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ORIGINAL PAPER

Metabolic adjustments in breeding female kittiwakes (*Rissa tridactyla*) include changes in kidney metabolic intensity

Bernt Rønning · Børge Moe · Olivier Chastel · Juli Broggi · Magdalene Langset · Claus Bech

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Abstract Black-legged kittiwakes (BLKIs) reduce self-maintenance cost through reductions in mass-specific basal metabolic rate (BMR), body mass and the size of visceral organs during the chick-rearing period. In the present study, we measured kidney in vitro oxygen consumption and plasma 3,3′,5-triiodo-L-thyronine (T3) levels of incubating and chick-rearing female BLKIs, to test whether the decrease in BMR is caused mainly by decreased metabolic intensity or simply by reductions in the size of organs with high metabolic intensity. Body mass and body condition were lower in chick-rearing birds compared with the incubating birds. In contrast to the previous findings, however, the kidney mass did not differ between the two breeding stages. Plasma T3 levels decreased substantially during the breeding season, indicating a reduction in BMR. Over the same period, kidney mass-specific oxygen consumption decreased (by 17.2%) from the incubating to the chick-rearing stage. Thus, the reduction in BMR found in breeding BLKIs seems partly explained by adjustments in metabolic intensity of visceral organs. Lowered metabolic intensity of visceral organs would permit increased allocation of energy to offspring at the expense of their own self-maintenance.

Keywords Kittiwake · Breeding · Metabolism · Thyroid hormones · Kidney

Abbreviations

BLKI	Black-legged kittiwake
BMR	Basal metabolic rate
CR	Chick rearing
INC	Incubating
T3	3,3′,5-triiodo-L-thyronine
VO_2	Oxygen consumption

Introduction

Reproduction is a stressful life-cycle event which in many bird species includes a reduction in body mass (Moreno 1989). From an energetic point of view, changes in the overall body mass are of less significance than the relative changes in size of organs comprising overall mass. This is because the specific metabolic rate varies substantially between tissues (Krebs 1950), and as a consequence different tissues contribute disproportionately to the whole-body metabolism. Thus, relative small, but highly metabolic active organs like liver, kidney and heart are expected to contribute disproportionately to the whole-body basal metabolism (Rolfe and Brown 1997). The size of visceral organs is known to be flexible, changing in response to different environmental and life-cycle events (Piersma and Lindstrøm 1997). If the metabolic intensity of these organs remains invariant as they change size, we would expect that

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B. Rønning (✉) · B. Moe · M. Langset · C. Bech
Department of Biology, Norwegian University of Science and Technology, 7491 Trondheim, Norway
e-mail: bernt.ronning@bio.ntnu.no

B. Moe
Division of Arctic Ecology, Norwegian Institute for Nature Research (NINA), 9296 Tromsø, Norway

O. Chastel
Centre d'Étude Biologiques de Chizé (CEBC), Centre National de la Recherche Scientifique, 79360 Villiers en Bois, France

J. Broggi
Department of Biology, University of Oulu, PO Box 3000, 90014 Oulu, Finland

changes in organ masses will directly influence the whole-body metabolism. This is supported by the findings from several studies that report significant correlations between basal metabolic rate (BMR) and mass of various highly metabolic active organs (Bech and Østnes 1999; Chappell et al. 1999; Piersma 2002; Moe et al. 2004, 2005). There is, however, considerable inconsistency between the studies regarding which organs correlates best with BMR. This implies that organ metabolic intensity may vary between species, and perhaps between life stages within species. Several studies have suggested that certain tissues may temporally vary in the species they studied (Merkt and Taylor 1994; Weber and Piersma 1996; Piersma et al. 2004). Furthermore, differences in activity of metabolic enzymes have been found in avian tissues undergoing mass change in both muscles (Selman and Evans 2005; Saunders and Klemm 1994) and visceral organs (Vézina and Williams 2005). Adjustments commonly reported in animals may be a complex process involving both changes in mass as well as metabolic intensity of constituent organs.

Thyroid hormones have long been known to influence metabolism in endothermic animals, but the mechanisms underlying these effects are still not fully understood (see reviews by Soboll 1993; Goglia et al. 2002; Silvestri et al. 2005). Various metabolic effects caused by thyroid hormones are established in birds (McNabb 2000). In house sparrows (*Passer domesticus*) and black-legged kittiwakes (BLKIs) (*Rissa tridactyla*) variation in plasma 3,3′,5-triiodo-L-thyronine (T3) is a significant determinant of the individual variation in mass-specific BMR (Chastel et al. 2003, unpublished results). In rats, in vitro O_2-consumption (VO_2) in various tissues is also shown to differ between individuals with different thyroid status (Barker and Klitgaard 1952; Ismail-Beigi and Edelman 1971; Somjen et al. 1981). Thus, thyroid hormones probably also play an important role in metabolic flexibility by modulating the metabolic intensity in different organs.

Breeding birds must allocate their energy optimally between offspring and self-maintenance so that lifetime reproductive success is maximised (Roff 1992; Stearns 1992). In Arctic breeding BLKIs both body mass and mass-specific BMR have been found to decrease substantially from incubation to the chick-rearing periods (Langseth et al. 2000; Bech et al. 2002; Moe et al. 2002), indicating a reduced energy allocation to self-maintenance. Langseth et al. (2000) found that the mass reduction of the kidney and the liver was disproportionately large compared to the overall reduction in body mass. However, although both the liver and kidney have a high mass-specific VO_2, the mass reduction in these organs could not alone explain the considerable reduction in mass-specific BMR. Thus, the reduction in organ masses may have been paralleled with an unknown degree of reduction in metabolic intensity in at least some of the visceral organs, further reducing BMR during the breeding period.

The aim of the present study is hence to go one step further in understanding the metabolic adjustments during breeding. We compared the plasma T3 concentration between incubating and chick-rearing female BLKIs. Variation in plasma T3 has previously been found to account for 60% of the individual variation in mass-specific BMR in this species (O. Chastel et al., unpublished results), and a difference in plasma T3 between the groups of birds sampled would thus indicate a change in BMR during the breeding season. We also obtained data on body mass and kidney mass which in earlier studies are found to change during the breeding season. In addition, we measured in vitro oxygen consumption of kidney slices to test if there was any decrease in metabolic intensity contributing to the decrease in mass-specific BMR during the breeding season. Because of the high metabolic intensity in kidney tissue, relatively small changes in kidney mass-specific VO_2 could have a significant impact on mass-specific BMR. If the reduction in BMR found in breeding BLKIs is partly explained by adjustments in organ metabolic intensity, we predict kidney mass-specific VO_2 to be lower in chick-rearing as compared to incubating birds.

Materials and methods

Study species

The BLKI is a Northern hemisphere medium-sized gull, having a circumpolar distribution. The birds used in the present study were breeding in a colony in Kongsfjorden, close to Ny-Ålesund, on the west coast of Svalbard (78°54′N, 12°13′E). The BLKIs on Svalbard breed from June to August. Because we were limiting the study to breeding females, we sexed birds by measuring head plus bill length in birds captured at nest. Individuals were sexed as females if head plus bill <92.1 mm (Barrett et al. 1985). The sex was later verified by DNA sexing (Fridolfsson and Ellegren 1999). The incubating birds (INC birds, $n = 9$) were collected in the period 4–8 July, and the chick-rearing birds (CR birds, $n = 8$) were collected from 27 to 29 July. The median hatch date at a nearby subcolony was 9 July in 2005. Thus, the INC birds were collected just prior to chick hatching and CR birds were collected when their chicks were approximately 3-weeks old.

Oxygen consumption measurements

After arrival to the laboratory (maximum 1 h after capture), the birds were euthanised with an intraperitoneal injection of sodium pentobarbitone (100 mg kg^{-1} body mass). The birds were then cut open and a small piece of the kidney (from the

cranial lobe) was cut out and weighed to the nearest 0.1 mg with a Sartorius digital scale (DWS, Elk Grove, IL, USA). The carcasses were then frozen for analyses of kidney mass at a later stage (see below). The kidney pieces used in the oxygen consumption measurements were immediately placed in an ice-cold Ringer's solution (in g/l: 8 NaCl, 0.4 KCl, 0.06 $Na_2HPO_4{\cdot}2H_2O$, 0.047 KH_2PO_4, 0.2 $MgSO_4{\cdot}7H_2O$, 4.76 Hepes, 0.442 $CaCl_2{\cdot}2H_2O$; adjusted to pH 7.4 with 4 N NaOH). The kidney pieces were gently stirred around in the Ringer's solution to wash out blood. A hand-held slicer, modified after Stadie and Riggs (1944), was used to slice the kidney samples to approximately 0.3 mm thick slices. Each slice was immediately transferred to an ice-cold Ringer's solution containing 10 mmol l^{-1} glucose.

The oxygen consumption measurements were obtained using a Strathkelvin respiration cell (RC-350, Glasgow, UK) with a Strathkelvin 1310 oxygen electrode (Glasgow, UK). The electrode was connected to a Strathkelvin 781 oxygen meter (Glasgow, UK) and the output reading was stored on a PC. The measurements were obtained at 40°C in a 2 ml medium (Ringer's solution, with the addition of 10 mmol l^{-1} glucose and 5 mmol l^{-1} sodium pyruvate). The tissues slices were gently blotted on filter paper and weighted (±0.1 mg) before added to the respiration cell. Oxygen consumption was measured for 4–8 min following thermal equilibration.

Body measurements and kidney dissection

Body mass was measured to the nearest 5 g, using a spring balance (MWT Mess und Wiegetechnik GmbH & Co. KG, Wennigsen, Germany), immediately after the birds were euthanased. In addition, measurements of the tarsus length and head plus bill length were taken as detailed in Moe et al. (2002). The birds were stored in air-tight plastic bags and transported frozen to the laboratory in Trondheim, where they were kept at −20°C. All dissections were performed within 5 months after capture. Kidneys were excised from semi-frozen carcasses, and the wet mass was determined by weighing the samples on a digital scale. However, because kidneys lost variable amounts of fluid when extracting tissues for metabolic measurements, we decided to instead use dry mass of kidneys to represent kidney size. The dry mass was found after drying the kidneys at 55°C until stable weights were achieved. When calculating total dry mass of the kidneys it was assumed that samples removed for metabolic measurements had the same water content as the kidney from which they were extracted.

Blood collection and T3 radioimmunoasseys

Within 3 min of capture in the field, a blood sample (maximum of 500 µl) was taken from the brachial vein, using a heparinised syringe. Within 1 h of collection, blood was centrifuged at 2,000 rpm in 8 min to separate the plasma from blood cells. The plasma was stored at −20°C until final T3 analyses. Total plasma concentrations of 3,3′,5-triiodo-L-thyronine (T3) were determined by radioimmunoassay at the CEBC as detailed in Chastel et al. (2003). Only one assay was performed and the intra-assay coefficient of variation was 2.6% ($n = 5$ replicates). All collections, and hence also blood samples, were collected in the afternoon to minimize the potential diurnal variation in plasma T3 (Klandorf et al. 1978).

Statistical analyses

Differences in body mass, body size, kidney mass, kidney VO_2 and plasma T3 between INC and CR birds were analysed using a one-way ANOVA. We used a general linear model (type III sum of squares) to analyse kidney mass-specific VO_2 in relation to plasma T3 concentration (covariate) and breeding stage (factor). We used biometrical measurements of tarsus and head plus bill in a principal component analysis to test if there was a difference in body size between birds from the two distinct groups (INC and CK birds, respectively). The first principal component (PC1) accounted for 51% of the variance and was used as an index of body size. All statistical analyses were performed using SPSS ver. 12.01 (SPPS Inc., Chicago, USA). The significance level was set at $P = 0.05$.

Results

Body mass was 12% lower in CR compared to INC birds ($F_{1,15} = 32.2$; $P < 0.001$, Table 1), despite body size not differing between these two groups ($F_{1,15} = 1.6$; $P = 0.225$, Table 1). Hence, the low body mass of CR birds reflected a reduced body condition and indicated that they had lost body mass during the chick-rearing period. However, the dry mass of kidney was not significantly different between the two breeding periods (Table 1).

Kidney mass-specific VO_2, measured in vitro, was 17.2% lower in CR compared to INC birds (2.19 and 2.64 ml $O_2\ g^{-1}\ h^{-1}$, respectively; $F_{1,15} = 21.6$; $P < 0.001$, Fig. 1). Plasma T3 concentration likewise decreased substantially (from 3.10 to 1.79 ng/ml plasma; $F_{1,15} = 7.4$; $P = 0.016$) during the breeding season (Fig. 1), suggesting a decline in mass-specific BMR from the incubation to the chick-rearing stage. When analysing the kidney mass-specific VO_2 we found a significant interaction between plasma T3 and breeding stage ($F_{1,13} = 4.8$; $P = 0.047$). Kidney mass-specific VO_2 correlated significantly with plasma T3 in the INC birds ($r^2 = 0.812$, $t = 5.492$; $P = 0.001$), whereas this was not the case for the CR birds ($r^2 = 0.031$, t = 0.438; $P = 0.677$, Fig. 2).

Table 1 Mean values and standard deviation (SD) of body mass, body size index and kidney dry mass in incubating and chick-rearing female black-legged kittiwakes

Parameters	Incubating birds (n = 9)		Chick-rearing birds (n = 8)		Breeding period differences		
	Mean	SD	Mean	SD	F	df	P
Body mass (g)	385.0	21.0	338.6	10.2	32.2	1, 15	<0.001
Body size index	0.23	0.52	−0.26	1.35	1.04	1, 15	0.324
Kidney dry mass (g)	0.952	0.040	0.980	0.080	0.85	1, 15	0.370

Body size index was extracted from a principal component analysis with the lengths of tarsus and head plus bill (see "Materials and methods")

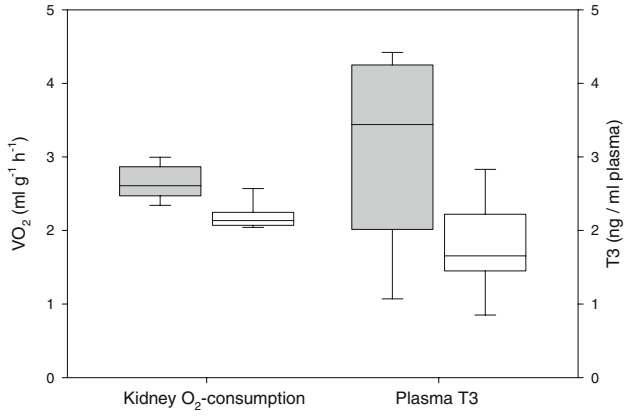

Fig. 1 Box plot showing median, upper and lower quartiles, and minimum and maximum values of kidney O_2-consumption and plasma T3 concentration in incubating (*grey boxes*, n = 9) and chick-rearing (*white boxes*, n = 8) female black-legged kittiwakes

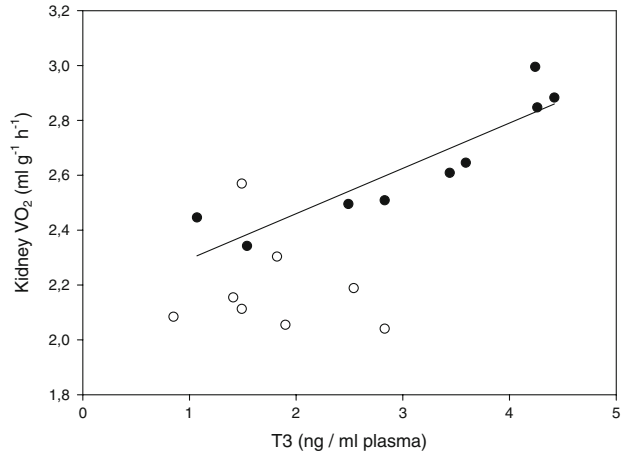

Fig. 2 Correlation between kidney O_2-consumption and plasma T3 concentration in incubating (*black circles*, n = 9) and chick-rearing (*open circles*, n = 8) female black-legged kittiwakes

Discussion

The breeding season has been suggested to be the most energy-demanding period for adult birds (Drent and Daan 1980). Consequently, many bird species have been observed to have a decrease in body mass during this stressful period (Moreno 1989). By spending endogenous energy reserves, breeding birds may be able to provide sufficient parental care, when resources are too scarce to cover the energetic demands from both offspring and self-maintenance (Ricklefs 1974; Moe et al. 2002). If breeding birds also lower their BMR, a higher proportion of the total available energy can be devoted to their offspring. Our study demonstrates that BLKIs change the metabolic intensity in a metabolically expensive organ, the kidney, during their breeding season. Furthermore, the lower metabolic intensity of the kidney of CR birds compared to INC birds was accompanied by lower body mass and plasma T3 concentration. The concomitant reductions in body mass, kidney metabolic intensity and plasma T3 concentration may represent one of the mechanisms that parents use to divert energy from self-maintenance to their offspring.

The 12% reduction in the body mass from the incubation to the chick-rearing period was of the same magnitude as previously found in female BLKIs from the same breeding area (~15%, Langseth et al. 2000; Moe et al. 2002). However, while Langseth et al. (2000) found that kidneys lost disproportionately more mass than the body as a whole, we did not detect a change in kidney mass in the birds we studied. Body condition in BLKIs at the end of the breeding season has been found to vary between years, probably due to inter-annual differences in foraging condition (Golet and Irons 1999). It is not known if differences in foraging condition could result in annual differences in mass and pattern of mass change in organs in breeding BLKIs. However, inter-annual differences in organ mass between breeding seasons as well as differences in the pattern of mass change between breeding stages has previously been reported in birds (Burness et al. 1998; Vézina and Williams 2003) indicating that this may be common.

The plasma T3 concentration was substantially lower in CR birds compared with INC birds. Given the strong correlation between plasma T3 and mass-specific BMR previously found in BLKIs (O. Chastel et al., unpublished results), it seems safe to conclude that this reflects the well known post-hatching BMR decrease observed in BLKIs (Langseth et al. 2000; Bech et al. 1999, 2002). The study by

Langseth et al. (2000) indicates that the BMR reduction during the breeding season in the BLKIs involves a reduction in metabolic intensity in some organs or tissues. This is in fact what the present study confirms: oxygen consumption in kidney slices decreased 17.2% from the incubation to the chick-rearing stages. Studies on both mammals and birds have suggested that reduced metabolic rate results from both reduction in metabolic intensity and modification in body composition (Merkt and Taylor 1994; Piersma et al. 2004). Several studies on seasonal variation in enzyme activity of various tissues support this idea. For example, several catabolic enzymes are known to vary seasonally in some migratory bird species (Lundgren and Kiessling 1985, 1986; Saunders and Klemm 1994). In captive red knots (*Calidris canutus*), Selman and Evans (2005) found that succinate dehydrogenase activity decreased in pectoral muscle and increased in small intestines during pre-migratory fattening. However, a seasonal variation in mass-specific citrate synthase (CS-activity) in the pectoralis muscle was not found in house finches (*Carpodacus mexicanus*) (O'Connor 1995). A change in CS-activity per unit mass between breeding stages was observed in the kidney of European starlings (Vézina and Williams 2005), supporting our findings that metabolic intensity in the kidney can change between breeding stages.

At a system-wide level, changes in thyroid hormones are known to influence BMR, and these hormones seem to be especially active in certain highly metabolic tissues like liver and kidney (Ismail-Beigi and Edelman 1971). In rats, injections of T3 have been shown to increase in vitro oxygen consumption in kidney slices (Barker and Klitgaard 1952; Ismail-Beigi and Edelman 1971; Somjen et al. 1981). Thus, the metabolic action of T3 seems to persist in surviving tissue slices in vitro (Barker and Klitgaard 1952). The active sodium potassium pump utilises more than half of the basal O_2-consumption in the kidney, at least in mammals (Clausen et al. 1991). Because T3 is known to stimulate cortical Na,K-ATPase activity (Somjen et al. 1981), modification of the Na,K-ATPase activity might be one factor explaining the correlation between plasma T3 levels and kidney oxygen consumption shown in the present study. However, a positive correlation between kidney mass-specific $\dot{V}O_2$ and plasma T3 was found only in the incubating birds (Fig. 2), which had higher plasma T3 concentrations than the chick-rearing birds. We have no obvious explanation for this observation other than it could be due to some physiological differences between birds in the different breeding stages; for example, differences in the ratios between concentration of total T3 and biological active free T3.

In summary, we found that both body mass and body condition decreased in female breeding BLKIs from the incubation to the chick-rearing stage. The dry mass of kidneys did not differ significantly between birds from the different breeding stages. This differs from the earlier studies on BLKIs breeding in Kongsfjorden, and indicates that the mass dynamics of visceral organs differ between breeding seasons. However, in spite of the lack of mass reduction in the kidney during the measurement period, there was a significant decrease in plasma T3 concentration indicating a reduction in mass-specific BMR. This was mirrored by the reduced metabolic intensity of kidney slices in the CR birds compared to INC birds. Adjustments in metabolic intensity seem thus to be one factor contributing to the phenotypic flexibility in BMR observed in breeding BLKIs. These results suggest that the reduction in BMR during the breeding season may be a complex process involving both changes in body mass, body composition and modifications in metabolic intensity. Thus, changes in metabolic intensity should be considered when examining the relationship between BMR and changes in body composition.

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