

Changes in body condition in breeding kittiwakes *Rissa tridactyla*

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We investigated the seasonal pattern of changes in body condition of breeding black-legged kittiwakes *Rissa tridactyla* in Svalbard (79°N) to evaluate whether changes in body condition were a consequence of the energetic demands of breeding (the reproductive stress hypothesis) or of voluntary anorexia to attain lower flight costs during chick rearing (the programmed anorexia hypothesis). Adult body condition was recorded from early egg laying to fledging and was examined in relation to date (relative to hatching), sex, parental time-budget, brood size and reproductive success. To distinguish between the two hypotheses we evaluate whether the reduction in body condition occurred during or ahead of the energetically most demanding part of the chick-rearing period. We combine our results on changes in body condition and time-budget with published information on field metabolic rate (FMR) and chick energy requirements from studies in the same colony.

Our calculations of adult energy requirements and energy intakes indicate that the first part of the chick-rearing period was energetically the most demanding period, because adult energy requirement per hour spent off the nest was highest in this period, and adults were time constrained because of the need for 24-h brooding of the chicks.

During the incubation period female body condition increased slightly, but significantly, while male body condition was stable. During the first part of the chick-rearing period, female and male body condition decreased by 14.8% and 8.4%, respectively. During the second part of the chick-rearing period, both male and female body condition remained stable. The reductions in body condition occurred during the phase which was suggested to be the energetically most demanding part of the chick-rearing period, thus supporting the reproductive stress hypothesis. Parental body condition during the incubation period was positively related to the probability of successfully fledging young, providing additional support for the reproductive stress hypothesis.

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Mass loss during breeding has been observed in many bird species (see review by Moreno 1989). It has generally been interpreted as a consequence of the energetic demands of breeding, the reproductive stress hypothesis (Ricklefs 1974, Harris 1979, Monaghan et al. 1989, Moreno 1989, Wendeln and Becker 1996) and has been used as an index of reproductive costs (Askenmo 1977, Bryant 1979, Nur 1984, Johnson et al. 1990). However, an alternative hypothesis explains the loss of body mass as an intrinsic process, known as programmed anorexia (Mrosovsky and Sherry 1980), a means of ensuring a

lower cost of foraging through decreased flight cost (Freed 1981, Norberg 1981). Flight is by far the most energetically costly activity in birds, with a metabolic rate 5–15 times higher than their basal metabolic rate (Norberg 1996). Flight costs are highly dependent on body mass. A low body mass during the breeding period, especially during the energetically demanding nestling period, would significantly decrease the cost of flying. By minimising the total cost of flying, more energy would be available for allocation to reproduction (Freed 1981, Norberg 1981).

Which of the above two hypotheses is true for most bird species has been the subject of several studies during the past decade (Hillström 1995, Sanz and Moreno 1995, Merkle and Barclay 1996). The two hypotheses are not mutually exclusive, since a stress-imposed mass loss will also lead to a saving in flight costs. The timing of body mass loss has been considered to enable a distinction to be made between the two hypotheses (Croll et al. 1991, Jones 1994). However, mass loss during the first part of the chick-rearing period has been interpreted both as programmed anorexia (Croll et al. 1991, Gaston and Jones 1989, Phillips and Furness 1997) and as a consequence of reproductive stress (Dijkstra et al. 1990, Wendeln and Becker 1996). Hence, whether the mass loss occurs during or ahead of the most energetically demanding part of the breeding cycle becomes a crucial question. However, the two hypotheses may attribute different meanings of the term 'energetically demanding'. In the programmed anorexia hypothesis (Freed 1981, Norberg 1981) the term refers strictly to the energetic costs of flight (search and transport of prey to the growing chicks). In the original reproductive stress hypothesis, as proposed by Nice (1937) and later by Ricklefs (1974), 'energetic demands' were given virtually the same meaning, the energetic costs of feeding chicks. Later, Nur (1984) distinguished between the physiological costs of feeding chicks and the energetic costs of both feeding and brooding chicks. Strictly speaking, the energetic cost of any breeding activity of a parent bird should be included when evaluating reproductive stress, as should the bird's capacity to cover these energy requirements by sufficient energy intake.

Body mass changes in breeding black-legged kittiwakes *Rissa tridactyla* have been investigated in northern Norway (Barrett et al. 1985) and Alaska (Golet and Irons 1999). Barrett et al. (1985) interpreted the observed mass loss in the kittiwakes as an adaptation to reduce the costs of flight, whereas Golet and Irons (1999) interpreted the observed reduction in body condition as a cost of reproduction. However, the precise temporal pattern of changes in body mass in the kittiwake has not been described.

To better understand the body mass dynamics of breeding kittiwakes, we investigated the pattern of changes in body condition of breeding birds throughout a breeding season, from early egg laying to fledging, in a population living in Svalbard (79°N). Body condition changes were examined in relation to date (relative to hatching), sex, breeding duties (nest attendance and foraging flights), brood size and reproductive success. We also used information on field metabolic rate (FMR, Fyhn et al. 2001) and chick energy requirements (Gabrielsen et al. 1992), obtained from studies conducted in the same colony, when discussing which part of the chick-rearing period is the energetically most demanding.

The reproductive stress hypothesis predicts that a reduction in body condition should occur during the energetically most demanding phase of breeding or during any phase in which the energetic demands are sufficient to cause a negative energy balance. By contrast, the programmed anorexia hypothesis predicts that a reduction in body condition should occur before the energetically most demanding period of breeding. The benefits of a low wing loading are greatest during the period in which the flight costs are highest.

We assume that if body condition before the energetically most demanding period is positively related to reproductive success (i.e. fledged young) this will support the reproductive stress hypothesis. Adults in high body condition may benefit from being able to draw upon endogenous reserves during the physiological stressful period and therefore fledge more young. If body condition before the energetically most demanding period is negatively related to reproductive success it will support the programmed anorexia hypothesis. Light adults may benefit from having lower flight costs when the flight demands are highest and therefore fledge more young.

Methods

Study area and birds

The study was carried out during the breeding season of 1997 in a colony of kittiwakes, Krykkjefjellet in the Kongsfjord, Svalbard (78° 55'N, 12° 20'E). The colony comprised 640 breeding pairs in 1981 (Mehlum and Bakken 1994), but has increased in size during the last two decades (F. Mehlum, pers. comm.). Nests from several parts of the colony were checked every second day throughout the breeding season (from 10 June to 12 August) to determine the timing of breeding in each nest. The date of hatching (day 0) of a nest was defined as the date on which the first egg hatched, and all subsequent events were related to this date.

Adult kittiwakes from a total of 114 nests were captured regularly throughout the breeding season. The birds were caught on the nests by using a telescopic fishing rod with a nylon snare fitted to its end. The first time an individual was caught it was weighed to the nearest 5 g, using a spring balance (Federwaage, Germany), and morphometric measurements (the lengths of head plus bill, tarsus and wing) were taken. It was then banded with a numbered metal ring from Stavanger Museum, Norway. Head plus bill length was measured with a sliding calliper from the back of the head to the tip of the bill, parallel to the cutting edge of the lower bill (Coulson et al. 1983). Tarsus length was measured with a sliding calliper from the notch on the back of the inter-tarsal joint to the edge appearing when the toes were bent 90° relative to the tarsus. Wing length was

measured with a stopped ruler from the carpal joint to the tip of the longest primary.

Sexing was based on the head plus bill length, assuming that within each breeding pair the largest bird was male. After visual inspection of the gonads of dissected kittiwakes (collected in 1997, 1998 and 1999) we found that this sexing method sexed 41 out of 42 birds correctly (98%).

If only one of the birds of a pair was caught, a head plus bill length of 92.1 mm was used as the discriminant value. Barrett et al. (1985) calculated this discriminant value in a population of kittiwakes on Hornøya (70° 22'N, 21° 10'E). They found that it sexed 87% of the birds correctly. Kittiwakes in the Kongsfjord do not differ in size from kittiwakes on Hornøya (head plus bill length ± 2 SE, Hornøya: males 89.2 ± 0.6 mm; females 94.5 ± 0.6 mm; Kongsfjord: males 89.3 ± 0.53 mm; females 94.0 ± 0.45 mm). The latter indicates that a discriminant value of 92.1 mm is appropriate for the Kongsfjord birds. Seventy-nine out of 86 (91.9%) individuals in pairs in which both adults were caught, would have been sexed correctly.

Parental attendance

Parental attendance pattern was recorded in a part of the colony during two continuous 24-h periods: 16–17 July (early in the chick-rearing period) and 30–31 July (late in the chick-rearing period). Based on a median hatching date (10 July) for that specific part of the colony, the mean age of the chicks in the nests was 6–7 and 20–21 days, respectively, during the observation periods. Nests were observed from the ground in front of the colony, without disturbing the birds. Presence or absence of the adults was recorded every 30 min during each observation period. When an individual kittiwake was recorded as present during two successive observations, it was assumed to have been present during 60 min. The number of foraging flights was defined as the numbers of returns made to the nest during the 24-h period. Distinction between the sexes was aided by colour-marking; females were marked red and males were marked blue, using a Penol marker. To avoid any bias caused by squatters, only pairs in which both adults were clearly marked were included in the analysis (22 pairs during the first period and 23 pairs during the second period).

Body condition

To calculate a body size index, we performed a principal components analysis (SPSS 1999) including measurements on head plus bill length, tarsus length and wing length of adults captured during the incubation period (Freeman and Jackson 1990). The first principal

component (PC1) accounted for 74.2% of the variance and was positively correlated with all three traits (head plus bill: $r = 0.88$, tarsus: $r = 0.87$, wing: $r = 0.83$, $P < 0.0001$, $N = 122$). The factor score from the PC1 was used as our body size index.

The relationship between body mass and body size during the incubation period differed significantly for males and females ($F_{1,119} = 4.0$, $P = 0.047$). Using PC1 we developed a least-squares regression for each sex that allowed us to predict the mass of a bird given its size (Fig. 1). Our body condition index (BC) was the residuals from these regressions (eq. 1):

$$BC = \frac{\text{obs. body mass} - \text{pred. body mass}}{\text{pred. body mass}} \times 100 \quad (1)$$

Analysis and statistics

To determine the possible effects of brood size on parental attendance or foraging flights, brood size was considered to be the actual brood size recorded at the time the observations were made. To study any possible effects of brood size on body condition, adult pairs were classified into two groups, those raising a single chick and those raising two chicks. Only pairs that kept two chicks alive for more than 75% of the total nestling period or kept two chicks alive until the last weighing were included.

The pattern of changes in body condition of breeding kittiwakes was tested by using general linear models (GLM) in SPSS v10.0 (SPSS 1999). The data for the three stages (incubation, first and second part of the

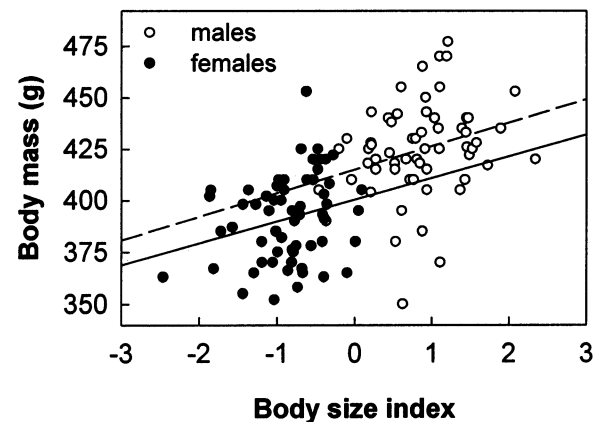


Fig. 1. Relationship between body mass and body size for male ($y = 11.4x + 414.9$, $N = 62$, $r^2 = 0.08$, $P = 0.025$, dashed line) and female ($y = 10.6x + 400.3$, $N = 60$, $r^2 = 0.06$, $P = 0.051$, solid line) kittiwakes during the incubation period in Svalbard (79°N). The body size index was obtained from a principal component analysis based on measurements on head plus bill-, tarsus- and wing length.

chick-rearing period) were analysed separately. The separation between the first and second part of the chick-rearing period was based on the finding that, for both male and female adult kittiwakes, the lowest body masses were recorded 16–17 days after hatching. In addition, their attendance pattern has been found to change when the chicks are at this age, presumably due to an increase in the thermoregulatory independence of the chicks (Gabrielsen et al. 1992). The first part of the chick-rearing period was therefore defined as the 16 first days after hatching, while the second part comprised the rest of the nestling period (from day 17 to fledging).

Body condition was entered as the dependent variable in the GLM analysis, while sex and brood size were factors, with date (relative to hatching) as a covariate. The initial global model included the main effects of sex, date and brood size, as well as the sex \times date and the brood size \times date interactions. Non-significant interaction terms were excluded in subsequent analyses.

To retain independence, a single mass was selected for each individual for each period, as follows: 20 randomised independent data sets were simulated, and the slope for the common regression was calculated, for each sex and period. After executing a linear regression on each of the twenty data sets, the data set with the slope closest to that of the common regression was chosen.

Changes in body condition (in %) from hatching to the second part of chick-rearing period were calculated by the following equation:

$$\text{Change in body condition (\%)} = \text{BC} - (f_{\text{inc}}(0) + f_{1.\text{c.r.}}(0)) \times \frac{1}{2} \quad (2)$$

BC = Observed body condition in the second part of the chick-rearing period,

$f_{\text{inc}}(0)$ = Predicted body condition at hatching (day 0) using the regression (body condition on date) obtained for the incubation period,

$f_{1.\text{c.r.}}(0)$ = Predicted body condition at hatching (day 0) using the regression (body condition on date) obtained for the first part of the chick-rearing period.

To test for a possible relationship between body condition and reproductive success we recorded the number of chicks of each breeding pair on day 30 post hatch. We assume that chicks that have attained this age fledge successfully. We obtained information on body condition during incubation and number of young fledged for 76 birds (28 pairs and 20 single birds). Only two of the 28 pairs fledged two young, while the rest fledged either one or zero young. We characterised the birds' reproductive success as 'fledging young' or 'not fledging young'. Hence, logistic

regression, using the logit-link function, was used to test for a possible relationship between body condition and reproductive success. Reproductive success was entered as the binary dependent variable, and body condition was entered as a covariate. The logistic regression was first executed with male or female body condition as covariates separately. Thereafter we executed it with the mean body condition of the parents within the 28 pairs as a covariate.

The t-test and the paired t-test were used to compare means of independent and paired samples, respectively. The nonparametric Mann-Whitney and Wilcoxon tests were used if the samples were not normally distributed. Means are reported with ± 1 SD. Correlation tests were made using Pearson correlation. Probabilities (α) of less than 0.05 were considered significant. All the statistical analyses were performed using SPSS v10.0.

Results

Body condition

Adult body mass during incubation showed a significant positive relationship to body size ($F_{1,119} = 9.4$, $P = 0.003$; Fig. 1), but the relationship between the sexes differed ($F_{1,119} = 4.0$, $P = 0.047$).

Since no significant interactions between sex and date were found ($F \leq 1.8$, $P \geq 0.18$), this indicates an almost parallel development of body condition in both sexes (Fig. 2A). However, separate linear regressions for the sexes revealed that a difference existed during the incubation period. Female body condition increased significantly during incubation ($F_{1,59} = 5.3$, $P = 0.025$), whereas male body condition did not ($F_{1,61} = 0.1$, $P = 0.7$). The increase in female body condition corresponded to an increase in body mass by 0.9 g d^{-1} ($y = 0.93x + 407$, $F_{1,61} = 5.6$, $P = 0.021$; Fig. 2B).

A significant negative relationship existed between body condition and date during the first part of the chick-rearing period ($F_{1,76} = 45.3$, $P < 0.0001$). No effect of brood size or of an interaction between brood size and date was found ($F \leq 2.1$, $P \geq 0.15$), indicating that adult body condition decreased independently of brood size during the first part of chick rearing. Separate linear regressions of body mass on date showed that females lost 4.0 g d^{-1} ($y = -4.0x + 395$, $r^2 = 0.44$, $N = 44$, $P < 0.0001$; Fig. 2B), and males lost 3.6 g d^{-1} ($y = -3.6x + 443$, $r^2 = 0.28$, $N = 40$, $P < 0.0001$; Fig. 2B) during this period.

During the second part of the chick-rearing period the body condition of both females and males stabilised at a low level (Fig. 2A). No effect of brood size or an interaction between brood size and date on body condition was found ($F < 0.88$, $P > 0.36$).

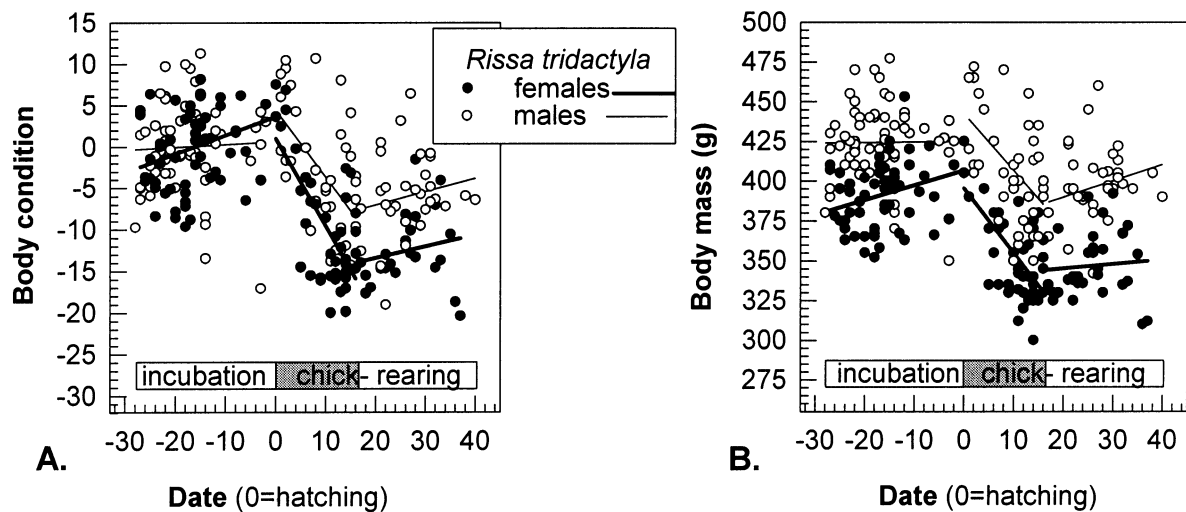


Fig. 2. Body condition (A) and body mass (B) of male and female kittiwakes breeding in Svalbard (79°N). Body condition is the percentage by which a bird's body mass differs from that predicted during the incubation period (given its size and sex). Regression lines and symbols are identical for both graphs. The first part of the chick-rearing period is from hatching to day 16 and the second part from day 17 to fledging. See text for statistics.

Cost of chick rearing

Females showed a greater reduction in body condition (-14.8%) from hatching to the second part of the chick-rearing period than males (-8.4%; t-test: $t = 4.9$, $df = 53$, $P < 0.0001$). There was no significant difference in body condition in adults raising one chick compared to adults raising two chicks (t-test: $t = 0.3$, $df = 30$, $P = 0.8$).

Body condition and reproductive success

The logistic regression showed a positive, but not significant, relationship between male body condition during the incubation period and number of young fledged ($B = 0.127$, $SE = 0.075$, $\chi^2 = 2.89$, $df = 1$, $N = 38$, $P = 0.089$). However, female body condition during the incubation period was significantly positively related to number of young fledged ($B = 0.172$, $SE = 0.082$, $\chi^2 = 4.40$, $df = 1$, $N = 38$, $P = 0.036$). The mean body condition of the parents within a pair was also significantly positively related to number of young fledged ($B = 0.399$, $SE = 0.177$, $\chi^2 = 5.1$, $df = 1$, $N = 28$, $P = 0.025$; Fig. 3).

Parental attendance

Observations of nest attendance and the daily number of foraging flights of the breeding adults were made in the first and second part of the chick-rearing period. During the first part the chicks were attended 24 hours a day by at least one of the parents, while in the second part of the chick-rearing period parental attendance

time was 55% lower (Mann-Whitney: $U = -5.6$, $P < 0.0001$; Fig. 4). The chicks were left unattended for 13.2 h d^{-1} in this period.

Males and females spent equal amounts of time on the nest in the first part of the chick-rearing period, while males spent more time on the nest than females in the second part (Table 1). In the first part of the chick-rearing period parental attendance was not dependent on brood size. However, in the second part males raising one chick spent more time on the nest

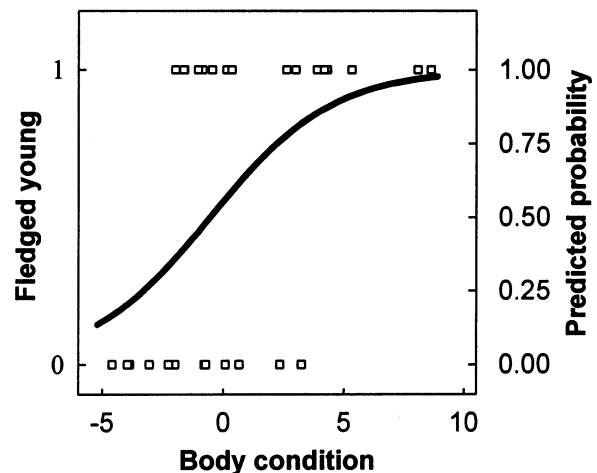


Fig. 3. Relationship between mean body condition of parents within a pair during incubation and number of young fledged (squares). 'Fledged young = 1' refers to one or two fledged young, while 'fledged young = 0' refers to zero fledged young. Given is the logistic regression (line) of the predicted probability of fledging young on mean body condition of parents. See text for statistics.

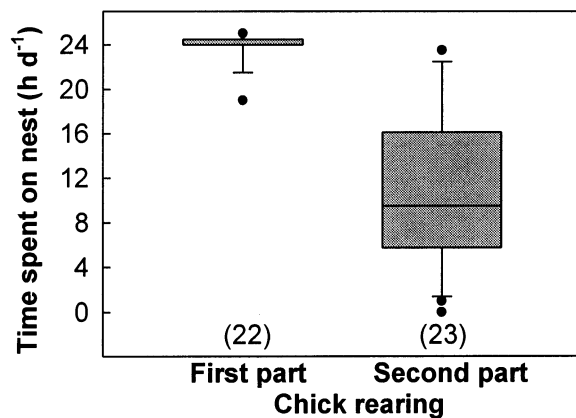


Fig. 4. Parental nest attendance (h d^{-1}) in the first and second parts of the chick-rearing period for pairs of breeding kittiwakes in Svalbard (79°N). Time spent on nest is the sum for both parents. Parental attendance was recorded during a 24-h observation on 16–17 and 30–31 July. The mean age of the chicks was 6–7 and 20–21 days, respectively. Plotted are the median, the 25th and the 75th percentiles, the 10th and the 90th percentiles and outlying data points. Number of pairs shown in parentheses. See text for statistics.

Table 1. Parental nest attendance (h d^{-1}). Mean values ± 1 SD. Values marked with asterisks differ significantly between early and late chick rearing. Parental attendance did not differ between the sexes during early chick rearing (paired t-test, $t = 1.29$, $df = 21$, $P = 0.2$) but did so during late chick rearing (Wilcoxon, $Z = -2.4$, $P = 0.016$). **: $P < 0.001$, ***: $P < 0.0001$.

	Early chick rearing (N = 22)	Late chick rearing (N = 23)
Males	11.2 ± 2.2	$6.7 \pm 5.4^{**}$
Females	12.5 ± 2.6	$4.1 \pm 3.0^{***}$

than males raising two chicks (t-test: $t = 2.3$, $df = 16.9$, $P = 0.035$).

Males and females made equal number of foraging flights both in the first and in the second part of the chick-rearing period (Wilcoxon: $Z < 1.6$, $P > 0.1$). The number of foraging flights was independent of brood size in the first part of the chick-rearing period. However, pairs raising one chick made significantly fewer foraging flights in the second compared to the first part of the chick-rearing period, while pairs raising two chicks made the same number of foraging flights in both periods (Table 2).

Table 2. Number of daily foraging flights for pairs of kittiwakes breeding in Svalbard given as means ± 1 SD. Sample sizes in parentheses. The number of foraging flights differs significantly (t-test, $P < 0.01$) between the early and late chick-rearing periods for pairs raising one chick. *: $P < 0.01$.

	Early chick rearing	Late chick rearing
Pairs with 1 chick	9.0 ± 2.1 (5)	5.1 ± 2.8 (18)*
Pairs with 2 chicks	8.0 ± 2.0 (17)	7.8 ± 3.3 (5)

Discussion

In the kittiwake, a near parallel change in body condition of both sexes would be expected during the incubation period, since their participation in incubation is virtually the same (Barrett 1978, Coulson and Wooller 1984). However, we found that female body condition increased significantly, while male body condition was stable during the incubation period. In the present study we did not measure the incubating adults' attendance time on the nest. Thus, we cannot assess whether the difference between the sexes in their pattern of body condition change is caused by differences in participation in incubation. However, our results are not consistent with a previous study on kittiwakes in northern Norway (Barrett et al. 1985), in which a stable body mass during the incubation period was reported for both sexes. One reason for this discrepancy could be that the authors did not relate their body mass data to hatching date, but to calendar date. Another reason could be that body mass patterns vary between years, as reported in the common tern *Sterna hirundo* (Wendeln and Becker 1996).

The body mass increase in females during the incubation period was due to deposition of lipids and build-up of lean mass (own unpubl. data). Female mass loss during the first part of the chick-rearing period was due to a reduction in both lipid and protein. The protein content was significantly reduced in muscles (breast and leg) and inner organs (liver, kidneys, heart and gut). The mass loss of males was most likely due to similar changes in body composition.

Adult kittiwakes exhibited a negative energy balance during the first part of the chick-rearing period, and consequently they drew on endogenous reserves. Because body mass was stable during the second part of the chick-rearing period energy expenditure equalled energy intake. Was the negative energy balance during the first part of the chick-rearing period caused by a voluntary anorexia, or were the energy requirements higher than the adults' foraging capacity? We combined our information on adult mass loss, mass loss composition (own unpubl. data) and time-budget with information on field metabolic rate (FMR, Fyhn et al. 2001) and chick energy requirements (Gabrielsen et al. 1992) to calculate adult energy requirements and energy intake. The FMR data were obtained in 1997 and 1998 in the same colony as we obtained our mass loss and time budget data. The chick energy requirement data were obtained from field and laboratory measurements on chicks in 1986 and 1987, also from the Krykkjefjellet colony (Gabrielsen et al. 1992). Table 3 lists the physiological and ecological parameters used in calculating the energy requirements and energy intake of an adult kittiwake during the first and the second parts of the chick-rearing period. We have not calculated sex-specific energy requirements, because we do not have information on how large proportions of the chicks'

Table 3. Physiological and ecological parameters used in calculating the energy requirements per day and the food requirements per hour spent off nest in breeding kittiwakes on Svalbard.

Parameters	Abbreviations used in equations 3 and 4	First part of the chick-rearing period	Second part of the chick-rearing period
Mean body mass (age of chicks in parentheses)		396 g (6 d old)	368 g (20 d old)
Mean mass change		-3.8 g d ⁻¹	0
Mass loss composition ¹		35% fat, 35% water, 30% protein	-
Energy release from mass loss ²	E _{mass loss}	75.1 kJ d ⁻¹ (3.8 g d ⁻¹ mass loss)	0
Field metabolic rate ³ (mean age of chicks in parentheses)	FMR	753 kJ d ⁻¹ (6 d old)	865 kJ d ⁻¹ (25 d old)
Mean brood size ⁴	B	1.76 chicks	1.23 chicks
Energy requirements per chick ⁵ (age of chicks in parentheses)	E _{chick}	262 kJ d ⁻¹ (6 d old)	750 kJ d ⁻¹ (22 d old)
Mean time spent off nest (mean age of chicks in parentheses)		12.2 h (6-7 d old)	18.6 h (20-21 d old)

1) Own unpublished data

2) Withers (1992); lipids 39.2 kJ g⁻¹ and proteins 20.1 kJ g⁻¹

3) Fyhn et al. (2001)

4) Mean brood size is the average number of chicks in the nests where parental attendance was quantified

5) Fig. 7 in Gabrielsen et al. (1992)

energy requirements females and males supply. Hence, we have calculated the average adult energy requirement and energy intake and assumed that the average adult supplies half of the daily energy requirements of its brood. Energy requirements and energy intake were calculated according to equations 3 and 4 (see Table 3 for explanations of the abbreviations used in the equations).

Energy requirement (kJ d⁻¹)

$$= \text{Adult FMR} + \frac{1}{2}B \times E_{\text{chick}} \quad (3)$$

Energy intake (kJ d⁻¹)

$$= \text{Adult FMR} - E_{\text{mass loss}} + \frac{1}{2}B \times E_{\text{chick}} \quad (4)$$

The daily energy requirement and energy intake of adults were highest during the second part of the chick-rearing period due to both higher FMR and higher energy requirements of the chicks (Fig. 5). However, the energy requirement per hour spent off the nest (hereafter ER_{h-1} off nest) was highest during the first part (82.4 kJ h⁻¹ vs 75.9 kJ h⁻¹). Adult energy intake per hour spent off the nest (hereafter EI_{h-1} off nest) was 76 kJ h⁻¹ during both periods.

According to the reproductive stress hypothesis the adults would not have the capacity to meet the energy requirement of 82.4 kJ h⁻¹, as calculated for the first part of the chick-rearing period. However, if their capacity to acquire energy is 76 kJ h⁻¹, as calculated for the energy intake, why don't they just increase the time spent off the nest to meet their daily energy

requirement? By spending one hour more per day off the nest the adults would have maintained energy balance and would not have lost body mass. However, the chicks would have been left unattended for two hours per day, which may be detrimental because of their inability to thermoregulate and their need for protection.

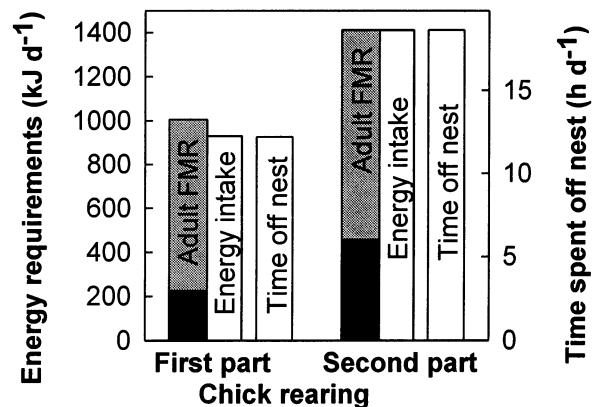


Fig. 5. Relationship between energy requirements, energy intake and time spent off the nest for adult kittiwakes in the first and second parts of the chick-rearing period. One adult energy requirement is calculated as the sum of the adult FMR (grey bars) and the energy requirements of half of the brood (black bars). The energy intake is calculated by subtracting the energy release of mass loss from the energy requirements. In the second part of the chick-rearing period there is no mass loss, and energy intake equals energy requirements. The physiological and ecological parameters used to calculate the energy requirements and the energy intake are given in Table 3. The equations for calculating the energy requirements and energy intake are given in the text.

According to the programmed anorexia hypothesis, adults would be capable of acquiring 82.4 kJ h^{-1} (or more) but voluntarily acquire less energy in order to lose mass and thereby reduce flight costs. Our calculation does not prove that adult capacity is lower than 82.4 kJ h^{-1} . However, it may indicate that since the adults do not meet the energy requirements during the part in which the ER_{h-1} off nest was calculated to be highest.

A weakness in our calculations of adult energy budgets is the lack of statistical testing. It is impossible to calculate standard errors for the various values used, which precludes the testing of whether the differences between energy intake and expenditure are statistically significant. The biological significance is already emphasised. The adults would have to leave the chicks unattended for 2 h per day to meet the daily energy requirement during the first part of the chick-rearing period, if their sustained capacity for acquiring energy equals the calculated EI_{h-1} off nest. An additional weakness is the lack of independent information on food availability. Our arguments about energy demand, energy intake and time available for foraging assume that the extrinsic limit on EI_{h-1} off nest remains constant throughout the study.

Of the hypotheses for mass loss we find the reproductive stress hypothesis most plausible. In terms of energy requirements per hour spent off the nest the first part of the chick-rearing period was calculated to be the most energetically demanding period, and the constraining factor is the time needed on the nest (Fig. 4). Young chicks' need for constant brooding by one of the parents limits the time available to the parents for foraging.

Recent studies on kittiwakes in Alaska and northern Norway have reported changes in body condition or body mass which are consistent with our results (Jacobsen et al. 1995, Pichl 1997, Golet et al. 1998, Golet and Irons 1999). However, these studies did not separate the early and late parts of the chick-rearing period to identify which one is the energetically most demanding. No previous study on kittiwakes has concluded that the first part of the chick-rearing period is the energetically most demanding. However, this has been reported in many pelagic seabirds (Ricklefs 1983, Salamolard and Weimerskirch 1993, Weimerskirch 1999).

In the original stress hypotheses of Nice (1937) and Ricklefs (1974) changes in body mass were interpreted as physiological costs of feeding chicks. The energy requirements of chicks are highest during the second part of the chick-rearing period. Hence, this period has commonly been regarded as the energetically most demanding for the adults (Freed 1981, Barrett et al. 1985, Croll et al. 1991, Merkle and Barclay 1996, Phillips and Furness 1997). However, information on the costs of feeding the chicks or adult energy expenditure is not necessarily sufficient to address the question of the

energetically most demanding phase of breeding. Our calculation of the energy budgets of breeding kittiwakes suggests that it is necessary to take into account both energy expenditure and energy intake as well as time available for foraging to identify the energetically most demanding phase of breeding and to evaluate physiological stress.

A stress-imposed mass loss during the first part of the chick-rearing period will also lead to savings in flight costs. These are highest during the second part of the chick-rearing period (Fyhn et al. 2001). However, if the observed mass loss is a consequence of physiological stress, the energetic benefit of lower flight costs are a by-product of that stress rather than a consequence of programmed anorexia.

Our results indicate that the breeding effort was sex dependent (Table 1) and females showed the greatest reduction in body condition between hatching and the second part of the chick-rearing period. A sex-specific pattern of reduction in body condition (or body mass) has also been found for many other avian species (see the review by Moreno 1989). Our findings are also consistent with the observed, sex-specific, pattern of reduction in body condition in breeding kittiwakes in Alaska (Golet and Irons 1999) and with the observed sex-specific variation in FMR within pairs of breeding kittiwakes (Fyhn et al. 2001).

We did not observe a brood-size dependent pattern in body condition despite our finding that adult breeding duties depended on brood-size during the last part of the chick-rearing period (Table 2). Brood size has an effect on adult FMR in the second part of the chick-rearing period (Fyhn et al. 2001). Our lack of clear brood-size dependent changes in body mass and body condition are nonetheless in contrast to the findings of many studies in which brood size was manipulated (Lindén and Møller 1989, Golet et al. 1998, Golet and Irons 1999). We therefore assume that differences in brood size may reflect quality differences between parents. Confounding factors, such as age and experience with resulting differences in the foraging capacity of breeding birds may mask brood-size dependent costs of chick rearing.

Adult body condition during the incubation period was positively related to the probability of successfully fledging young. This result implies that it is advantageous to be in good body condition before the onset of chick rearing. It may indicate that female mass gain during the incubation period is adaptive. The females are presumably low on stored nutrients after egg laying, and to successfully fledge young they benefit from improving their body condition before the onset of chick rearing. Our finding that body condition during incubation was positively related to fledging success is in accordance with several other studies. In the European kestrel *Falco tinnunculus*, the sparrowhawk *Accipiter nisus*, the pied flycatcher *Ficedula hypoleuca* and

in the common tern female body mass during the incubation period correlated positively with reproductive success (Drent and Daan 1980, Newton and Marquiss 1984, Lifjeld and Slagsvold 1986, Wendeln and Becker 1999).

Our calculations of the adult energy budget indicate that the first part of the chick-rearing period was the energetically most demanding part. Our finding that body condition during incubation was positively related to the probability of successfully fledging young supports the reproductive stress hypothesis. Further, female mass increase and male mass conservation during the incubation period may be additional arguments against the programmed anorexia hypothesis. It would seem paradoxical that kittiwakes should conserve or gain endogenous reserves during the incubation period if they were programmed to lose mass abruptly after hatching, as required by the programmed anorexia hypothesis. Phillips and Furness (1997) have argued that female arctic skuas *Stercorarius parasiticus* conserve their energy reserves during incubation as an insurance against natural fluctuations in food availability and/or to enable an early re-laying should the initial breeding attempt be unsuccessful. They found that female arctic skuas maintained a stable body mass during incubation, followed by an abrupt mass loss interpreted as an effect of programmed anorexia. However, we interpret the mass conservation (males) and the mass increase (females) of kittiwakes during the incubation period as a strategy for meeting a predictable and demanding period that severely reduces body condition. Individuals that store or conserve endogenous energy during the incubation period may attain a higher capacity to allocate energy to the chicks at the expense of their own feeding time.

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