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Repeatability of basal metabolism in breeding female kittiwakes *Rissa tridactyla*

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We studied kittiwakes (*Rissa tridactyla*) breeding near Ny-Ålesund (79° N, 12° E) on Svalbard. In 1997, the basal metabolic rates (BMRs) of 17 breeding females were measured during the incubation and chick-rearing periods. The mean body mass of the kittiwakes decreased significantly (by 10%) between the incubation and chick-rearing periods. At the same time, both the whole-body and mass-specific BMRs decreased significantly. There was a positive and significant relationship between the BMR residuals from the incubation period and those from the chick-rearing period. Thus, the BMR of incubating female kittiwakes is a significant predictor of their BMR during the chick-rearing period. New BMR data were collected in 1998 from ten of these females, measured around the chick-hatching date. Repeatability values were calculated using either (i) the data for eight individuals for which three BMR measurements existed, or (ii) all the data from both years, yielding significant repeatabilities of 0.52 and 0.35, respectively. These values indicate that between 48 and 65% of the observed variation in BMR is due to intraindividual variability, while between-individual variability accounts for 35–52% of the variation in the BMR. This is the first report of a significant repeatability of the BMR of an endothermic organism across an elapsed time of more than one day.

Keywords: adaptive evolution; endotherms; metabolic rate; repeatability

1. INTRODUCTION

Individual variation is an important characteristic in any population of organisms. Variation is the fundament on which natural selection works in order to shape organisms adaptively to changing environments. However, even though individual variation is a cornerstone for the theory of evolution by natural selection (Darwin 1859), it is only in the past few decades that the study of individual physiological variation has gained momentum (Bennett 1987; Pough 1989; Hayes & Jenkins 1997; Jenkins 1997).

For a certain biological trait to evolve (or change) through natural selection, three fundamental prerequisites must be fulfilled. First, variation in the trait must necessarily be capable of influencing the inclusive fitness of individuals. Second, the between-individual variation should be consistent. Thus, the variation should not merely be a product of stochastic variations, either in the environment or at the individual level. The variation should be consistent, i.e. a high and significant repeatability should be found. Third, the trait must be heritable.

Studies of the repeatability of physiological parameters have mainly been done on traits that are related to the aerobic performance of an organism, e.g. running speed (Huey & Dunham 1987; Van Berkum & Tsuji 1987), maximum aerobic capacity, induced either by exercise or cold exposure (Hayes 1989*a*,*b*; Garland & Bennett 1990; Hayes & Chappell 1990; Chappell *et al.* 1995, 1996), the resting metabolic rate (Hayes *et al.* 1998) or the field metabolic rate (FMR) (the average metabolism of an individual measured over a longer time-scale—usually one or two days; Berteaux *et al.* 1996). All of these indices of aerobic performance are intuitive characteristics of the endurance performance of individual organisms, e.g. by characterizing their capacity to escape from predators or their ability to be more active or to cope with more severe weather conditions in other ways. However, the repeatability of the basal metabolic rate (BMR) has so far not been considered in this context. The BMR represents the lowest sustainable aerobic metabolism of a resting, post-absorptive, endothermic organism which involves no thermoregulatory costs (Brody 1945; IUPS Thermal Commission 1987). It is thus a significant component of the aerobic performance of endotherms. The BMR is probably one of the most widely measured physiological variables of endotherms and an immense amount of BMR data has been published.

The BMR of different endothermic species varies greatly within and between species. This variation has often been attributed to adaptations either to specific environmental conditions or to certain behavioural traits of the species. In birds, for instance, a high BMR has been found to be characteristic of species living in the colder climates of higher latitudes (Ellis 1984; Gabrielsen *et al.* 1988; Bryant & Furness 1995), in species that live in aquatic environments (Bennett & Harvey 1987) and in species with a high level of aerobic activity (Kersten & Piersma 1987). Similarly, a low BMR has been said to be characteristic of tropical birds (Hails 1983; Pettit *et al.* 1985), of birds

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living on islands (McNab 1994) and of night-active birds (Bennett & Harvey 1987). Intraspecific metabolic correlations with specific environments have also been described. In house finches (*Carpodacus mexicanus*), for example, those individuals living in Colorado and Michigan have a significantly higher winter BMR compared to those individuals living in southern California, which experience much milder winters (Root *et al.* 1991).

Despite the underlying assumption that the BMR of birds and mammals will have undergone adaptive changes when exploiting different ecological niches, there are no published studies in which all of the above-mentioned prerequisites for the adaptive evolution of the BMR have been investigated. The only report of repeatability of the BMR is that of Hayes *et al.* (1992), who reported a very high value when individual mice were tested within the same day. In the present study, we report on an initial investigation of the repeatability of the BMR over extended time periods in an Arctic breeding seabird, the kittiwake (*Rissa tridactyla*).

2. MATERIAL AND METHODS

(a) *Study area and animals*

We studied kittiwakes in a colony at Kongsfjorden, Svalbard (78°54′ N, 12°13′ E), *ca.* 7 km west of Ny-Ålesund, during the breeding seasons of 1997 and 1998. More than 600 pairs of kittiwakes breed in the colony ('Krykkjefjellet') every year, together with 50–100 Brünnich's guillemots (*Uria lomvia*) and five to ten pairs of black guillemots (*Cepphus grylle*) (Mehlum & Fjeld 1987). During the breeding season the birds experience continuous daylight and the mean ambient temperature during the warmest summer month (July) is 4.5 °C.

In 1997, the females of 24 breeding pairs were chosen at random and their BMRs measured during the incubation period. During the chick-rearing period we were able to catch 17 of these individuals again for the purpose of obtaining a second measurement of BMR. During the breeding season of 1998, the BMR was measured in ten females which had either their BMR measured twice in 1997 (eight individuals) or only once in 1997 (two individuals). The BMR measurements in 1998 were obtained just prior to hatching time.

The birds were caught on their nests in the colony using a fishing pole fitted with a terminal noose. The kittiwakes were then transported in an open boat to the laboratory in Ny-Ålesund within 1 h of capture. After the metabolic experiments were completed, the birds were released outside the laboratory, on average 18.3 h (s.d. = 5.0 h and range 11–28 h) after capture. After release, the kittiwakes either went straight to sea (apparently to feed) or straight back to the colony. When compared with control nests from other parts of the colony, we did not observe any apparent effects on the breeding performance of the experimental females as a result of our handling. In three out of the ten experimental nests used in 1998 in which the BMR was obtained prior to the time of hatching, the eggs did not actually hatch. For these nests we estimated the most likely hatching date, based on either the egg-laying dates, assuming a brooding period of 28 days (Mehlum 1989) or on the appearance of fractures in the eggs.

(b) *Measurements of oxygen consumption*

Rates of oxygen consumption (V_{O_2}) were measured using open flow-through respirometry. Outside air was dried over silica gel and drawn through an *ca.* 25-l temperature-controlled metabolic chamber with a flow rate of approximately 2.2 l min^{-1}. The actual flow rates were measured by the use of 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 measured using an oxygen analyser (type 244A, Servomex Ltd, Crowborough, UK). The oxygen analyser was calibrated using dry outside air (set to 20.95% oxygen) and pure stock nitrogen. The rates of oxygen consumption were calculated using formula 3A in Withers (1977), assuming a respiratory quotient of 0.8 and corrected for wash-out delay in the system by the method described by Niimi (1978). In this way, we obtained the instantaneous oxygen consumption rates. Metabolic rate values (W) were subsequently calculated from the values of the oxygen consumption rate using a conversion factor of 20.1 kJ per litre of oxygen. The birds were confined to the metabolic chamber for a minimum time of 8 h and the minimum value of oxygen consumption used to calculate the BMR was obtained on average 13.3 h (s.d. = 5.5 h and range 5–24 h) after the birds had been captured in the field. The BMR was calculated from the lowest 25 min running average (see below) of instantaneous oxygen consumption during exposure to thermoneutral conditions. The body mass was measured (to an accuracy of 1 g) immediately before and after the experiment. A linear decrease in body mass was assumed when assessing the body mass value used in calculating the mass-specific oxygen consumption. Measurements of BMR were obtained at all times during the diurnal cycle. There was no effect of the time of measurements, probably due to the continuous daylight at this high latitude.

The use of a 25 min running average procedure for obtaining the lowest metabolic rate was shown to be justified after plotting the minimum values of V_{O_2} calculated in three randomly selected experimental runs using mean times which varied from 2 to 45 min. These curves revealed that the use of too short an averaging interval results in very low minimum values of the BMR, thereby underestimating the true BMR level. On the other hand, the use of too long averaging periods would include periods of restlessness which results in increased BMR values and, thus, an overestimation of the BMR. However, at intermediate averaging periods, the minimum BMR values calculated changed relatively little (see Meerlo *et al.* (1997) for a description of this procedure).

The ambient temperatures (T_a) during the experiments were measured using a copper-constantan thermocouple (type 0.005, California Fine Wire Co., CA, USA) placed inside the metabolic chamber. All readings of T_a, as well as the voltage output from the oxygen analyser and the mass flow meter, were initially stored at 1 min intervals on a data logger (Grant Squirrel, type 1203, Grant Instruments Ltd, Cambridge, UK) and later transferred to a computer for analysis.

(c) *Statistical analyses*

The values are presented as means ± 1 s.d. Coefficients of variation (CVs) were calculated as s.d. × 100/mean. Comparisons of two mean values were made using the Student's *t*-test. In the case of a failed normality test, a Mann–Whitney ranked-sum test was used. For comparisons of more than two mean values, a one-way ANOVA was used. The removal of body mass as a common factor in the correlations was achieved by using the residual values in the correlations. Residual values were calculated as the percentage of the expected values for each year separately: the residual BMR values were therefore computed as (measured BMR/predicted BMR) × 100, from which the

Table 1. *Descriptive statistics for body mass, oxygen consumption (V_{O_2}) and the calculated BMRs for 17 female kittiwakes measured during the incubation and chick-rearing periods in 1997*

(Also shown are the results of paired *t*-tests comparing the two measuring periods in 1997.)

	incubation period			chick-rearing period			paired *t*-test	
	mean ± s.d.	range	CV	mean ± s.d.	range	CV	*t*	*p*
body mass (g)	345.50 ± 13.7	327.00–370.0	3.4	311.90 ± 20.5	282.00–355.0	6.6	5.42	< 0.0001
V_{O_2} (ml min^{-1})	9.92 ± 1.12	8.31–12.70	11.3	7.57 ± 1.40	5.81–10.77	18.4	5.07	< 0.001
BMR (W kg^{-1})	9.62 ± 1.11	8.41–12.65	11.5	8.08 ± 1.01	6.62–10.25	12.5	4.55	< 0.001

predicted BMR was obtained from a linear regression (least-squares method) of $\log_{10}$ BMR on $\log_{10}$ body mass.

The repeatability of the BMR was calculated from the variance components derived from a one-way ANOVA test, as described by Lessells & Boag (1987). Because the mean values of the BMR varied between the experimental periods and years, we were unable to use the actual BMR values in the ANOVA test. Instead, we used the residual values, based on individual regressions of $\log_{10}$ BMR on $\log_{10}$ body mass for each of the three experimental periods. In this way, equal mean values were assured.

All the statistical analyses were performed using SigmaStat software (v. 2.03, SPSS Inc.). The results were considered statistically significant at values of $p \leqslant 0.05$.

3. RESULTS

The BMR measurements during the incubation period in 1997 were made between 18 June and 3 July, while the BMR measurements made during the chick-rearing period were obtained between 17 and 31 July. Even though the time periods for both of the measuring periods thus lasted for approximately two weeks, the time window was much smaller when assessed from the actual breeding schedules of the individual pairs. We used the hatching date of the first egg as a standard reference point. The BMR measurements made during the incubation period were obtained 16.5 ± 2.0 days (range 13–20 days) before hatching, while the BMR measurements during the chick-rearing period were obtained 13.8 ± 1.7 days (range 9–17 days) after hatching. The mean time between the two BMR measurements was 30.3 ± 2.1 days (range 27–34 days). During the 1998 breeding season the BMR measurements were obtained on average 3.6 ± 4.1 days (range −1 to 11 days) before hatching.

In 1997 the T_a measured inside the metabolic chamber was 10.3 ± 2.0 °C during the incubation period and 12.7 ± 3.6 °C during the chick-rearing period. In 1998 the value was 12.8 ± 1.4 °C. The T_a measured during the first incubation period in 1997 differed significantly from the other two values (*t*-test, $t \geqslant 2.35$ and $p \leqslant 0.025$). However, all three values of T_a are well within the thermoneutral range, which extends down to *ca.* 5 °C for kittiwakes breeding on Svalbard (Gabrielsen *et al.* 1988). In addition, the V_{O_2} values were not significantly influenced by T_a ($p \geqslant 0.19$) within either of the three experimental series.

In 1997, the body mass of the female kittiwakes decreased by nearly 10% between the incubation period (mean mass of 346 g) and the chick-rearing period (mean mass of 312 g; see table 1). The body masses of the females in 1998 (mean mass of 360 g, table 2) did not differ significantly from the incubation masses in 1997 ($p = 0.06$), although they were significantly higher than the body mass values measured during the chick-rearing period in 1997 ($p < 0.001$).

Table 2. *Descriptive statistics for body mass, oxygen consumption (V_{O_2}) and the calculated BMR for ten females measured at the time of hatching in 1998*

	mean ± s.d.	range	CV
body mass (g)	359.80 ± 23.8	323.00–394.0	6.6
V_{O_2} (ml min^{-1})	9.90 ± 1.36	8.35–12.99	13.7
BMR (W kg^{-1})	9.24 ± 1.33	7.88–12.48	14.4

In 1997, the BMR decreased significantly (paired *t*-test, $t = 4.55$ and $p = 0.0003$), from 9.62 ± 1.11 W kg^{-1} during the incubation period to 8.08 ± 1.01 W kg^{-1} during the chick-rearing period (table 1). The BMR recorded later in the season was thus 85% of the BMR measured earlier in the breeding season. All but three out of the 17 females that were measured twice in 1997 showed a decrease in their BMR values. The mean BMR value during the 1998 breeding season was 9.24 ± 1.33 W kg^{-1} (table 2), which was not significantly different from the mean BMR measured during the incubation period in 1997 ($p = 0.42$).

There was a strong correlation between body mass and BMR when the 1997 season values were considered as a whole. Thus, $\log_{10}$ BMR (W) was linearly related to $\log_{10}$ body mass (g) by the equation $\log_{10}$ BMR $= -2.27 + 1.28 \times \log_{10}$ body mass ($r = 0.66$, $F_{1,32} = 24.0$ and $p < 0.001$; figure 1). The changes in BMR were significantly correlated with the changes in body mass (figure 2). Hence, those individuals which experienced the largest decrease in body mass showed the largest decrease in BMR. Significant correlations were found when both the mass-dependent (W) and mass-specific (W kg^{-1}) metabolic rates were used (figure 2). This indicates that the change in BMR was not solely an effect of a decrease in body mass, but was also attributable to a change in metabolic intensity.

We calculated the residual BMR values based on the regression line describing the relationship between $\log_{10}$ BMR and $\log_{10}$ body mass (figure 1) and then regressed the BMR residuals from the incubation period with those from the chick-rearing period. This relationship proved to be both positive and significant ($r = 0.642$, $F_{1,15} = 10.6$ and $p = 0.0055$; figure 3). Hence, individuals with a high BMR relative to their body mass during the incubation period also had a relatively high BMR during the chick-rearing period.

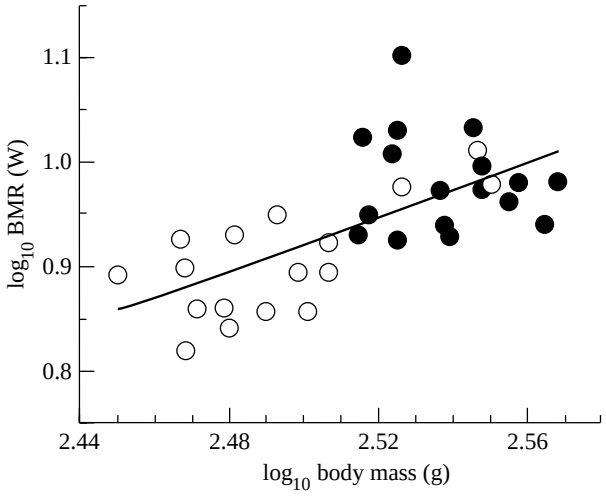

Figure 1. Log_{10} BMR (W) as a function of $\log_{10}$ body mass (g) of 17 female kittiwakes (*Rissa tridactyla*) measured during the incubation (filled circles) and chick-rearing (open circles) periods.

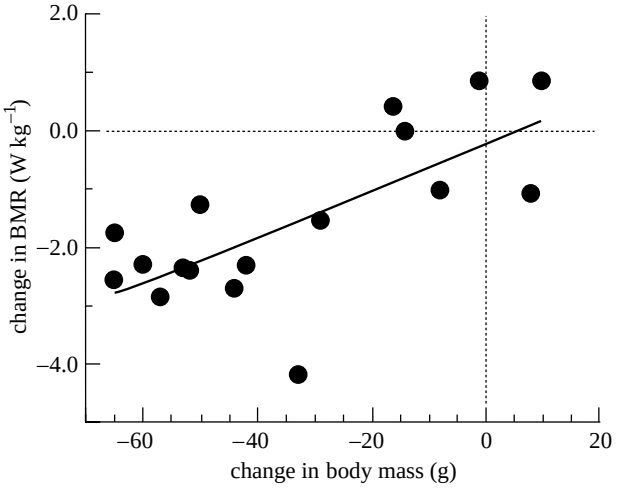

Figure 2. Relationship between change in body mass (g) and change in mass-specific BMR ($W\,kg^{-1}$) between the incubation and chick-rearing periods for breeding female kittiwakes.

For all birds measured in both years of the study, the BMR residuals calculated from the 1998 data did not correlate significantly with the BMR residuals calculated from either of the two separate measuring periods in 1997 ($p \geqslant 0.18$). However, when using the data from the eight individuals for which we had a complete set of BMR measurements (three measurements from each female from the incubation and chick-rearing periods in 1997 and just before hatching time in 1998), a repeatability of 0.520 ($F_{8,17} = 4.25$ and $p < 0.006$; table 3) was found (based on variance components from a one-way ANOVA; Lessells & Boag 1987). In addition, when all the data (eight individuals for which we had three BMR measurements and 11 individuals for which we obtained only two BMR measurements) were incorporated in the ANOVA test, a repeatability of 0.347 ($F_{18,27} = 2.28$ and $p = 0.028$; table 3) was found. Taken together, these repeatability values indicate that 48–65% of the observed variation in the BMR residuals is due to intraindividual variability. Between-individual variability would thus account for

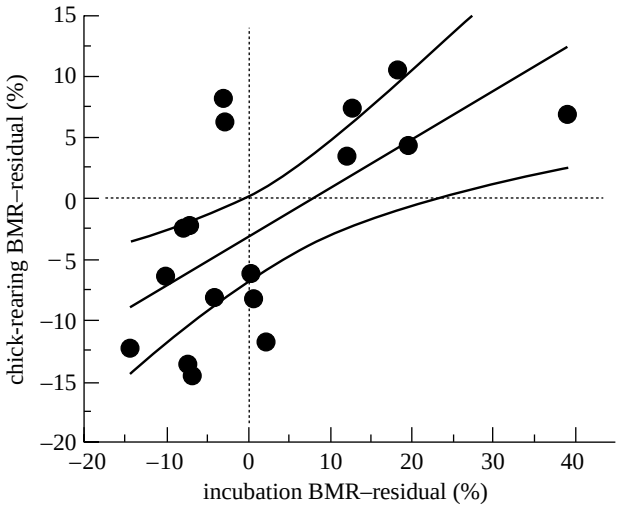

Figure 3. Residual values of the BMR of female kittiwakes during the chick-rearing period as a function of the residual BMR values during the incubation period. Residual values are expressed as a percentage of the expected values based on all the values of the BMR measured in 1997. Regression lines (see text for details) and 95% confidence intervals are shown.

35–52% of the observed variation in the BMR residuals of breeding female kittiwakes.

4. DISCUSSION

The observed variation in the BMR values of the female kittiwakes (values of CV between 11.5 and 14.4% for the mass-specific rates; tables 1 and 2) lie within the ranges of variation reported in other avian BMR studies. For example, Burness *et al.* (1998), after recalculating the data of Dutenhoffer & Swanson (1996), reported CV values varying between 4.5 and 21% (mean CV of 11.4%) in ten species of passerine birds. In a study of North Atlantic seabirds, Bryant & Furness (1995) presented BMR values for 11 species, with CV values ranging between 5.6 and 31.5% (mean CV of 13.2%). In one of the species studied by Bryant & Furness (1995), the kittiwake, the CV was as high as 31.5%. In another study on kittiwakes from Svalbard, a CV value for the BMR of only 4.9% was found (Gabrielsen *et al.* 1988). Consequently, our CV values for the BMR of kittiwakes thus lie well within the range of those reported previously for this species as well as those reported for other bird species (Bryant & Furness 1995; Burness *et al.* 1998).

The above results emphasize the fact that, in a natural population of seabirds, substantial interindividual variations in BMR values exist. However, for these variations to be 'targeted' by natural selection, the BMRs of individuals in the populations must be relatively consistent over time. Thus, there should be a high and significant repeatability of individual BMRs relative to those of the population. Hence, the main question that we addressed in the present study was: Do individual kittiwakes have a consistent BMR (relative to the mass-adjusted population mean) over time? Two of the findings of the present study indicate that this is at least partly the case.

First, the significant relationship obtained between the residual BMR values during the incubation period and the residual BMR values during chick-rearing period

Table 3. *Analysis of variance for calculation of the repeatability of the BMR in breeding female kittiwakes*

(The analysis is based on either all measurements of the BMR made in both 1997 and 1998 comprising eight individuals with three measurements each and 11 individuals with two measurements each or only the individuals for which three measurements existed (two in 1997 and one in 1998). The values used in the ANOVA are the residual values, expressed as a percentage of the expected values within each of the three separate experimental periods.)

source of variation	d.f.	sum of squares	mean squares	F	p
all measurements in 1997 and 1998					
between	18	3570.6	198.4	2.24	0.028
within	27	2394.6	88.7	—	—
total	45	5965.2	—	—	—
individuals with three measurements					
between	7	2502.0	357.4	4.53	0.006
within	16	1263.0	78.9	—	—
total	23	3765.0	—	—	—

(figure 3) clearly indicates that a significant repeatability existed, at least over a duration of one month. Hence, the BMR of incubating female kittiwakes is a significant predictor of the BMR during the chick-rearing period. Second, the calculated values of overall repeatability over one month and one year, which in both cases reached statistical significance (see table 3), clearly show that the BMR is a repeatable physiological parameter, although the intraindividual variation explained a greater proportion (48–65%) of the overall variation than the between-individual variation (35–52%). It should be emphasized that we use the term 'repeatability' despite large changes in the population mean value for the BMR. Hence, 'individual consistency' could have been used as another appropriate term, since the individuals are not defending a specific level of BMR.

An important factor that needs to be considered when evaluating the magnitude of the repeatability is the time-scale over which the repeatability is measured. It seems obvious that shorter time intervals between measurements will result in higher values of repeatabilities, simply because of a relatively unchanged physiological 'status' of each individual. At long time intervals between measurements, there is a greater chance that the physiological status of each individual in a population will change. The degree of repeatability can therefore be expected to decrease. Such a decrease in repeatability has been described by Chappell *et al.* (1996) for the red junglefowl (*Gallus gallus*). The repeatability of exercise-induced maximal V_{O_2} was 0.93 (r-value for a linear regression of residual values) when measured at intervals of only 2 h. However, at intervals of 180 days the repeatability value had decreased to 0.52 (Chappell *et al.* 1996). In the present study, the repeatability values are based on measurements obtained over a relatively long time period (one month to one year). It is thus of great interest that we obtained significant repeatabilities for both time periods, including the BMR measurements obtained over a one-year period (table 3).

In order to assess the biological significance of a repeatability value varying between 0.35 and 0.52, as found in the present study, our values should be compared with other reported repeatability values for aerobic performances characteristic of endotherms. However, this would seem to be the first report of the repeatability of BMRs over more than one day. Except for the very high repeatability values for *Mus musculus*, which were measured twice within the same experimental run and, thus, left little room for variability (Hayes *et al.* 1992), we are not aware of any other studies of repeatability of BMRs with which we can compare our values. However, there are two published values of the repeatability of FMRs for populations of small mammals (Speakman *et al.* 1994; Berteaux *et al.* 1996). Both studies reported repeatability values (0.269 and 0.236, respectively; see Berteaux *et al.* 1996) for the FMR that are smaller than the values reported for the BMR in the present study. One can only speculate whether these are genuine ones and, if so, what would be the biological significance of such a difference in the repeatability between BMR and FMR values. If the repeatability of BMRs generally proves to be higher than that of FMRs, it could reflect the fact that the BMR represents anatomical and physiological treatises of an animal (Daan *et al.* 1990; Burness *et al.* 1998), whereas FMRs include behavioural variation as well (Nagy 1989) and, thus, have a higher potential lability.

Over the time period (approximately one month) for which we found a significant repeatability of BMR in 1997, the female kittiwakes underwent several significant physiological changes. On average, they lost 9.7% of their initial body mass (table 1), most of which was due to loss of body fat built up during the incubation period (Moe 1998). In addition, these females also showed a significant reduction in size of some internal organs (e.g. the heart and liver) as well as in the pectoral muscles (Moe 1998). In recent years, there has been a growing appreciation that the body composition of birds and mammals is not invariant but may undergo significant short-term alterations in response to changing environmental parameters (Piersma & Lindström 1997). Since the BMR has been proved to be closely related to body composition (Daan *et al.* 1990; Piersma *et al.* 1996; Weber & Piersma 1996; Meerlo *et al.* 1997; Burness *et al.* 1998; Chappell *et al.* 1999), it should also be considered as a flexible parameter. It is therefore interesting that, despite the substantial changes in body composition of the female kittiwakes during the breeding season, the BMR values of the incubating females were still significant predictors of BMR during the chick-rearing period (figure 3). Thus,

the repeatability was observed over a period during which the physiological status of the birds changed greatly.

At present, we cannot attribute fitness differences to the between-individual variation in the BMR of the kittiwakes we examined. However, physiological and ecological data for other bird species suggest that relationships exist between metabolic rate and fitness. For instance, a positive correlation between social dominance and the BMR has been reported for four species of passerine birds (Røskaft *et al*. 1986; Hogstad 1987; Bryant & Newton 1994). Assuming that dominance would confer an increased fitness, through either higher reproductive output or an increased survival rate, those individuals with the highest fitness would then be expected to also have the highest BMR. It is thus possible that our finding of a persistent BMR at the individual level indicates that hierarchical benefits will persist as well and might be selected unless 'trade-offs' at times offset this selection. Such a trade-off could exist, since it would be energetically more expensive to maintain a high BMR at the cost of maintaining the internal organs involved in 'setting' the BMR (such as the heart, kidney, liver and gut; Daan *et al*. 1990; Burness *et al*. 1998).

In summary, we found a significant repeatability of the BMR in breeding female kittiwakes—the first time, to our knowledge, this has been documented for an endotherm over periods of more than one day. Our values for the repeatabilities indicate that 48–65% of the variance in the BMR is due to intraindividual variability, while between-individual variation accounts for 35–52% of the variation. It is conceivable that this repeatable BMR variation has an impact on fitness, but whether or not selection could affect the BMR depends on whether the variance is heritable.

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