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Review

The energy economy of the arctic-breeding Kittiwake (*Rissa tridactyla*): a review[☆]

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Abstract

The present paper reviews recent studies on changes in body mass, body composition and rates of energy expenditure during the breeding season in the black-legged Kittiwake (*Rissa tridactyla*) on Svalbard (79 °N). The main characteristic of the energy budget is a pronounced decrease in body mass as well as basal metabolic rate (BMR) after the eggs have hatched. While most internal organs lose mass in direct proportion to the general decrease in body mass, the liver and kidney masses decrease to a disproportionately greater extent. Since both the liver and the kidney have high intrinsic metabolic rates, these results support an earlier notion that the reduction in body mass is an adaptation to reduce maintenance costs. Alternatively, the reduced BMR is due to a decrease in energy uptake from the gastrointestinal tract, thereby ensuring that undigested food is ready to be regurgitated to the chicks. At the end of the chick-rearing period, the field metabolic rate (FMR) reaches its highest level, probably due to an increased workload associated with chick feeding. This occurs at a time of low body mass and BMR. A pronounced increase in the metabolic scope (FMR/BMR) during the latter part of the chick-rearing period demonstrates that BMR and FMR may change independently of each other and that the ratio FMR/BMR may not be a good measure of energy stress.

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The reproductive period is often considered a period during which the energy budgets of animals are especially strained. In birds, the reproductive period may be especially demanding, because it

often involves an increased activity of the adults and a reallocation of energy from self-maintenance and survival to investment in egg-formation, incubation, and growth of the chicks. At the same time, the energy budget has to be managed in such a manner that both the current survival of offspring is ensured, and, simultaneously, the body condition of the adults maintained such that their own future reproductive potential is not compromised (Sibley and Calow, 1986; Williams, 1966).

For many bird species, the high energy expenditure during the breeding season, caused, for example, by the higher frequency of foraging trips, have historically been assumed to result in a 'stress' situation that causes the body mass to

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decrease (the reproductive stress hypothesis; Nice, 1937; Ricklefs, 1974; Nur, 1984; Moreno, 1989). The mass changes have consequently been assumed to represent the reproductive costs (e.g. Nur, 1984). The decrease in body mass could, however, also be considered as an adaptation that enhances breeding success by reducing the cost of flying, hence reducing the foraging costs (the flight-adaptation hypothesis; Freed, 1981; Norberg, 1981). A decrease in body mass during the chick-rearing period—whatever its underlying reason—represents a dilemma for the birds, since a low body mass may potentially compromise the aerobic machinery necessary for the increased foraging activity. There have been few studies aimed at disentangling this interrelationship between body mass changes and metabolic changes during the chick-rearing period in birds.

In a series of recent studies, we have investigated the energetics of reproduction in black-legged Kittiwakes (*Rissa tridactyla*) breeding in the arctic. More specifically, we have reported on changes in energy expenditure [basal metabolic rates (BMR) and field metabolic rates (FMR)] as well as changes in body reserves throughout the breeding season on Svalbard at 79°N (Bech et al., 1999; Langseth et al., 2000, 2001; Fyhn et al., 2001; Moe et al., 2002). In the present paper we review these results, with special emphasis on the changes in body mass and metabolic rate from the incubation period to the chick-rearing period.

2. Study area

The black-legged Kittiwake (hereafter called only the ‘Kittiwake’) is a medium-sized gull living in the northern parts of the Atlantic, including the Barents Sea region. In these northernmost breeding areas the breeding period is characterised by continuous daylight. The average ambient temperature in July is only approximately 4.5 °C. The species may experience periods of unfavourable weather conditions and even summer snowfall. Our study area was a colony of Kittiwakes breeding at ‘Krykkjefjellet’ in Kongsfjorden on the east coast of Svalbard (78°54’N, 12°13’E). Our own studies, which are referred to in this review, were carried out during the summers of 1997–1999.

3. Results

3.1. Body mass

In most avian species, including seabirds, a decrease in body mass is observed during the breeding period (Moreno, 1989). This was also the case for the Kittiwakes breeding on Svalbard. After a stable, or even increased, body mass during the incubation period, the body mass decreased immediately after hatching (Moe et al., 2002). During the first part of the chick-rearing period (from hatching to 16 days post-hatching), body mass decreased by 16 and 11% for females and males, respectively (Moe et al., 2002). During the remainder of the chick-rearing period, body mass, and hence also body condition, remained stable for both sexes.

Moe et al. (2002) have argued that the reduced body mass observed in the Kittiwakes may be in line with the ‘reproductive stress’ hypothesis. The adult Kittiwakes are time-constrained because of the need to attend the chicks 24-h a day during the first part of the chick-rearing period. Also, calculations of energy budgets show that the energy requirements per hour spent off the nest are actually highest during the first part of the chick-rearing period, compared to the second part (average values of 82.4 and 75.9 kJ h⁻¹, respectively; Moe et al., 2002).

3.2. Body composition

Parallel to the changes in overall body mass from incubation to chick-rearing, significant changes in body composition were found in the Kittiwakes. Langseth et al. (2000) reported changes in the mass of the kidney and liver, from the incubation to the chick-rearing period, that were larger than expected based on the changes in overall body mass. Thus, while body mass decreased to 87% of its incubation value, that of the kidney decreased to 67% and of the liver to only 59% of their incubation period values. The changes in liver mass are especially noteworthy, showing a reduction in wet mass from 24 g to only 14 g. Other measured body components (breast and leg muscles, heart and intestine) all changed in a nearly direct proportion to the general change in body mass (Langseth et al., 2000).

There are few published data with which these results can be compared. In a recent study, Niizuma

et al. (2001) showed that in Leach's Storm-petrels (*Oceanodroma leucorhoa*), the liver mass also decreased from incubation to late chick-rearing; from 1.38 to 1.16 g. However, this reduction was of the same relative magnitude as that of the reduction in total body mass (decreased from 47.2 to 38.9 g). In the storm-petrels, in contrast to the Kittiwakes, the decrease in body mass was mainly due to a loss in skin mass, including subcutaneous adipose tissue. Niizuma et al. (2001) argued that the storm-petrels benefited from the loss of body mass by decreasing their flight costs at a time during which the birds have to fly between the foraging areas and the breeding areas carrying heavy food loads. Hence, these authors argue in favour of the flight-adaptation hypothesis.

If the sole purpose of a reduced body mass were to ensure lower flight costs during chick-rearing, as indicated by the 'flight-adaptation hypothesis', it seems unlikely that the size of such important organs as the liver and the kidney would be reduced so much. A reduction in mass from 24 to 14 g for the liver (Langseth et al., 2000) more likely signifies some change in the metabolic function of the birds. The organ mass changes hence support the reproductive stress hypothesis.

3.3. Basal metabolic rate

Since the liver and the kidney are known to have a particularly high intrinsic metabolic intensity (Krebs, 1950; Burrin et al., 1988; Scott and Evans, 1992), one could presume that the reduction in body mass from the incubation period to the chick-rearing period in the Kittiwakes would lead to changes in the basal metabolic rate (BMR). This is exactly what has been reported (Bech et al., 1999; Langseth et al., 2000, 2001). The BMR of female Kittiwakes was relatively constant during the incubation period, being 1.75 and 1.65 ml O₂ g⁻¹ h⁻¹ for the early and late parts of the incubation period, respectively. During the chick-rearing period BMR fell significantly, to values of 1.45 and 1.25 ml O₂ g⁻¹ h⁻¹ approximately 2 weeks and 3–4 weeks, respectively, into the chick-rearing period (Bech et al., 1999; Langseth et al., 2000). A link between the liver mass and BMR was likewise shown by a separate analysis of a group of adult Kittiwakes for which information on both BMR and body composition was available. This analysis showed that the liver was the only significant predictor of BMR, explaining 62% of

the variation in BMR (Langseth et al., 2000). The importance of the liver as a significant organ in determining metabolic heat production has been shown previously for both young and adult birds (e.g. Bech and Østnes, 1999; Chappell et al., 1999).

3.4. Field metabolic rate

The FMR of breeding Kittiwakes has been reported from the early as well as the late chick rearing period by Fyhn et al. (2001). Gabrielsen and Mehlum (2002) have in addition reported values from the pre-incubation and incubation periods, obtained from Kittiwakes breeding in the same colony. Taken together, these studies have revealed FMR-values, which varied roughly approximately 800 kJ day⁻¹ (Fig. 1). The FMR values for the Kittiwakes breeding on Svalbard are approximately what would be expected when compared with those of other marine bird species, which, by avian standards, generally have high FMRs (Brit-Friesen et al., 1989; Nagy et al., 1999; Ellis and Gabrielsen, 2001).

Looking in more detail at the temporal pattern of FMR throughout the breeding period (Fig. 1), one can see that there is a pronounced increase in FMR during the course of the chick-rearing period, amounting to an increase of 24% (from 736 kJ day⁻¹ during early chick-rearing to 915 kJ day⁻¹ during late chick-rearing; Fyhn et al., 2001). Hence, what seems to characterise the chick-rearing period is, on the one hand, a pronounced increase in FMR at the end of the period and, also, on the other hand, a rather low FMR during early chick-rearing period. This is further supported by a mean pre-incubation FMR-value of 772 kJ day⁻¹ for Kittiwakes in the same colony (Gabrielsen and Mehlum, 2002); a value which is also higher than that recorded during the early incubation period (Fig. 1).

4. Overview and conclusions

Ever since Drent and Daan (1980) published their paper on 'the prudent parent', the ratio between FMR and BMR (the 'sustained metabolic scope') has repeatedly been given importance when assessing the energy loads of birds and other groups of animals. A maximum ratio for FMR/BMR of approximately 4.0–4.5 was also claimed (Drent and Daan, 1980), although some studies

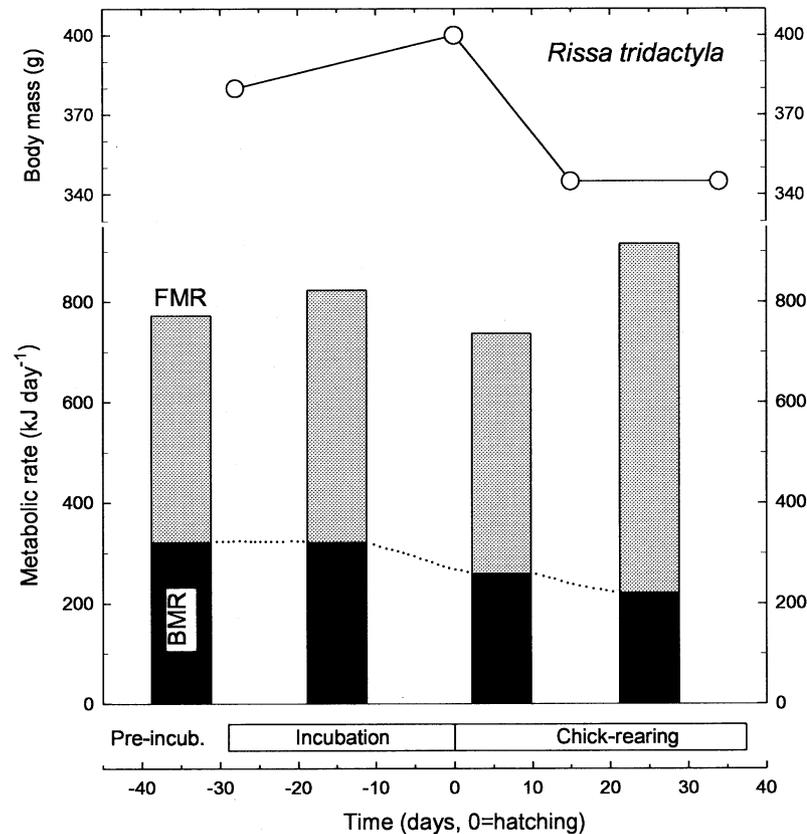


Fig. 1. Body mass, basal metabolic rate (BMR) and field metabolic rate (FMR) in relation to time during the breeding season in kittiwakes (*Rissa tridactyla*) on Svalbard. Time is given relative to the date of breeding (hatching time equals time 0) for each individual Kittiwake for which information was obtained. Data (average values) taken from Bech et al. (1999), Fyhn et al. (2001), Gabrielsen and Mehlum (2002) and Moe et al. (2002).

have shown that FMR may be as high as seven times the BMR (Hammond and Diamond, 1997). In a recent review on seabird energetics, Ellis and Gabrielsen (2001) report values of FMR up to six times the BMR. Our own studies on Kittiwakes have demonstrated that the FMR/BMR ratio may vary throughout the breeding period (Fig. 1). During the pre-incubation and incubation periods FMR was approximately 2.5 times BMR, while the ratio increased to 2.7 and 3.9 during the early and late parts of the incubation period, respectively. Since the first part of the chick-rearing period is energetically the most 'demanding' (Moe et al., 2002), we argue that the FMR to BMR ratio is not necessarily a good indicator of energy stress. Whether an organism is energy-stressed or not probably depends more on the ratio between energy intake and expenditure than on the actual level of energy expenditure. There may, therefore, not necessarily be a relationship between the FMR/

BMR ratio and energy stress in birds, which may be energetically stressed with a relatively low FMR/BMR ratio.

The suggestion of a maximum limit to the ratio between FMR and BMR (whatever its magnitude) has originated from the suggestion that there could be a functional link between BMR and FMR (Nagy 1987; Bryant, 1991; Koteja, 1991; Ricklefs et al., 1996; Hammond and Diamond, 1997). Hammond and Diamond (1997) suggested that high levels of FMR induce high maintenance costs because of enlargement in the energy-supplying organs, which in turn will increase the BMR. An important finding from our studies is that the FMR and BMR may actually change independently of each other and in opposite directions (Fig. 1). Hence, our results do not support the idea of a functional coupling between FMR and BMR. We have no explanation for this apparent paradox, which enables the Kittiwakes to increase their

daily energy expenditure, while at the same time they decrease their metabolic machinery dramatically.

Although we suggest that the mass loss at the beginning of the chick-rearing period is likely to be caused by some reproductive ‘stress’, rather than as a result of an adaptive change (Moe et al., 2002), the lower mass will nonetheless result in lower flight costs. In a similar manner one can also argue that the lowering of the BMR, whatever the underlying physiological mechanisms, will be beneficial for the adults, since they will have to expend less energy on maintenance costs (Langseth et al., 2001). The lower BMR of chick-rearing Kittiwakes will cause these birds to spend less energy in fuelling their own metabolic machinery. In effect, they may allocate more of their available energy into food-gathering for their offspring. This would be particularly beneficial if the BMR and FMR are ‘decoupled’, as indeed seems to be the case in Kittiwakes. A decrease in BMR in response to an increased workload has also been reported for other bird species. The Zebra finch (*Taeniopygia guttata*) compensated for an increased workload with a decrease in BMR (Deerenberg et al., 1998), and male White-crowned Sparrow (*Zonotrichia leucophrys gambelii*), which were implanted with testosterone, increased their activity level, while at the same time their BMR decreased (Wikelski et al., 1999).

An alternative explanation for the decrease in adult body mass and BMR after hatching could lie in the way the Kittiwakes feed their chicks. During the first part of the chick-rearing period, the adults feed the chicks small amounts of regurgitated food at short intervals. Consequently, the chicks are fed more frequently than the shift in parental duties would imply. For such a feeding strategy to function, the food for the chicks must be kept as ‘undigested’ as possible by the adults. Hence, the distinct loss of body mass at hatching might be caused by some, as yet unknown, changes in the digestive machinery, which ensures that the food is kept ‘fresh’ in the gastrointestinal tract but, simultaneously, causes a decrease in the food absorption rate of the adults. A striking parallel is presented by the King penguin (*Aptenodytes patagonicus*), in which, also, the digestive functions are partly altered to allow the adults to carry fresh food for a prolonged length of time (Gauthier-Clerc et al., 2000). Since food reduction generally causes large effects on liver size (Goodmann and

Ruderman, 1980; Burrin et al., 1988), our observations for the Kittiwakes of a mass decline primarily of the liver, is also indicative of some form of ‘starvation’.

This model of ‘self-inflicted metabolic stress’ in the Kittiwakes would be in agreement with the observed changes in body mass, body composition, FMR as well as BMR. Hence, the observation of a disproportionate decrease in liver mass indicates that some metabolic ‘downscaling’ occurs, which, in turn, will also lower the BMR. The daily energy expenditure must consequently partly be sustained by the use of endogenous reserves during early chick-rearing, causing the body mass to decrease. Although this model might seem speculative, and we have so far no suggestions to make as to the physiological mechanisms involved, the model seems attractive and deserves further studies.

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References

- Bech, C., Østnes, J.E., 1999. Influence of body composition on the metabolic rate of nestling European shags (*Phalacrocorax aristotelis*). *J. Comp. Physiol. B* 169, 263–270.
- Bech, C., Langseth, I., Gabrielsen, G.W., 1999. Repeatability of basal metabolism of breeding female Kittiwakes *Rissa tridactyla*. *Proc. R. Soc. Lond. B* 266, 2161–2167.
- Brit-Friesen, V.L., Montevecchi, W.A., Cairns, D.K., Macko, S.A., 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology* 70, 357–367.
- Bryant, D.M., 1991. Constraints on energy expenditure by birds. In: Bell, B.D., Cossee, R.O., Flux, J.E.C., Heather, B.D., Hitchmough, R.A., Robertson, C.J.R., Williams, M.J. (Eds.), *Acta XX Congressus Internationalis Ornithologici*. New Zealand Ornithological Congress Trust Board, Wellington, pp. 1989–2001.
- Burrin, D.G., Britton, R.A., Ferrell, C.L., 1988. Visceral organ size and hepatocyte metabolic activity in fed and fasted rats. *J. Nutr.* 118, 1547–1552.
- Chappell, M.A., Bech, C., Buttemer, W.A., 1999. The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. *J. Exp. Biol.* 202, 2269–2279.
- Deerenberg, C., Overkamp, G.J.F., Visser, G.H., Daan, S., 1998. Compensation in resting metabolism for experimentally increased activity. *J. Comp. Physiol.* 168B, 507–512.

- Drent, R.H., Daan, S., 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68, 225–252.
- Ellis, H.I., Gabrielsen, G.W., 2001. Energetics of free-ranging seabirds. In: Schreiber, E.A., Burger, J. (Eds.), *Biology of Marine Birds*. CRC Press, Boca Raton, Florida, pp. 359–407.
- Freed, L.A., 1981. Loss of mass in breeding wrens: stress or adaptation? *Ecology* 62, 1179–1186.
- Fyhn, M., Gabrielsen, G.W., Nordøy, E.S., Moe, B., Langseth, I., Bech, C., 2001. Individual variation in field metabolic rate of Kittiwakes (*Rissa tridactyla*) during the chick-rearing period. *Physiol. Biochem. Zool.* 74, 343–355.
- Gabrielsen, G.W., Mehlum, F., 2002. Energy expenditure of Kittiwakes (*Rissa tridactyla*) during the pre-breeding and incubation periods. *Polar Biol.* (submitted).
- Gauthier-Clerc, M., LeMaho, Y., Clerquin, Y., Drault, S., Handrich, Y., 2000. Penguin fathers preserve food for their chicks. *Nature* 408, 928–929.
- Goodmann, M.N., Ruderman, N.B., 1980. Starvation in the rat I. Effect of age and obesity on organ weights, RNA, DNA and protein. *Am. J. Physiol.* 239, E269–276.
- Hammond, K.A., Diamond, J., 1997. Maximum sustained energy budgets in humans and animals. *Nature* 386, 457–462.
- Koteja, P., 1991. On the relation between basal and field metabolic rates in birds and mammals. *Funct. Ecol.* 5, 56–64.
- Krebs, H.A., 1950. Body size and tissue respiration. *Biochim. Biophys. Acta* 4, 249–269.
- Langseth, I., Moe, B., Fyhn, M., Gabrielsen, G.W., Bech, C., 2000. Flexibility of Basal Metabolic Rate in Arctic breeding Kittiwakes (*Rissa tridactyla*). In: Heldmaier, G., Klingenspor, M. (Eds.), *Life in the Cold*. Springer-Verlag, Heidelberg and New York, pp. 471–477.
- Langseth, I., Moe, B., Bech, C., 2001. Body mass reduction in breeding female Kittiwakes (*Rissa tridactyla*); an adaptation to reduce maintenance costs? *Atlantic Seabirds* 3, 165–178.
- Moe, B., Langseth, I., Fyhn, M., Gabrielsen, G.W., Bech, C., 2002. Changes in body condition in breeding Kittiwakes *Rissa tridactyla*. *J. Avian Biol.* 33, (in press).
- Moreno, J., 1989. Strategies of mass changes in breeding birds. *Biol. J. Linn. Soc.* 37, 297–310.
- Nagy, K.A., 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monographs* 57, 111–128.
- Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.* 19, 247–277.
- Nice, M.M., 1937. Studies in the life history of the Song Sparrow I. A population study of the Song Sparrow. *Trans. Linn. Soc. New York* 4, 1–247.
- Niizuma, Y., Takahashi, A., Sasaki, N., Hayama, S.-I., Tokita, N., Watanuki, Y., 2001. Benefits of mass reduction for commuting flight with heavy food load in Leach's storm-petrel, *Oceanodroma leucorhoa*. *Ecol. Research* 16, 197–203.
- Norberg, R.A., 1981. Temporary weight decrease in breeding birds may result in more fledged young. *Am. Nat.* 118, 838–850.
- Nur, N., 1984. The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. *J. Anim. Ecol.* 53, 479–496.
- Ricklefs, R.E., 1974. Energetics of reproduction in birds. In: Paynter, R.A. (Ed.), *Avian Energetics*. Nuttall Ornithological Club, Cambridge, pp. 152–292.
- Ricklefs, R.E., Konarzewski, M., Daan, S., 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *Am. Nat.* 147, 1047–1071.
- Scott, I., Evans, P.R., 1992. The metabolic output of avian (*Sturnus vulgaris*, *Calidris alpina*) adipose tissue, liver and skeletal muscle: implications for BMR/body mass relationships. *Comp. Biochem. Physiol.* 103A, 329–332.
- Sibley, R.M., Calow, P., 1986. *Physiological Ecology of Animals. An Evolutionary Approach*. Blackwell Scientific Publications, Oxford and London.
- Wikelski, M., Lynn, S., Breuner, C., Wingfield, J.C., Kenagy, G.J., 1999. Energy metabolism, testosterone and corticosterone in white-crowned sparrows. *J. Comp. Physiol.* 185A, 463–470.
- Williams, G.C., 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am. Nat.* 100, 687–690.