Individual Variation in Field Metabolic Rate of Kittiwakes (*Rissa tridactyla*) during the Chick-Rearing Period

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ABSTRACT

Field metabolic rate (FMR), using the doubly labelled water (DLW) method, was measured in free-ranging adult kittiwakes (*Rissa tridactyla*) early and late in the chick-rearing period at Svalbard, Norway. Individual variation in FMR was analysed by comparing FMR with body mass, sex, nest attendance, chick age, brood size, and basal metabolic rate (BMR). Mean FMR of kittiwakes during the chick-rearing period was 27.0 ± 0.9 (SE) W kg^{-1}, while the individual variation (calculated as coefficient of variation [CV]) in FMR was 24%. Sex, time spent away from the nest, age of the chicks, and brood size contributed significantly to FMR and explained 65% of the variation in FMR. The FMR increased by 32% from early until late in the chick-rearing period. This occurred simultaneously with an increase in the time spent away from the nest. In 15 of 20 pairs, one of the mates had 15% or higher (mean of the 15 pairs, 22% ± 8%) FMR (W kg^{-1}) than their partner, even though the mates spent equal amounts of time away from the nest. This indicates an intrapair conflict in FMR. The variation in total FMR of pairs was 40% less than the individual variation, and total FMR of pairs increased with age of the chicks. This indicates that the mates adjust their energy expenditure within a relatively constant FMR determined by the energy needs of the chicks. Individual variation in FMR could not be explained by variation in body mass or BMR. BMR measured late in the chick-rearing period was 26% lower than previous measurements of BMR from the prebreeding and incubation periods. The increase in FMR and simultaneous decrease in BMR caused a 40% increase in metabolic intensity (FMR/BMR) of kittiwakes during the chick-rearing period. It is suggested that the metabolic intensity is not a proper measure of the metabolic load in seabirds.

Introduction

The efficiency of acquiring and spending energy is of utmost importance for survival and reproductive success of an animal. Individual variation in the animal's capacity to adjust energy expenditure might, therefore, influence fitness. Even so, most studies have regarded individual variation in field metabolic rate (FMR) as unwanted noise, and few studies have investigated the proximate causes of this variation in free-ranging birds (see Tindbergen and Dietz 1994; Nagy et al. 1999*a*). A large interspecific variation in FMR (the highest being almost six times greater than the lowest) exists after adjusting for body mass and phylogenetic order (Nagy et al. 1999*b*). Intraspecifically, the relationship between FMR and body mass is not as pronounced as interspecific comparisons (e.g., Speakman et al. 1994; Tindbergen and Dietz 1994). To understand the individual variation in FMR, it is therefore necessary to identify factors other than body mass and phylogeny that may influence FMR in birds.

Because activity comprises the largest part of FMR, variation in cost of locomotion is one important factor influencing FMR. Breeding birds frequently fly to and from the nest, and different distances to the foraging area could conceivably contribute to variation in FMR. Differences in the workload between sexes caused by unequal sharing of breeding duties have also been shown to cause considerable differences in FMR (e.g., Williams 1987; Masman et al. 1989). For birds rearing dependent chicks, the energy needs of the chicks often comprise a large fraction of the food gathered by the parents (Ricklefs and Williams 1984), thus influencing FMR of the parent. In species where the chicks' energy demands increase from hatching to fledging, age of the chicks could cause additional increases in the FMR of the parents. Although this relationship has not been shown previously in seabirds, it is expected, considering the high foraging costs of many seabirds (Konarzewski et al. 1993). Seabirds

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collect less food than terrestrial species with the same level of energy expenditure and thus have higher foraging costs (Konarzewski et al. 1993). Similarly, one would expect that the higher energy demands of a larger brood would be reflected in the parents' FMR. A positive correlation between natural brood size and FMR has only been found in some terrestrial bird species (Hails and Bryant 1979; Williams 1987). Until now, a similar correlation has not been observed in seabirds.

The higher basal metabolic rate (BMR) of birds (Nagy et al. 1999*b*) has been suggested as one explanation for the higher FMR of birds compared with mammals. A similar proposal has been made between groups of birds, for example, marine versus terrestrial birds (Bennett and Harvey 1987). Intraspecifically, however, a similar relationship among individuals is yet to be found (Nagy et al. 1999*a*). It has been suggested that BMR represents the metabolic machinery that limits metabolic output (Daan et al. 1990). Individual variations in BMR might therefore be reflected in the individual variations in FMR of animals working close to their physiological capacity. The breeding season has been suggested to be the most energy-demanding period for adult birds (Drent and Daan 1980). Seabirds in the Arctic breed at low ambient and seawater temperatures with high foraging and thermoregulatory costs; hence, it is suggested that they work close to their physiological capacity during the breeding season. Arctic breeding seabirds should, therefore, be ideal for the study of an intraspecific relationship between FMR and BMR.

During the arctic summer on Svalbard, Norway, kittiwakes (*Rissa tridactyla*) breed close to the northernmost limits of the breeding range. Previous studies on kittiwakes have indicated an individual variation in FMR of 30%–40% (coefficient of variation) during the breeding season (Gabrielsen et al. 1987; Thomson et al. 1998; G. W. Gabrielsen and F. Mehlum, unpublished data). Kittiwakes often rear two chicks that achieve adult body mass before fledging (Barrett 1978). From hatching to fledging (ca. 35 d; Barrett and Runde 1980), the chicks show a threefold increase in their energy demands (Gabrielsen et al. 1992). The harsh climatic conditions at Svalbard and the rapid growth to adult size involving a corresponding increase in energy demands of the chicks could indicate that the adult kittiwakes in these areas work close to their physiological capacity. Under such conditions, individual variations in acquiring and spending energy may have direct consequences for the reproductive success of kittiwakes. This species should therefore be an excellent model for studying the factors that cause the variation in FMR.

The aim of this study was to examine the most important factors contributing to the individual variation in FMR of breeding kittiwakes. Thus, energy expenditure was estimated from CO_2 production using the doubly labelled water (DLW) method in individuals experiencing different energy constraints. Factors considered in untangling the causes of individual variation in FMR were body mass, sex, nest attendance, chick age, brood size, and BMR.

Material and Methods

Birds

Kittiwakes (*Rissa tridactyla*) rearing chicks in a small ($n \approx$ 200 pairs) colony 8 km east of Ny-Ålesund, Kongsfjorden, Svalbard, Norway (78°55′N, 11°58′E), were studied. The studies were performed between July 13 and August 10 in 1997 and between July 23 and August 6 in 1998. The experiments were performed under licence of Norwegian Veterinary Authorities and the Governor of Svalbard.

Weather

Temperature, wind speed, and precipitation were measured at the Research Station of the Norwegian Polar Institute in Ny-Ålesund. Weather conditions during the study periods in 1997 and 1998 were not significantly different from those of a standard year. The mean ambient temperature during the chick-rearing period (from mean hatching date until the studies were finished, 22 and 26 d in 1997 and 1998, respectively) was 5.5°C (SD = 1.3°C), mean wind speed was 4 m s^{-1} (SD = 2 m s^{-1}), and total precipitation was 39.6 mm. There was continuous daylight during the chick-rearing period. The colony was in the shade from 0800 to 2000 hours.

Biometric Measurements

The birds were caught on their nest using a 7-m-long pole with a noose at the end. Immediately after being captured, the birds were placed in a nylon bag and weighed. Initially, the birds were sexed by measuring head and bill lengths (females <92 and males >92 mm) using a slide caliper (±0.01 mm) according to Barrett (1978). The individual with the largest head in a pair was assumed to be the male (Coulson et al. 1983). This method has been shown to sex kittiwakes with 87% accuracy (Barrett et al. 1985). For other purposes, 32 birds were killed after the experiments and were sexed correctly. To identify the birds at the nest, the males and females were colour marked on their heads with permanent markers. Body mass was measured in the field using Pesola spring balances (±5 g) in 1997 and a Sartorius BL 3100 (Sartorius AG, Göttingen) electronic balance (±0.01 g) in 1998. In the laboratory (BMR measurements), body mass was measured using a Mettler PE16 (Mettler Instruments AG, Greifensee-Zurich) electronic balance (±0.001 g).

Behavioural Studies

Nest attendance of the birds was recorded to study the effect of handling in the DLW experiment. Nest attendance was quantified by recording the individuals attending the nest, the duration and number of foraging trips, and the total time spent away from the nest. In addition, changes in nest attendance were also recorded when the chicks grew older. The pattern of nest attendance was compared with the FMR measurements. In 1997, nest attendance was recorded every 20 min for 24 h before the DLW injection and for 24 h 1 d after the DLW injection. In 1998, nest attendance was continuously recorded for 24 h before the DLW injection and at intervals every 20–60 min between the DLW injection and recapture. Direct visual observations of the behaviour were performed from a beach 20 m away from the colony.

Field Metabolic Rate

The DLW method (Lifson and McClintock 1966; Nagy 1980) was used to estimate FMR of adult kittiwakes with small (5–10 d old) and large (19–24 d old) chicks. A total of three DLW series were performed, two in 1997 and one in 1998. In 1997, both birds in 12 pairs were injected with DLW when the chicks were 5–7 d old. Of these, 12 birds (six females and six males) were reinjected when the chicks were 19–21 d old. In 1998, both birds in 11 pairs, in addition to two females and three males (a total of 27 birds), were injected with DLW when the chicks were 21–23 d old. The birds in 1997 and 1998 were injected with 1.2 and 1.1 mL DLW ($^3H_2{}^{18}O$), respectively, containing 90.4%–91.5% $H_2{}^{18}O$ (YEDA-Stable Isotopes, Rahavot, Israel) and 0.4 mCi ^3H_2O (New England Nuclear). The dose was injected intramuscularly into the pectoral muscle using a 2.5-mL syringe. The entire procedure lasted 5 min. The birds were placed in a cage covered with a blanket for at least 1 h to let the isotopes become completely equilibrated with the body water (Degen et al. 1981). A blood sample was taken by carefully puncturing a brachial vein with a needle and collecting the droplets that formed around the wound into 4 × 70-μL heparinized glass capillary tubes. These tubes were immediately flame sealed and refrigerated until analysis. All birds returned to their nests within 5 h after release. During the next 3 d, we managed to recapture 30 of the birds in 1997 and all of the birds in 1998 for a second blood sample. In addition, a third blood sample was taken within 3 d postinjection from 15 and 23 birds in 1997 and 1998, respectively.

The analyses of isotope levels in blood samples were performed at University of California, Los Angeles. Blood samples were vacuum distilled to obtain pure water. Tritiated water was measured for specific activities by liquid scintillation, and the ^{18}O levels were measured by the proton-activation method (Wood et al. 1975). Four of the blood samples in 1997 were rejected because of problems with isotope levels (K. A. Nagy, personal communication). In two of these samples, the levels of ^{18}O were <5% above background level in the final samples, and in the other two samples, the values of ^3H were unaccountably high in the final samples, probably because of contamination. FMR was finally estimated for both birds in nine pairs and another eight individual birds, giving a total of 26 kittiwakes in 1997, and both birds of 11 pairs and another five individual birds, a total of 27 kittiwakes, in 1998. In each year, blood samples from three nonmanipulated kittiwakes were collected as described above to determine background levels of ^3H and ^{18}O in kittiwakes. The background levels were 33 and 25 cpm for ^3H and 1,996 and 2,032 ppm for ^{18}O in 1997 and 1998, respectively.

Body water volumes were estimated from the dilution volumes of injected $H_2{}^{18}O$ at day 1 of the experiments. Body water volumes at recapture were estimated on the basis of the measured body mass and by assuming the birds had the same fraction of body water content throughout the experiment (Nagy 1983). This assumption could be wrong, as most of the body mass changes in seabirds during DLW studies are caused by stomach content and unassimilated water (Roby and Ricklefs 1986). However, because it has been estimated that body mass has to change >50% to have significant impact on the estimation of CO_2 production (Nagy 1980) and the largest body mass change in this study was only 8%, we feel justified in using this assumption. Carbon dioxide production and water flux between DLW equilibration and recapture were estimated for each bird using Equation (2) in Nagy (1980) and Equation (4) in Nagy and Costa (1980), respectively, as modified from Lifson and McClintock (1966). These equations adjust for physical fractionation effects and account for the background enrichment of ^3H and ^{18}O of the blood as a single compartment. Hence, the equations assume that the exchange of hydrogen from the nonaquatic hydrogen pool balances the difference in dilution space between hydrogen and oxygen (Speakman 1990). FMR (expressed in watts) was calculated using a caloric equivalent of 25.6 J mL $CO_2{}^{-1}$ produced. The caloric equivalent for CO_2 was based on analysis of fat and protein content of regurgitated samples from kittiwakes during the experimental periods, assuming that the energy for FMR was mainly derived from catabolism of ingested food. This assumption is based on the fact that body mass changed very little during the measurement period (Tables 2, 3).

The most abundant food items eaten by kittiwakes during the chick-rearing period were the teleost *Boreogadus saida*, the crustaceans *Thysanoessa* sp. and *Parathemisto libellula*, the mollusc *Limacina helicini*, and the annelid *Nereis* sp. One sample (range 10–60 g wet weight) of each of the five food items was homogenised in a food processor and dried at 56°C to constant mass using an incubator (Termaks, Bergen, Norway). Protein (Kjeldahl nitrogen extraction) and fat content (fat extraction using methyl ether) were determined from dry samples. The caloric equivalent of CO_2 production was estimated assuming that only fat and protein contributed to the energy of the food. The caloric equivalent for the species analysed varied by less than ±1% (coefficient of variation [CV]). The mean caloric equivalent of all food samples was, therefore, used in the calculation.

Basal Metabolic Rate

After the DLW experiments were finished late in the chick-rearing period, rates of oxygen consumption ($\dot{V}O_2$) were measured using open-circuit respirometry on 12 (seven females and five males) and 15 (nine females and six males) of the kittiwakes used in the DLW experiments in 1997 and 1998, respectively. The birds were caught on the nest and placed in cages before being transported to the laboratory of the Norwegian Polar Institute in Ny-Ålesund. The transport lasted approximately 45 min. To ascertain that the kittiwakes were in a postabsorptive state when the $\dot{V}O_2$ measurement started, the kittiwakes were kept in the cage for at least 3 h (7.6 ± 4.6 [SD] h) before being placed into a metabolic chamber. The experimental setup was identical to the one described by Bech et al. (1999). Outside air was dried over silica gel and drawn through a 25-L temperature-controlled metabolic chamber with a flow rate of approximately 2.2 L min^{-1}. The actual flow rates were measured using a calibrated mass flow meter (type 201C-FA, Bronkhorts Hi-tek, Ruurlo, The Netherlands). An aliquot of the effluent air was dried over silica gel, and the oxygen concentration was measured using an oxygen analyser (type 244A, Servomex, Crowborough, U.K.). To allow a period of adaptation to the new surroundings, the first hour of metabolic measurements was not used in the calculation of $\dot{V}O_2$. The $\dot{V}O_2$ used for BMR calculation was measured, on average, 6.6 ± 2.1 (SD) h after the kittiwakes were placed in the chamber. Previous metabolic studies on kittiwakes have revealed no diurnal variations in BMR (Bryant and Furness 1995; G. W. Gabrielsen and F. Mehlum, unpublished data). The metabolic measurements were, therefore, performed both during day- and nighttime. Each bird was weighed immediately before and after the experiment, and a linear decrease in body mass during the metabolic measurement was assumed when assessing whole body $\dot{V}O_2$ (mL O_2 min^{-1}) to mass specific $\dot{V}O_2$ (mL O_2 g^{-1} h^{-1}). The rates of $\dot{V}O_2$ were calculated using formula (3A) in Withers (1977) and corrected for washout delay in the system by the method described by Niimi (1978). Measurements of BMR, based on short measurement intervals (<5 min), give high stochastic variance. This is in contrast to long intervals (>30 min) that may include periods of activity. The choice of an intermediate interval gives the least rise in $\dot{V}O_2$ with increasing intervals (Hayes et al. 1992; Meerlo et al. 1997). By plotting the $\dot{V}O_2$ of three randomly selected kittiwakes, based on intervals from 2 to 60 min, an interval of 25 min gave the most stable $\dot{V}O_2$ and was, therefore, used when calculating BMR (Bech et al. 1999). In this study, a respiratory quotient of 0.73 was assumed. This assumption is based on previous measurements of $\dot{V}O_2$ and CO_2 production in kittiwakes, using almost the same procedure as in this study (G. W. Gabrielsen and F. Mehlum, unpublished data). This gives a caloric equivalent of 19.9 J mL $O_2{}^{-1}$ consumed when converting $\dot{V}O_2$ to energy expenditure.

Mass-specific BMR (W kg^{-1}) of kittiwakes rearing young chicks was estimated from measurements of BMR on kittiwakes early in the chick-rearing period (Bech et al. 1999). This BMR was used to express metabolic intensity (FMR/BMR) of kittiwakes rearing small chicks in this study. The average measured BMR (W kg^{-1}) of kittiwakes rearing large chicks was used to express metabolic intensity for those kittiwakes ($n = 12$) in which individual BMR measurements were not performed.

Statistics

The values are presented as $\overline{X} \pm 1$ SE if not otherwise noted. The individual variation is expressed as the CV, calculated as SD × $100/\overline{X}$. Two-tailed Student's *t*-tests were used to compare two independent, normally distributed means. Paired *t*-tests were used to test for differences between two measurements on the same individuals within a group. Relationships between two variables were examined using least square regression analysis. Standard linear multiple regression analysis was performed to test FMR (dependent variable) against sex, body mass, age of the chicks, brood size, time off nest, and BMR (independent variables). In 1997, FMR was measured twice during the chick-rearing period of the same birds. To be able to perform parametric tests, FMR from kittiwakes rearing old chicks in 1997 was excluded from further analysis. Year did not have any influence on the results (Student's *t*-test), and data obtained from 1997 and 1998 were, therefore, pooled. To examine the effect of sex on FMR, mass-dependent FMR was used as the dependent variable because body mass was significantly different between the sexes ($P < 0.001$). BMR did not show any relationship with FMR and was therefore excluded as a variable. The regression analysis was performed using sex, brood size, time off nest, and age of chicks as independent variables. Sex and brood size were categorical variables. Time off the nest and the age of the chick were continuous variables. There was no effect of covariance between independent variables used in the analysis.

The repeatability of the FMR was calculated from the variance components derived from a one-way ANOVA test, as described by Lessels and Boag (1987). Because the mean values of FMR varied between the experimental periods, we were unable to use the actual FMRs in the ANOVA test. Instead, we used residual values based on values of individual regressions of log FMR on log sex, chick age, time off nest, and brood size for the first day and second day in each experimental period. The predicted FMRs were thereby obtained from multiple regression analysis as described above. In this way, equal mean values were assumed. All statistical tests were performed using Statistica 5.0, and the results were considered significant when $P < 0.05$.

Results

Effect of Handling

There were no significant differences between sexes in nest attendance among kittiwakes raising either small or large chicks. In the experiments in 1997, the behavioural studies started 1 d after the DLW injection. The handling associated with the use of the DLW method had no influence on the nest attendance in the first DLW experiment (Fig. 1). In the second DLW experiment in 1997, the kittiwakes showed a reduced nest attendance from 7.4 ± 1.7 h d^{-1} before injection to 4.1 ± 1.2 h d^{-1} after injection. During the same period, however, unmanipulated kittiwakes showed a reduction in nest attendance almost identical to the DLW-injected birds (Fig. 1). During the experiment in 1998, when the behavioural studies started immediately after the injection, there was a significant reduction ($P < 0.001$) in the time spent on the nest the day following the DLW injection (10.4 ± 0.8 and 6.7 ± 0.7 h d^{-1} before and after injection, respectively). When comparing the nest attendance before injection with days 2 and 3 after injection, there was a significant reduction in the nest attendance (from 10.4 ± 0.8 to 9.2 ± 1.2 h d^{-1}; $P < 0.01$, paired *t*-test).

FMR

The FMRs of individuals are presented in Tables 1–3. There was a significant correlation ($r^2 = 0.50$, $P < 0.001$) between the FMR from the first and second recapture after injection ($n = 32$) during the DLW experiment early in 1997 and late in 1998 (Fig. 2). A repeatability of 0.64 ($P < 0.01$) was found for FMR between the first and second day of the DLW experiments. This indicates a good repeatability of FMR in kittiwakes, at least over an interval of 1 d. The similar mean of FMR between days indicates that the reduced nest attendance because of handling had no effect on total energy expenditure of breeding kittiwakes during the DLW experiment.

The FMR of kittiwakes rearing small chicks in 1997 was 22.3 ± 0.6 W kg^{-1} (4.1 ± 0.1 mL CO_2 g^{-1} h^{-1}; Fig. 3). The FMR of kittiwakes rearing larger chicks was 33.4 ± 4.4 W kg^{-1} (4.7 ± 0.6 mL CO_2 g^{-1} h^{-1}) in 1997 and 29.5 ± 1.1 W kg^{-1} (4.2 ± 0.2 mL CO_2 g^{-1} h^{-1}) in 1998. The 32% difference in FMR between kittiwakes rearing small chicks in 1997 and larger chicks in 1998 was significant ($P < 0.001$). There was a tendency ($P < 0.07$) toward an increase in FMR of 50% in kittiwakes during the chick-rearing period in 1997 (Fig. 3).

Body Mass

Female body mass was significantly ($P < 0.001$) less than male body mass during the entire chick-rearing period. Both sexes showed a decrease in body mass of about 8% in 1997 and 6% in 1998 between the early (382 ± 7 g) and late (350 ± 14 g in 1997 and 362 ± 6 g in 1998) chick-rearing periods. There was a significant positive correlation ($r^2 = 0.19$, $P < 0.05$) between FMR (W kg^{-1}) and body mass among kittiwakes raising small chicks (FMR = 0.02 × BM [g] + 2.58). There was no such relationship among kittiwakes raising large chicks.

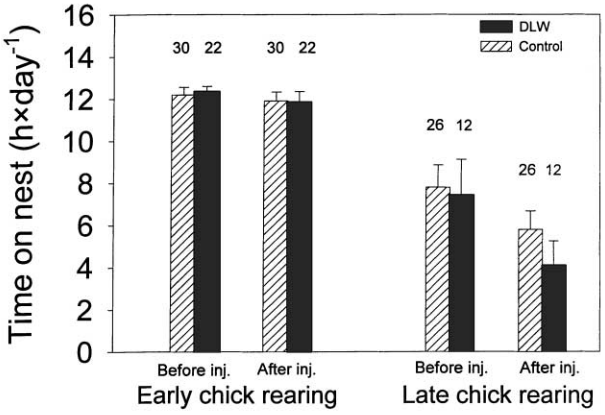

Figure 1. Nest attendance of kittiwakes before and after injection of doubly labelled water (DLW) early and late in the chick-rearing period in Kongsfjorden, Svalbard, Norway, July 15–30, 1997. The control group consisted of birds not injected with DLW. Data are presented as $\overline{X} \pm 1$ SE, with number of individuals indicated above each column.

BMR

The BMR of individuals are presented in Tables 2 and 3. There were no significant differences between the BMR measurements performed with adults rearing old chicks between 1997 and 1998 or between sexes. There were no correlations between the measured BMR and time of the day, time from catching at the nest, or time spent in the metabolic chamber.

The mean body mass of the birds during the BMR measurements was 328 ± 5 g. Mean BMR was 7.2 ± 0.1 W kg^{-1} (1.3 ± 0.03 mL O_2 g^{-1} h^{-1}). There was a significant correlation ($r^2 = 0.39$, $P < 0.001$) between mass-dependent BMR (W kg^{-1}) and body mass. There was no relationship between mass-specific BMR and FMR ($r^2 = 0.06$, $P = 0.4$).

The metabolic intensity (FMR/BMR) increased from 2.6 × BMR (range 2.1–3.2) to 4.2 × BMR (range 2.7–5.9) when rearing small and large chicks, respectively. Among individual kittiwakes in which both FMR and BMR were measured (only in birds rearing large chicks, $n = 27$), the metabolic intensity was 4.3 × BMR (range 2.8–6.3).

Sex

There were no differences in FMR between sexes when data were pooled ($P = 0.11$ in 1997 and $P = 0.41$ in 1998). In 14 of 20 pairs examined, however, the female had on average 23% higher FMR than the male. The females and males within pairs

Table 1: Field metabolic rate (FMR), time spent away from the nest, and age of the chicks of kittiwake breeding pairs in Kongsfjorden, Svalbard, Norway, in 1997 and 1998

			Males		Females		
Nest	Brood Size	Chick Age	FMR (W kg^{-1})	Time Off Nest (%)	FMR (W kg^{-1})	Time Off Nest (%)	Total FMR of the Pair[a] (W kg^{-1})
Early chick rearing:							
E06	1	7	20.5	46	24.2	52	44.6
E08	2	7	20.3	69	25.3	52	45.6
E14	2	5	22.0	54	24.7	44	46.6
E20	2	7	21.9	40	27.2	56	49.1
E26	2	7	21.7	52	25.7	48	47.5
F07	2	5–6	19.5	40	24.7	60	44.2
B67	2	5–6	18.6	…	19.9	…	38.5
E30	2	5	23.5	52	23.0	46	46.5
E32	2	5	25.4	50	20.0	50	45.5
Mean ± SE	1.9 ± .3	6 ± 1	21.5 ± .7	50 ± 3	23.8 ± .8	51 ± 2	45.3 ± 1.0
CV (%)			10		10		7
Late chick rearing:							
E11	2	26	26.9	56	33.8	100	60.6
E21	1	27	24.5	60	38.2	78	62.7
E08	1	27	27.1	60	31.8	70	58.8
E32	1	25	22.2	63	30.8	62	53.0
E20	2	23	32.1	74	28.4	64	60.5
E23	2	25	27.6	81	34.7	83	62.3
E19	2	23	31.4	89	33.0	87	64.5
E14	1	25	19.8	…	24.9	57	44.6
E33	1	25	29.6	63	23.8	72	53.4
E35	2	27	39.6	…	32.1	…	71.7
E31	1	25	38.4	…	22.3	50	60.8
Mean ± SE	1.5 ± .5	25 ± 1	29.0 ± 1.9	68 ± 4	30.3 ± 1.5	72 ± 5	59.6 ± 2.1
CV (%)			21		16		12

[a] The sum of FMR from the male and female in a pair.

spent similar time away from the nest during the chick-rearing period ($P = 0.31$ and $P = 0.16$ for kittiwakes raising small and large chicks, respectively).

Nest Attendance

The nest attendance between 1000 and 2200 hours was the same as between 2200 and 1000 hours. The nest attendance was similar between sexes, except for females with old chicks in 1997, when the females spent less time ($P < 0.03$) at the nest when compared with the males (5.1 ± 0.7 vs. 8.0 ± 1.1 h d^{-1}). In 1997, the kittiwakes showed a significant reduction in nest attendance ($P < 0.001$) as the chicks grew older (12.1 ± 0.2 vs. 6.5 ± 0.7 h d^{-1}; Figs. 1, 4). In 1998, kittiwakes with older chicks spent a significantly longer time (10.4 ± 0.7 h d^{-1}) on the nest ($P < 0.001$) compared with birds having chicks of the same age in 1997 but significantly less time ($P < 0.001$) compared with birds with small chicks from 1997.

There was no relationship between FMR and time spent away from the nest in 1997. However, a positive significant relationship ($r^2 = 0.50$, $P < 0.0001$) was found between FMR and time spent away from the nest in adult kittiwakes raising small chicks in 1997 and in birds raising large chicks in 1998 (Fig. 4; FMR [W kg^{-1}] $= 0.21 \times T + 13.03$, where T is the fraction [percentage] of time spent away from the nest between injection and recapture). When the chicks were small, there was a correlation ($r^2 = 0.33$, $P < 0.01$) between FMR and the number of times the parents returned to the nest (FMR [W kg^{-1}] $= 1.34 \times p + 17.74$, where p is number of times the parents returned to their nest between injection and recapture). No such correlation was found among kittiwakes having old chicks in 1997 and 1998.

Brood Size

Among kittiwakes with small chicks, there were no differences in nest attendance between birds rearing one or two chicks. As

Table 2: Field metabolic rate (FMR), average body mass, body mass change, total body water (TBW), water turnover rate (H_2O), age of the chick, and brood size of breeding kittiwakes in Kongsfjorden, Svalbard, Norway, July 19–31, 1997

Nest	Sex	Elapsed Time (d)	Body Mass (g)	Δ Body Mass (% d^{-1})	TBW (mL)	H_2O (mL d^{-1})	FMR (mL CO_2 g^{-1} h^{-1})	FMR (W kg^{-1})	$\dot{V}o_2$ (mL O_2 g^{-1} h^{-1})	BMR (W kg^{-1})	Brood Size	Chick Age (d)
Early chick rearing:												
B67	F	2.2	329	−.3	209	227	2.8	19.9	…	…	2	5–6
B67	M	2	393	−2.9	240	161	2.6	18.6	…	…	2	5–6
E06	F	2	364	−1.1	217	156	3.4	24.2	1.3	7.2	1	7
E06	M	2	403	−1.8	238	184	2.9	20.5	…	…	1	7
E08	F	2.1	361	−.4	205	204	3.6	25.3	1.2	6.6	2	7
E08	M	2.1	369	−7	268	229	2.9	20.3	1.7	9.4	2	7
E14	F	2	383	−.8	231	192	3.5	24.7	1.3	7.2	2	5
E14	M	2.2	433	−.4	327	212	3.1	22	1.2	6.6	2	5
E18	F	2.1	383	1.1	215	141	2.6	18.3	…	…	1	7
E20	F	2	371	.1	211	204	3.8	27.2	1.4	7.7	2	7
E20	M	2.7	368	−.5	212	232	3.1	21.9	…	…	2	7
E25	M	2	397	2.5	238	223	3.2	22.9	1.4	7.7	2	8
E26	F	2	350	−1.6	201	146	3.6	25.7	1.6	8.8	2	7
E26	M	2	434	3.1	230	231	3.1	21.7	…	…	2	7
E30	F	2	346	−1.2	212	147	3.2	23	1.5	8.3	2	5
E30	M	2	363	−.7	212	198	3.3	23.5	1.3	7.2	2	5
E32	F	2	363	−.7	214	215	2.8	20	1.1	6.1	2	5
E32	M	2	420	1.2	265	207	3.6	25.4	1.1	6.1	2	5
F07	F	2.1	374	−4.7	232	203	3.5	24.7	…	…	2	5–6
F07	M	2.1	389	−2.8	259	191	2.8	19.5	…	…	2	5–6
B72	M	2.1	440	8.2	242	221	2.7	19.3	…	…	2	5–6
$\overline{X}$ ± SE		2.1 ± .03	382 ± 7	−.5 ± .7	232 ± 6	196 ± 4	3.1 ± .1	22.3 ± .6	1.3 ± .2	7.4 ± .3		6 ± .2
Late chick rearing:												
E32	M	2.8	405	3.5	28	308	4.0	28.1			2	20
E32	F	2.0	341	2.6	206	338	2.8	19.5			2	20
E08	F	2.1	329	3.3	214	524	6.1	43.1			2	22
E26	F	2.1	329	2.3	212	300	4.8	34.3			2	22
E20	F	2.1	348	2.6	212	448	5.9	42.1			2	22
$\overline{X}$ ± SE		2.2 ± .1	350 ± 14	2.9 ± .2	226 ± 15	343 ± 43	4.7 ± .6	33.4 ± 4.4				21 ± .4

Note. Also included are measurements of basal metabolic rate (BMR) using open-circuit respirometry in the laboratory.

Table 3: Field metabolic rate (FMR), average body mass, body mass change, total body water (TBW), water turnover rate (H_2O), age of the chick, and brood size of breeding kittiwakes in Kongsfjorden, Svalbard, Norway, July 27–31, 1998

Nest	Sex	Elapsed Time (d)	Body Mass (g)	Δ Body Mass (% d^{-1})	TBW (mL)	H_2O (mL d^{-1})	FMR (mL CO_2 $g^{-1}h^{-1}$)	FMR (W kg^{-1})	$\dot{V}o_2$ (mL O_2 g^{-1} h^{-1})	BMR (W kg^{-1})	Brood Size	Chick Age (d)
E06	M	1	384	11.4	194	188	3.3	23.7	…	…	1	25
E08	F	2	344	−.3	220	192	4.5	31.8	1.2	6.6	1	27
E08	M	2.1	360	.7	219	130	3.8	27.1	1.2	6.6	1	27
E11	F	1.9	330	1.7	216	372	4.8	33.8	1.2	6.6	2	26
E11	M	2.2	340	1	195	247	3.8	26.9	…	…	2	26
E13	M	2.3	383	0	228	267	3.2	23	…	…	1	27
E14	F	2.1	359	.3	204	183	3.5	24.9	1.3	7.2	1	25
E14	M	3.2	401	.9	269	211	2.8	19.8	1.3	7.2	1	25
E15	F	2.9	322	.8	185	250	3.5	24.6	…	…	1	27
E18	F	2.2	328	2.1	200	230	5.2	37.2	…	…	2	21
E19	F	2.2	351	.9	207	368	4.7	33	1.2	6.6	2	23
E19	M	1.1	367	3.1	217	731	4.4	31.4	…	…	2	23
E20	F	2.1	338	1.3	202	208	4	28.4	1.3	7.2	2	23
E20	M	2.4	346	−.1	211	242	4.5	32.1	…	…	2	23
E21	F	2.2	330	2.6	195	226	5.4	38.2	1.3	7.2	1	27
E21	M	2.1	393	.5	239	236	3.5	24.5	1.3	7.2	1	27
E22	M	2.4	402	1.1	243	241	4.9	34.6	…	…	1	27
E23	F	1.1	341	5.6	191	250	4.9	34.7	…	…	2	25
E23	M	2.4	370	.1	219	172	3.9	27.6	…	…	2	25
E31	F	2.2	331	−.2	193	223	3.1	22.3	…	…	1	25
E31	M	1.7	433	11.3	245	246	5.4	38.4	1.1	6.1	1	25
E32	F	2	323	2.4	196	196	4.3	30.8	1.3	7.2	1	25
E32	M	2.2	392	.1	230	196	3.1	22.2	1.1	6.1	1	25
E33	F	2.3	363	1.5	211	154	3.4	23.8	1.5	8.3	1	25
E33	M	2.1	376	.8	223	215	4.2	29.6	…	…	1	25
E35	F	2.9	331	1.8	193	271	4.5	32.1	1.4	7.7	2	27
E35	M	1	353	6.3	216	295	5.6	39.6	1.2	6.6	2	27
$\bar{X}$ ± SE		2.1 ± .1	359 ± 6	2.1 ± 3.1	213 ± 4	208 ± 5	4.2 ± .2	29.5 ± 1.1	1.3 ± .1	7.1 ± .1	1.4 ± .1	25.3 ± .3

Note. Also included are measurements of basal metabolic rate (BMR) using open-circuit respirometry in the laboratory.

the chicks grew older, kittiwakes with two chicks showed a reduced nest attendance ($P < 0.01$) compared with kittiwakes having one chick (4.6 ± 1.0 vs. 8.4 ± 0.7 h d^{-1}; data from 1998). The difference in nest attendance and brood size was reflected in the FMR. Kittiwakes having two old chicks had 18% higher FMR ($P < 0.01$) compared with kittiwakes having one old chick (32.4 ± 1.2 W kg^{-1}, $n = 11$, vs. 27.6 ± 1.5 W kg^{-1}, $n = 16$). Because of uneven distribution of kittiwakes raising one or two chicks in the experiments in 1997 (18 birds with two chicks and three birds with one chick), a relationship between FMR and brood size was impossible to examine in the 1997 data set.

Individual Variation in FMR

The individual variation in FMR, expressed as CV, of kittiwakes rearing small chicks in 1997 and large chicks in 1997 and 1998, was 12%, 30%, and 19%, respectively. The mean individual variation in FMR during the chick-rearing period was 24% (CV). The independent variables used in the standard linear multiple regression analysis were sex, brood size, age of the chicks, and time spent away from the nest. Using these variables, FMR was predicted with an $r^2 = 0.65$ ($P < 0.0001$), indicating that 65% of the individual variation in FMR could be explained by the independent variables. Sex ($P < 0.01$), brood size ($P < 0.009$), age of chicks ($P < 0.003$), and time off nest ($P < 0.04$) contributed significantly to the individual variation in FMR.

Discussion

Effect of Handling and Repeatability of FMR

A change in activity level of the kittiwakes caused by the DLW experiment would diminish the value of the estimated FMR. The kittiwakes attending the DLW experiment exhibited reduced nest attendance during the day following the injection. However, our observations suggest that the birds behaved normally on the second day. The lack of a change in nest attendance

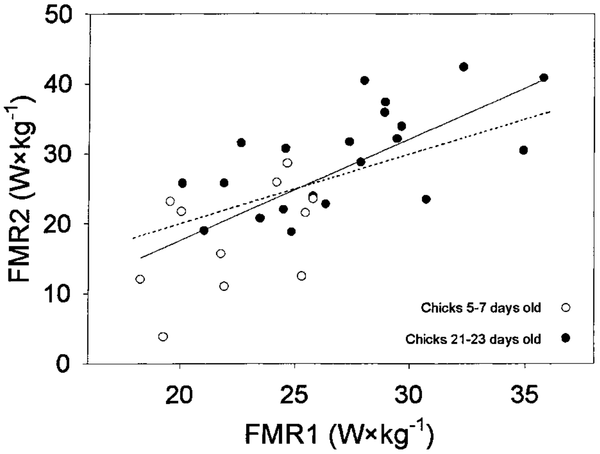

Figure 2. Relationship between field metabolic rate (FMR), measured with doubly labelled water (DLW), on the first (FMR1) and second day (FMR2) after DLW injection for breeding kittiwakes in Kongsfjorden, Svalbard, Norway, early and late in the chick-rearing period. Symbols represent measurements of individual kittiwakes. The correlation between FMR (W kg^{-1}) from the first (x) and second day (y) after DLW injection is shown by the solid line and expressed by the equation $y = 1.45x - 11.46$ ($r^2 = 0.50$, $P < 0.0001$). The dotted line indicates the relationship in which FMR1 equals FMR2.

in 1997 is most likely because the behavioural studies started 1 d after the injection. Furthermore, the similar mean FMR during the first and second recapture periods (Fig. 2) indicates that the change in nest attendance caused by handling did not cause a significant change in activity level. This finding is in accordance with DLW studies in Northern gannets (*Sula bassanus*), in which changes in behaviour caused by handling did not influence FMR (Birt-Friesen et al. 1989).

The difference in FMR between kittiwakes rearing small chicks in 1997 and those rearing large chicks in 1998 may have been caused by an annual effect (e.g., climatic differences or a difference in prey distribution). However, similar FMR among kittiwakes rearing large chicks in 1997 and 1998 suggests that the two years were comparable. In addition, hatching date, chick mortality, and chick growth were similar between the two years (M. Fyhn, I. Langseth, I. Naess, G. W. Gabrielsen, and C. Bech, unpublished data).

FMR of kittiwakes in this study showed high repeatability between the first and second day of each experiment (Fig. 2). Repeatability in FMR of birds has previously only been shown in female pied flycatchers (*Ficedula hypoleuca*; Potti et al. 1999). This study supports the suggestion by Berteaux et al. (1996) that repeatability in FMR is only expected to occur in animals experiencing energy-demanding periods.

Individual Variation in FMR

In this study, we have identified several important factors (sex, time spent away from the nest, age of the chicks, and brood size) that explain 65% of the individual variation in FMR of breeding kittiwakes.

The similar FMR between pairs indicates that the parents adjust their energy expenditure according to the chicks' energy needs, indicated by an increase of 31% in the total FMR of pairs from early to late chick-rearing period. Summation of FMR in both mates of a pair showed that the variation in FMR between pairs was almost 40% less than the individual variation in FMR (7% variation between pairs vs. 11% among individuals with small chicks and 12% variation between pairs vs. 19% among individuals with large chicks). In 15 of 20 pairs, one of the mates had 15% or higher (mean of the 15 pairs: 22% ± 8%) FMR than their partner, which indicates an intrapair conflict in FMR. Thus, to cover the energy needs of the growing chicks, the parents appear to adjust their FMR relative to the work effort of their mate. This might mask sex differences in FMR if the mates within pairs are not considered. Other species that share chick-rearing duties have also been shown to adjust their work effort in response to the energy needs of the chicks and body condition of the partner (Lorentsen 1996; Erikstad et al. 1997; Tveraa et al. 1997).

Sex Differences

The tendency toward higher mass-specific FMR of females within pairs is in contrast to previous studies on FMR in kittiwakes. Thomson et al. (1998) found that male kittiwakes had significantly higher FMR during incubation than females, whereas neither Gabrielsen et al. (1987) nor Golet (1999) found any sex differences in FMR of breeding kittiwakes. The higher FMR of males in the study of Thomson et al. (1998) was mainly explained by males spending more time away from the nest

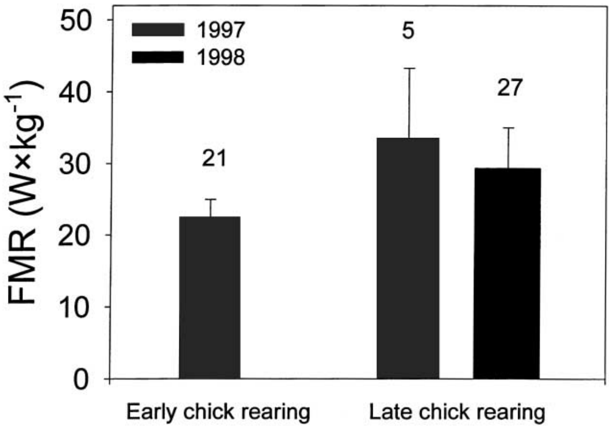

Figure 3. Field metabolic rate (FMR), measured with doubly labelled water, of breeding kittiwakes related to the age of the chicks in Kongsfjorden, Svalbard, Norway, in 1997 (July 15–31) and in 1998 (July 26–31). Data are presented as $\overline{X} \pm 1$ SE, with number of individuals indicated above each column.

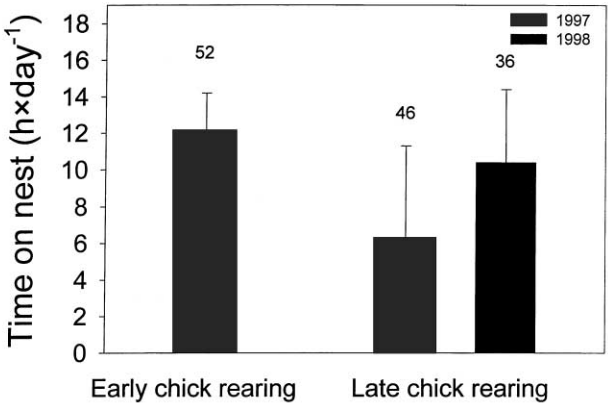

Figure 4. Nest attendance of breeding kittiwakes in Kongsfjorden, Svalbard, Norway, early (chicks 5–10 d old) and late (chicks 21–26 d old) in the chick-rearing period in 1997 and 1998. Data are presented as $\overline{X} \pm 1$ SE, with number of individuals indicated above each column.

than females, thus indicating higher activity. In this study, however, there was no difference in nest attendance between the sexes that could explain a higher FMR of females within a pair. The lack of difference in nest attendance between sexes is in accordance with previous studies of kittiwakes (Wanless and Harris 1992; Coulson and Johnson 1993). This study, however, indicates that work effort could differ between sexes even if the total time spent on the nest is the same.

Brood Size

This study is the first to show a significant correlation between FMR and natural brood size in a seabird species. When comparing kittiwakes rearing either one or two old chicks of similar age, the latter had significantly higher FMR and were absent from the nest for longer periods of time. A positive relationship between FMR and brood size is likely to be expected considering that growth rates and body mass of kittiwake chicks are independent of brood size (Barrett 1996). Hence, the energy needs of two old chicks comprise about 50% of the total food intake by the parents (Gabrielsen et al. 1992; this study). The amount of energy allocated to the chicks is high compared with other species of seabirds, which allocate about 15%–25% of the food to the chicks (Roby and Ricklefs 1986; Konarzewski et al. 1993), but is comparable to passerines (65%; Ricklefs and Williams 1984). A high energy allocation into the chicks of kittiwakes compared with other seabirds therefore is in agreement with the correlation between FMR and brood size found in this study.

Chick Age

The FMR of kittiwakes rearing small chicks in this study is similar to that found by Gabrielsen et al. (1987) on Hopen Island, Svalbard. The 32% higher FMR of kittiwakes rearing large chicks is reflected in the change in nest attendance as the chicks grow older (Fig. 4). Time spent away from the nest contributed significantly to the variation in FMR. When rearing small chicks, one of the parents attended the nest at all times. When the chicks became older, both parents left the nest for longer periods to forage. This study is, therefore, in accordance with previous studies on nest attendance of kittiwakes during the chick-rearing period (Gabrielsen et al. 1992; Wanless and Harris 1992).

Feeding Frequency

When the chicks are young, they frequently have to be fed small meals. During this period, the parents returned to the nest approximately every third hour, and there was a positive correlation between FMR and feeding frequency. The same relationship has been shown in small passerines (Bryant 1988, 1997; Tindbergen and Dietz 1994). Early in the chick-rearing period, the variation in foraging time is limited, so the cost of transport could influence the variation in FMR. Later in the chick-rearing period, the parents returned to the nest only one to two times per day, and total time spent away from the nest was the most important variable. This is in agreement with the strong correlation between FMR and time spent away from the nest late in the chick-rearing period (Fig. 5).

Cost of Locomotion

Cost of locomotion associated with foraging might be considered the most important factor influencing FMR in seabirds (Obst et al. 1987; Birt-Friesen et al. 1989; Montevecchi et al. 1992; Gabrielsen 1996). Early in the chick-rearing period, when the birds frequently returned to the colony, they were foraging close to the colony. The distance to the foraging area was estimated from the time budgets to be <10 km from the colony. When the chicks become older, the time budgets indicate that the parents are able to forage farther from the colony. The parents are also able to adjust the amount of food delivered per meal according to the energy needs of the chicks (Lorentsen 1996). An increased energy cost of transport late in the chick-rearing period is therefore possible. However, tracking of kittiwakes wearing VHF transmitters showed that they foraged mostly within 7 km from the colony in Kongsfjorden, Svalbard, even though the chicks were large (M. Fyhn, E. S. Nordøy, and G. W. Gabrielsen, unpublished data). This may indicate that the use of different areas for foraging does not contribute to the variation of FMR found in this study. Previous telemetry studies on kittiwakes from the same area have also shown for-

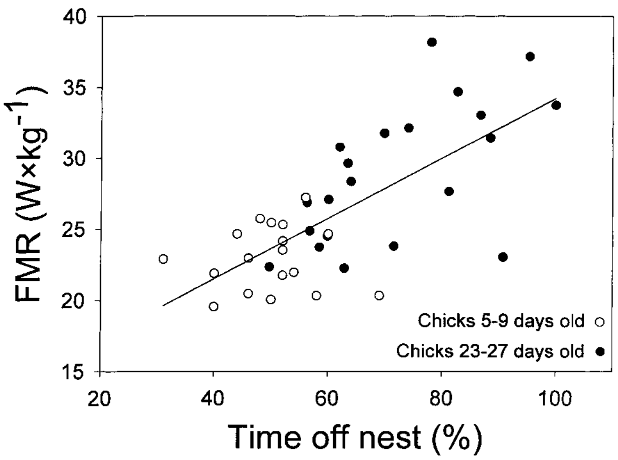

Figure 5. Relationship between field metabolic rate (FMR), measured with the doubly labelled water (DLW) method, and the fraction of the time between DLW injection and recapture spent away from the nest for kittiwakes early and late in the chick-rearing period in Kongsfjorden, Svalbard, Norway. The correlation between FMR (y) and the fraction (x) of the experimental period spent away from the nest is shown by the solid line, expressed by the equation $y = 0.21x + 13.03$ ($P < 0.0001$, $r^2 = 0.50$).

aging distances of 10 km during the chick-rearing period (Gabrielsen and Mehlum 1989). The foraging range of kittiwakes in the Kongsfjorden area is small when compared with tracking studies of kittiwakes in Alaska, where the distance to the foraging areas varied between 20 and 200 km (Irons 1998).

An increase in FMR is most likely explained by a threefold increase in energy demand of the chicks from hatching until fledging (Gabrielsen et al. 1992). However, increased energy demands of the chicks are not necessarily responsible for the entire increase in the parents' FMR. While the kittiwakes lost body mass and used their endogenous energy reserves early in the chick-rearing period, they maintained body mass and covered their entire energy demand by food intake during the last part of the chick-rearing period. Thus, the increase in FMR is therefore most likely explained by an increase in energy expenditure caused by searching for food to cover both the energy requirements of the parent and the chick(s).

Metabolic Intensity

The average metabolic intensity early in the chick-rearing period of 2.6 × BMR is in accordance with the study of Gabrielsen et al. (1987) on kittiwakes at Hopen Island, Svalbard. The average metabolic intensity late in the chick-rearing period of 4.3 × BMR is similar to the maximum level of energy expenditure of 4.0 × BMR suggested by Drent and Daan (1980) for birds during reproduction. Moreover, 60% of the kittiwakes exceeded the suggested maximum level of energy expenditure. This supports findings in other studies of seabirds (Birt-Friesen et al. 1989), terrestrial birds (Bryant and Tatner 1991), and mammals (Westerterp et al. 1986; Hammond et al. 1994) that show that animals might exceed the 4 × BMR level of energy expenditure for shorter periods of time (d).

Even though the kittiwakes in this study might be assumed from the above to work close to their physiological capacity, there was no correlation between FMR and BMR. Therefore, this study does not support an intraspecific correlation between FMR and BMR. At this time, such a correlation has not been found in any intraspecific study examining the relationship between FMR and BMR (Peterson et al. 1998; Nagy et al. 1999*b*).

The increase in metabolic intensity among kittiwakes during the chick-rearing period is primarily caused by the increase in FMR. However, the BMR of kittiwakes in this study was about 25% lower than measurements of BMR of kittiwakes during incubation from the same area (Gabrielsen et al. 1988; Bech et al. 1999). This reduction in the denominator also contributed to the increased metabolic intensity. Thomson et al. (1998) and G. W. Gabrielsen and F. Mehlum (unpublished data) compared the metabolic intensity of kittiwakes between incubation and chick rearing and concluded that the two periods were of similar work loads for the birds. However, they used BMR measured during incubation as the denominator in both periods. Using the BMR from this study, kittiwakes rearing old chicks have a 40% higher work load, when expressed as metabolic intensity, than incubating kittiwakes (G. W. Gabrielsen and F. Mehlum, unpublished data) from the same area. This illustrates that when metabolic intensity is used as an indication of the energetic load of the animal, the BMR should ideally be measured on the same individuals, but more important, the measurements should be performed during the same period as that of the measured FMR. However, it might be that metabolic intensity is not a proper measure of the work load of the animal.

In summary, this study has identified that sex, time spent away from the nest, age of the chicks, and brood size to a large extent can explain the individual variation in FMR of breeding kittiwakes. Body mass or BMR did not explain any of the variation in FMR in breeding kittiwakes. This is the first study to show a significant relationship between FMR and brood size and age of chicks in seabirds.

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