Variation in Energy Expenditure among Black-Legged Kittiwakes: Effects of Activity-Specific Metabolic Rates and Activity Budgets

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ABSTRACT

We sought to determine the effect of variation in time-activity budgets (TABs) and foraging behavior on energy expenditure rates of parent black-legged kittiwakes (*Rissa tridactyla*). We quantified TABs using direct observations of radio-tagged adults and simultaneously measured field metabolic rates (FMR) of these same individuals ($n = 20$) using the doubly labeled water technique. Estimated metabolic rates of kittiwakes attending their brood at the nest or loafing near the colony were similar (ca. 1.3 × basal metabolic rate [BMR]), although loafing during foraging trips was more costly (2.9 × BMR). Metabolic rates during commuting flight (7.3 × BMR) and prey-searching flight (6.2 × BMR) were similar, while metabolic rates during plunge diving were much higher (ca. 47 × BMR). The proportion of the measurement interval spent foraging had a positive effect on FMR ($R^2 = 0.68$), while the combined proportion of time engaged in nest attendance and loafing near the colony had a negative effect on FMR ($R^2 = 0.72$). Thus, more than two-thirds of the variation in kittiwake FMR could be explained by the allocation of time among various activities. The high energetic cost of plunge diving relative to straight flight and searching flight suggests that kittiwakes can optimize their foraging strategy under conditions of low food availability by commuting long distances to feed in areas where gross foraging efficiency is high.

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Introduction

Identification of the ecological factors that affect energy expenditure rates has been a primary concern of avian energetics research (Bryant and Tatner 1991; Bryant 1997). Progress in understanding how ecology influences the allocation of energy to various competing functions (i.e., survival, growth, storage, reproduction) has been hampered, however, by substantial interindividual variation in energy expenditure rates (Ricklefs and Williams 1984; Bryant and Tatner 1991). The magnitude of this interindividual variation ("noise") often overrides any effect of ecological factors ("signal"), and most of the interindividual variation in energy expenditure rates has eluded explanation.

Seabirds have figured prominently in studies of ecological energetics because of the stringent energetic constraints imposed by the geographic separation of breeding and foraging areas (Lack 1968; Ricklefs 1983). Energy expenditure rates in seabirds are responsive to a variety of extrinsic factors such as oceanic regime (Birt-Friesen et al. 1989), weather conditions (Jouventin and Weimerskirch 1990; Furness and Bryant 1996), brood size (Fyhn et al. 2001), and food availability (Jodice et al. 2002). Field metabolic rates (FMRs) may also vary as a result of individual differences in foraging strategy or reproductive effort (Irons 1993; Golet et al. 2000). But studies of seabird energetics have not avoided the difficulty of substantial unexplained variation in energy expenditure rates among individuals, even within a species and during a particular stage of the annual cycle (Ellis and Gabrielsen 2001). Partitioning this variation into the portion that is relevant to avian life histories, as opposed to that which reflects individual differences in metabolic intensity or efficiency (Ellis 1984), remains a challenge.

Regardless of the underlying causes of individual differences in energy expenditure rates, the large differences in activity-specific metabolic rates (e.g., nest attendance vs. flight) should make energy expenditure rates sensitive to variation in how seabirds allocate time to various activities (i.e., time-activity budgets [TABs]). In seabirds, energy expenditure rates during

incubation have been reported to be as low as 0.8 to 2 × basal metabolic rate (BMR; Grant and Whittow 1983; Grant 1984; Obst et al. 1987), while rates during flight may be as high as 14 × BMR (Birt-Friesen et al. 1989). Metabolic costs of more intensive foraging modes in seabirds, such as plunge diving, have not yet been directly measured but are likely to exceed the costs of flight. For example, the short, dynamic flights used by some passerines while foraging may elevate energy expenditure to at least 20 × BMR (Tatner and Bryant 1986; Bautista et. al. 1998; Nudds and Bryant 2000). On the basis of these estimates, it is likely that FMRs of seabirds can vary substantially with the proportion of time engaged in these different activities.

Understanding the relationship between the allocation of time to various activities and energy expenditure rates has been constrained by the difficulty of simultaneously recording detailed TABs in free-ranging birds and measuring their metabolic rates. This has presented a special challenge in seabirds, which may cover substantial distances during a single foraging trip. Estimates of activity-specific metabolic rates in free-ranging seabirds have typically been restricted to estimates of metabolic rate during nest attendance or, by subtraction, during foraging trips away from the nest (Ellis and Gabrielsen 2001). Estimates of metabolic rate during flight have been derived from doubly labeled water (DLW) studies that have simultaneously deployed time-activity recorders (Birt-Friesen et al. 1989) or have simply recorded time away from the nest and assumed that birds did not alight during that time (a reasonable assumption for marine species that cannot alight on water, such as sooty terns [*Sterna fuscata*]; Flint and Nagy 1984). Although time-activity recorders may allow for quantification of inactive time during foraging trips, this technique does not allow for the identification of the proportion of time spent in different types of flight or foraging activities; therefore, the effect of various foraging activities on energy expenditure cannot be determined.

Our goal was to relate variation in field metabolic rates of free-ranging seabirds to variation in their TABs. We used the DLW technique to measure FMRs of parent black-legged kittiwakes (*Rissa tridactyla*) and simultaneously recorded detailed TABs for these same individuals. Previous studies of energy expenditure rates in free-ranging seabirds in general and kittiwakes in particular have demonstrated that variation in FMRs among individuals within a population can be substantial (Gabrielsen et al. 1987; Obst and Nagy 1992; Golet et al. 2000; Nagy et al. 2001). We hypothesized that among-individual variation in energy expenditure rates of seabirds is primarily a reflection of differences in TABs (as opposed to individual differences in activity-specific metabolic costs) and can be predicted largely on the basis of differences in TABs.

Our first objective was to quantify metabolic costs across the range of seabird activities (i.e., nest attendance, loafing, various flight modes, various foraging activities). We predicted that nest attendance and loafing would incur similar costs, which would

be far lower than those required for flight. We also predicted that foraging activities would incur a higher metabolic cost than straight flight because the former requires a significant degree of maneuvering, changes in airspeed and altitude, as well as lift off from the water surface.

Our second objective was to determine the extent to which variation in FMRs was accounted for by differences in TABs and by attributes of foraging trips at sea (e.g., prey type, duration of the foraging trip, maximum distance from the colony attained during the foraging trip). We predicted that the proportion of time allocated to foraging would account for a substantial proportion of the variation in FMR because most activities that require a high rate of energy expenditure (i.e., flight-based activities) occur during foraging trips and because the duration and intensity of foraging trips can vary substantially among individual kittiwakes (Suryan and Irons 2000).

Material and Methods

Focal Species and Study Sites

Black-legged kittiwakes are small gulls (Laridae) that nest colonially on sea cliffs throughout much of the circumpolar north. Kittiwakes are monogamous, and both sexes participate in incubation and brood rearing. In Alaska, kittiwakes tend to lay one- or two-egg clutches. Foraging usually involves back-and-forth flight when searching for prey ("searching flight") and plunge diving when attempting to capture prey. Less frequently, kittiwakes may feed on the surface of the water or kleptoparasitize other seabirds. Major prey in this part of the species' range include pelagic schooling fishes such as Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), and, to a lesser extent, juvenile gadids (Gadidae), euphausiids (e.g., *Thysanoessa* spp.), and other planktonic crustacea. Kittiwakes from this population also forage on offal and discards from fish processors (Roby et al. 2000). Kittiwakes are sexually dimorphic with respect to body size, with males tending to be slightly larger than females (Jodice et al. 2000).

We conducted this experiment from July 20 to August 8, 1999, at the kittiwake breeding colony in Shoup Bay, Alaska. The colony is located on an island in a fjord near Valdez, Alaska, in northeastern Prince William Sound (61°09′N, 146°37′W). During the 1990s, this was the largest and most productive kittiwake colony in Prince William Sound, with ca. 7,500 breeding pairs of kittiwakes.

Radio Telemetry and Time-Activity Budgets

We used noose poles and leg nooses to capture parent kittiwakes at their nest sites during daylight hours (Hogan 1985; Benson and Suryan 1999). We attached radio transmitters (mass = 10 g; Advanced Telemetry Systems, Isanti, Minn.) ventrally at the base of the tail feathers with two nylon cable ties and instant

adhesive. The complete transmitter package weighed less than 3% of adult body mass. We measured body mass (± 0.1 g) as well as length of head plus bill and flattened wing (to ± 0.1 mm). Radio-tagged kittiwakes were sexed using morphometric models that were based on these latter two measures and that had an accuracy rate of approximately 93% (Jodice et al. 2000).

Once radio-tagged birds were injected with DLW and released, we attempted to continuously record activity for at least one complete foraging trip or until the injected kittiwake was recaptured. Radio signals of kittiwakes at the colony were monitored with four-element Yagi and two-element "H" antennas. We used binoculars and a spotting scope from a small island about 100 m from the colony to observe injected birds on colony and to continuously record their activity. Activities recorded included nest attendance and flight caused by any source of disturbance on colony. Occasionally, birds departed the colony but did not initiate foraging trips. These birds often loafed at a nearby stream or on floating ice in Shoup Bay. For these events, we recorded flight time, loafing time, and any disturbance flight.

Once an injected bird departed on a foraging trip, we tracked it with a telemetry receiver and a four-element Yagi antenna from a 7.3-m Boston Whaler capable of traveling 65 km h^{-1}. The distance between the boat-tracking team and the radio-tagged kittiwake at sea varied from ca. 100 to 700 m, depending on circumstances, and we attempted to maintain constant visual contact. Birds were occasionally lost from view, although radio contact was rarely lost. In all cases, we remained at a sufficient distance from the radio-tagged bird to minimize the risk of affecting the bird's behavior. Activities recorded during foraging trips via visual observations and telemetry included time engaged in straight (or commuting) flight, searching flight, surface feeding, and loafing. We also recorded the number of plunge dives by each bird (which we converted to time by assuming that each plunge dive lasted on average 20 s; R. M. Suryan, personal communication), the maximum distance from the colony attained during the foraging trip, the duration of the foraging trip in minutes, whether kittiwakes made use of fish offal from processing plants during the foraging trip, and the proportion of plunge dives that occurred in foraging flocks.

Doubly Labeled Water Methodology

We used the DLW technique (Lifson and McClintock 1966) to measure CO_2 production of radio-tagged kittiwakes. All birds selected for the DLW experiment were radio tagged ≥ 4 d before capture for DLW injection. This allowed birds to acclimate to the radio transmitter before measuring FMR. Before capture for DLW injection, we monitored colony attendance of all radio-tagged kittiwakes regularly via telemetry to ensure that all tagged birds were displaying normal attendance patterns.

We captured radio-tagged parent kittiwakes on their nests

for the DLW experiment using the same techniques previously described. Captured birds were transported a short distance by skiff from the colony to a field camp for processing. For each bird, we measured body mass (± 0.1 g). We also recorded the number of chicks in the brood and measured chick wing length. Chick age was then estimated from regressions of chick age on chick wing length on the basis of known-age chicks from Shoup Bay in 1999 (chick age $= 2.57 + 0.122 \times$ wing length; adjusted $R^2 = 0.95$). The mean (± 1 SD) age of the nestlings of injected adults was 19.0 ± 8.6 d posthatch, although chicks ranged in age from 7 to 30 d posthatch (kittiwake chicks fledge at 35–40 d posthatch). We restricted the experiment to adults with chicks in this general age range to minimize potential differences in adult provisioning effort and hence energy expenditure rate because of either low food intake capacity of young nestlings (Gabrielsen et al. 1992) or reduced adult provisioning of full-grown nestlings near fledging.

We used a 1-cc Hamilton gas-tight syringe to administer an intraperitoneal injection of 0.8 mL of a mixture of $H_2^{18}O$ and ^2H_2O to birds immediately after capture. This dosage allowed for collection of blood samples up to 52 h postequilibration with ^{18}O levels sufficiently elevated above background to allow for accurate measurement of CO_2 production. The enrichment of ^{18}O and ^2H in the mixture was 59.0 and 34.4 atom percent, respectively, on the basis of the suppliers' values. We verified the enrichment of both isotopes by quantitatively diluting the DLW with distilled water and then analyzing the diluted sample along with the blood samples. In all cases, the final enrichments for ^{18}O and ^2H were at least 0.02 atom percent above background levels.

We followed two different handling protocols after injecting subjects with DLW. The first nine birds were wrapped in cloth bags immediately following injection and placed in a dark box for 1 h to allow the labeled water to equilibrate with the body water pool. We then collected an initial blood sample of approximately 100 μL by puncturing the brachial vein with a 23-gauge needle and collecting blood in nonheparinized microhematocrit tubes. Tubes were filled to about 30% of capacity, and the blood samples were centered within the tubes. We used a propane torch to flame seal tubes immediately after blood collection. Blood samples were kept refrigerated at ca. 5°C until analyzed. Following the recapture of each individual, we collected a final blood sample. This is referred to as the double-sample technique (Speakman 1997).

The last 11 birds were released immediately following injection. No initial blood sample was collected. On recapture, a blood sample was taken following procedures previously outlined. This process is referred to as the single-sample technique (Speakman 1997) and was used to minimize disturbance to birds that may have been associated with the equilibration period (Obst et al. 1987). Regardless of whether birds were subjected to the single- or double-sample technique, they were released before 1400 hours. We also captured and bled but did

not inject an additional six adult kittiwakes to establish background isotope levels.

Calculating Rates of CO_2 Production

Rates of CO_2 production for double- and single-sample birds were calculated using different procedures. In each case, however, background, initial, and final blood samples were always analyzed in triplicate following the procedures described by Jodice et al. (2002). Herein, isotope concentrations and other measures are presented ± 1 SD.

We estimated the amount of body water (N_O, moles) at the start of the measurement interval for each bird subjected to the double-sample technique by using the plateau method, which is based on ^{18}O dilution (Visser et al. 2000):

$$N_O = \frac{Q(C_{DO} - C_{IO})}{(C_{IO} - C_{BO})}, \tag{1}$$

where Q represents the size of the dose (moles), C_{DO} represents the concentration of the ^{18}O isotope of the dose (atom percent), C_{IO} represents the ^{18}O concentration of the initial blood sample, and C_{BO} represents the average ^{18}O concentration of the background samples (for $n = 6$ kittiwakes, $C_{BO} = 0.1992 \pm 0.00032$ atom percent).

For the same bird, its amount of body water (N_H, moles) was simultaneously estimated on the basis of ^2H dilution of the same dose:

$$N_H = \frac{Q(C_{DH} - C_{IH})}{(C_{IH} - C_{BH})}, \tag{2}$$

where C_{DH} represents the concentration of the ^2H isotope of the dose (atom percent), C_{IH} represents the ^2H concentration of the initial blood sample, and C_{BH} represents the average ^2H concentration of the background samples (for $n = 6$ kittiwakes, $C_{BH} = 0.0145 \pm 0.00007$ atom percent). For each bird, its dilution space ratio ($R_{dilspace}$, dimensionless) was calculated as

$$R_{dilspace} = \frac{N_H}{N_O}, \tag{3}$$

and the average $R_{dilspace}$ was 1.022 ± 0.0061.

For each bird, the fractional turnover rate of the ^{18}O isotope (k_O, h^{-1}) was calculated with

$$k_O = \frac{[\ln(C_{IO} - C_{BO}) - \ln(C_{FO} - C_{BO})]}{t}, \tag{4}$$

where C_{FO} represents the ^{18}O concentration of the final blood sample and t represents the time elapsed between taking the initial and final blood sample (h). The average

value of k_O was 1.33 ± 0.578. Similarly, the fractional turnover rate of the ^2H isotope (k_D, h^{-1}) was calculated with

$$k_D = \frac{[\ln(C_{IH} - C_{BH}) - \ln(C_{FH} - C_{BH})]}{t}, \tag{5}$$

where C_{FH} represents the ^2H concentration of the final blood sample (atom percent). The average value of k_D was 1.08 ± 0.519. Last, the rate of CO_2 production (rCO_2, mL h^{-1}) for each individual was calculated with

$$rCO_2 = 22{,}400 \times \left(\frac{N_{OAVG}}{2.078}\right) \times (k_O - k_D) - 0.0062\, N_{OAVG} \times k_D \tag{6}$$

(i.e., Eq. [7.17] from Speakman 1997), where N_{OAVG} represents the average size of the body water pool during the measurement. It was calculated using the initial and final body masses, assuming that the percentage of body water (as assessed from isotope dilution at the start of the measurement) remained constant during the measurement.

Because the application of the single-sample protocol involves the taking of only one sample at the end of the observation period (henceforth, also referred to as final sample), the values for N_O, N_D, C_{IO}, and C_{IH} for each bird have to be assessed indirectly (Webster and Weathers 1989; Speakman 1997). On the basis of the information obtained for the two sample birds, it was found that N_O consisted of $60.9\% \pm 1.75\%$ of the initial body mass. In addition, it was found that the slope of the relationship between N_O and body mass did not statistically differ from 0 ($P = 0.1$), enabling us to calculate each individual's N_O by applying the value of 60.9% for all single-sample birds.

This relationship was used to calculate N_O for each single-sample bird. Subsequently, its N_D value was calculated by multiplication of N_O with the average $R_{dilspace}$ value of 1.022.

Next, C_{IO} was estimated by applying N_O, C_{BO}, and Q in Equation (1). Similarly, C_{ID} was estimated by applying N_D, C_{BD}, and Q in Equation (2). These values can subsequently be used to calculate k_O (Eq. [4]) and k_D (Eq. [5]), where t represents in this case the time interval between the injection time plus 1 h and the taking of the final sample. With these values and the enrichment values of the final sample, rCO_2 can be calculated with Equation (6).

Measuring Field Metabolic Rates

We expressed CO_2 production rates on a mass-specific basis (mL CO_2 g^{-1} h^{-1}) for all analyses. We also present daily energy expenditure (DEE; kJ d^{-1}) for comparative purposes. DEE was calculated on the basis of equations in Speakman (1997), using an energetic equivalent of 27.33 kJ L CO_2 respired^{-1}, appro-

priate for a protein- and lipid-rich diet (Gessaman and Nagy 1988).

We examined the relationship between mass-specific field metabolic rate (msFMR) and measurement interval (i.e., the time between initial and final blood sample collection for double-sample birds or the time between 1 h postrelease and final blood sample collection for single-sample birds) to determine whether measurement of energy expenditure might be biased by any diurnal pattern in kittiwake activity. Measurement intervals ranged from 5.8 to 33.2 h. We regressed msFMR on the deviation of the measurement interval from 24 h (Speakman 1997) but found no relationship ($t_{21} = 0.72$, $P = 0.48$); therefore, we used unadjusted msFMR values in all subsequent analyses.

Estimating Activity-Specific Metabolic Costs

We estimated kittiwake metabolic rates during seven focal activities: nest attendance, loafing near the colony (i.e., not during a foraging trip), loafing during a foraging trip, straight flight (i.e., flapping flight that did not involve a substantial degree of maneuvering or diving), searching flight (i.e., back-and-forth flight patterns associated with searching for prey), plunge diving for prey, and surface feeding for prey. On average, these seven activities accounted for 92.4% ± 4.6% of each individual's TAB. We did not estimate metabolic costs for the following activities: flight that occurred in response to our capture attempts, handling time, and time during which the bird was not observed.

We used a suite of 13 linear regression models and a model selection approach (Burnham and Anderson 1998) to estimate the specific metabolic rate for each of the seven focal activities (Table 1). For each linear model, msFMR was the dependent variable. We limited the number of independent variables in each model to three or fewer. Each independent variable was the proportion of time (min h^{-1}) engaged in one of the seven focal activities. Individual models were not designed to represent any specific hypothesis, as is often the case in such a model selection approach, because each model was instead designed to avoid overfitting and multicollinearity. We chose not to estimate activity-specific metabolic costs with either a series of simple linear regression models (i.e., one model per activity) or one multiple linear regression model that included all seven activities because the former would be more likely to result in biased estimates of activity-specific metabolic costs (Wilson and Culik 1993), while the latter would likely suffer from overfitting and multicollinearity.

Once the models were developed, we proceeded as follows. First, we ran each model (Table 1). Second, we calculated the Akaike Information Criteria statistic corrected for small sample size (AIC$_c$) for each model. The AIC$_c$ is based on each model's residual sums of squares, the number of estimable parameters in the model, and the sample size (Burnham and Anderson 1998). Third, we used the AIC$_c$ statistic to rank all models

according to the probability of each being the most parsimonious and plausible given the available data (we present ΔAIC$_c$, or the difference between the AIC$_c$ value for the highest-ranked model and the AIC$_c$ value for the model under consideration). We did this so that activity-specific metabolic rates could be estimated using those models that best described the data. Fourth, for those activity variables that appeared in the highest-ranked model only, we calculated each activity-specific metabolic cost to kittiwakes using the coefficient and SE terms for each variable (the procedure for the remaining variables is described below).

On the basis of the units of the regressed variables, the coefficient for each activity was interpreted as the incremental metabolic cost that accrued while individuals were engaged in the measured activity. This incremental metabolic cost was measured as mL CO_2 g^{-1} min engaged in the activity^{-1}. Multiplying the coefficient by 60 yielded the incremental metabolic cost to the individual as mL CO_2 g^{-1} h^{-1} while engaged in that activity. Total metabolism during each activity was then estimated by summing the intercept term from that multiple linear regression (MLR) model with each of the scaled coefficients (Flint and Nagy 1984). These values were then reported as multiples of kittiwake BMR (1.197 mL CO_2 g^{-1} h^{-1}; Gabrielsen et al. 1988). This calculation step can be described as FMR during activity as a multiple of BMR = [intercept + (coefficient × 60)]/1.197.

To estimate metabolic costs for the remaining focal activities (i.e., those variables not included in the highest-ranked model), we advanced to the next highest-ranked model and repeated the procedure previously described. If, however, this next highest-ranked model contained at least one activity for which metabolic costs had already been estimated from a higher-ranked model, we skipped the entire model and advanced to the next model (this occurred only once; see "Results"). The primary purpose for doing so was to avoid compromising the integrity of activity-specific metabolic costs by taking them out of context of the original model (i.e., by using an intercept term and coefficient from one model while ignoring another coefficient from the same model because the activity that it represented had already been accounted for in a higher-ranked model). This procedure was repeated until metabolic costs were estimated for each of the seven focal activities.

As a means of assessing the reliability of our activity-specific metabolic rate estimates, we compared results from the previous analyses with estimates derived from three additional analyses. First, we conducted simple linear regressions with msFMR as the response variable and each of the seven focal activities as an independent variable. Second, we repeated the previous MLR analysis using a resampling procedure. We did this to ensure that our relatively small sample size was not producing unreliable coefficient estimates. For each model, we conducted 1,000 regressions. We compared the median values of the intercept

Table 1: Model selection statistics from linear regression models of mass-specific field metabolic rate (mL CO_2 g^{-1} h^{-1}) on activities of black-legged kittiwake parents at the Shoup Bay colony, Prince William Sound, Alaska, July 20–August 8, 1999

Model Parameters	K	Residual Sums of Squares	ΔAIC_c
Nest attendance, loafing near colony, surface feeding	5	4.49	.00
Searching flight, commuting flight	4	5.79	1.47
Loafing near colony	3	8.60	6.21
Plunge diving, loafing during foraging trip	4	7.76	7.32
Loafing near colony, loafing during foraging trip, surface feeding	5	6.70	8.01
Searching flight, nest attendance	4	8.48	9.10
Searching flight	4	10.41	10.03
Loafing during foraging trip	3	10.48	10.17
Commuting flight, plunge diving	4	8.96	10.20
Commuting flight	3	10.57	10.34
Plunge diving	3	12.24	13.27
Nest attendance	3	14.06	16.04
Surface feeding	3	16.68	19.46

Note. K = number of parameters in model + 1 for intercept + 1 for variance estimator. AIC_c = Akaike Information Criteria statistic corrected for small sample size.

and coefficient terms from each of the 1,000 regressions with those from the MLR analysis previously described.

Third, we used a series of simple linear regression models where the response variable was the field metabolic rate that accrued only during the foraging trip (estimated from the activity-specific metabolic rates for time spent attending the nest and loafing near the colony) and the independent variables were minutes per hour of the foraging trip engaged in commuting flight, searching flight, plunge diving, surface feeding, or loafing during the foraging trip. We estimated activity-specific metabolic rates for each of these five independent variables on the basis of the coefficients and intercept terms from each regression model, as previously described.

Effects of Time-Activity Budgets on Field Metabolic Rates

We conducted another series of linear models to determine the extent to which TABs accounted for variation in kittiwake msFMR. The dependent variable in these analyses was msFMR. There were seven independent variables available. Three were based on the proportion of time (min h^{-1}) kittiwakes were engaged in an activity (nest attendance, loafing near the colony, foraging trip) relative to the entire DLW measurement interval. The other four variables were based on the proportion of the foraging trip (min h^{-1}) kittiwakes were engaged in loafing, straight flight, searching flight, or plunge diving. R^2 values were used to compare the amount of variation accounted for in each model; those models with the highest R^2 values were deemed to account for the most variation in msFMR. We also assessed the degree to which a suite of additional procedural, foraging

trip, or individual attributes increased the explanatory ability of the preceding models.

Means are presented as ± 1 SD, and regression coefficients and multiples of BMR are presented as ± 1 SE unless noted otherwise. Min h^{-1} refers to average minutes engaged in the activity per hour of the DLW measurement interval unless noted otherwise.

Results

Time-Activity Budgets

We recorded comprehensive TABs (i.e., activity recorded for >85% of the measurement interval), recaptured, and measured energy expenditure rates for 20 kittiwakes (Appendix). All injected birds continued attending their nests following the first and second captures. DLW measurement intervals during which TABs were recorded averaged 12.6 $\pm$ 6.6 h (range = 5.8 to 33.2 h). The duration of the measurement interval did not vary with sex, brood size, chick age, or any of the possible two-way interactions of these terms ($F_{1,12} < 1.1$, $P > 0.3$). The average proportion of the DLW measurement interval for which we recorded TABs was 98.2%.

The mean proportion of the measurement interval that injected kittiwakes engaged in each of the seven focal activities was nest attendance = 28.2% $\pm$ 16.8%, loafing during foraging trip = 21.4% $\pm$ 15.8%, loafing near colony = 16.6% $\pm$ 20.6%, straight flight = 13.3% $\pm$ 7.3%, searching flight = 10.2% $\pm$ 9.5%, surface feeding = 1.9% $\pm$ 3.5%, and plunge diving = 0.9% $\pm$ 0.7%. There were no significant differences between sexes in proportion of time spent in each activity

Table 2: Multiple linear regression coefficients used to estimate the activity-specific metabolic cost of black-legged kittiwake parents at the Shoup Bay colony, Prince William Sound, Alaska, July 20–August 8, 1999

Behavior	Coefficient	SE	P Value	Intercept	Adjusted R^2	Metabolic Cost (mL CO_2 g^{-1} h^{-1})[a]	($\times$ BMR ± 1 SE)[b]
Nest attendance (1)[c]	−.050	.012	.002	4.855	.68	1.85	1.5 $\pm$ .3
Loafing near colony (1)[c]	−.058	.010	.001	4.855	.68	1.38	1.1 $\pm$ .5
Surface feeding (1)	−.043	.059	.476	4.855	.68	2.27	1.9 $\pm$ 2.9
Commuting flight (2)[d]	.113	.031	.002	2.015	.61	8.79	7.3 $\pm$ 1.6
Searching flight (2)[d]	.090	.023	.002	2.015	.61	7.41	6.2 $\pm$ 1.1
Plunge diving (4)	.891	.364	.026	2.283	.48	55.74	46.6 $\pm$ 15.9
Loafing on foraging trip (4)	.052	.017	.006	2.283	.48	5.40	4.5 $\pm$ .9
Loafing on foraging trip (revised)[e]	−.081	.041	.069	8.34	.15	3.48	2.8 $\pm$ 2.1

Note. The total metabolic cost to the individual during each behavior is presented as mass-specific field metabolic rate (mL CO_2 g^{-1} h^{-1}) and as a multiple of basal metabolic rate (i.e., $\times$ BMR). Number in parentheses is the model rank from Table 1.

[a] msFMR while engaged in activity calculated as intercept $\pm$ (coefficient $\times$ 60).

[b] BMR = 1.197 mL CO_2 g^{-1} h^{-1} (Gabrielsen et al. 1988); multiple of BMR calculated as [intercept + (coefficient $\times$ 60)]/1.197.

[c] Coefficients not significantly different ($P = 0.6$).

[d] Coefficients not significantly different ($P = 0.5$).

[e] Results from regression of msFMR during foraging trip only on minutes per hour of the foraging trip spent loafing.

($P > 0.1$ for each activity). There was, however, a significant difference in TABs between birds subjected to the double- or single-sample injection protocol. Double-sample birds spent a greater proportion of the DLW measurement interval inactive near the colony (29.7% $\pm$ 24.2%) than did single-sample birds (5.8% $\pm$ 7.5%; $t_{9.3} = 2.8$ for unequal variances, $P = 0.02$). Consequently, double-sample birds also spent a smaller proportion of the DLW measurement interval on foraging trips (34.0% $\pm$ 31.3%) than did single-sample birds (59.8% $\pm$ 13.7%; $t_{10.5} = 2.3$ for unequal variances, $P = 0.04$).

The mean proportion of the DLW measurement interval allocated to foraging trips was 48.2% $\pm$ 26.2% (range = 0% to 86%) and did not differ by sex ($t_{18} = 2.1$, $P = 0.18$). On average, injected kittiwakes tended to spend a greater proportion of the foraging trip active (55.9% $\pm$ 15.7%) than loafing (40.2% $\pm$ 18.3%; paired $t_{16} = 2.0$, $P = 0.05$). Kittiwakes spent a greater proportion of the foraging trip engaged in straight flight (28.1% $\pm$ 11.8%) than searching flight (21.0% $\pm$ 14.1%); much smaller proportions of the foraging trip were engaged in either surface feeding (4.6% $\pm$ 6.8%) or plunge diving (2.1% $\pm$ 1.3%; repeated-measures ANOVA, $F_{3, 51} = 40.2$, $P < 0.0001$).

Field Metabolic Rates

Mass-specific FMRs in this study ranged from 1.55 to 5.56 mL CO_2 g^{-1} h^{-1}. Mean msFMRs of male and female kittiwakes were 3.30 $\pm$ 1.10 and 3.61 $\pm$ 0.77 mL CO_2 g^{-1} h^{-1}, respectively. Although this difference was not significant ($t_{18} = 1.1$, $P = 0.40$), the power to detect a difference at an α level of 0.10 was only 0.20. Mean msFMR of kittiwakes subjected to the single-

and double-sample procedures were 3.75 $\pm$ 0.8 and 3.10 $\pm$ 1.0 mL CO_2 g^{-1} h^{-1}, respectively. Although this difference was not statistically significant ($t_{18} = 1.6$, $P = 0.12$), the power to detect a difference at an α level of 0.10 was only 0.49. Kittiwake msFMR was not related to age of chicks ($R^2 = 0.16$, $P = 0.12$), nor was there a difference in msFMR between parents of one- and two-chick broods ($t_{18} = 0.3$, $P = 0.3$).

The mean msFMR was 3.45 $\pm$ 0.94 mL CO_2 g^{-1} h^{-1} when data for the two sexes were pooled. This is similar ($F_{2, 111} = 0.8$, $P = 0.47$) to average msFMR reported by Roby et al. (2000) for kittiwakes nesting at Shoup Bay in 1997 and 1998 (3.25 $\pm$ 0.56 mL CO_2 g^{-1} h^{-1}) and to values reported by Golet et al. (2000) for kittiwakes nesting at Shoup Bay in 1992 (3.21 $\pm$ 1.2 mL CO_2 g^{-1} h^{-1}). Therefore, msFMRs of kittiwakes in this study did not appear to be biased due to birds carrying radio transmitters, the relatively short DLW measurement intervals, or the handling procedure. Mean DEE of male and female kittiwakes in this study was 934.4 $\pm$ 300.7 kJ d^{-1} and 839.5 $\pm$ 253.8 kJ d^{-1}, respectively.

Activity-Specific Metabolic Rates

The rankings and AIC statistics from the linear models used to estimate activity-specific metabolic costs are presented in Table 1. We used models ranked first, second, and fourth in Table 1 to estimate total metabolic costs that accrued to individuals during each activity (Table 2).

Metabolic costs to kittiwakes during nest attendance (1.5 $\pm$ 0.3 $\times$ BMR) and while loafing near the colony (1.1 $\pm$ 0.5 $\times$ BMR) were similar ($t_{37} = 0.5$ for difference between regression coefficients, $P = 0.6$; Table 2; Fig. 1a, 1b). Metabolic
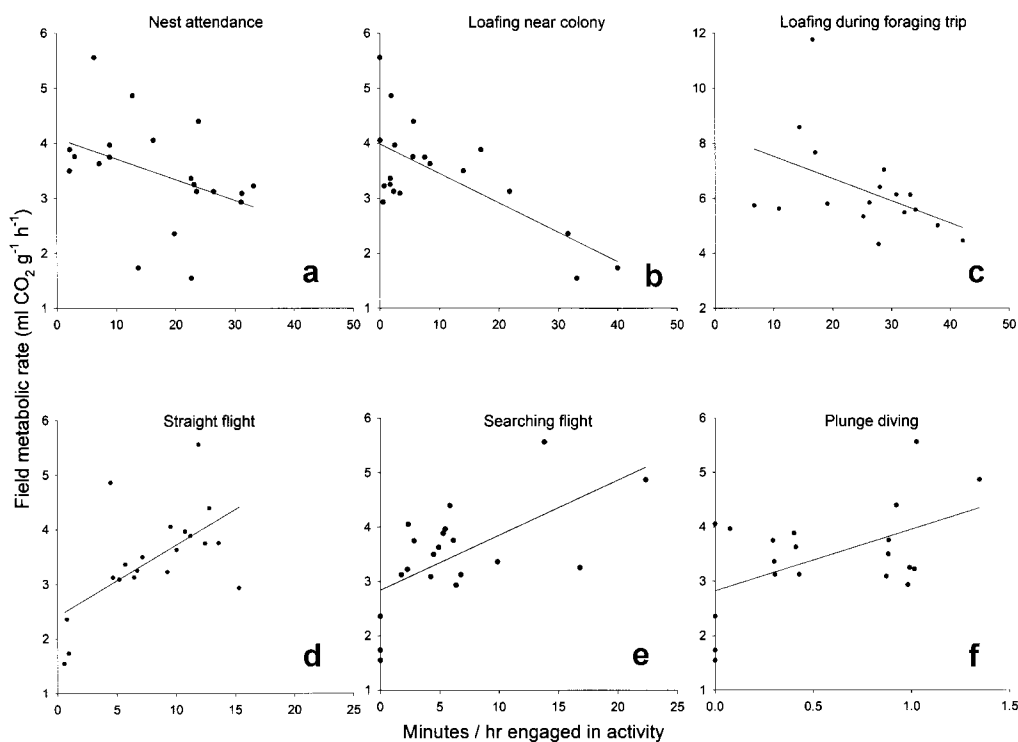
Figure 1. Relationships of mass-specific field metabolic rates (mL CO_2 g^{-1} h^{-1}) of radio-tagged black-legged kittiwakes to proportion of time (min h^{-1}) engaged in each of six activities recorded during chick rearing at the Shoup Bay colony, Prince William Sound, Alaska, July 20–August 8, 1999. Plots were produced from simple linear regressions, although multiple linear regressions were used to calculate coefficients for estimation of activity-specific metabolic rates (except 1c; see "Results"). Note that the range of values along the X-axes varies among plots.

costs during searching flight (6.2 ± 1.1 × BMR) and commuting flight (7.3 ± 1.6 × BMR) were similar ($t_{37} = 0.6$ for difference between regression coefficients, $P = 0.5$; Table 2; Fig. 1d, 1e). The metabolic cost during plunge diving (46.6 ± 15.9 × BMR) was substantially higher than for any other activity (Table 2; Fig. 1f). Surface feeding (1.9 ± 2.9 × BMR) was the only activity whose coefficient did not differ significantly from 0, indicating that there was no apparent relationship between time engaged in this activity and msFMR (Table 2).

The metabolic cost that accrued while loafing during a foraging trip was estimated to be 4.5 ± 0.9 × BMR (Table 2). Results from an alternate regression analysis (see "Material and Methods") using the response variable of metabolic rate during the foraging trip instead of metabolic rate during the entire DLW measurement interval, however, indicated that the metabolic rate of kittiwakes while loafing during the foraging trip was 2.8 ± 2.1 × BMR (Table 2; Fig. 1c). We believe this estimate of 2.8 × BMR is a more accurate assessment of the cost of loafing during foraging trips when compared with the costs of loafing near the colony and the cost of nest attendance. We suggest that the elevated estimate of 4.5 × BMR is a direct reflection of the cost of the foraging trip itself, which is estimated to be 4.2 × BMR. In fact, the proportion of the DLW

measurement interval that kittiwakes spent on a foraging trip and the proportion of the DLW measurement interval that kittiwakes loafed during the foraging trip were strongly correlated ($r = 0.89$). In contrast, the proportion of the DLW measurement interval that kittiwakes spent on a foraging trip and the proportion of the foraging trip that kittiwakes loafed were only moderately correlated ($r = 0.45$). Thus, the supplementary analysis based on foraging trip FMR is likely to be more accurate for the variable of loafing during the foraging trip (Fig. 1c). For each of the other six focal activities, coefficients and activity-specific metabolic rate estimates derived from the three additional analyses were well within ±1 SE of the original estimates and in some cases were nearly identical to the original estimates.

Accounting for Variation in msFMR with TABs

Nest attendance explained 16% of the variability in kittiwake msFMR (Table 3, model A). In contrast, 72% of the variation in msFMR was accounted for by adding a variable for loafing near the colony to the above model (Table 3, model B). Other models that examined the relationship between msFMR and various attributes of kittiwake TABs (e.g., duration of the for-

Table 3: Effect of time-activity budget variables on mass-specific field metabolic rate of black-legged kittiwake parents at the Shoup Bay colony, Prince William Sound, Alaska, July 20–August 8, 1999

ID and Model	P	Model R^2
All birds included:		
A. $4.1 - .04 \times$ min h^{-1} attending the nest	.07	.165
B. $4.8 - .06 \times$ min h^{-1} loafing near colony	<.001	.724
$- .05 \times$ min h^{-1} attending the nest	.001	
C. $6.9 - .08 \times$ min h^{-1} inactive	<.001	.649
D. $1.9 + .09 \times$ min h^{-1} active	<.001	.682
E. $1.9 + .05 \times$ min h^{-1} on foraging trip	<.001	.679
Birds that did not forage excluded:		
F. $4.7 - .05 \times$ min h^{-1} loafing near colony	.07	.433
$- .04 \times$ min h^{-1} attending the nest	.001	
G. $2.3 + .04 \times$ min h^{-1} on foraging trip	.009	.375
H. $2.3 + .04 \times$ min h^{-1} on foraging trip	.02	.376
$+ .002 \times$ min h^{-1} of foraging trip in straight flight	.9	
I. $1.2 + .05 \times$ min h^{-1} on foraging trip	.009	.413
$+ .19 \times$ min h^{-1} of foraging trip plunge diving	.3	
J. $2.1 + .04 \times$ min h^{-1} on foraging trip	.007	.439
$+ .02 \times$ min h^{-1} of foraging trip in searching flight	.2	
K. $2.0 + .04 \times$ min h^{-1} on foraging trip	.007	.440
$+ .02 \times$ min h^{-1} of foraging trip actively foraging	.2	

Note. Units for independent variables are minutes per hour of the doubly labeled water measurement interval invested in that activity, unless specified otherwise. Models A–E include all birds ($n = 20$), while models F–K include only those birds that went on foraging trips ($n = 17$). P values are listed in order of the independent variables in the model.

aging trip) explained 65%–68% of the variability in the data (Table 3, models C–E).

We also evaluated models that included only birds that engaged in foraging trips ($n = 17$; Table 3, models F–K). The model that best explained the variability in kittiwake msFMR from this set of models included independent variables for the proportion of time on the foraging trip and the proportion of the foraging trip during which birds were actively foraging (model K; $R^2 = 0.44$). A comparison among models F–K suggests that variation in the incidence of plunge diving and searching flight were responsible for a moderate proportion of the variation in metabolic costs during a foraging trip.

We examined how the addition of a series of single variables (foraging trip and individual attributes) affected R^2 values from models F and K. These models were chosen because they represented two major facets of TABs for those birds that undertook foraging trips: activities that reduced average FMR the more time was allocated to them (i.e., nest attendance and loafing) and activities that elevated average FMR the more time was allocated to them (i.e., flight and active foraging). The additional variables examined were prey type (young-of-year [YOY] fish, older than YOY fish, or use of offal from fish processors), maximum distance traveled from the colony (km;

mean = 31.8 ± 21.5), average wind speed (m s^{-1}; mean = 3.8 ± 2.0) obtained from a nearby weather station during the DLW measurement interval, the proportion of foraging attempts that occurred within a foraging flock (i.e., birds not foraging singly; mean = 70% ± 30%), the DLW injection protocol (i.e., single- or double-sample technique; see "Material and Methods"), sex, brood size, chick age, body mass at time of capture, and minutes per hour of the DLW measurement interval during which the individual was being pursued for capture and was being handled. The addition of each variable to models F and K increased the R^2 value of the original models by an average of only 6.6% ± 6.1%. In no case were the coefficients for the added variables significant ($P > 0.18$).

Discussion

Activity-Specific Metabolic Rates

Our estimate of metabolic rate during brood attendance (1.5 ± 0.3 × BMR) is similar to that reported for kittiwakes in Norway (1.9 ± 0.6 × BMR; Gabrielsen et al. 1987) and well within the range of estimates for other seabirds (0.8 to 4.7 × BMR; Grant and Whittow 1983; Birt-Friesen et al. 1989; Adams et al. 1991; Obst and Nagy 1992; Ballance 1995). Our

Table 4: Metabolic rate during flight estimated with the doubly labeled water technique in free-ranging seabirds

Common Name	Metabolic Rate during Flight ($\times$ BMR $\pm$ 1 SE)[a]	References
Grey-headed albatross	3.2	Costa and Prince 1987
Wandering albatross	2.3	Adams et al. 1986
Wilson's storm-petrel	4.2 $\pm$ .4	Obst et al. 1987
Northern gannet	11.9 $\pm$ 3.5	Birt-Friesen et al. 1989
Red-footed booby	4.5 $\pm$ .8	Ballance 1995
Black-legged kittiwake	6.9 $\pm$ 1.9	This study
Black-legged kittiwake	7.5 $\pm$ 1.5	This study
Sooty tern	4.8 $\pm$ .6	Flint and Nagy 1984

Note. Metabolic rate during flight is integrated among all flight types except in black-legged kittiwakes where costs for commuting and searching flight are listed in that order. Flight time was estimated from previous studies of time-activity budgets for grey-headed albatross (*Diomedea chrysostoma*) and wandering albatrosses (*Diomedea exulans*); assumed to be 100% of time at sea for Wilson's storm-petrel (*Oceanites oceanicus*), red-footed booby (*Sula sula*), and sooty tern (*Sterna fuscata*); measured via activity recorders for northern gannets (*Sula bassanus*); and measured via direct observation for black-legged kittiwakes (*Rissa tridactyla*).

[a] BMR was predicted for grey-headed albatross, directly measured for Wilson's storm-petrel and northern gannet, and measured on the same species during a different study for all others.

estimate is, however, slightly higher than that predicted from an allometric equation based on metabolic rates from 10 species of seabirds (1.1 × BMR) reported in Birt-Friesen et al. (1989).

The metabolic rate of kittiwakes while loafing during a foraging trip (2.8 ± 2.1 × BMR) was greater than that estimated while loafing near the colony (1.1 ± 0.5 × BMR). This difference may be due in part to an elevation in thermostatic costs experienced by kittiwakes while loafing away from the colony (Ellis 1984; Birt-Friesen et al. 1989); during foraging trips, kittiwakes tend to rest on either small, exposed islets or the water surface. Elevated metabolic rates experienced by kittiwakes while loafing during foraging trips may also be due to energetic costs associated with heat increment of feeding (HIF). HIF peaks soon after prey are consumed and, in other seabirds, elevates metabolic rates by 40%–80% over postabsorptive resting metabolic rates (Baudinette et al. 1986; Croll and McClaren 1993; Hawkins et al. 1997). The metabolic rates associated with loafing during foraging trips were the most likely to be affected by HIF costs because kittiwakes tend to loaf following successful feeding bouts. In contrast, the potential for HIF costs to substantially bias estimates of metabolic rates during other activities is limited given the low probability that HIF consistently peaked during any one activity other than loafing during the foraging trip.

Estimates of flight costs for seabirds are rare. Metabolic rate during flight has yet to be measured directly or indirectly in black-legged kittiwakes, and although estimates of flight cost for other larids are available, these are based on either mass-loss studies or wind-tunnel experiments (Berger et al. 1970; Tucker 1972; Dolnik and Gavrilov 1973). Six published studies used the DLW technique to measure the energetic cost of flight in free-ranging seabirds (Flint and Nagy 1984; Adams et al. 1986; Costa and Prince 1987; Obst et al. 1987; Birt-Friesen et al. 1989; Ballance 1995; Table 4). FMR during flight in these species ranged from 2.3 × BMR (wandering albatross [*Diomedea exulans*]; Adams et al. 1986) to >11 × BMR (northern gannet [*Sula bassanus*]; Birt-Friesen et al. 1989).

We compared our empirical estimate of the metabolic costs of straight flight in kittiwakes with predicted costs from (1) an allometric model developed specifically to predict seabird flight cost (Birt-Friesen et al. 1989), (2) an allometric model developed to predict flight costs across a range of avian families (Nudds and Bryant 2000), and (3) an aerodynamic model (Pennycuick 1989). For the allometric models, we assumed an average body mass of 400 g for adult kittiwakes, and for the aerodynamic model, we used a range of wing morphology values (wingspan = 0.889, 0.914, and 1.04 m; aspect ratio = 8, 9, and 10) that were appropriate for this species (Pennycuick 1987). We used default values provided by the aerodynamic modeling program for all other input variables except BMR, which we set to 3.63 W (Gabrielsen et al. 1988).

Our empirical estimate of metabolic rate during commuting flight (7.3 ± 1.6 × BMR) was intermediate between predictions from the aerodynamic model and the general allometric model but much higher than that of the seabird allometric model. Predicted flight cost from the seabird allometric model (Birt-Friesen et al. 1989) was 2.8 × BMR, while the prediction from the general avian allometric model (Nudds and Bryant 2000) was 8.4 × BMR. Predicted maximum range power, P_{mr}, from the aerodynamic model ranged from 20.2 to 22.5 W, and the

median P_{mr} was 21 W, or ca. 5.8 × BMR. This suggests that kittiwakes do not possess specialized adaptations to reduce flight costs, as in several highly pelagic seabirds included in the seabird allometric model (i.e., albatrosses, storm-petrels, sooty terns; Table 4).

Metabolic rate during plunge diving has not been estimated in piscivorous birds either directly or indirectly. Our estimate for the cost of plunge diving (47 ± 16 × BMR) was more than six times our estimate for commuting flight (7.3 ± 1.6 × BMR). The power requirements of plunge diving are evidently high, and this may account for the elevated FMRs of seabird species that use this foraging technique (Birt-Friesen et al. 1989; Adams et al. 1991). Plunge diving in kittiwakes is likely to be energetically expensive because it requires some degree of underwater propulsion, vertical takeoff from the water's surface (occasionally with an additional payload of food), and aerobatic maneuvers with wet plumage. Our estimate for the cost of plunge diving in kittiwakes is within the range of previously published metabolic costs for similarly intense activities in birds. For example, short, intense flights in zebra finches (*Taeniopygia guttata*) and starlings (*Sturnus vulgaris*) have been estimated at 28 × BMR (Nudds and Bryant 2000) and 39 to 69 × BMR (Westerterp and Drent 1985; Bautista et al. 1998), respectively, while the metabolic rate of rheas (*Rhea americana*) during intense running sessions was measured at 36 × resting metabolic rate (Bundle et al. 1999). Our estimate of the metabolic cost for plunge diving should be viewed cautiously, however, because this activity comprises such a small portion of the total TAB that even a small sampling error with respect to time engaged in the activity could result in a change to the estimated metabolic rate during that activity (Nudds and Bryant 2000).

Effects of Time-Activity Budgets on FMR

Differences in TABs among individuals accounted for as much as 72% of the variation in kittiwake FMRs when all subjects were considered and as much as 45% of the variation in FMR when only those birds that went on foraging trips were considered (Table 3). These results provide strong support for our initial hypothesis that variation in TABs strongly affects FMRs. If only the proportion of time spent attending the nest was considered, however, then the proportion of FMR variation accounted for decreased to only 16%. The additional foraging trip and individual-based attributes that we considered did not substantially improve the explanatory ability of any of our models.

Investigations of seabird FMRs rarely have an opportunity to directly measure TAB variables other than nest attendance (Ellis and Gabrielsen 2001). The reciprocal of nest attendance is often used as an index for time at sea, and time at sea is frequently equated with duration of the foraging trip. Most studies of seabird energetics that estimate foraging trip duration

in this manner report positive correlations between FMR and time at sea (e.g., Adams et al. 1991; Obst and Nagy 1992; Thompson et al. 1998; Fyhn et al. 2001; Nagy et al. 2001). Furness and Bryant (1996) and Golet et al. (2000), however, detected no correlation between estimated time at sea and FMR in northern fulmars and black-legged kittiwakes, respectively. Nest attendance may be a misleading measure of foraging intensity because although parent seabirds not attending the nest are typically considered to be foraging at sea, we observed that these individuals may invest substantial amounts of time loafing either near the colony or at some distant location.

The unexplained variation in the relationship between FMRs and TABs in our study may be due in part to individual variation or extrinsic factors for which we did not account. Sampling error associated with the measurement of TABs also may have accounted for some of the unexplained variability, although we minimized TAB sampling error by (1) recording only activities that were distinct enough to allow little opportunity to misclassify behavior and (2) maximizing the amount of the DLW measurement interval for which behavior was recorded (98% on average). We also minimized sampling error in our estimates of FMR by employing lab protocols that specifically addressed the short DLW measurement intervals we encountered (see "Material and Methods"). Furthermore, our estimates of TABs, FMRs, and their interrelationship were not adversely affected by any atypical behavior that kittiwakes may have exhibited (e.g., the extended loafing activity immediately following release that we observed in some double-sample birds) because (1) the TAB and FMR data were recorded simultaneously and accurately (i.e., birds were known to be loafing and not flying while off colony) and (2) the FMR of the individuals in question was consistent with their activity level (i.e., lower FMRs were recorded for less active individuals).

In conclusion, our study demonstrated that metabolic rates of free-ranging adult kittiwakes raising young were strongly and positively affected by the proportion of time dedicated to the foraging trip. This single variable explained 68% of the variation in kittiwake FMR and thus provides a useful means to estimate FMR for kittiwakes. Consequently, the majority of among-individual variation in measurements of FMR can be attributed to variation in TABs rather than intrinsic differences in the energetic efficiency of individuals.

Our data also suggest that parent kittiwakes can accrue substantial energy savings by increasing the proportion of time spent attending their brood, loafing near the colony, or, to a lesser extent, loafing during the foraging trip. Because kittiwakes also accrue survival benefits when energy expenditure rates are reduced during the breeding season (Golet et al. 1998, 2000), kittiwakes should maximize time engaged in nest attendance or loafing as long as doing so does not compromise lifetime reproductive output. Experiments involving supplemental feeding and brood removal support this prediction. Kittiwakes provided with supplemental food exhibited higher brood atten-

dance and, consequently, lower energy expenditure rates compared with control birds (Gill et al. 2002; Jodice et al. 2002). Kittiwakes relieved of their broods had lower energy expenditure rates and higher survival than did control birds (Golet et al. 1998, 2000). Presumably, the lower FMRs of experimental birds in each study were due to a reduction in foraging activity.

Estimated flight costs in kittiwakes were well within the range of other seabirds, while estimated costs of plunge diving were approximately six times those of flight. The relative metabolic costs of these foraging activities suggest that kittiwakes can extend foraging trip distances at a much lower cost than they can increase the intensity of plunge diving to capture prey. These differences in costs may explain why kittiwakes tend to increase foraging range, rather than increase foraging intensity, when food availability decreases (Suryan and Irons 2000). Future studies of kittiwake breeding ecology should measure the proportion of time allocated to foraging trips whenever this is feasible because it can explain much of the variation in field metabolic rates and reproductive effort of adult kittiwakes.

Appendix

Table A1: Energy expenditure rates and activity measures of 20 radio-tagged black-legged kittiwake parents at the Shoup Bay colony, Prince William Sound, Alaska, July 20–August 8, 1999

Sex	Body Mass (g)	Measurement Interval (h)	% Time on Foraging Trip	Total Energy Expenditure (kJ)	Field Metabolic Rate (mL CO_2 g^{-1} h^{-1})
M	429.2	13.0	42.3	670.0	4.39
M	496.6	7.7	0	244.8	2.36
M	383.4	22.6	81.7	890.0	3.75
M	475.8	8.5	0	191.3	1.73
M	437.2	8.9	0	164.0	1.55
M	404.4	11.8	37.6	401.0	3.09
F	367.6	6.5	65.7	259.5	3.96
M	387.9	11.8	61.9	485.8	3.88
F	394.4	13.1	16.6	440.4	3.12
M	464.3	14.4	58.6	732.1	3.75
M	441.3	10.8	64.4	689.8	4.86
F	333.6	9.9	41.9	292.2	2.93
F	418.5	14.6	48.6	557.4	3.12
F	400.0	5.8	51.7	249.8	3.36
F	369.8	14.3	42.0	498.3	3.22
F	356.5	8.9	70.3	392.0	4.05
M	445.0	21.3	68.6	990.2	3.63
F	369.4	8.8	85.7	548.1	5.56
F	365.4	33.2	71.6	1,193.2	3.50
F	346.1	6.6	54.4	232.9	3.25

Note. Birds from rows 1–9 were subjected to the double-sample technique, while individuals from rows 10–20 were subjected to the single-sample technique.

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