

# DAILY ENERGY EXPENDITURE AND ENERGY UTILIZATION OF FREE-RANGING BLACK-LEGGED KITTIWAKES<sup>1</sup>

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**Abstract.** Rates of CO<sub>2</sub> production by breeding Black-legged Kittiwakes (*Rissa tridactyla*) (mean mass, 386 g) were measured by using doubly-labeled water. Kittiwakes alternated days on and off the nest, while they brooded their nestlings. Field metabolic rates (FMR) in nonforaging birds averaged 2.43 ml CO<sub>2</sub>/g·hr, or 596 kJ/day. This is 1.9 times the basal metabolic rate (BMR), measured in the laboratory to be 1.31 ml CO<sub>2</sub>/g·hr, or 314 kJ/day. FMRs in foraging birds averaged 4.04 ml CO<sub>2</sub>/g·hr, or 992 kJ/day which is 3.2 times BMR.

The rate of food consumption by an adult kittiwake, calculated on the basis of the chemical composition and digestibility of capelin (*Mallotus villosus*, the most important dietary item at Hopen Island) was 315 g of fresh matter per bird every other day. A colony of 3,000 breeding pairs of kittiwakes at Hopen Island, using the fishing grounds around the island, would consume about 1,245 kg of fresh fish per day, and add about 76 kg (dry matter) of guano to the marine ecosystem during the chick-rearing period.

**Key words:** *Arctic; seabird energetics; doubly-labeled water; field metabolic rate; food consumption.*

## INTRODUCTION

The Barents Sea and the waters surrounding Svalbard are highly productive and support large populations of marine mammals and one of the world's greatest concentrations of seabirds (Zenkevitch 1963). These birds constitute a major component of the marine ecosystem and they form an important linkage between the terrestrial and marine ecosystems in the Svalbard area. Black-legged Kittiwakes (*Rissa tridactyla*) comprise a large fraction of the seabird biomass. Thus, studies of kittiwake feeding habits, food requirements, and assimilation efficiency are of great importance in order to determine the energy flow through the ecosystem.

Until recently, the role of seabirds in the arctic marine food chain has been estimated from models of seabird energetics (Wiens and Scott 1975, Furness 1978, Croxall and Prince 1982, Furness and Cooper 1982, Furness and Barrett 1985), which are based on time-energy budget (TEB) studies of individual species. The TEB method involves field measurements of the

amounts of time that birds spend in various activities, along with laboratory-based estimates of the energetic cost of these activities (Gessaman 1973, King 1974, Kendeigh et al. 1977). The TEB method is difficult to apply to many seabirds, because they travel long distances to forage and may be unobservable for days at a time. Moreover, recent studies have shown that TEB estimates may contain large errors, depending on the specific TEB method that is employed (Williams and Nagy 1984a, Weathers et al. 1984, but see Nagy et al. 1984).

It is now possible to measure field metabolic rates (FMR) of birds directly, by using the doubly-labeled water method. This technique, used in conjunction with time budget measurements and determinations of diet composition, has yielded much information about food and energy requirements of wild birds (Weathers and Nagy 1980, Williams and Nagy 1984a, Nagy et al. 1984, Bryant et al. 1985). Validation studies on birds have shown that DLW measurements are within  $\pm 10\%$  of direct gravimetric measurements of CO<sub>2</sub> production, indicating reasonable accuracy for such studies (Williams and Nagy 1984b).

The main goal of the present study was to determine the field metabolic rates and food requirements of breeding Black-legged Kittiwakes.

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## MATERIALS AND METHODS

### BIRDS

Black-legged Kittiwakes breeding on Hopen Island (76°30'N and 25°03'E), in the Svalbard archipelago, were studied from 31 July until 8 August 1984. Between 2,000 and 3,000 pairs of kittiwakes breed annually in the colony we studied on the eastern coast of Hopen. Kittiwakes on Hopen lay one or two eggs and they usually fledge one chick (R. T. Barrett, unpubl.). Kittiwake chicks were about 5 to 10 days old when we performed our study, and both parents were making foraging trips.

### WEATHER

The weather conditions were measured at Hopen Radio, 500 m away from the colony, every third hour. The weather during the study period was characterized by low temperatures, fog, and strong winds. The mean air temperature was 4.4°C (range, 1.2–12°C), daily average rainfall was 0.4 mm (range, 0.1–1.2 mm) and mean wind speed was 9 m/sec (range, 2–24 m/sec). The ocean surface temperature was about 3.0°C. There was continuous, 24 hr light at Hopen during the study period.

### DLW

Metabolic rates (CO<sub>2</sub> production) and water flux rates were measured using the doubly-labeled water method (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980) in one or both members of breeding pairs. A total of 24 adult kittiwakes were caught on the nest. Each was placed in a nylon bag and carried to the field laboratory 500 m from the colony. Birds were injected in the pectoral muscle with 1.2 ml of water containing 97.11% oxygen-18 and 0.4 mc of tritium, and were held in a wooden box for 1.0 to 1.5 hr while the isotopes mixed thoroughly in body water fluid (Degen et al. 1981, Williams and Nagy 1984b). Birds were weighed to ±5 g on a Pesola spring balance, head and bill lengths were measured to ±1 mm to determine sex (males > 92 and females < 92 mm) (Mehlum, unpubl.), and each was marked with individual patterns on the head using picric acid and indian ink. A blood sample (ca. 1 ml) was taken from a wing vein before release. Most of the birds returned to their nest within 10 to 30 min after release, and all were relieved at the nest by their mates during the next 24 hr. Over the next eight

days, marked birds were recaptured, weighed, and sampled, some more than once. Visual observations of the colony were made four times each day to check if birds were present. We obtained separate measurement intervals covering brooding of young only ("on nest"), as well as periods away from the nest ("off nest") that included foraging.

Blood samples were centrifuged in heparinized microhematocrit capillary tubes, and were vacuum-distilled to obtain pure water. Isotope levels in the water were measured by liquid scintillation spectrometry (for tritium) and proton activation analysis (for oxygen-18, Wood et al. 1975). Rates of CO<sub>2</sub> production were calculated by using equation 2 in Nagy (1980), and water flux rates were calculated by using equation 4 in Nagy and Costa (1980). Body water volumes were estimated at initial capture from dilution of injected oxygen-18 (Nagy 1980). Water volumes at recaptures were calculated as initial fractional water content multiplied with body mass at recapture.

### FOOD CONSUMPTION

Field metabolic rates were converted from units of CO<sub>2</sub> production to units of energy (J) by using the factor 26.5 J/ml CO<sub>2</sub>. This factor was calculated from the chemical composition of capelin (74.4% water, 10.1% fat, 13.4% protein, and 1.9% ash; Utne 1976), using energy equivalents for fat and protein from Schmidt-Nielsen (1975). This calculation involves the assumption that the proportions of dietary fat and protein assimilated were the same as their proportions in the diet, and that kittiwakes ate only capelin during our study. In fact, kittiwakes fed primarily on capelin, but they consumed some arctic cod and various species of crustaceans as well (Mehlum and Giertz 1984; Lydersen et al. 1985; Giertz et al. 1985; R. T. Barrett, pers. comm.). However, the conversion factors for these diet items should be within 10% of that for capelin, due to similarities in the conversion factors for protein and fat (Schmidt-Nielsen 1975).

The amount of food an adult kittiwake would have to consume to satisfy its daily energy requirement (as measured with doubly-labeled water) was calculated from the energy content and energy assimilation efficiency for capelin. These fish contain 25.7 kJ/g dry matter, and 76% of this energy is available for metabolism by kittiwakes (Gabrielsen, Mehlum, and Brekke, unpubl. data). Thus, with a water content of 74.4%,

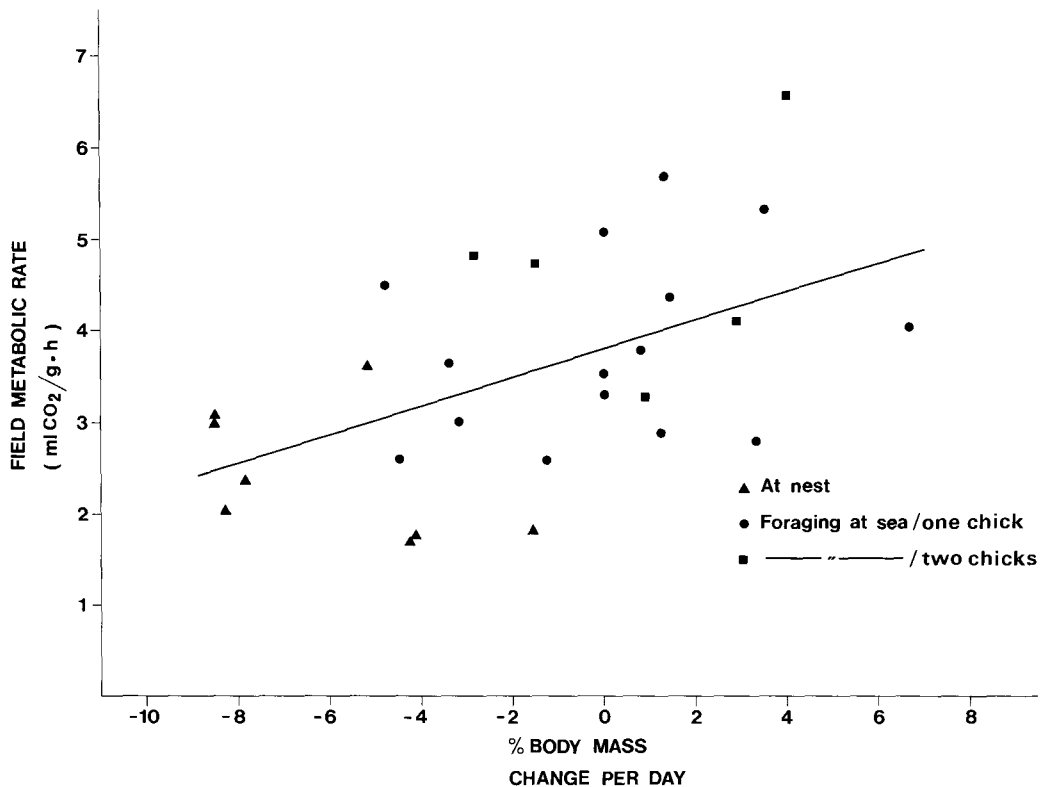


FIGURE 1. Relationship between field metabolic rate, measured with doubly-labeled water, and rate of increase or decrease in body mass for breeding adult kittiwakes at Hopen. The line is the least squares regression, where  $y = 3.82 + 0.16x$ ,  $r^2 = 0.26$ ,  $F_{1,26} = 9.06$ ,  $P < 0.01$ .

capelin contain 5.0 kJ metabolizable energy per g of fresh matter.

#### STATISTICS

Two-tailed *t*-tests were used to determine the significance of differences between means. Results are reported as mean  $\pm$  standard deviation. The regression line in Figure 1 was calculated by using the least-squares method of linear regression.

#### RESULTS

##### BODY MASS

Female kittiwakes had significantly lower body masses ( $367 \pm 11$  g) than did males ( $399 \pm 29$  g,  $P < 0.01$ ). However, there were no significant differences in mass-specific rates of  $\text{CO}_2$  production or water flux, or rates of body mass change between sexes, so mean body mass (386 g) and mean values for the rate processes were used in subsequent calculations. Kittiwakes maintained

body masses on average while foraging, but they lost body mass while brooding on their nests (Table 1).

##### FIELD METABOLIC RATE

Basal metabolic rate (BMR) measured in the laboratory was  $1.31 \text{ ml CO}_2/\text{g}\cdot\text{hr}$  or  $314 \text{ kJ/day}$  (Gabrielsen et al., unpubl.). Field metabolic rate ( $\text{CO}_2$  production) of foraging birds averaged  $4.04 \pm 1.11 \text{ ml CO}_2/\text{g}\cdot\text{hr}$  which is equivalent to  $992 \pm 273 \text{ kJ/day}$ , or 3.16 times BMR (Table 1). Non-foraging birds had significantly lower ( $P < 0.01$ ) metabolic rates, averaging  $2.43 \pm 0.73 \text{ ml CO}_2/\text{g}\cdot\text{hr}$ , or  $596 \pm 179 \text{ kJ/day}$  (1.90 times BMR).

There was a tendency (not statistically significant) toward higher field metabolic rates during foraging in parents that had two chicks ( $4.71 \pm 1.41 \text{ ml CO}_2/\text{g}\cdot\text{hr}$ ,  $n = 3$ ) than in parents having one chick ( $3.87 \pm 1.01 \text{ ml CO}_2/\text{g}\cdot\text{hr}$ ,  $n = 16$ ; see Fig. 1). There was a significant correlation between field metabolic rate and % body mass

TABLE 1. Field metabolic rate, water influx and body mass of adult kittiwakes on Hopen Island, 31 July to 8 August 1984.

Animal	Sex	Body mass		Field metabolic rate		Water influx rate	Measurement period (days)
		Mean, g	Change, %/day	ml CO <sub>2</sub> /g·hr	kJ/day	ml/day	
<b>While off nest</b>							
2	M	452.5	-3.38	3.64	1,048	115	0.98
2†	M	447.5	+1.29	5.69	1,619	277	0.99
3	M	387.5	+0.89	3.78	932	158	1.48
4*	F	352.5	+2.90	4.12	924	171	1.47
4*†	F	367.5	+4.00	6.60	1,543	366	1.02
5	F	372.5	+1.25	2.87	680	143	1.07
5†	F	375.0	0	5.19	1,238	241	1.45
8†	M	395.0	+3.49	5.31	1,334	246	1.45
8	M	412.5	+3.31	2.78	729	217	1.10
9	M	402.5	-3.08	3.01	771	217	2.02
10*†	F	367.5	-2.85	4.83	1,129	196	1.43
10*	F	362.5	+0.88	3.30	761	231	1.57
11†	M	432.5	+1.41	4.37	1,202	190	0.82
11	M	435.0	0	3.30	703	198	1.05
13	M	400.0	-4.46	2.62	667	209	1.12
15	M	387.5	-1.16	2.60	641	137	1.11
15	M	377.5	-4.79	4.51	1,083	244	0.83
19	M	400.0	+6.64	4.04	1,028	207	1.13
21*	F	365.0	-1.49	4.73	1,098	172	1.86
23	F	340.0	0	3.54	765	179	1.66
Mean		391.6	+0.24	4.04	995	206	
SD		31.5	3.01	1.11	290	56	
<b>While on nest</b>							
6	F	367.5	-8.30	2.06	481	51	0.82
6	F	362.5	-4.23	1.70	392	27	1.02
7	F	342.5	-1.57	1.83	399	34	0.93
12	F	387.5	-7.87	2.36	582	38	0.82
19	M	400.0	-8.52	3.00	763	46	0.88
20	M	395.0	-8.53	3.11	781	36	0.89
20	M	372.5	-4.15	1.74	412	47	0.97
23	F	365.0	-5.20	3.61	838	33	0.83
Mean		374.1	-6.05	2.43	581	39	
SD		19.1	2.63	0.73	188	8	

\* Nest contained two chicks.

† Off nest during windy day.

change per day in kittiwakes (Fig. 1; least-squares regression analysis;  $F_{1,26} = 9.06$ ,  $P < 0.01$ ). Weather conditions also affected field metabolic rate. There was a significant increase ( $P < 0.001$ ) in energy expenditure of foraging birds during a 24-hr period of strong southwesterly winds from  $3.44 \pm 0.59$  ml CO<sub>2</sub>/g·hr ( $n = 5$ , wind speed = 7.8 m/sec) before, or  $3.67 \pm 0.92$  ml CO<sub>2</sub>/g·hr ( $n = 6$ , wind speed = 8.3 m/sec) after strong winds to  $5.33 \pm 0.77$  ml CO<sub>2</sub>/g·hr ( $n = 6$ , wind speed = 12.8 m/sec) during strong winds.

Rates of water influx were highest ( $P < 0.01$ ) when kittiwakes were off their nest (Table 1). Body water contents averaged  $61.4 \pm 2.2\%$  of body mass ( $n = 17$ ).

Visual observation of six marked birds by telescope, checked each 30 min, showed that kittiwakes at Hopen Island spent an average of 23 hr away from the nest (range, 17.0–29.5 hr). Both parents participated in brooding and feeding of the chicks. The brooding birds remained on the nest until relieved by their mates. Three of 17 studied kittiwakes raised two chicks.

#### FOOD CONSUMPTION

The amount of food a typical adult kittiwake would have to consume to satisfy its own energy requirements was calculated from field metabolic rate measurements as follows. Energy expenditure during one day on the nest was 597

kJ/bird, and one day foraging cost 992 kJ/bird to give a total two-day expenditure of 1589 kJ/bird. At a metabolizable energy yield of 5.0 kJ/g fresh mass of food (see above), the kittiwake must consume 315 g fresh food or about 82% of its body mass. All of this food would be consumed on the day the bird foraged.

We can check this estimate of feeding rate by calculating its associated water influx rate, and comparing this with actual influxes measured with tritiated water. A mass of 315 g of capelin, at 74.4% water, contains 234 ml of H<sub>2</sub>O. Metabolically-produced water, from oxidation of assimilated protein and lipid, would provide an additional 0.122 ml H<sub>2</sub>O/g fresh food (conversion factors from Schmidt-Nielsen 1975), for a total water yield of 272 ml H<sub>2</sub>O/315 g capelin consumed. This is about 11% higher than the measured two-day water influx of 245 ml H<sub>2</sub>O/bird (Table 1). The difference may be due to our assumption that 100% of the diet was capelin, which has a relatively high water content. Ingestion of other foods with lower water contents would improve the agreement. Moreover, measured water influxes in Table 1 may underestimate those in kittiwakes maintaining steady-state, because our experimental birds, on average, were slowly losing body mass (Table 1). Thus, they were probably not eating quite enough food to meet their energy expenditures, with the difference coming from energy stored in their bodies. This comparison suggests that the feeding rate estimated from energy expenditure is reasonable, and that kittiwakes consumed little or no sea water while foraging.

## DISCUSSION

The FMR of free-ranging kittiwakes was ca. 1.9 times BMR when brooding and ca. 3.1 times BMR when they were off their nests. These values are in accordance with studies of other species in which isotopically-labeled water has been used on breeding birds (Utter 1971, Utter and LeFebvre 1973, Hails and Bryant 1979, Bryant and Westerterp 1980, Weathers and Nagy 1980, Nagy et al. 1984, Ricklefs and Williams 1984). Hails and Bryant (1979) found higher FMR in male Common House-Martins (*Delichon urbica*) feeding their broods. Male European Starlings (*Sturnus vulgaris*) expended less energy during the middle of the nesting period than females (Ricklefs and Williams 1984). In our study there was no significant difference between males and fe-

males in FMR. Our study was performed during a short period when the adults were brooding and feeding their chicks. A longer experimental period, more measurements, and stable weather conditions are required to explore for possible sexual differences in FMR. Feeding modes are probably very different in seabirds as compared with house-martins or starlings. Seabirds forage at a much longer distance from the nest than do martins or starlings.

At Hopen both parents shared in feeding of their chicks. Three of 17 parents studied were feeding two chicks. FMRs averaged ca. 3.0 times BMR in parents feeding one chick, and ca. 3.6 times BMR in parents feeding two chicks, but this difference is not statistically significant due to high variability in FMR data (Fig. 1). Although Ricklefs and Williams (1984) found that FMR was independent of brood size in starlings, Hails and Bryant (1979) found a significant correlation between FMR and brood mass in male house-martins. An increase in brood size from three to four young entails an average increase in energy expenditure by female house-martins of 18%. This is in accordance with our study which indicated an FMR increase of 20% in kittiwakes feeding two chicks. The parents of two chicks probably have to spend more time flying while searching for food, and they may also spend more energy to carry a greater mass of food from the foraging area. Purple Martins (*Progne subis*) and house-martins showed an increase in energy expenditure with increased rate of food delivery to the brood (Utter and LeFebvre 1973, Hails and Bryant 1979, Bryant and Westerterp 1983).

Bryant and Westerterp (1983) found a significant correlation between FMR and weather factors (ambient temperature and windspeed). Fair weather (warm and calm days) resulted in higher energy expenditure. This was associated with better food supply (flying insects), more time spent in flight and a greater amount of food brought to the nestlings. Foraging kittiwakes showed a significant increase in FMR during one day of heavy wind. This is probably not due to an increased cost of capturing prey, but rather to an increased energy cost for flapping flight. The energy cost of flight in free-living birds should not be calculated as a given multiple of BMR, as is done in many models (summarized by Flint and Nagy 1984). Behavior and aerodynamic properties are certainly important factors, but weath-

er also has a large influence on the energy expenditure during flight. High wind increases flapping time at the expense of gliding or soaring in kittiwakes.

Behavioral observations of six marked pairs of kittiwakes on Hopen island showed that they spent an average of 23 hr away from their nests during the chick rearing period. We assume that kittiwakes spent much of their time foraging while not on their nests, but they may also have been resting at the breeding island. During the experimental period, flocks of several hundred kittiwakes were often seen resting close to the breeding colony. Most often these birds were sitting with their heads under their wings, but they were also seen preening. Thus, our measurements of FMR and water flux during off-nest periods may include periods of rest as well as foraging bouts.

Kendeigh et al. (1977) provide equations for estimating daily energy expenditure of birds, and these have often been used in models for estimating energetics of seabird populations (Wiens and Scott 1975, Furness 1978, Furness and Cooper 1982, Furness and Barrett 1985). These equations compensate for the effect of temperature on energy metabolism, but Kendeigh et al. (1977) suggest that they may underestimate metabolism for birds breeding at high latitude. Nagy et al. (1984) made DLW measurements of FMR in Jackass Penguins (*Spheniscus demersus*), and found close agreement with the predictions from Furness and Cooper's (1982) bioenergetic model, which is based on Kendeigh's equations. Kendeigh's equation (0°C) predicts a daily energy expenditure for a 386-g kittiwake of 443 kJ/day. Actual FMRs were 36% higher in kittiwakes on the nest, and 123% higher for birds off the nest.

Walsberg's (1983) equation for daily energy expenditure, based on studies of 42 avian species, gives an estimate of 479 kJ/day for a 386-g kittiwake. Actual FMRs were 21% higher (on nest) and 108% higher (off nest, Table 1). These comparisons indicate that caution should be taken when modelling energetics of northern seabirds using equations by Kendeigh et al. (1977) and Walsberg (1983) to estimate daily energy expenditure.

A breeding kittiwake eats an average of 315 g of fresh capelin every other day (assuming a diet of capelin only). This represents only the food an adult needs for its own energy requirements, and does not include food given to its young. Based on metabolism and growth rate measure-

ments on growing kittiwake chicks (Gabrielsen and Mehlum, unpubl.), and assuming that they have the same assimilation efficiency as adults, we estimated that a 10-day-old chick would consume about 100 g of fresh food each day. Thus, the food requirements of the two adults and one chick (age 10 days) at a typical nest would be 415 g fresh fish per day. A colony of 3,000 breeding pairs (including one chick in each nest) of kittiwakes would therefore consume about 1245 kg of capelin per day. At a dry matter digestibility of about 75% (Gabrielsen and Mehlum, unpubl.), we estimate that about 76 kg (dry matter) of nitrogen-rich guano is added to the Hopen island ecosystem each day by this colony alone. Much of this guano is deposited on the terrestrial portion of the system.

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