

FIELD METABOLIC RATES OF KITTIWAKES *RISSA TRIDACTYLA* DURING INCUBATION AND CHICK REARING

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We used doubly labelled water to study the field metabolic rates of breeding Kittiwakes *Rissa tridactyla* during the incubation phase, and to compare these with the metabolic rates of Kittiwakes rearing chicks. During the incubation phase, birds with two eggs spent an average (\pm SE) of 915 ± 134 kJ day⁻¹. This was similar to published estimates of Kittiwake energy expenditure during the chick-rearing phase, and similar to our own measurements of metabolic rates in a small number of birds rearing two chicks (863 ± 177 kJ day⁻¹). Our results corroborate the current view that incubation is not a phase of low energy expenditure, even in a large bird like the Kittiwake, and even in a species where both parents incubate. There was high variability of energy expenditure between birds, and this was largely because birds spent varying proportions of their time on and off the nest and did not show simple diurnal cycles under the conditions of 24 hour daylight. Birds spent 559 ± 197 kJ day⁻¹ while at the nest, and 1241 ± 154 kJ day⁻¹ away. Males had higher energy expenditure than females, and this was because they spent more time off the nest, not because they were bigger. There was no evidence that metabolic rates were influenced by wind speed or temperature. In order to look at whether birds had to work harder to incubate larger clutches we placed an extra egg in some nests and measured metabolic rates of the adults. Those with an extra egg spent 1011 ± 163 kJ day⁻¹ which was not significantly greater than the 915 kJ day⁻¹ spent by those with their normal clutch size.

Key words: *Rissa tridactyla* - Field metabolic rate - incubation - seabirds - reproductive energetics - doubly-labelled water

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INTRODUCTION

Traditionally, it has been assumed that rearing chicks is a phase of the breeding season when birds have to work particularly hard and that incubation is comparatively easy (Lack 1947; references in Van der Werf 1992). Although many small birds (12-85 g) do indeed have higher metabolic rates when rearing chicks than when incubating eggs, metabolic rates during incubation are on average only c. 20% below those during chick rearing (Tatner & Bryant 1993). For species where

only one parent is involved in incubation, Williams (1991, 1996) has argued that birds work just as hard during incubation as they do during chick-rearing. There has, however, been less attention given to the possibility that incubation could entail high energy expenditure even in species where both parents incubate, and there has been little work on the field metabolic rates of large birds during different stages of the breeding season (though see Masman *et al.* 1988; Pettit *et al.* 1988; Birt-Friesen *et al.* 1989). Because the costs of measuring energy expenditure with doubly la-

belled water increase with body size, many workers have concentrated on smaller species, and the reviews of both Williams (1991), and Tatner & Bryant (1993) included no studies of birds weighing more than 85 g. In order to gain a better understanding of the reproductive energetics of a large species with biparental incubation, we aim here to: (1) measure metabolic rates of Kittiwakes *Rissa tridactyla* during the incubation phase, (2) compare these with information on metabolic rates of Kittiwakes rearing chicks, (3) compare metabolic rates of birds while at the nest and while off the nest, (4) compare the metabolic rates of the males and females, (5) look at whether metabolic rates during incubation are higher in severe weather, and (6) look at whether birds have to work harder if they are given an extra egg to incubate.

METHODS

Study species and study site

We selected the Kittiwake as our study species for four main reasons. Firstly, it is relatively large (average (\pm SE) body mass for birds studied = 404.2 ± 7.1 g, $n = 17$; Table 1). Second, both parents share the incubation duties. Third, it has been found that metabolic rates can feasibly be measured in this species using the doubly-labelled water technique (Gabrielsen *et al.* 1987; Bryant 1989; Tatner & Bryant 1989), and fourthly, results for this species can be compared with published estimates of field metabolic rates during the chick-rearing phase of the breeding season (Gabrielsen *et al.* 1987). The Kittiwake can be caught on the nest using a fowling pole, and has not been found to be severely affected by disturbance in contrast to some other seabird species (e.g. Uttley *et al.* 1994). We conducted all our fieldwork on the island of Hornøya in North-East arctic Norway ($70^{\circ}22'N$, $31^{\circ}10'E$). This island holds a large Kittiwake colony of about 20 000 pairs. Many nests are situated on accessible low cliffs and rocky outcrops, making data collection safe and practical. Because of its high latitude, Hornøya experi-

ences continuous daylight during the Kittiwake breeding season, and the birds did not show a simple diurnal cycle, but instead alternated time on and off the nest irregularly with their mates (Table 1). Kittiwakes on Hornøya bred between May and August, they laid clutches of 1-3 eggs, and some birds which failed laid a second clutch. Hatching success (\pm SE) was only $37 \pm 3.5\%$, suggesting that breeding conditions were poor. Causes of nest-failure could rarely be proved, but some nests were predated by Herring Gulls *Larus argentatus*. In order to test whether energy expenditure was affected by wind and temperature, we mounted a min-max thermometer in the colony, 1m above the ground, protected from direct sunlight, and we obtained wind speed data from the local weather station on the mainland. During the period when energy expenditures were being measured, daily minimum temperatures varied between 3 and 8°C, daily maximum temperatures varied between 6 and 19°C, and wind speed varied between 3 and 30 m s⁻¹.

Measuring energy expenditure

We used the doubly labelled water technique (Tatner & Bryant 1989) to measure energy expenditure. In order to apply this technique to Kittiwakes incubating their normal clutches of 2 eggs, seven adults were caught on their nests during the early incubation phase. They were weighed, individually dye-marked with picric acid, and injected intraperitoneally with 3 ml of doubly labelled water containing 15 atom% ¹⁸O and 5 atom% Deuterium. Birds were kept in a wooden box for one hour while the isotopes mixed evenly through the body and then blood samples were taken from the brachial or femoral vein and stored in flame-sealed glass capillaries. So that energy expenditure could be calculated from rates of isotope depletion, further blood samples were taken from birds recaptured once or twice on their nests at intervals as near as possible to 24 or 48 hours after release.

Isotope ratio mass spectrometry on repeated blood samples was used firstly to estimate water loss from rates of deuterium depletion, and sec-

Table 1. Energy expenditures, body mass values and relative nest attendance of Kittiwakes during incubation and chick rearing. Note that repeat measurements were taken on birds with ring numbers MA22750 and MA22989.

Category	Ring Number	Body Mass (g)	Energy Expenditure			Sex	Attendance ¹	Period
			ml CO ₂ g ⁻¹ hr ⁻¹	kJ day ⁻¹	kJ g ⁻¹ day ⁻¹			
Incubation - 2 eggs	MA22722	349	1.79	398	1.14	F	15/16 (2)	22hr 20min
	MA22750	382	2.59	629	1.65	F	14/27 (3)	21hr 5min
	MA22750	390	1.39	344	0.88	F	17/22 (4)	25hr 5min
	MA22969	451	3.22	925	2.05	M	22/41 (3)	32hr 15min
	MA21114	403	5.91	1515	3.76	M	7/23 (3)	38hr 55min
	MA22959	407	3.57	925	2.27	M	1/44 (1)	39hr 15min
	MA21124	397	3.19	806	2.03	F	1/27 (2)	27hr 10min
	MA23059	438	4.89	1363	3.11	F	1/33 (1)	32hr 20min
Incubation - 2 + 1 eggs	MA21138	380	1.87	451	1.19	F	29/43 (2)	36hr 25min
	MA22728	368	3.31	774	2.10	F	17/17 (0)	26hr 50min
	MA22977	403	5.22	1339	3.32	F	4/32 (2)	30hr 15min
	673954	450	3.43	982	2.18	F	16/34 (4)	29hr 50min
	MA21125	435	6.26	1733	3.98	M	12/33 (2)	47hr 5min
	MA22989	443	2.80	789	1.78	F	10/44 (2)	43hr 5min
	MA22989	429	4.83	1319	3.07	F	-	11hr 30min
2 chicks	MA21140	402	1.64	420	1.05	F	1/19 (1)	29hr 40min
	MA23081	383	4.40	1072	2.80	F	-	35hr 55min
	MA23079	395	4.68	1177	2.98	M	-	41hr 15min
	MA23082	388	3.17	782	2.02	F	-	68hr 10min

¹Attendance refers to the number of nest-checks at which the bird was present on the nest divided by the total number of nest-checks. In brackets () is shown the number of times birds and their mates changed over at the nest during the period of observation.

only, after correcting for this water loss, rates of ¹⁸O depletion were used to estimate CO₂ production. These rates of CO₂ production were then converted to metabolic rates assuming 26.5 J per ml CO₂ (Tatner & Bryant 1989). All blood samples were analysed in duplicate to check for consistency. Blood samples were checked and calibrated against standards. The full protocol for the doubly labelled water technique is outlined in Tatner & Bryant (1989), and their methods were followed throughout.

Although Gabrielsen *et al.* (1987) have published extensive comparable results on the field metabolic rates of Kittiwakes rearing chicks, we

caught and injected a further four birds rearing two large chicks to check if metabolic rates were similar in this study. In order to look at whether birds would have to work harder if they had clutches of three eggs rather than two, we added an extra egg to the nests of six further birds and measured the metabolic rates of these birds in the same way. We decided to manipulate clutch size experimentally rather than simply comparing birds with natural clutches of two or three eggs, because birds choosing to lay bigger clutches may be higher quality parents capable of rearing more offspring without additional effort (Partridge 1989).

Because the study was conducted under conditions of 24-hour daylight and because the birds do not show simple diurnal cycles, the normal benefits of resampling isotopes after exactly 24 or 48 hours are less pronounced. Males and females irregularly alternated time foraging at sea and time on the nest (Table 1) and, like Gabrielsen *et al.* (1987), we found this gave rise to substantial variation between measurements of energy expenditure. Birds could be caught on the nest but not while they were foraging at sea, and so the individual measurements thus include birds which had spent varying amounts of time doing each activity. Because foraging bouts were shorter than those observed by Gabrielsen *et al.* (1987), it was not possible simply to divide birds into those at sea and those on the nest, but using a telescope we observed birds regularly throughout the period at hourly or half-hourly intervals and noted whether they were at the nest or not. This was not possible for 3 birds studied during the chick-rearing period because their nests could not easily be observed except from nearby, and this would have caused disturbance.

Data analysis

The full data set is shown in Table 1. Multiple measurements of energy expenditure were made for birds with ring numbers MA22750 and MA22989. For bird MA22750, data from the two sampling periods were summed to produce single measurements of energy expenditure and nest attendance for the combined period. For bird MA22989, attendance data were not collected throughout the second period, so data for only the first sampling period were used. We used Proc Genmod of SAS (SAS Institute Inc. 1997) to test all hypotheses within the framework of generalised linear models. After checking the distributional assumptions, normal errors were used to model energy expenditure (kJ day^{-1}), and so the models were similar to unbalanced analyses of (co-)variance. Attendance data were modelled using a binomial error structure, treating each nest-check as the unit of observation, but 'nesting' individual nests within the variables of interest in

order to contend with the non-independence of repeated observations on individual nests. We have used likelihood-ratio tests to compare models and test the significance of effects throughout, and have quoted the appropriate chi-square statistic where required. Full details of this modelling approach can be found in SAS Institute Inc. (1997).

We tested whether energy expenditure differed between birds incubating 2 eggs and those rearing 2 chicks. We looked at whether an intercept-only model (energy expenditure common to both periods) could be significantly improved by adding 'stage-of-breeding' to the model, and we estimated average energy expenditure during the two stages by fitting 'stage-of-breeding' and suppressing the intercept. We tested whether the high variability of energy expenditure was related to nest attendance by adding the proportion of nest-checks when the bird was on the nest to an intercept-only model of energy expenditure (kJ day^{-1}). We then estimated energy expenditure of birds on and off the nest by fitting a model with 'proportion of time at the nest', and 'proportion of time off the nest'. This model contained no intercept. We tested whether energy expenditure differed between males and females by adding 'sex' to an intercept-only model, and we estimated the average energy-expenditure of males and females by suppressing the intercept and fitting only 'sex'. We then tested whether the nest-attendance of males and females differed, by dropping 'sex' from a model containing 'sex' and 'individual-within-sex'. We then tested whether the effect of sex on energy expenditure was due to anything else apart from attendance, by adding 'sex' to a model containing 'proportion-of-time-at-nest' and 'proportion-of-time-away-from-nest'. We similarly tested for an effect of body mass on energy expenditure, and looked at whether this persisted after controlling for sex and nest-attendance. In the same way, we tested for an effect of giving birds an extra egg, and we tested for effects of wind speed, minimum temperature, and maximum temperature. We also used interaction terms between each of these variables and 'proportion-of-time-at-nest' or 'proportion-of-time-

away-from-nest' in order to look at whether sex, body mass, clutch size, or weather conditions might specifically affect only energy expenditure on the nest, or energy expenditure off it, though in no case could we find such effects.

RESULTS

Details of all measurements of energy expenditure are given in Table 1, together with information on the body mass, sex, and nest-attendance patterns of the individual birds. Birds incubating clutches of two eggs had an energy expenditure (\pm SE) of 915 ± 134 kJ day⁻¹ ($n = 7$). This was not significantly different from the energy expenditure of birds rearing two chicks (863 ± 177 kJ day⁻¹, $n = 4$). Assuming a resting metabolic rate of 314 kJ day⁻¹ (Gabrielsen *et al.* 1987), expenditure during incubation represents 2.91 x RMR and expenditure during chick-rearing represents 2.75 x RMR. Energy expenditure was affected significantly by the proportion of time the birds spent at the nest ($\chi^2_1 = 4.50$, $P = 0.034$). Birds at the nest spent an average (\pm SE) of 559 ± 197 kJ day⁻¹, birds off the nest spent 1241 ± 154 kJ day⁻¹.

Energy expenditure differed significantly between the sexes ($\chi^2_1 = 4.11$, $P = 0.043$), with males spending 1274 ± 172 kJ day⁻¹ and females spending 820 ± 115 kJ day⁻¹. However, males spent significantly more time away from the nest ($\chi^2_1 = 8.20$, $P < 0.0001$), and the effect of sex did not persist after controlling for attendance. Further, energy expenditure increased significantly with body mass ($\chi^2_1 = 4.43$, $P = 0.035$), with birds spending an extra 6.85 ± 2.98 kJ day⁻¹ for each additional gram. The effect of body mass did not, however, persist after controlling for sex or for nest-attendance. We therefore propose that males have a higher energy expenditure, not because they are bigger, but simply because they spend less time at the nest. Birds given an extra egg had an average energy expenditure of 1011 ± 163 kJ day⁻¹ ($n = 6$), and this was not significantly greater than the expenditure of those with their natural clutch of two eggs, regardless of whether or

not we controlled for nest-attendance. There was no evidence that minimum temperature, maximum temperature, or wind speed affected daily energy expenditure.

DISCUSSION

Tatner & Bryant (1993) developed geometric mean regression and iterative non-linear regression models to describe the relationship between body mass and field metabolic rates of small birds during incubation. Extrapolation of these for a bird of 404.2 g yields estimates of 799 kJ day⁻¹ and 763 kJ day⁻¹ respectively. These values lie well within the range of estimates made here, though small deviations would clearly be difficult to detect given the high variability in the data. The results found here are therefore not atypical of what might be extrapolated from other, smaller, species.

Though energy expenditure may vary between studies according to many other factors such as weather, location, food abundance and conditions for breeding, and although the low hatching success of birds in the study colony ($37 \pm 3.5\%$) might suggest breeding conditions were poor, the metabolic rates we observed here during incubation are similar to, or even slightly above, those found by Gabrielsen *et al.* (1987) in his study of birds rearing chicks. They calculated an average energy expenditure of 992 kJ day⁻¹ (range 641-1619) for actively foraging birds and 596 kJ day⁻¹ (range 392-838) for birds tending chicks at the nest. They proposed that a typical bird would expend on average 794 kJ day⁻¹ (range 392-1619) during the chick-rearing phase. These values are similar to those found in the four birds for which we measured energy expenditure during the chick-rearing period, although the influence of nest attendance on our measurements of energy expenditure during the chick rearing period cannot be assessed here because attendance data could not be collected for 3 of the 4 birds.

These data, for a larger species, are therefore consistent with Tatner & Bryant's (1993) sugges-

tion that incubation may also be an energetically costly phase of the breeding season since the metabolic rates of Kittiwakes were comparable during the stages of incubation and chick-rearing. Our data further indicate that high costs during the incubation phase were not restricted to periods of harsh weather.

One striking feature of these data is the high variability between individuals. This is unlikely to be due simply to measurement error: all samples were replicated and checked against standards, and Nagy (1980) has shown that the errors in the doubly labelled water technique are generally no more than $\pm 10\%$. Much of the variability was found to be real variance in energy expenditure due to differences in the amount of time spent by birds at the nest, and this arose largely because the study was conducted under conditions of 24 hour daylight where diurnal cycles are not pronounced. Energy expenditure off the nest was more than double that on the nest. There was no evidence that energy expenditure varied according to weather conditions and, although it varied significantly according to body mass and sex, our data suggest that the effect of body mass was due to sex, and the effect of sex was itself due to differences in the amount of time spent at the nest.

When energy expenditure off the nest is so much higher than energy expenditure on the nest, this inevitably leads to the question of whether incubation *per se* can be considered expensive. We would suggest that it must be expensive because the overall expenditure is similar to that of birds rearing chicks. Incubating on a nest may involve lower energy expenditure than foraging, but it involves no energy intake whatsoever; all energy spent while on the nest must be balanced by additional energy intake at sea. The act of incubation itself cannot therefore be taken in isolation. However, not all energy spent while off the nest need necessarily be spent acquiring energy for incubation. It may be that the birds, particularly the males, engage in activities such as extra-pair courtship. It is notable that males have a higher energy expenditure than females and that they spend more time off the nest. The apparent high 'costs

of incubation' may therefore partly be high costs of other activities. Furthermore, not all the energy spent on the nest need necessarily be due entirely to incubation. Between nest-observations, there may be short sallies to tackle competitors threatening their nest-site, or predators threatening them or their young. The expenditure of 559 kJ day⁻¹ on the nest, which equates to 1.8 x RMR (Gabrielsen *et al.* 1987), may include the costs of these activities.

Although energy expenditure was high during incubation, there was no evidence that it increased with clutch size; the higher energy expenditures of birds with an extra egg were not significantly different from those of birds with their normal clutch of two eggs. Most other studies have found a relationship between clutch size and energy expenditure (Thomson *et al.* 1998). The lack of a relationship in these data may simply represent a failure to detect a relationship due to the low statistical power inherent in small sample sizes and high variability.

Gabrielsen & Mehlum (in press) found similar patterns of energy expenditure among Kittiwakes breeding on Svalbard.

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SAMENVATTING

Om de kosten van de ouderlijke zorg voor de jongen te kwantificeren, werd het energieverbruik van Drieteenmeeuwen *Rissa tridactyla* in Noord-Noorwegen tijdens het bebroeden van eieren vergeleken met het energieverbruik tijdens de verzorging van de kuikens. Er werd gebruik gemaakt van de 'zwaarwater-methode'. Tijdens het bebroeden van legsels van twee eieren gaven de vogels gemiddeld 915 kJ dag⁻¹ uit. Dit getal was vergelijkbaar met het gemiddelde energieverbruik van Drieteenmeeuwen die twee jongen verzorgden, zoals bleek uit eigen metingen (gemiddeld 863 kJ dag⁻¹) en gegevens uit de literatuur. Dit betekent dat het bebroeden van eieren, zelfs voor een relatief grote vogel als de Drieteenmeeuw, waarbij beide ouders aan de broedzorg deelnemen, niet noodzakelijkerwijs 'relatief goedkoop' is, zoals vroeger meestal werd gedacht. Wel waren er bij dit onderzoek grote verschillen in energieverbruik tussen individuele vogels. Een deel van deze variatie kon worden verklaard uit de tijdsbesteding van de vogels. Drieteenmeeuwen die voornamelijk op het nest aanwezig waren, hadden een energieverbruik van 559 kJ dag⁻¹, terwijl vogels die nauwelijks op het nest aanwezig waren, een veel hoger energieverbruik hadden (1241 kJ dag⁻¹). Ook hadden de wat grotere mannetjes een hoger energieverbruik dan de vrouwtjes, maar dat was eerder het gevolg van het feit dat ze minder tijd op het nest doorbrachten dan dat ze groter waren. Windsnelheid en luchttemperatuur waren niet gecorreleerd met het energieverbruik. Om te zien of Drieteenmeeuwen die meer eieren warm moeten houden, ook meer energie verbruiken, werd in enkele nesten een extra ei gelegd. Zulke vogels gaven gemiddeld 1011 kJ dag⁻¹ uit, een gemiddelde dat statistisch niet verschilde van het energieverbruik van 915 kJ dag⁻¹ van Drieteenmeeuwen met een normale legselgrootte van twee eieren. (TP)

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