

# REDUCTION IN BODY MASS AND BASAL METABOLIC RATE IN BREEDING FEMALE BLACK-LEGGED KITTIWAKES *RISSA TRIDACTYLA*: AN ADAPTATION TO REDUCE MAINTENANCE COSTS?

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Langseth I., Moe B. & Bech C. 2001. Reduction in body mass and basal metabolic rate in breeding female Black-legged Kittiwakes *Rissa tridactyla*: An adaptation to reduce maintenance costs? *Atlantic Seabirds* 3(4): 165-178. *We studied changes in body mass and basal metabolic rates (BMR) in breeding female Black-legged Kittiwakes Rissa tridactyla on Svalbard (79°N, 12°E) in 1997 and 1998. Measurements of body masses and BMR were obtained two weeks before hatching, at hatching, early in the chick-rearing period and late in the chick-rearing period. During incubation, body mass and mass specific BMR remained relatively stable. From hatching to late chick-rearing, body mass and mass specific BMR decreased by 12% and 26% respectively. However, from about two weeks up to about four weeks into the chick-rearing period, body mass and BMR did not change significantly. Whole body BMR scales with body mass<sup>2.18</sup>. This exponent is greater than that expected for a homomorphic variation in BMR, and indicates that the reduction in BMR must involve properties other than an overall body mass reduction. The simultaneous reduction in body mass and BMR could result from a negative energy balance, leading to a reduction in the masses of metabolically active organs. Alternatively, a reduction in BMR could be an adaptation to compensate for an elevated activity level during the chick-rearing period. By a reduction in the adult's maintenance costs, more energy can be allocated for promoting chick growth.*

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## INTRODUCTION

Most birds face an energetic challenge during reproduction because this period often involves an increase in activity and a reallocation of energy from self maintenance and survival to egg formation, incubation and chick growth. Since both time and energy may be limiting resources, the adult birds often experience a reduction in body mass, and consequently also in body condition, during reproduction (Moreno 1989). This reduction in body mass has generally been considered to be a consequence of energetic stress (Ricklefs 1974; Harris 1979; Drent & Daan 1980; Ricklefs & Husserl 1984; Monaghan *et al.* 1989; Moreno 1989). However, some evidence exists that a reduction in body mass is part of a mechanism that compensates for the increased level of activity during reproduction, either by reducing the cost of flying (Freed 1981; Norberg 1981) or by reducing energy consumption at rest (Deerenberg *et al.* 1998).

The basal metabolic rate (BMR) is defined as the rate of energy transformation in an endothermic organism in a rested, awakened, fasting and thermoneutral state (IUPS Thermal Commission 1987), and is considered as an obligatory part of the total energy expenditure. Allometric relationships between BMR and body mass (BM) reveal mass exponents of 0.60–0.82, depending on taxonomic level (Elgar & Harvey 1987; Bennet & Harvey 1987). This partially reflects the relationship between body surface and volume, which roughly calibrates with  $BM^{0.67}$ . Heusner (1984) stated that when body mass changes while other properties that affect the metabolic rate (temperature, density, mass-specific enthalpy, chemical composition, form) remain unchanged, energy turnover should calibrate approximately with  $BM^{0.67}$ , also called a homomorphic variation. Considerable deviations are often noted from the allometric relationships and interspecific variation in BMR has been considered as an adaptation to environmental differences and ways of living (Bennet & Harvey 1987). There is also increasing evidence that even within single species BMR is a flexible parameter that changes with season, or with other external or internal factors (Daan *et al.* 1989; Piersma *et al.* 1996). Intra-individual mass-exponents in excess of 1.0 have been found in birds (Daan *et al.* 1989; Deerenberg *et al.* 1998). This indicates that change in body mass also may include a change in other properties that can alter metabolic intensity.

The possible impact of an alteration in BMR on total energy expenditure is not clear. Some argue that since BMR represents the cost of keeping the metabolic machinery operative, the BMR-level should reflect the total capacity of this machinery. BMR and the maximal sustained metabolic rate should then be closely linked (Drent & Daan 1980; Daan *et al.* 1990; Hammond & Diamond 1997). In this case it would be advantageous to have a high BMR in periods with elevated energetic demands in order to be able to increase the total energy turnover, and a reduction in BMR would consequently reflect a reduced maximal metabolic capacity. Other studies have failed to find any relationships between BMR and the maximal metabolic rate within a species (Hayes *et al.* 1992; Konarzewski & Diamond 1994; Meerlo *et al.* 1997). This would argue in favour of a possible benefit of a decrease in BMR during energy demanding periods, since a reduction in BMR will enable more of the available energy to be allocated into other activities, such as reproduction (Gadgil & Bossert 1970).

Black-legged Kittiwakes *Rissa tridactyla* lose mass during chick rearing (Moe *et al.* 2001), a period in which both their activity level and total energy expenditure increases (Fyhn *et al.* 2001). The aim of the present study was to investigate whether a change in body mass of breeding female Black-legged Kittiwakes corresponds with changes in their BMR and to discuss what possible impact this would have on their energy balance.

## MATERIALS &amp; METHODS

The study was performed in a Black-legged Kittiwake colony at Kongsfjorden (78°54'N 12°13'E), 7 km west of Ny-Ålesund on Svalbard. In this colony about 600 Black-legged Kittiwake pairs breed with 50-100 Brünnich's Guillemots *Uria lomvia* and five to ten pairs of Black Guillemots *Cepphus grylle* (Mehlum & Fjeld 1987). The birds experience continuous daylight throughout the breeding season.

In two breeding seasons, 11 June-13 August 1997 and 19 June-29 July 1998, the colony was visited on a regular basis in order to record nest contents and hatching dates. Females used in the experiments were randomly selected after their sex, based on biometric measurements, had been confirmed. They were all breeding but no consideration was taken of their clutch or brood size (mainly because of an insufficient number of single egg/chick nests). The adult birds were captured when sitting on their nests, using a fishing pole fitted with a terminal noose. On the first capture, measurements of head+bill (skull) length were obtained to the nearest 0.1 mm, using a flexible ruler. Body masses were obtained to the nearest 1.0 g on every capture occasion, using a spring balance. For pairs for which data from both adults were obtained, the sexes were differentiated according to their relative size, the smaller (in both body mass and size) being the female. This method gave 98% correct determination when sexing Black-legged Kittiwakes on Hornøya, 70°N (Pichl 1997). When only one individual in a pair was captured, the females were assumed to have a skull length of less than 92.1 mm, and males were assumed to have a skull length of more than 92.1 mm. This method gave 87% correct determination when sexing Black-legged Kittiwakes on Hornøya (Barrett *et al.* 1985). We managed to capture the partner of all but one of the experimental birds. This female had a skull length of 91.4 mm, which is well beyond (0.7 mm) the limit of 92.1 mm, and we are therefore trusting that all the experimental birds were females.

Altogether we obtained 67 measurements of BMR in 40 female Black-legged Kittiwakes, of which 24 measurements were made during the incubation period (in 1997), 10 just around hatching time (in 1998), 17 about two weeks after hatching (in 1997) and 16 late during the chick-rearing period (7 in 1997 and 9 in 1998). Metabolic rates were measured indirectly as the rates of oxygen consumption in resting post-absorptive individuals, using open flow-through respirometry. After capture in the field, the Black-legged Kittiwakes were placed in a cage and transported to a laboratory in Ny-Ålesund for BMR-measurements. Within 7 hours (on average) the Black-legged Kittiwakes were placed in a metabolic chamber of approximately 25 l, in which the ambient temperature ( $T_a$ ) was measured using a copper-constantan thermocouple (California Fine Wire Co., type 0.005). Dry outside air was drawn through the

chamber at a rate of *ca.* 2.2 l min<sup>-1</sup>. The actual flow-rate was constantly measured by a flow-meter (Bronkhorts Hi-tek, type 201C-FA). Effluent air was dried over silica-gel and a fraction of the dry effluent air was directed into an oxygen analyser (Servomex, type 244A) for measurement of oxygen concentration. Readings of  $T_a$  and the voltage output of the flow-meter and the oxygen-analyser were recorded every minute by a data-logger (Grant Squirrel, type 1203) and transferred to a computer for further analysis. The birds were weighed to the nearest 1.0 g immediately before and after each experiment, which on average lasted for 10 hours. A linear decrease in body mass was assumed when calculating the body mass, from which the mass-specific BMR was calculated. The birds (except 16, which were sacrificed and used in studies of body composition) were released outside the laboratory. All were observed back on their nests within a couple of hours afterwards.

Rates of oxygen consumption were calculated using formula 3A in Withers (1977) and assuming a respiratory quotient of 0.8. We used the method described by Niimi (1978) in order to correct for washout delay and to obtain instantaneous rates. The minimum 25 minutes running mean was considered to represent the basal metabolic rate (for further details on method see Bech *et al.* 1999). Oxygen consumption values were converted into Watts (W) using a factor of 20.1 kJ per litre of oxygen.

A number of nests, 48 in 1997 and 55 in 1998, were randomly selected as controls. Hatching rates, chick growth and chick survival were similar for the experimental nests and the control nests (*pers. obs.*). Hence, removal of the females from their nests during the BMR measurements did not seem to have any deleterious effect on reproduction. The mean body mass and BMR values obtained during the incubation period did not differ significantly between the two seasons (1997 and 1998), nor did the means obtained during the chick rearing period. Hence, we have not analysed the data for the two seasons separately in this study. All statistical analyses were performed using SigmaStat software (SPSS Inc., v. 2.03). Values are presented as means  $\pm$  1 standard deviation (SD) and the results were considered statistically significant at values of  $P \leq 0.05$ . The National Committee for Animal Research (Forsøksdyruttvalget) in Norway approved the experimental protocol for the experiments. Permissions to work in the colony and the collection of individuals for analyses of body composition were obtained from the Governor of Svalbard (*ref.* 96/00569-2 and 98/00469-5).

## RESULTS

The body masses of female Black-legged Kittiwakes recorded in the field two weeks prior to hatching and around hatching time did not differ significantly (on average  $387 \pm 24$  g,  $n = 33$ ), nor did the body mass values obtained early and later on in the chick-rearing period (on average  $342 \pm 16$  g,  $n = 31$ ). However, the latter mean is significantly lower (about 12%) than the incubation period mean value ( $t$ -test,  $t = 8.663$ ,  $df = 62$ ,  $P < 0.001$ ). The body masses of the female Black-legged Kittiwakes recorded in the laboratory at the same time as the BMR values were recorded (hereafter called the lab body masses) are lower than the body masses recorded earlier in the field due to the intervening fasting period. There was no significant difference in relative body mass decrease between the five groups (Kruskal-Wallis one way ANOVA on ranks,  $H = 6.87$ ,  $P = 0.076$ ) and the reduction was on average  $9.1 \pm 3.2\%$  ( $n = 64$ , we failed to obtain field body masses for three individuals.).

The mean lab body masses for the females two weeks prior to hatching, around hatching, two weeks into the chick rearing period and late in the chick rearing period were  $347 \pm 20$  g ( $n = 24$ ),  $360 \pm 24$  g ( $n = 10$ ),  $312 \pm 20$  g ( $n = 17$ ),  $313 \pm 11$  g ( $n = 7$ ) and  $312 \pm 13$  g ( $n = 9$ ) respectively (Fig. 1). The two body mass means obtained during the incubation period were not significantly different from each other, nor were the three body mass means obtained during the chick-rearing period. However, the mean values obtained during the incubation period were significantly different from the three mean values for the chick-rearing period (one-way ANOVA followed by a Student-Newmann-Keul procedure for pairwise comparisons,  $F_{4,62}$ ,  $P < 0.0001$ ). This suggests that body mass declined from incubation to the chick-rearing period.

The ambient temperatures recorded during the BMR measurement periods ranged from 7–24 °C. There was no significant relationship between  $T_a$  and the metabolic rates measured either in the incubation period or in the chick-rearing period. Thus we considered all the measurements to lie within the thermoneutral zone for Black-legged Kittiwakes on Svalbard, which has previously been found to include temperatures from 5°C up to at least 20°C (Gabrielsen *et al.* 1988).

The time from capture in the field to the actual BMR measurement ranged from 5–24 hours. The minimum time of 5 hours may seem insufficient for the birds to become post-absorptive since 5 hours is the approximate retention time of Black-legged Kittiwakes (Hilton *et al.* 1998). However, the time from capture to the end of the experiment was never less than 10 hours. The minimum metabolic rate recorded as little as 5 hours after capture may indicate that the birds had already been fasting before capture. In addition, Hawkins *et al.* (1997) showed that in Brünnich's Guillemots the effect of heat

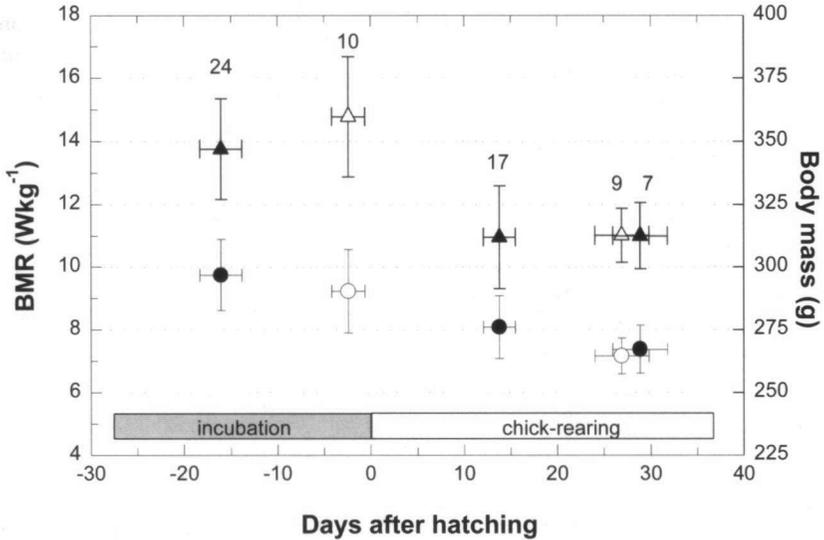


Figure 1. Mass specific BMR (circles) and corresponding body masses (triangles) of breeding female Black-legged Kittiwakes in 1997 (filled symbols) and 1998 (open symbols). Data are presented as mean values  $\pm$  1 SD, with numbers of individuals shown above the symbols. Time of hatching of the first chick in a clutch indicated by 0 on the x-axis.

Figuur 1. Massa-specifieke BMR (cirkels) en de bijbehorende massa (driehoeken) van broedende wijfjes Drieteenmeeuwen in 1997 (zwarte symbolen) en 1998 (open symbolen). De gegevens zijn weergegeven als gemiddelden  $\pm$  1 SD, met het aantal individuen boven de symbolen. Het moment van uitkomen van het eerste kuiken is als 0 op de x-as weergegeven.

increment of feeding (HIF) lasted for 85 minutes after intake of Polar Cod (*Boreogadus saida*). Assuming a similar effect of HIF on Kittiwakes, a period of 5 hours from last feeding opportunity to measurement should not affect the BMR-values.

Mass specific BMR changed in line with change in body mass (Fig. 1). For the two recordings made during the incubation period BMR values were  $9.75 \pm 1.14 \text{ W kg}^{-1}$  ( $n = 24$ ) and  $9.23 \pm 1.33 \text{ W kg}^{-1}$  ( $n = 10$ ) respectively. These values are not significantly different from each other. Two weeks into the chick rearing period mean BMR was  $8.08 \pm 1.01 \text{ W kg}^{-1}$  ( $n = 17$ ) and late in the chick rearing period the means were  $7.16 \pm 0.57 \text{ W kg}^{-1}$  ( $n = 7$ ) and  $7.38 \pm 0.77 \text{ W kg}^{-1}$  ( $n = 9$ ) (Fig. 1). These last three mean values are not significantly

different from each other, but they are all significantly different from the mean values obtained during the incubation period (one-way ANOVA followed by a Student-Newmann-Keul procedure for pairwise comparisons,  $F_{4,62}$ ,  $P < 0.0001$ ).

Since mass-specific BMR decreases with body mass, a reduction in body mass will have an even stronger effect on the whole-body BMR. The relationship between whole-body BMR and lab body mass of breeding female Black-legged Kittiwakes is described by the equation:

$$(1) \quad \text{BMR} = 9.1 * 10^{-6} \text{ BM}^{2.18}$$

(least square linear regression,  $R = 0.80$ ,  $n = 40$ ,  $df = 38$ ,  $P < 0.001$ ) where BMR is in W and BM is body mass in g. Only one BMR measurement of each individual is included in the analysis, giving  $n = 40$ . Equation 1 can further be used to eliminate body mass as a determining factor and to calculate residual values of BMR

$$(2) \quad \text{BMR}_{\text{residual}} = \text{BMR}_{\text{measured}} / \text{BMR}_{\text{predicted by eq. 1}} * 100$$

A regression between  $\text{BMR}_{\text{residual}}$  and the corresponding stage of breeding gives a significant, negative relationship:

$$(3) \quad \text{BMR}_{\text{residual}} = 104.7 - 0.4 * \text{days after hatching}$$

(least square linear regression,  $R = -0.47$ ,  $n = 40$ ,  $df = 38$ ,  $P = 0.002$ ) where  $\text{BMR}_{\text{residual}}$  is in percent (Fig. 2).

## DISCUSSION

The Black-legged Kittiwake has a biparental care system, both sexes taking an equal share in both the incubation period, which normally lasts for 27 days, and the chick-rearing period (Mehlum 1990). The chicks attain thermal independence about one week after hatching (Barrett 1978), but are constantly brooded for another 10 days (Gabrielsen *et al.* 1992). They are dependent on food provisioning until fledging time, 5-6 weeks after hatching (Mehlum 1990). Moe *et al.* (2001) studied the body mass dynamics of breeding male and female Black-legged Kittiwakes in the same colony as in the present study. Their findings showed that body mass change closely followed the changes in activity levels during different stages of the breeding cycle. During the incubation period, when activity levels are low, body mass remained stable or showed a slight increase. After hatching, the parents must provide both food and heat to their fast growing chicks and consequently less energy and time will be

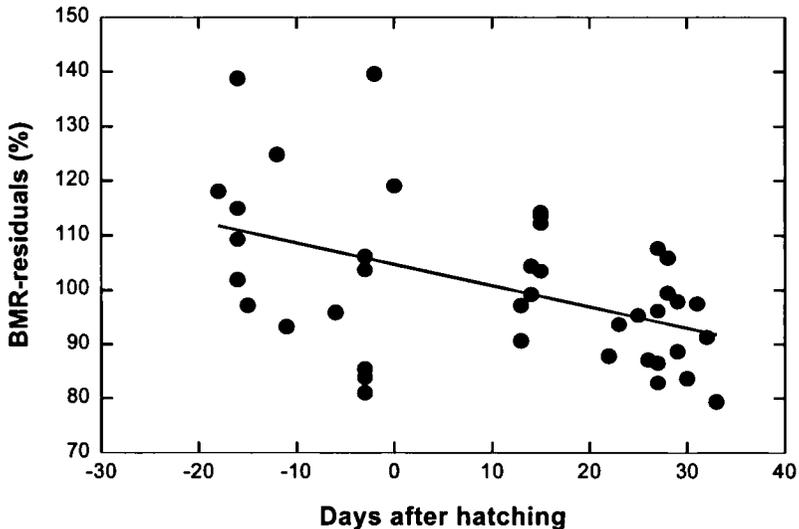


Figure 2. Relationship between the residuals of the regression of whole-body BMR and body mass (equation 1) and days after hatching of breeding female Black-legged Kittiwakes ( $n = 40$ , linear regression:  $R = -0.47$ ,  $df = 38$ ,  $P = 0.002$ ).

Figuur 2. Het verband tussen de residuen van de regressie van BMR en massa (formule 1) en het aantal dagen na het uitkomen van de jongen bij broedende wijfjes Drieteenmeeuwen ( $n = 40$ ; lineaire regressie  $R = -0.47$ ,  $df = 38$ ,  $P = 0.002$ ).

available for self-maintenance. The result is a decrease in parental body mass. During the last part of the chick-rearing period the chicks can be left alone for longer periods and, even though their total energy demand increases, more time is available to provide for the adults' own maintenance requirements. The result is that the adult body masses level off. The body mass changes of the female Black-legged Kittiwakes observed in the present study agrees with the findings of Moe *et al.* (2001) and of Wendeln & Becker (1996) in Common Terns *Sterna hirundo*.

From the time of capture in the field until the BMR measurements were made in the laboratory, the body masses of the females decreased by approximately 9%. This was mainly due to emptying of the gut during the fasting period. The degree of body mass reduction was similar in all five groups and the changes in the lab body masses, in consequence, showed the same pattern of change as the field body masses.

Gabrielsen *et al.* (1988) measured the oxygen consumption of 16 adult Black-legged Kittiwakes, of both sexes, on Svalbard in June/July and found a resting metabolic rate (RMR) of  $1.64 \text{ ml O}_2 \text{ g}^{-1}\text{h}^{-1}$  ( $= 9.16 \text{ W kg}^{-1}$ , mean body mass 365 g). Even though the precise reproductive stage for these individuals was not reported, we assume, based on the dates, that the measurements were made during the incubation period. In four Black-legged Kittiwakes in Scotland, mean BMR was found to be  $1.62 \text{ ml O}_2 \text{ g}^{-1}\text{h}^{-1}$  ( $= 9.05 \text{ W kg}^{-1}$ , mean body mass 305 g, Bryant & Furness 1995). Neither the sex nor the reproductive stage of these individuals was stated. Our own values of BMR from the incubation period (9.75 and  $9.23 \text{ W kg}^{-1}$ ) lie within the range of these previous measurements of BMR in Black-legged Kittiwakes, but our values from the chick-rearing period (8.08, 7.16 and  $7.38 \text{ W kg}^{-1}$ ) are lower.

The mass specific BMR of female Black-legged Kittiwakes decreases in line with body mass during the chick-rearing period. This implies that the whole body BMR is reduced by more than would have been expected from an effect of a decrease in body mass alone. Accordingly, BMR changes in proportion to  $\text{BM}^{2.18}$  (see eq. 1). This mass exponent exceeds the exponent expected for a homomorphic variation in BMR (0.67), and it indicates that lightweight individuals have a relative, as well as an absolute, lower BMR than heavier individuals, and that a small change in body mass will have a profound effect on the BMR. This is further demonstrated by the relationship between the residuals of BMR and the days after hatching (Fig. 2), which shows that during incubation females even have relatively higher BMR than would be expected by their high body masses.

High mass-exponents have also been found in other birds in situations that may resemble those experienced during the chick-rearing period. In female Kestrels *Falco tinnunculus*, with varying nutritional conditions, the exponent was 1.6 (Daan *et al.* 1989). In a study of Zebra Finches *Taeniopygia guttata*, with experimentally increased workloads, the intra-individual mass exponent of the metabolic rate was 2.30 (Deerenberg *et al.* 1998). Obviously, in these studies, including our own, the change in metabolic intensity must have involved mechanisms other than an overall body mass change.

A growing understanding exists as to how an inter- and intra-specific variation in BMR reflects variations in body composition (Daan *et al.* 1990; Weber & Piersma 1996). Different organs and tissues vary in their intrinsic metabolic rates (Krebs 1950). Organs such as the liver, heart, kidney and intestine have high metabolic rates, whereas fat and muscle tissues have low metabolic rates. In this way, BMR level may reflect the relative sizes of different organs (Daan *et al.* 1990). Within an individual, a rearrangement of body composition may be an adaptation or a response to different situations according to a use/disuse principle (Piersma & Lindström 1997) and this may in

turn lead to changes in BMR. In individual Kestrels that were kept on either high maintenance regimes (*ad libitum* food intake) or low maintenance regimes (resembling body condition during the late chick-rearing period), Daan *et al.* (1989) found that nocturnal BMR was lower during the low maintenance regime than during the high maintenance regime. This was partly due to a greater depression of the nocturnal body temperature. In addition, analyses of body composition revealed a disproportionate reduction in heart and kidney lean mass, and the authors surmised that the variation in BMR reflected variation in the masses of these metabolically highly active organs. A study of the changes in body composition of breeding female Black-legged Kittiwakes has produced similar results (Langseth *et al.* 2000). From incubation to chick-rearing there was a mass reduction in most of the internal organs in the chick rearing period, but a disproportionate decrease in the liver and kidney masses. These organs are both metabolically highly active and a positive relationship between liver mass and mass-specific BMR has been reported in small mammals (Konarzewski & Diamond 1994; 1995) and some birds (Bech & Østnes 1999; Chappell *et al.* 1999). However, one cannot ignore that the mass of the skeleton and the plumage probably will remain relatively constant with a change in body mass. Thus, with a reduction in body mass, the relative mass of skeleton and plumage will increase. Since these tissues have low, or even zero, metabolism this could also lead to a reduction in mass-specific BMR with a reduction in total body mass.

In small mammals there seems to be a mobilisation of the supply organs (e.g. intestine and liver) in connection with reproduction (Hammond & Diamond 1997). The metabolic machinery must apparently be upgraded in order to be able to support the extra energy demands faced during pregnancy and lactation. This may also cause a rise in BMR. In breeding female Brown Long-Eared Bats *Plecotus auritus* BMR increased from pregnancy until after parturition, despite a decrease in body mass (McLean & Speakman 2000). For the Black-legged Kittiwakes it would thus seem unlikely that a reduction in BMR, as a consequence of a reduction in the kidney and liver masses, represents an adaptation to a period during which the energy demands are considered to increase. In small mammals atrophy of the liver is found to be a response to starvation and to a negative energy balance (Goodman & Ruderman 1980; Burrin *et al.* 1988). This could also be the case for Black-legged Kittiwakes during the chick-rearing period, when limitations in both time and food intake may render the birds unable to maintain a positive energy balance.

The field metabolic rate (FMR) of breeding Black-legged Kittiwakes on Svalbard increases throughout the chick-rearing period (Fyhn *et al.* 2001). Hence, it does not seem that a reduction in the masses of internal organs, which occurs in parallel to a reduction in BMR, affects their ability to increase their

total energy expenditure. Thus, it is tempting to speculate that a reduction in BMR during the chick rearing period may be a mechanism that minimises maintenance costs, which in turn enables the adult birds to allocate more energy to chick-growth without greatly increasing their total energy consumption. Such a mechanism will be advantageous in situations where both food and time are limiting resources and costs are associated with increasing the food intake. In some species of birds, a reduction in RMR has been found to compensate for increased activity. Deerenberg *et al.* (1998) manipulated the workload of individual Zebra Finches by experimentally increasing the amount of activity (number of hops) required to get access to food. They found that for individuals with a high workload daily energy expenditure and daily food intake were lower than for individuals with a low workload. The difference was larger than could be explained by a reduction in the body mass of the high-workload individuals. Deerenberg *et al.* (1998) concluded that the high-workload individuals compensated (or even over-compensated) by behaviourally increasing their efficiency and by decreasing their RMR, both during the night and the inactive hours of the day. Although this study did not explain the physiological mechanisms underlying the reduction in RMR, it did show that even though the birds had *ad libitum* access to food they compensated for the increased activity by reducing their body mass and RMR rather than increasing their food intake. A similar change in RMR was found in male White-crowned Sparrows *Zonotrichia leucophrys gambelii* with varying testosterone levels (Wikelski *et al.* 1999). Males (both intact and castrated) with testosterone implants showed an increased activity level, but a decrease in both body mass and RMR, compared with pre-implantation values.

These findings of a body mass related reduction in RMR in Zebra Finches and White-crowned Sparrows in connection with an increase in activity, resemble our finding of a reduction in BMR in female Black-legged Kittiwakes during the chick-rearing period. One can speculate that whereas female mammals must mobilise the metabolic machinery in order to support the growing foetus and later the endogenous milk production, birds, in contrast, seem to be able to slow down their metabolic intensity at rest as a compensation for the increased workload during reproduction. However, the question still remains as to whether Black-legged Kittiwakes lose body mass because of limited food and time resources, or whether there are costs associated with increasing food intake, such as increased predation risk, which exceed the costs of losing weight. Obviously there must also be costs associated with reducing metabolic rate at rest, otherwise it would have been energetically advantageous to maintain a constant low metabolic rate. A reduction in body mass may involve a depletion of body reserves that normally serve as insurance against starvation (Lima 1986), and a reduction in BMR may result in damage to the

immunological defence mechanism (Deerenberg *et al.* 1997). In order to further elucidate whether free-living Black-legged Kittiwakes really do compensate for increased activity during the chick-rearing period by reducing their body mass and BMR, or whether this is merely a consequence of energetic stress, manipulative experiments are called for, either by increasing food availability or by increasing the workload.

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#### TERUGLOPEND LICHAAMSGEWICHT EN BASAALMETABOLISME BIJ BROEDENDE WIJFJES DRIETEENMEEUWEN *RISSA TRIDACTYLA*: EEN AANPASSING OM ONDERHOUDSKOSTEN TE BEPERKEN?

*Veranderingen in lichaamsgewicht en basaalmetabolisme (BMR) werden onderzocht bij broedende wijfjes Drieteenmeeuwen Rissa tridactyla op West-Spitsbergen (79°NB, 12°OL) in 1997 en 1998. Massabepalingen en metingen van het BMR werden verricht tijdens het broeden (twee weken voor het uitkomen van de eieren), rondom het uitkomen van de eieren, in de eerste dagen van jongenzorg en vlak voor het uitvliegen van de jongen. Gedurende het bebroeden van de eieren waren massa en BMR beide tamelijk stabiel, maar vanaf het moment van uitkomen tot het moment van uitvliegen namen massa en BMR respectievelijk met 12% en 26% af. Vanaf twee weken tot ongeveer vier weken in de periode van jongenzorg werden er echter geen veranderingen gevonden. Het BMR gemeten voor het gehele lichaam verhoudt zich als lichaamsmassa<sup>2.18</sup>. Deze exponent is groter dan verwacht voor een homomorfe variatie van het BMR en dit suggereert dat er andere factoren een rol spelen dan alleen een afnemend lichaamsgewicht. Het tegelijkertijd afnemen van massa en BMR zou het resultaat kunnen zijn van een negatieve energiebalans met als gevolg daarvan een teruglopende massa van de metabolisch actieve organen. Aan de andere kant zou een teruglopend BMR een aanpassing kunnen zijn om de verhoogde activiteit samenhangend met de jongenzorg op te vangen. Een reductie van de onderhoudskosten van de volwassen vogels zorgt ervoor dat meer energie kan worden gestoken in de jongenzorg waardoor de kuikens sneller kunnen groeien.*

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