatial distributions of foraging birds have been observed around different colonies. In the southern and central Bering Sea, auklets typically forage just offshore island colonies (Hunt et al. 1978). In contrast, birds breeding on islands in the northern Bering Sea often forage at sites more than 50 km offshore (Hunt and Harrison 1990; Hunt, Harrison, and Cooney 1990).

We compared the foraging ecology and field metabolism of least auklets breeding on St. George, St. Matthew, and St. Lawrence Islands (fig. 1). Our objectives here are (1) to compare field metabolic rates (FMRs) of birds with commute distances varying by more than an order of magnitude, (2) to deduce patterns of energy use and acquisition by integrating FMR data with observed foraging radii and other behavioral information in a simple model, and (3) to use insights derived from the model to explore the ecological impacts of physical and biological differences among the marine environments of the three islands.

Material and Methods

Overview

Fieldwork for this study included both sea-based and land-based components. Data obtained at sea (and their role in this study) consisted of bird counts conducted during transects (for determining auklet foraging distributions), vertical plankton tows (for estimating food densities and availability of alternative prey species), and collections of food samples from foraging

Fig. 1. Locator map showing the geographic context of our study. The edge of the continental shelf is indicated by the dotted line.

birds (for determining the species composition of adult diets). Data obtained ashore at colonies included doubly labeled water measurements (for estimating rates of energy utilization) and collections of food regurgitations from adults (for determining the species composition of meals fed to chicks).

We focused on the Kookoolik colony on St. Lawrence Island and the colony near Glory of Russia Cape on St. Matthew Island. Fieldwork was conducted on and around St. Lawrence Island from August 4 to August 11, 1985, and on and around St. Matthew Island from August 14 to August 21, 1985. Various operations were carried out during different portions of these periods, but because of the short overall durations of the two island studies (8 d each), collection of different kinds of data was nearly synoptic (table 1). At both colonies, nests contained chicks during the course of the study.

Supplemental auklet surveys were conducted at sea around St. George Island between July 28 and August 5, 1987. These surveys allowed us to place the results from earlier studies of auklets on that island (Roby and Brink 1986; Roby and Ricklefs 1986) in a context that facilitates comparison with our data from St. Matthew and St. Lawrence Islands.

Field Procedures

Rates of energy utilization were measured in adult least auklets by means of the doubly labeled water method (Lifson and McClintock 1966; Nagy 1983). At both St. Lawrence and St. Matthew Island colonies, adults were captured by stretching mist nets flat over regions of scree under which nests were located. Birds were trapped in the nets as they emerged from the nests to depart for sea or as they attempted to deliver meals to their chicks after

TABLE 1
Durations of different types of data collection, August 1985

Data	Base	St. Lawrence Island Dates	St. Matthew Island Dates
Bird surveys	Sea	8–11	14–21
Plankton tows	Sea	4–10	15–21
Food samples	Sea	8–10	19
Doubly labeled water	Land	6–8	16–18
Regurgitations	Land	6–8	16–19

returning from sea. Captured birds were weighed to the nearest 0.5 g with a Pesola spring balance, banded with U.S. Fish and Wildlife Service aluminum bands, and marked for future recognition with light spots of paint on the tips of the feathers of the upper breast.

Forty birds with chicks were given intrapectoral (muscle) injections of 0.3144 mL doubly labeled water ($^3HH^{18}O$). Isotope enrichments in the injection solution were 0.33 mCi ^3H per milliliter and 97 atom % ^{18}O. Injected birds were held for 1 h in individual cloth bags to allow the injected isotope to equilibrate with the body water. After 1 h, two 70-μL blood samples were taken by puncturing the brachial vein and filling heparinized capillary tubes. The capillary tubes were sealed with Critocaps and stored in a shaded area (4°C) for up to 2 d.

After initial blood samples were taken, birds were released near the point of capture. In all but one case, the injected birds flew immediately out to sea. We checked nets every 30–60 min throughout the day. When an injected bird was found again in the net, it was removed and reweighed, and a second blood sample was taken and processed as above. The bird was again released near the point of capture. In several cases, injected individuals were captured a third time, and a third blood sample was taken.

Adults (injected and noninjected) often regurgitated food loads from their sublingual pouch upon hitting the net. We routinely scraped these regurgitations from the rocks under the nets. In addition, food samples were obtained from auklets collected at sea at locations where large numbers of birds were observed. All food samples were preserved individually in 85% ethanol for later identification.

To determine the foraging distributions of least auklets at sea, we conducted counts from the bridge of the research vessel *Alpha Helix* while the ship was underway on transects radiating from each island. All birds observed on the water within a 300-m arc from directly ahead of the ship to 90° off the beam were counted, and data were entered directly into a handheld microcomputer.

Zooplankton abundance and community structure were determined by conducting vertical tows of a 1-m diameter, 505-μm mesh plankton net when the boat stopped at sampling stations. The net was towed from a position 3–4 m above sea bottom to the surface, with mean tow depths of 32 m (St. Matthew Island) and 29 m (St. Lawrence Island).

Analysis of Samples and Calculations

Blood samples were analyzed in the laboratory of K. A. Nagy at the Laboratory of Biomedical and Environmental Sciences, UCLA. Water was removed from

the blood samples with a vacuum microdistillation technique. Tritium concentration in each water sample was measured in duplicate by adding 10 μL of the distillate to 7 mL of scintillant and counting ^3H activity on a liquid scintillation counter until the coefficient of variation was 0.7%. Oxygen-18 concentrations were measured with the proton activation method (Wood et al. 1975; Nagy 1983) and subsequent counting of ^{18}F with a gamma counter. Oxygen-18 samples were counted in triplicate for each blood sample until coefficients of variation were ≤1.0% for each group of triplicates. Tritium and ^{18}O levels were corrected for background by measuring ^3H activity and the ^{18}O concentration in blood samples taken from six uninjected birds (four from St. Lawrence Island and two from St. Matthew Island). The means of these background values were subtracted from the isotope levels measured in each of the samples from injected birds before proceeding with calculations of CO_2 production.

Total body water volume was determined from the ^{18}O levels in initial blood samples via the isotope dilution space method (Nagy 1983). Rates of CO_2 production were calculated from initial and final isotope levels and water fraction via equation (2) in Roby and Ricklefs (1986). Field metabolic rate was calculated from CO_2 production by assuming an energy equivalent of 26.8 J (mL CO_2)$^{-1}$ (Roby and Ricklefs 1986). For birds that were recaptured twice ($n = 3$), we calculated an overall time-averaged FMR using the data from the two successive measurement intervals.

Because auklets were recaptured opportunistically, the measurement period was not 24 h (St. Lawrence Island, 23.3–32.9 h, $\bar{X} = 28.1$ h; St. Matthew Island, 22.1–30.0 h, $\bar{X} = 26.4$ h). We therefore standardized the observed FMRs to a 24-h period by adjusting for the nocturnal proportion of the measurement period during which auklets were inactive and assumed to have energy expenditures near the basal metabolic rate (BMR). For this adjustment, the mean BMR of least auklets on St. Lawrence and St. Matthew Islands was assumed to be the same as that of auklets breeding on St. George Island, 4.79 kJ h^{-1} (Roby and Ricklefs 1986). At both St. Matthew and St. Lawrence Islands, auklets typically departed between morning civil twilight and sunrise, and they returned for the night between sunset and evening civil twilight (B. S. Obst, R. W. Russell, G. L. Hunt, Jr., Z. A. Eppley, and N. M. Harrison, personal observation). We used values of 7.6 h (St. Matthew Island) and 5.9 h (St. Lawrence Island) as estimates of the duration of nocturnal inactivity. These values represent the length of time from the midpoint between sunset and evening civil twilight to the midpoint between morning civil twilight and sunrise at the respective latitudes of the islands for the dates of the doubly labeled water studies.

Food samples were identified and quantified by microscopic examination in the laboratory. The relative importance of different prey species was assessed by counting the total number of prey items in each food sample and computing the percentage of each prey type represented in each sample. Our identifications were completed prior to the description of *Neocalanus flemingeri,* which is very similar to the better-known *Neocalanus plumchrus* (Miller 1988; Miller and Clemons 1988). Our taxon *N. plumchrus* therefore includes an unknown proportion of *N. flemingeri.*

Statistical Analyses

Bird survey data from the radial transects were reduced by constructing cumulative frequency distributions (CFDs) of the distance of foraging auklets from each island. We used pairwise two-sample Kolmogorov-Smirnov tests (Sokal and Rohlf 1981) to look for differences in the at-sea distribution of foraging birds around the three colonies. The null hypothesis for these tests was that the maximum difference between the CFDs of birds from any two islands was no greater than might be expected by chance alone. In a strict sense, the assumptions underlying this test (or any other statistical test) are not rigorously met because transect observations do not provide random samples of birds. Venrick (1986) conducted Monte Carlo studies and showed that when individuals from a population are not sampled randomly, the resulting distribution of the Kolmogorov-Smirnov statistic is dependent on the spatial heterogeneity of the population. Specifically, Type I error rates increase with increasing spatial heterogeneity. In our study, the potential for Type I error is reduced because we apply the Kolmogorov-Smirnov test to CFDs assembled from multiple radial transects from each island (i.e., determinations of foraging distributions of birds are based on extensive sampling effort in both dimensions of two-dimensional horizontal space). Because we conducted nonorthogonal comparisons among the islands, we employed Bonferroni adjustments of significance levels to protect against Type I error from multiple tests.

Copepod densities around St. Matthew and St. Lawrence Islands were compared by means of a *t*-test. Food samples and regurgitations were analyzed with Mann-Whitney *U*-tests because these data were not normally distributed. The FMR data were analyzed with a parametric ANOVA. Because of the relatively small sample sizes generated by the doubly labeled water study, we chose a significance level of $P = 0.1$ to reject the null hypothesis of homogeneity of mean FMRs among the three islands. We estimated the power of this statistical test by generating 100 samples of normally distributed data with means, variances, and sample sizes as in our study and then count-

ing the number of times (out of 100) that the null hypothesis would be correctly rejected.

Results

Foraging Distributions

Transect effort and mean bird densities around the three colonies are shown in table 2. At-sea distributions of auklets differed strikingly around the three colonies (fig. 2). Median foraging distances determined from transect observations were 4.9 km, 5.0 km, and 56.0 km for birds from St. George, St. Matthew, and St. Lawrence Islands, respectively. Kolmogorov-Smirnov tests showed that the at-sea distributions of foraging birds did not differ between St. George and St. Matthew Islands (D_{max} = 0.078, not significant) but that the distribution around St. Lawrence Island was significantly different from distributions at both St. George Island (D_{max} = 0.825, $P < 0.0001$) and St. Matthew Island (D_{max} = 0.901, $P < 0.0001$).

Food and Plankton Samples

At St. Matthew Island, the copepod *Calanus marshallae* was the most abundant prey item in both food samples from birds collected at sea ($\bar{X}$ = 92.9% ± 5.4% SE, n = 6, range = 66.1%–100.0%) and regurgitations ($\bar{X}$ = 97.7% ± 0.4% SE, n = 31, range = 90.9%–100.0%). The percentage of *C. marshallae* represented did not differ significantly between food samples and regurgitations (U = 86.5, P = 0.79).

   In contrast, *C. marshallae* was absent from food samples from St. Lawrence Island, where *Neocalanus plumchrus* and *Neocalanus cristatus* were im-

TABLE 2

Pelagic survey data used to determine at-sea foraging distributions of least auklets

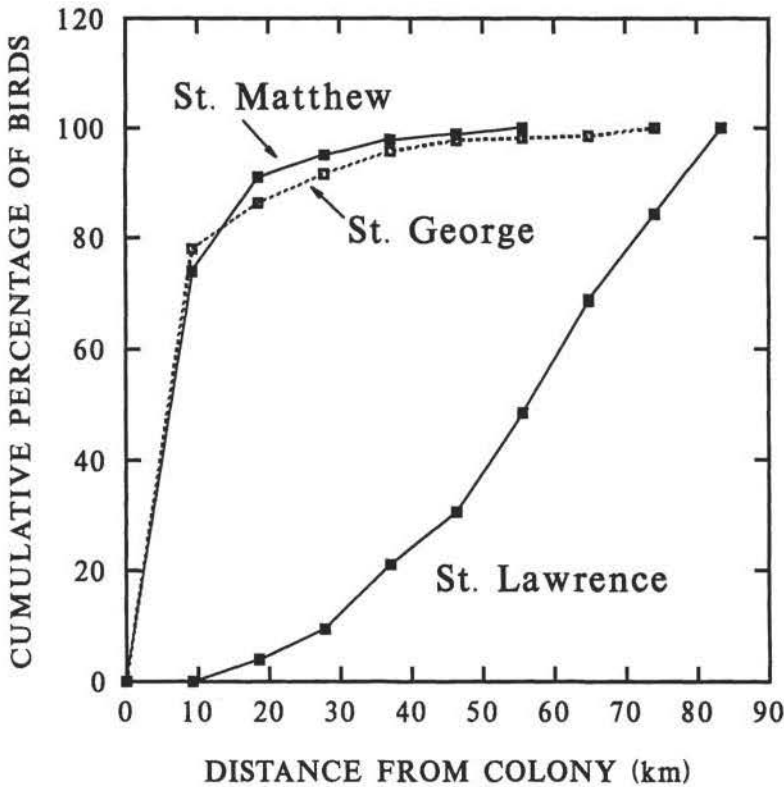| Colony	Year	Transect Effort (km)	Number of Auklets on Water	Mean Auklet Density (Birds km^{-2})
St. George Island	1987	593	495	2.8
St. Matthew Island ...	1985	322	1,508	15.6
St. Lawrence Island ...	1985	250	6,911	92.1

Fig. 2. Comparative distributions of least auklets around three islands in the Bering Sea. The data are presented as cumulative frequency distributions, with cumulative percentage of the total number of auklets observed on the water plotted against distance from each island.

portant prey items. At St. Lawrence, these two species were more predominant in regurgitations ($\bar{X}$ = 88.9% ± 1.4% SE, n = 25, range = 72.9%–98.8%) than in food samples taken from birds at sea ($\bar{X}$ = 32.9% ± 4.8% SE, n = 35, range = 0%–78.9%). This difference was statistically significant (U = 4.50, P < 0.0001). Reasons for this difference are not known with certainty, but the stomach samples generally contained few identifiable prey items, whereas regurgitations contained up to several thousand. Furthermore, because of their small size and high surface-to-volume ratios, copepods are probably subject to more rapid digestion than are any larger prey items that may occasionally be taken, thereby deflating the apparent importance of copepods in food samples obtained from stomachs of birds at sea. In contrast, food loads in sublingual pouches, which were being carried to the chicks, were generally regurgitated intact and did not suffer from this potential source of bias. For these reasons, we feel that the data from regurgitations

reflect the typical composition of auklet diets more accurately and precisely than do the data from stomach samples.

Vertical plankton tows conducted within 10 km of St. Matthew Island indicated that densities of *C. marshallae* averaged 50.9 m^{-3} (± 12.0 SE, n = 12 tows). Offshore St. Lawrence Island, densities of the two larger copepods varied with distance from the island (fig. 3). Patterns in the horizontal distributions of *N. plumchrus* and *N. cristatus* were very similar, with both species peaking in density in a band approximately 30–60 km offshore (fig. 3). Copepod densities in the most important foraging area for St. Lawrence auklets (40–65 km offshore; see fig. 2) averaged 50.6 m^{-3} (*N. plumchrus*) and 2.3 m^{-3} (*N. cristatus*), with a combined mean of 52.9 m^{-3} (± 14.1 SE, n = 9 tows). Comparison of total copepod densities between the auklets' principal foraging grounds off St. Matthew Island (<10 km offshore) and off St. Lawrence Island (40–65 km offshore) indicated that variances were homogeneous (Bartlett's test, X^2 = 0.001, df = 1, P = 0.97) and that the difference in mean density was not significant (t = 0.11, df = 19, P = 0.91).
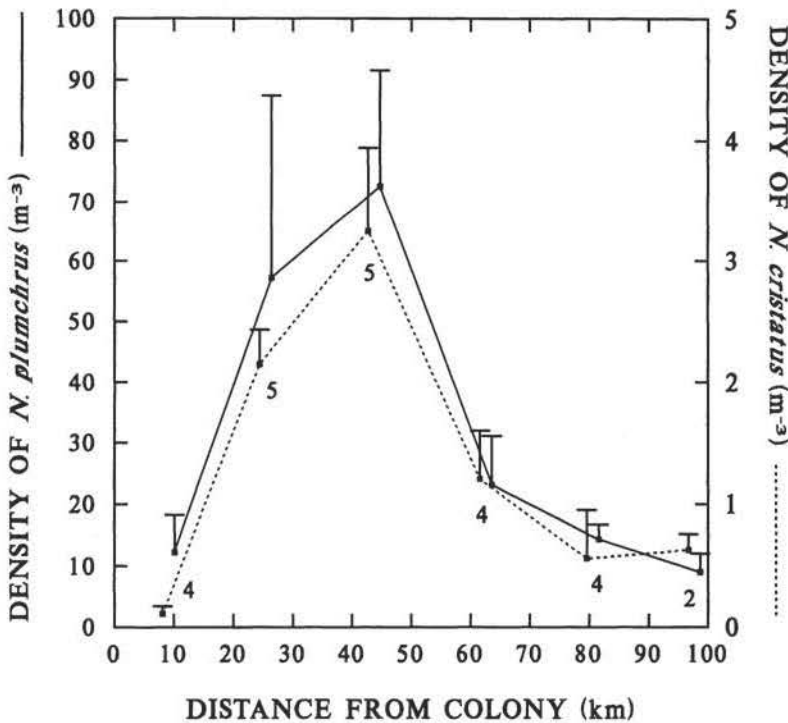

Fig. 3. *Densities of the copepods* Neocalanus plumchrus *and* Neocalanus cristatus *in relation to the distance offshore from the focal colony on St. Lawrence Island. Numbers indicate sample sizes (numbers of vertical net tows), and error bars indicate SEs.*

We measured the sizes of the three principal copepod prey species represented in food samples from least auklets. Mean lengths of *C. marshallae, N. plumchrus,* and *N. cristatus* were 3.9 mm, 4.8 mm, and 9.5 mm ($n = 50$ each), with no overlap.

Field Metabolism

Field metabolic rates of birds from the three colonies are shown in table 3. Variances were homogeneous among the islands (Bartlett's test, $X^2 = 2.2$, df = 2, $P > 0.1$). A parametric ANOVA did not detect a significant difference among birds from the three colonies ($F_{2,31} = 0.25$, $P > 0.75$). However, the power of this test, estimated via simulation, was only 32%. In other words, we had only a 32% chance of rejecting the null hypothesis if it was in fact false, given the sample sizes and variances observed. The difference between mean FMRs from any two islands would have had to exceed approximately 40–50 kJ d^{-1} in order for us to have been able to judge these means to be significantly different using Fisher's least significant difference (LSD) procedure.

Body masses of auklets from the three islands were very similar (table 3). Masses of individual birds typically varied during the interval between initial capture and recapture (table 3), but rates of body mass change did not differ among the three islands (ANOVA, $F_{2,32} = 2.05$, $P > 0.1$). Zero fell within 95% confidence intervals constructed around mean rates of mass change for each island, which suggests that auklets were in a state of energy balance during the course of the study.

Energy Economy of Breeding Auklets

We can use data from this study and information gleaned from the literature to reconstruct time and energy budgets of least auklets rearing chicks at the three island colonies. Birds breeding on all three islands spend most of the day at sea but spend the night inactive at the colony (Bédard 1969; Roby and Brink 1986; B. S. Obst, R. W. Russell, G. L. Hunt, Jr., Z. A. Eppley, and N. M. Harrison, personal observation). We assume that energetic costs during periods of nocturnal inactivity are close to BMR. We neglect possible thermoregulatory costs because there is no information on the microclimate in the nest crevices; however, we suspect that ambient temperature in a crevice may remain within the auklets' thermoneutral zone.

During the day, the birds forage at sea and only return to the colony briefly to drop off chick meals. An auklet's daily time budget is therefore divided principally between nocturnal inactivity, commuting between the colony

Energy metabolism and foraging ecology of least auklets

	St. George Island	St. Matthew Island	St. Lawrence Island
Body mass (g)	83.5	78.8 ± 2.0 (3)	78.6 ± 1.9 (7)
Body mass change (g d^{-1})	+.9 ± .6 (25)	−1.8 ± 1.5 (3)	−1.6 ± 1.8 (7)
Field metabolic rate (kJ d^{-1})	357.9 ± 9.0 (24)	338.0 ± 47.9 (3)	353.5 ± 14.6 (7)
Median foraging radius (km)	4.9	5.0	56.0
Principal prey species	*Neocalanus plumchrus* *Calanus marshallae* *Neocalanus cristatus*	*Calanus marshallae*	*Neocalanus plumchrus* *Neocalanus cristatus*

Note. Values shown are mean ± SE, with sample sizes indicated in parentheses. Physiological data for birds on St. George Island are from Roby and Ricklefs (1986); SEs and sample sizes were not available for body mass. Information on prey species for St. George Island is from Bradstreet (1985) and Roby and Brink (1986).

and foraging sites, resting on the sea surface, and diving for food. We denote these respective time allocations by T_n, T_t, T_r, and T_d (h d^{-1}) and the associated energetic costs by E_n, E_t, E_r, and E_d (kJ h^{-1}). Field metabolic rate can then be expressed as

$$FMR = E_n T_n + E_t T_t + E_r T_r + E_d T_d. \tag{1}$$

As explained earlier, we estimated T_n to be 7.6 h d^{-1} at St. Matthew Island and 5.9 h d^{-1} at St. Lawrence Island during our studies. During the St. George Island study, T_n was 7.8 h d^{-1} (Roby and Brink 1986).

The amount of time spent commuting between the colony and foraging sites is related to flight speed (V; km h^{-1}), foraging radius (R; km trip^{-1}), and the number of daily round-trip commutes (C; trips d^{-1}); thus,

$$T_t = (2 \cdot C \cdot R)/V. \tag{2}$$

We took V and E_t to correspond to the maximum-range speed (V_{mr}) predicted from Pennycuick's (1975, 1989) flight mechanics theory. Both V_{mr} and E_t are dependent on R and C because (1) the length of a commute affects body mass, which in turn affects flight speed and flight cost, and (2) the number of commutes determines the payload mass that must be transported during each return trip, which also affects flight speed and cost (Pennycuick 1975, 1989). We calculated V_{mr} and E_t with the software in Pennycuick (1989). Wingspan, body mass, and payload mass are important determinants of flight performance. The mean wingspan of 15 auklets measured on St. George Island was 0.34 m (Roby and Ricklefs 1986). Mean body masses from the three islands were assumed (table 3). The payload mass transported during each return trip is a function of daily food consumption by chicks and the number of trips undertaken to meet this demand. It is not known whether chick provisioning rates varied among colonies, but we assume here that they did not. Food requirements of auklet chicks on St. George Island averaged 13.9 g per parent per day (Roby and Brink 1986). We assume that the digestion of meals consumed by adult auklets occurs while the birds are at sea. Payload mass is therefore calculated as 13.9 g divided by the number of return trips made by each parent per day. The predicted flight speeds and costs that we calculated using Program 1 in Pennycuick (1989) are shown in table 4.

The remaining information required to reconstruct time and energy budgets concerns the number of round-trip commutes undertaken each day. Data are available from St. George Island, where adult auklets delivered an average of 2.6 chick-meals d^{-1} (Roby and Brink 1986). St. Matthew Island birds were assumed to be similar to St. George Island birds in this regard

TABLE 4

Estimated maximum-range flight speeds and costs for least auklets
as a function of flight leg and the number of commutes
undertaken each day

Colony	Daily Commutes	Flight Leg	V_{mr} (km h^{-1})	E_t (kJ h^{-1})
St. George Island	. . .	Outbound	45.4	33.8
St. George Island	2	Inbound	46.4	38.2
St. George Island	3	Inbound	46.1	36.8
St. Matthew Island	. . .	Outbound	44.6	31.0
St. Matthew Island	2	Inbound	45.7	35.2
St. Matthew Island	3	Inbound	45.4	33.8
St. Lawrence Island . . .	. . .	Outbound	44.5	30.5
St. Lawrence Island . . .	1	Inbound	46.4	38.8
St. Lawrence Island . . .	2	Inbound	45.5	34.7

Note. Measures of flight performance for the outbound leg are independent of the daily number of commutes because birds carry no payload on the outbound leg.

because of the nearly identical foraging distributions of auklets from the two islands (fig. 2). Our analyses indicated that it would be impossible for auklets from St. Lawrence Island to have completed more than two daily foraging trips to the median foraging distance, given the observed energy expenditures (table 3) and the theoretical cost of flight (table 4). Furthermore, it seems unlikely that St. Lawrence Island auklets completed only a single trip per day because the payload that would have had to have been transported (13.9 g) would constitute about 18% of body mass, whereas the maximum capacity of the least auklet's gular pouch is only about 12% of body mass (Bédard 1969). These interpretations are consistent with observed patterns of colony attendance on St. Lawrence Island, which generally suggest that auklets make two foraging trips per day (Bédard 1969; Piatt, Roberts, and Hatch 1990a; Piatt et al. 1990b).

The total at-sea component of the energy budget ($E_r T_r + E_d T_d$) can now be calculated with equations (1) and (2) and the data in tables 3 and 4. Time and energy budgets reconstructed in this way are shown graphically in figure 4, under the assumption that birds from St. Lawrence Island completed two daily foraging trips and birds from the other islands completed three daily trips. Although some birds from St. George and St. Matthew
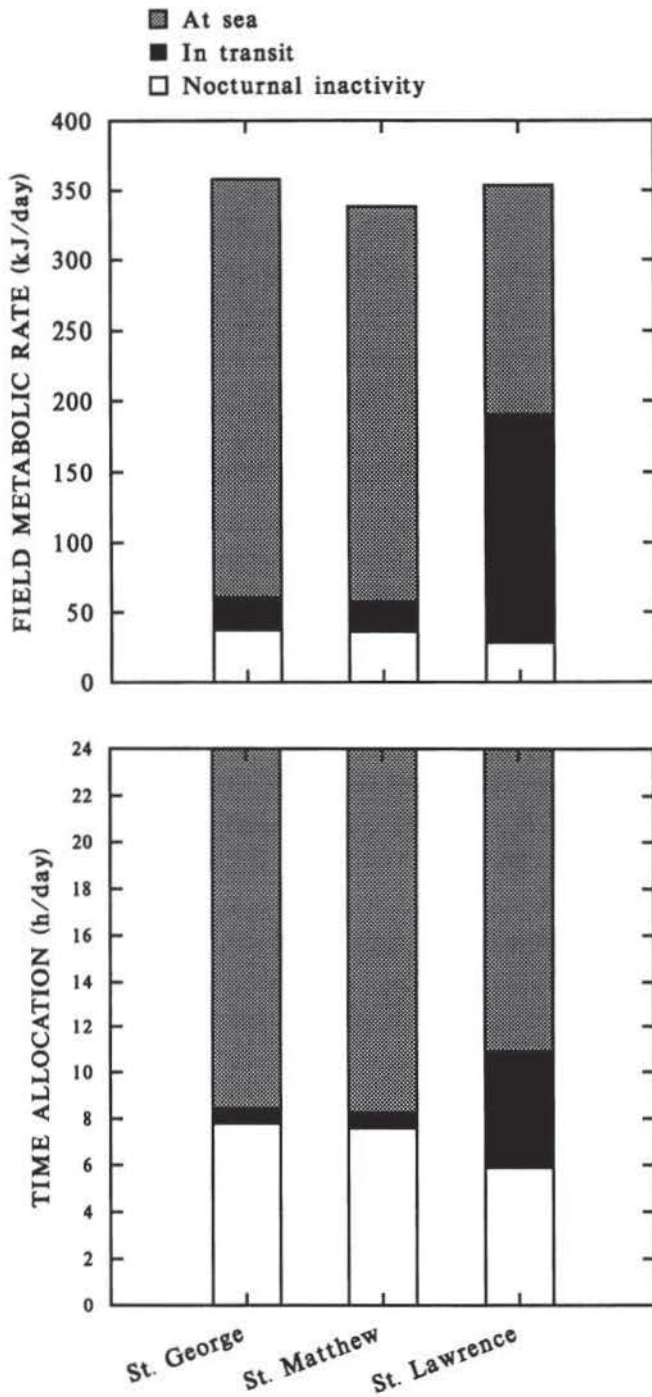
Fig. 4. Reconstructed energy budgets (top) and time budgets (bottom) of least auklets from the three islands studied. Budgets are based on the assumption that birds from St. Lawrence Island make two foraging trips per day and birds from the other islands make three trips per day.

Islands may have made only two trips (since the mean chick-meal delivery rate on St. George Island was 2.6 d^{-1}; Roby and Brink 1986), the reconstructed budgets for these islands are relatively insensitive to the number of trips assumed because of the small flight distances involved.

Finally, it is of interest to assess the foraging performance of auklets on each of the islands. We will characterize foraging performance in terms of the proportion of time at sea spent underwater and the rate of energy intake while underwater. Both of these values are dependent on T_d. To estimate T_d, information on E_r and E_d is required. Unfortunately, no information is available on these energetic costs in small alcids. In a laboratory study of larger alcids (murres, *Uria* spp., body mass ca. 1 kg), absorptive resting metabolic rates on water in the thermoneutral zone exceeded BMRs by about 50% (Croll and McLaren 1993). Water temperatures in our study areas were below the lower critical temperature for the much smaller least auklets (10°–15°C; Roby and Ricklefs 1986), so thermoregulatory contributions to E_r were probably significant. We assumed a value of 2 × BMR for E_r.

The cost of underwater locomotion is also poorly understood. Laboratory studies of penguins (Butler and Woakes 1984; Baudinette and Gill 1985; Culik and Wilson 1991; Kooyman et al. 1992), murres (Croll and McLaren 1993), and ducks (Woakes and Butler 1983; Stephenson 1994) have yielded widely varying measurements in the range 1–5 × BMR. In contrast, field studies of free-living penguins have suggested higher figures (5–10 × BMR) that seem generally comparable to the cost of flapping flight (Nagy, Siegfried, and Wilson 1984; Gales and Green 1990; Chappell et al. 1993). Because of the wide disparity among results from these different studies, we did not attempt to estimate E_d and instead performed a sensitivity analysis to examine the dependence of estimated measures of foraging performance on the value of E_d assumed. After substituting $T_r = 24 - T_n - T_t - T_d$ into equation (1) and then rearranging, we have

$$T_d = [\text{FMR} - E_n T_n - E_t T_t - E_r(24 - T_n - T_t)]/(E_d - E_r). \qquad (3)$$

Recalling our assumptions about the values of E_n (= BMR), E_r (= 2 × BMR), E_t (table 4), and time budgets (fig. 4), we can solve equation (3) for a range of hypothetical values of E_d. The dependence of T_d on the assumed value of E_d is shown in figure 5 (top), where T_d is expressed as the proportion of nontransit sea time spent underwater (i.e., $T_d/[T_r + T_d]$).

To estimate the rate of energy intake realized by auklets while underwater, we need an energy balance equation. Meals fed to chicks at the St. George Island colony were made up of 78.6% water, 9.6% fat, 7.2% protein, and 1.3% carbohydrate (Roby and Ricklefs 1986). These materials yield 0, 39.8,
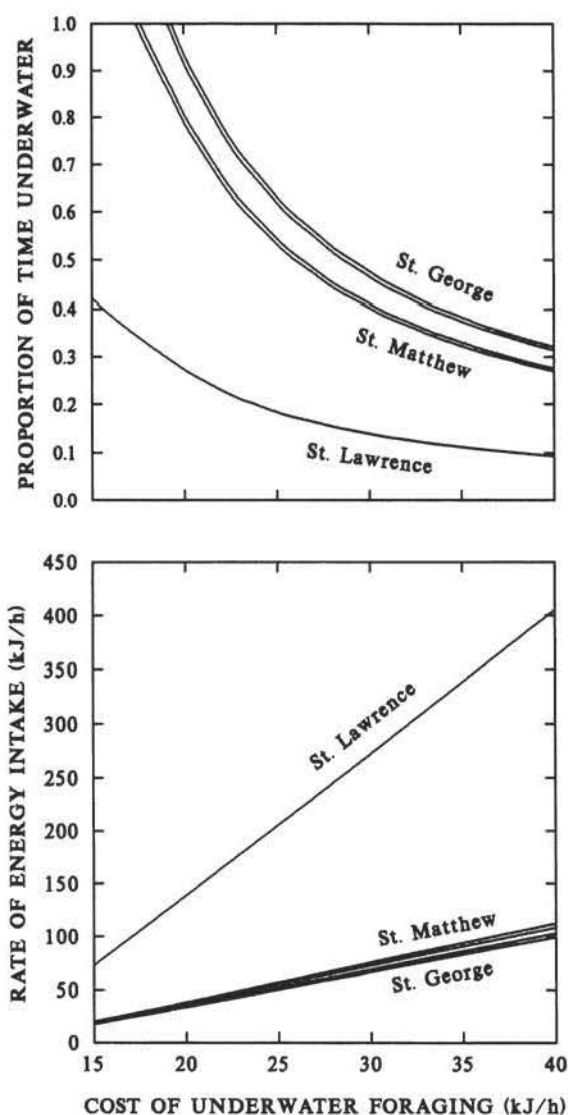
Fig. 5. Sensitivity analyses showing the dependence of measures of forag-
ing performance on the cost of underwater locomotion assumed in the
model. The top figure shows the proportion of nonflight time spent diving,
and the bottom figure shows the average gross rate of energy intake while
underwater. Analyses are shown for St. Lawrence Island birds undertak-
ing two foraging trips daily. Analyses for St. Matthew and St. George Is-
lands are shown separately for two and three daily foraging trips. (In the
top panel, upper curves indicate results for two trips and lower curves
indicate results for three trips; in the lower panel, upper curves indicate
results for three trips and lower curves indicate results for two trips.)

18.8, and 16.7 kJ g^{-1}, respectively, so auklet meals have an overall energy density of 5.39 kJ g^{-1}. As chicks consume 13.9 g per parent per day (Roby and Brink 1986), the energy equivalent of an auklet chick's food require-ments is calculated to be 74.9 kJ d^{-1} per parent. Of the total amount of energy in auklet meals, 83.8% is metabolizable (Roby and Ricklefs 1986). An energy balance equation for an adult auklet during the chick-rearing period is therefore given by

$$Y_d T_d = (FMR/.838) + 74.9, \tag{4}$$

where Y_d denotes the gross rate of energy acquisition while actively diving for food (kJ h^{-1}). In equation (4), the expression on the left represents daily gross energy acquisition, and the expression on the right represents daily gross energy demands. We assume that these two values are equal because our data did not indicate any significant trends in body mass change. Further support for the assumption of energy balance is provided in a recent study by Jones (1994), who found that breeding least auklets undergo an abrupt, programmed loss of mass at the time when the chicks hatch but that body mass then remains stable during the chick-rearing period.

Rates of energy intake while underwater can now be calculated for auklets foraging around each of the three colonies by means of equation (4), the FMR data (table 3), and the estimates of T_d obtained from equation (3). Estimates of Y_d were highly sensitive to the cost of underwater locomotion assumed (fig. 5, bottom). However, this analysis suggests that rate of energy intake by St. Lawrence Island birds was approximately four times the rate realized by birds from the other two islands *regardless of the actual cost of underwater locomotion* (fig. 5, bottom).

Discussion

Despite a greater than 10-fold difference in mean foraging radius, mean energy expenditures differed by less than 6% among auklets from the three colonies. It should be noted, however, that although a statistical test did not indicate a significant difference, the Type II error rate was high because of our small sample sizes. A simulation showed that even if the null hy-pothesis was false, we would fail to reject it 68% of the time, given our sample sizes and variances. Nevertheless, we would argue that the observed differences were ecologically unimportant, even if we had been able to declare them statistically significant. If total energy expenditures were di-rectly related to the proportion of time allocated to energetically costly

flight, as might be expected, then FMRs of auklets from St. Lawrence Island should have been much higher than those of birds from the other two islands. This was not the case, and, in fact, mean FMR tended to be highest in auklets breeding on St. George Island, where the birds foraged just offshore. Despite their much greater allocation of time to energetically costly commuting flight, mean daily energy expenditures of St. Lawrence Island auklets were actually lower than those of St. George Island birds, and only 5% higher than those of St. Matthew Island birds. These results suggest that even in heavily wing-loaded seabirds such as auklets, long-distance commuting between colony and feeding areas need not significantly change total adult energy expenditures.

Although we did not study the compensatory mechanism directly, our model indicates that the added cost of commuting for auklets from St. Lawrence Island was probably offset by a reduction in total underwater foraging costs resulting from greater foraging efficiency. The difference between estimated rates of energy intake by auklets from St. Lawrence Island and auklets from the other islands was approximately fourfold. What factors might have been responsible for such a large difference in foraging efficiency?

Differences in rates of energy intake while underwater could be due to differences in prey abundance, the energy content of prey, and/or the distribution of prey in the water column. Our plankton studies did not indicate a significant difference in overall prey abundance between St. Matthew and St. Lawrence Islands, so this explanation seems unlikely. However, the taxonomic composition of the copepod fauna differed radically between the islands. Large, energy-rich *Neocalanus* copepods were absent from the middle shelf domain waters near St. Matthew Island. Collections at sea and regurgitations from netted birds showed that the dominant prey of St. Matthew Island auklets was *C. marshallae,* which, at about 4 mm, is smaller than the typical prey of auklets from St. Lawrence Island (Harrison 1987; Hunt et al. 1990). The difference in energy content between *C. marshallae* and *Neocalanus* spp. is even greater than suggested by the differences in length because the former species is a slighter copepod that stores less lipid (S. Smith, personal communication in Hunt and Harrison [1990]). Thus, although the numerical density of copepods did not differ significantly between the islands, differences in the energy content of individual prey items almost certainly resulted in differences in overall energy density in the water column. Higher rates of energy intake by St. Lawrence Island auklets therefore probably resulted partly from their ability to exploit more energy-rich prey.

Although mean copepod densities did not differ between the auklets' foraging areas around St. Lawrence and St. Matthew Islands, the availability

of a food resource to a consumer depends on both the absolute abundance of the food in the environment and its accessibility. Food accessibility can be defined as the relative difficulty of reaching a food item (Moermond 1990), and it is very likely that differences between the marine environments of the different islands have important impacts on food accessibility.

At about 80 g, least auklets have an estimated maximum diving depth of 15 m (calculated with the regression equation for alcids in Burger [1991]). The depth-averaged levels of copepod density reported here are based on net tows conducted from a depth of about 30 m, so only about half of the water column sampled by our plankton nets was accessible to the auklets. Although vertical heterogeneity in prey density was not quantified by our plankton tows, previous studies in the region demonstrated an important source of such heterogeneity. North of St. Lawrence Island, the Anadyr current forms a bottom layer, intruding eastward under Bering Shelf water. Density differences between these two water masses are large, and a strong, stable, and shallow pycnocline is often present offshore. Least auklets from St. Lawrence Island did not feed near shore, where waters were vertically mixed, but were instead consistently concentrated over the stably stratified water offshore (Hunt et. al 1990). Copepods and other zooplankton are known to accumulate at interfaces between water layers (Harder 1968; Barroclough, Lebrasseur, and Kennedy 1969), and Hunt et al. (1990; see their figs. 6, 7, 9, 12, 15) presented acoustic evidence of dense plankton layers at and above the pycnocline (ca. 10–15 m depth) off St. Lawrence Island. They hypothesized that auklets preferentially foraged over the offshore, stratified water because prey availability was enhanced there. Foraging over a shallow, stable pycnocline should result in higher food accessibility and lower search and pursuit costs because (1) the presence of near-surface food layers is spatially predictable, (2) diving depth required to reach these shallow food layers is reduced, and (3) prey is concentrated in these layers (i.e., the mean distance between prey items is smaller).

In contrast to St. Lawrence Island, St. Matthew Island is located in the middle domain of the Bering Sea Shelf (Springer and Roseneau 1985). The only area where we encountered large numbers of foraging auklets was in Sarichef Strait off the northwest end of the island, where copepods may have been concentrated to some extent by a tidal rip over a shallow sill. We found no evidence of auklets foraging over the near-surface scattering layers offshore St. Matthew Island, which were dominated by jellyfish (K. O. Coyle et al., unpublished data). We therefore conclude that differences in both the energy density of prey and the accessibility of prey in the waters surrounding St. Lawrence and St. Matthew Islands are likely sources of variation in the foraging efficiency of least auklets.

Although our assumptions and predictions seem plausible in light of available information, several caveats should be noted. First, we have assumed that when departing from their colonies, auklets follow straight flight paths to foraging sites and that after arriving at these sites, the birds do not again engage in flight until the return trip is initiated, when they return directly to the colony. However, the pelagic distributions of auklets show intriguing patterns of spatial autocorrelation across a wide range of scales, which may derive from multiscale searching behavior at sea (Russell et al. 1992). If auklets employ such multiscale foraging strategies, then our estimates of time and energy allocations to flight are probably conservatively biased. Second, we used a theoretical model (Pennycuick 1975, 1989) to estimate flight speeds and costs. If the theory is wrong, or if auklets fly at speeds other than V_{mr} during the chick-rearing period (cf. Norberg 1981; McLaughlin and Montgomerie 1985), then our calculations are obviously inaccurate. Third, we had no information on the energetic cost of resting on the water, and we assumed that this cost was 2 × BMR on the basis of studies of other, larger species. Finally, we assumed that the amount of food delivered to chicks did not vary among islands. Recent studies of other alcid species lend some support to this assumption. In particular, Burger and Piatt (1990) found that rates at which common murres fed their chicks did not vary significantly among years, even though the abundance of capelin (the murres' principal prey) varied up to 10-fold within and between years.

The similarity of mean energy expenditures among least auklets in such diverse ecological situations is striking and raises the question of whether observed FMRs were at or near some biologically important benchmark level. Drent and Daan (1980) postulated the existence of a "general energetic upper level for sustained work" of 4.0 × BMR in parent birds feeding their young. Peterson, Nagy, and Diamond (1990) termed the ratio of sustained FMR to BMR "sustained metabolic scope." Compilations of published data on breeding seabirds have shown that although sustained metabolic scope does indeed tend to cluster around 3 or 4, it nevertheless varies considerably (1.6–6.6) among different species (Birt-Friesen et al. 1989; Mehlum, Gabrielsen, and Nagy 1993). Although the 4.0 × BMR hypothesis can now be rejected as a general rule (Peterson et al. 1990; Koteja 1991), few workers have considered the alternative possibility that breeding birds may have a species-specific preferred level of energy expenditure that is relatively invariant, even across an array of widely varying environments (but see Montevecchi, Birt-Friesen, and Cairns 1992).

In least auklets, the mean sustained metabolic scope of birds breeding on different islands in the Bering Sea showed little variation, ranging from 2.94 on St. Matthew Island to 3.11 on St. George Island. Despite this ho-

mogeneity of mean daily energetic expenditures, allocations to various compartments of time and energy budgets (e.g., commuting vs. foraging) appeared to be highly flexible and responsive to variation in the marine environment. These observations suggest that least auklets may have a pre-ferred level of daily energy expenditure of about $3 \times$ BMR, although the high levels of variation in FMR indicate that this level is below any upper ceiling on FMR that may exist for the species.

Conclusions concerning the existence of a characteristic species-specific preferred level of energy expenditure will have to await a more robust field sampling program. Our FMR sample sizes were very low, as is often the case in doubly labeled water studies. Furthermore, logistical constraints prohibited at-sea observations of the behavior of the specific birds for which FMR was measured, and some of our conclusions are necessarily contingent upon the assumption that the study birds employed "typical" auklet behavior (i.e., that they foraged at the midpoint of the distribution of birds away from the colony). It is important to stress that while mean FMRs showed re-markably little variation *among* colonies, measured FMRs were quite variable *within* colonies, which suggests that our assumptions concerning typical auklet behavior were probably oversimplified. Obtaining simultaneous FMR measurements and activity budgets for individual seabirds remains a difficult challenge for the future—although not an insurmountable one, in light of the recent successes with satellite telemetry (Weimerskirch et al. 1993; Jou-ventin et al. 1994).

Our findings indicate that interpretation of the energetic ecology of sea-birds can benefit significantly from information regarding foraging distri-butions, diet, and prey availability. However, because investment in chicks is a potential energy "sink" that was not accounted for in our studies, we are unable to assess the selective impact of intercolony variation in foraging radius. The effects of variable commute distances on chick provisioning rates and other aspects of auklet reproductive performance such as growth rates and fledging success are presently unknown and should be explored in future studies.

Acknowledgments

Literature Cited

ANDERSON, D. J., and R. E. RICKLEFS. 1987. Radio-tracking masked and blue-footed boobies (*Sula* sp.) in the Galapagos Islands. Natl. Geogr. Res. 3:152–163.

ANDERSSON, M. 1978. Optimal foraging area: size and allocation of search effort. Theor. Popul. Biol. 13:397–409.

BARROCLOUGH, W. E., R. J. LEBRASSEUR, and O. D. KENNEDY. 1969. Shallow scattering layer in the subarctic Pacific Ocean: detection by high-frequency echo sounder. Science 166:611–613.

BAUDINETTE, R. V., and P. GILL. 1985. The energetics of "flying" and "paddling" in water: locomotion in penguins and ducks. J. Comp. Physiol. 155B:373–380.

BÉDARD, J. 1969. Feeding of the least, crested, and parakeet auklets on St. Lawrence Island, Alaska. Can. J. Zool. 47:1025–1050.

BIRT-FRIESEN, V. L., W. A. MONTEVECCHI, D. K. CAIRNS, and S. A. MACKO. 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. Ecology 70:357–367.

BRADSTREET, M. S. W. 1985. Feeding studies. Pages 257–306 in S. R. JOHNSON, ed. Population estimation, productivity, and food habits of nesting seabirds at Cape Peirce and the Pribilof Islands, Bering Sea, Alaska. Report by LGL Ecological Research Associates to Minerals Management Service, Anchorage, Alaska.

BROWN, R. G. B. 1976. The foraging range of breeding dovekies, *Alle alle*. Can. Field-Nat. 90:166–168.

BURGER, A. E. 1991. Maximum diving depths and underwater foraging in alcids and penguins. Pages 9–15 in W. A. MONTEVECCHI and A. J. GASTON, eds. Studies of high-latitude seabirds. I. Behavioural, energetic, and oceanographic aspects of seabird feeding ecology. Occasional paper 68. Canadian Wildlife Service.

BURGER, A. E., and J. F. PIATT. 1990. Flexible time budgets in breeding common murres: buffers against variable prey abundance. Stud. Avian Biol. 14:71–83.

BUTLER, P. J., and A. J. WOAKES. 1984. Heart rate and aerobic metabolism in Humboldt penguins, *Spheniscus humboldti,* during voluntary dives. J. Exp. Biol. 108:419–428.

CHAPPELL, M. A., V. H. SHOEMAKER, D. N. JANES, S. K. MALONEY, and T. L. BUCHER. 1993. Energetics of foraging in breeding Adélie penguins. Ecology 74:2450–2461.

CROLL, D. A., and E. MCLAREN. 1993. Diving metabolism and thermoregulation in common and thick-billed murres. J. Comp. Physiol. 163B:160–166.

CULIK, B., and R. P. WILSON. 1991. Energetics of under-water swimming in Adélie penguins (*Pygoscelis adeliae*). J. Comp. Physiol. 161B:285–291.

DRENT, R. H., and S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

FASOLA, M., and G. BOGLIANI. 1990. Foraging ranges of an assemblage of Mediterranean seabirds. Colonial Waterbirds 13:72–74.

FLINT, E. N. 1991. Time and energy limits to the foraging radius of sooty terns *Sterna fuscata*. Ibis 133:43–46.

GALES, R., and B. GREEN. 1990. The annual energetics cycle of little penguins (*Eudyptula minor*). Ecology 71:2297–2312.

HARDER, W. 1968. Reactions of plankton organisms to water stratification. Limnol. Oceanogr. 13:156–168.

HARRISON, N. M. 1987. Foraging behavior and coexistence of seabirds in the Bering Sea. Ph.D. diss. University of California, Irvine. 82 pp.

HUNT, G. L., and N. M. HARRISON. 1990. Foraging habitat and prey taken by least auklets at King Island, Alaska. Mar. Ecol. Prog. Ser. 65:141–150.

HUNT, G. L., N. M. HARRISON, and R. T. COONEY. 1990. The influence of hydrographic structure and prey abundance on foraging of least auklets. Stud. Avian Biol. 14:7–22.

HUNT, G. L., B. MAYER, W. RODSTROM, and R. SQUIBB. 1978. Reproductive ecology, foods, and foraging areas of seabirds nesting on the Pribilof Islands. Pages 570–775 in Environmental assessment of the Alaskan continental shelf. Annual reports of principal investigators. Vol. 1. National Oceanic and Atmospheric Administration, Outer Continental Shelf Environmental Assessment Program, Boulder, Colo.

JONES, I. L. 1994. Mass changes of least auklets *Aethia pusilla* during the breeding season: evidence for programmed loss of mass. J. Anim. Ecol. 63:71–78.

JOUVENTIN, P., D. CAPDEVILLE, F. CUENOT-CHAILLET, and C. BOITEAU. 1994. Exploitation of pelagic resources by a non-flying seabird: satellite tracking of the king penguin throughout the breeding cycle. Mar. Ecol. Prog. Ser. 106:11–19.

KOOYMAN, G. L., Y. CHEREL, Y. LE MAHO, J. P. CROXALL, P. H. THORSON, V. RIDOUX, and C. A. KOOYMAN. 1992. Diving behavior and energetics during foraging cycles in king penguins. Ecol. Monogr. 62:143–163.

KOTEJA, P. 1991. On the relation between basal and field metabolic rates in birds and mammals. Funct. Ecol. 5:56–64.

KULETZ, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots. M.S. thesis. University of California, Irvine. 79 pp.

LIFSON, N., and R. McCLINTOCK. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. J. Theor. Biol. 12:46–74.

McLAUGHLIN, R. L., and R. D. MONTGOMERIE. 1985. Flight speeds of central place foragers: female Lapland longspurs feeding nestlings. Anim. Behav. 33:810–816.

MEHLUM, F., G. W. GABRIELSEN, and K. A. NAGY. 1993. Energy expenditure by black guillemots (*Cepphus grylle*) during chick-rearing. Colonial Waterbirds 16:45–52.

MILLER, C. B. 1988. *Neocalanus flemingeri,* a new species of Colanidae (Copepoda: Calanoida) from the subarctic Pacific Ocean, with a comparative redescription of *Neocalanus plumchrus* Marukowa. Prog. Oceanogr. 20:223–273.

MILLER, C. B., and M. J. CLEMONS. 1988. Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. Prog. Oceanogr. 20:293–313.

MOERMOND, T. C. 1990. Foraging behaviour: the influence of food accessibility on food choice and habitat selection. Pages 341–344 in R. VAN DEN ELZEN, K.-L. SCHUCHMANN, and K. SCHMIDT-KOENIG, eds. Proceedings of the international centennial meeting of the Deutsche Ornithologen-Gesellschaft, Current Topics in Avian Biology. Deutschen Ornithologen-Gesellschaft, Bonn.

MONTEVECCHI, W. A., V. L. BIRT-FRIESEN, and D. K. CAIRNS. 1992. Reproductive energetics and prey harvest of Leach's storm-petrels in the northwest Atlantic. Ecology 73:823–832.

NAGY, K. A. 1983. The doubly labeled water ($^3HH^{18}O$) method: a guide to its use. Publication 12-1417. University of California, Los Angeles.

NAGY, K. A., W. R. SIEGFRIED, and R. P. WILSON. 1984. Energy utilization by free-ranging jackass penguins, *Spheniscus demersus.* Ecology 65:1648–1655.

NORBERG, R. A. 1981. Optimal flight speed in birds when feeding young. J. Anim. Ecol. 50:473–477.

PENNYCUICK, C. J. 1975. Mechanics of flight. Pages 1–75 in D. S. FARNER and J. R. KING, eds. Avian biology. Vol. 5. Academic Press, New York.

———. 1987. Flight of seabirds. Pages 43–62 in J. P. CROXALL, ed. Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge.

———. 1989. Bird flight performance: a practical calculation manual. Oxford University Press, Oxford. 153 pp.

PENNYCUICK, C. J., J. P. CROXALL, and P. A. PRINCE. 1984. Scaling of foraging radius and growth rate in petrels and albatrosses (Procellariiformes). Ornis Scand. 15: 145–154.

PETERSON, C. C., K. A. NAGY, and J. DIAMOND. 1990. Sustained metabolic scope. Proc. Natl. Acad. Sci. USA 87:2324–2328.

PIATT, J. F., B. D. ROBERTS, and S. A. HATCH. 1990a. Colony attendance and population monitoring of least and crested auklets on St. Lawrence Island, Alaska. Condor 92:97–106.

PIATT, J. F., B. D. ROBERTS, W. W. LIDSTER, J. L. WELLS, and S. A. HATCH. 1990b. Effects of human disturbance on breeding least and crested auklets at St. Lawrence Island, Alaska. Auk 107:342–350.

ROBY, D. D., and K. L. BRINK. 1986. Breeding biology of least auklets on the Pribilof Islands, Alaska. Condor 88:336–346.

ROBY, D. D., and R. E. RICKLEFS. 1986. Energy expenditure in adult least auklets and diving petrels during the chick-rearing period. Physiol. Zool. 59:661–678.

RUSSELL, R. W., G. L. HUNT, K. O. COYLE, and R. T. COONEY. 1992. Foraging in a fractal environment: spatial patterns in a marine predator-prey system. Landscape Ecol. 7:195–209.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. 2d ed. Freeman, New York. 859 pp.

SPRINGER, A. M., and D. G. ROSENEAU. 1985. Copepod-based food webs: auklets and oceanography in the Bering Sea. Mar. Ecol. Prog. Ser. 21:229–237.

STEPHENSON, R. 1994. Diving energetics in lesser scaup (*Aythya affinis,* Eyton). J. Exp. Biol. 190:155–178.

VENRICK, E. L. 1986. The Smirnov statistic: an incorrect test for vertical distribution patterns. Deep-Sea Res. 33:1275–1277.

WANLESS, S., M. P. HARRIS, and J. A. MORRIS. 1990. A comparison of feeding areas used by individual common murres (*Uria aalge*), razorbills (*Alca torda*) and an Atlantic puffin (*Fratercula arctica*) during the breeding season. Colonial Waterbirds 13:16–24.

———. 1991. Foraging range and feeding locations of shags *Phalacrocorax aristotelis* during chick rearing. Ibis 133:30–36.

WEIMERSKIRCH, H., J. A. BARTLE, P. JOUVENTIN, and J. C. STAHL. 1988. Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. Condor 90:214–219.

WEIMERSKIRCH, H., M. SALAMOLARD, F. SARRAZIN, and P. JOUVENTIN. 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. Auk 110:325–342.

WILSON, R. P., K. A. NAGY, and B. S. OBST. 1989. Foraging ranges of penguins. Polar Rec. 25:303–307.

WOAKES, A. J., and P. J. BUTLER. 1983. Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. J. Exp. Biol. 107:311–329.

WOOD, R. A., K. A. NAGY, N. S. MACDONALD, S. T. WAKAKUWA, R. J. BECKMAN, and H. KAAZ. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. Anal. Chem. 47:646–650.