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Raising young reduces body condition and fat stores in black-legged kittiwakes

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Abstract We conducted a manipulative experiment to investigate how raising chicks affects the body condition (body mass scaled by body size) and body composition (percent fat vs. lean mass) of black-legged kittiwakes (*Rissa tridactyla*). For 4 consecutive years (1991–1994) we removed eggs from randomly selected nests and then compared adults raising chicks with adults that had their eggs removed. At the end of the chick-rearing period, adults raising chicks were significantly lighter for their size than adults that had their eggs removed. Adults raising chicks also had a significantly lower percent body fat (by 28%) than adults from manipulated nests. The difference in percent body fat between the two groups was apparent at all levels of condition, suggesting that adults that are raising chicks apportion their reserves differently than adults that are working only to meet their own metabolic needs. End-of-season body condition of adults from manipulated and unmanipulated nests varied significantly among 5 years of study, and appeared to reflect differences in local foraging conditions. In all years, females were in worse condition than males at the end of the breeding season. This sex-specific condition difference did not, however, appear to indicate a greater short-term reproductive cost among females. Females were lighter for their size than males in both the manipulated and unmanipulated groups. Our results suggest that adult kittiwakes compromise their body condition and body composition during chick rearing to increase the likelihood of successfully fledging young, even though such adjustments may decrease their own post-reproductive survival probabilities. Prior to estimating the body composition of the experimental birds, we evaluated the usefulness of several noninvasive techniques for predicting fat mass in kittiwakes. We used cross-validation techniques to compare multiple regression models that included total body electrical conductivity (TOBEC), total body water (TBW), and morphometric measurements as independent variables. The most parsimonious model for predicting fat mass was based on TOBEC and mass measurements. TBW and morphometrics were of little utility in predicting fat mass in kittiwakes. Previous studies that have evaluated the usefulness of TOBEC as a predictor of fat mass have shown mixed results. We suggest that the size of the experimental subject relative to the size of the TOBEC measurement chamber may affect the accuracy of this technique.

Key words Birds · Body condition · Cost of reproduction · Fat · TOBEC

Introduction

All organisms that reproduce more than once during their lifetime face the dual challenge of maximizing current reproductive success, and the probability of survival to the next breeding attempt. These two goals place distinct, and often conflicting, selective pressures on breeding adults. From the standpoint of managing energy stores, individuals may maximize reproductive success by investing as much as possible in their offspring, but such a strategy may compromise their own chances for survival (Williams 1966; Stearns 1976, 1992; Roff 1992). Because energy stores devoted to raising young are not available for self-maintenance, breeding animals may face declines in body condition (body mass scaled by body size) if they do not sufficiently increase their own energy inputs (the principle of allocation, Calow 1984). When reductions in body condition occur, they sometimes have non-trivial consequences. In birds, for example, brood (or clutch) size manipulation studies that have demonstrated effects on adult body

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condition have also often demonstrated effects on adult survival (Golet et al. 1998).

Despite the apparent costs of low body condition for adult birds, there may also be benefits. Adult birds that are light for their size have reduced wing loading, and this may increase the efficiency with which they transport prey to their chicks. Increased efficiency in prey delivery may promote high reproductive success, thus conferring a fitness benefit to birds that allow their body condition to decline during the chick provisioning stage. In fact, evidence suggests that mass loss in breeding birds may at times result from programmed intrinsic processes (the programmed anorexia hypothesis) which are not the result of stress (Blem 1976; Freed 1981; Norberg 1981; Moreno 1989; Croll et al. 1991; Gaston and Perin 1993; Jones 1994). When raising chicks, birds therefore appear to face conflicting selective pressures: To keep survival probability high, it may be advantageous to maintain a high level of body condition; however, to maximize current reproductive success, it may be beneficial to allow body condition to decline, so prey can be delivered more efficiently.

Further conflict may be envisioned when examining the forces that shape how adult birds partition their energy reserves. Because fat has roughly twice the energy content of lean mass on a per gram basis (Schmidt-Nielsen 1990), birds may maximize their survival probability by storing fat during the breeding season. Evidence from field studies provides support, as fat stores and over-winter survival have been found to be positively correlated (Lima 1986; Blem 1990). To maximize current reproductive success, however, it may beneficial for birds to allocate relatively more of their energy reserves to lean mass. Because protein turnover is needed for muscle repair, stores of lean mass (i.e., protein) are especially important during periods of high exercise, such as flight (Piersma 1990; Evans et al. 1992). Finally, the costs and benefits of how birds partition their energy reserves during the breeding season are likely to vary depending upon the foraging ecology of the species. For seabirds, which make frequent, long-distance foraging trips to gather food for their chicks, the benefits of reduced wing loading and low body fat may be greater than for species that forage more locally.

To better understand the mechanisms and consequences of mass loss in breeding birds we removed eggs from randomly selected black-legged kittiwake (*Rissa tridactyla*) nests during 4 consecutive years. Because adults from manipulated nests did not raise chicks, we assumed that their body condition and body composition were set simply to maximize survival to the next breeding season. Among adults raising young, however, we assumed that these levels were set as a compromise between the need to successfully raise offspring and the need to survive to reproduce again. Given these assumptions, we hypothesized that adults raising chicks have lower body condition, and a lower percent body fat than adults that have their eggs removed. Because we randomly selected nests for eggs removal, our comparison groups were theoretically composed of adults of equal abilities. Thus potential confounding factors (e.g., age, experience) were controlled for in our experiment, and we were able to ascribe observed differences in body condition and body composition to the reproductive state of the birds (breeding vs. non-breeding).

Because none of the noninvasive techniques that we were interested in using to characterize body composition in our experimental birds had been validated for use with kittiwakes, and because species-specific calibrations are recommended (Scott et al. 1991; Skagen et al. 1993), we undertook a validation study of our own. We compared the relative utility of total body electrical conductivity (TOBEC, Keim et al. 1988; Walsberg 1988), total body water (TBW, Degen et al. 1981; Ellis and Jehl 1991; Groscolas et al. 1991; Reilly and Fedak 1990), and mass and size measurements (morphometrics) for predicting fat mass in a set of kittiwakes that were collected from our study population. After determining which technique worked best, we applied it our experimental birds so we could study how body composition is affected by chick rearing. Thus in addition to being an investigation of how body composition (and body condition) is affected by raising chicks, this paper is an evaluation of different noninvasive methods for determining body composition. This study was part of a larger investigation of reproductive costs in kittiwakes in which we investigated adult energetics and interyear variability in survival and fecundity costs (Golet et al. 1998; Golet 1999).

Materials and methods

Assessing body condition

Kittiwakes were studied at the Shoup Bay colony, Prince William Sound, Alaska from 1991 to 1995. We determined adult kittiwake body condition by scaling body mass by body size (Reid 1987; Hamer et al. 1993). This involved three steps: establishing an index for body size in kittiwakes, developing predictive equations to relate body size to body mass in the study population at large, and applying measurements of experimental birds to these equations to generate individual body condition estimates. This method of estimating body condition is recommended over other techniques because it provides an estimate of condition that is independent of the structural size of the individual (Piersma 1984; Reid 1987; Piersma and Davidson 1991; Jakob et al. 1996).

To establish our body size index, we performed a principal components analysis (PCA, SYSTAT 1997) on measurements of adults captured during our 1991 banding effort. In total, 843 adults were captured on 11–19 May 1991, in 19 firings of a 50-foot wide rocket net (kittiwakes were attending their nest sites at this stage, but had not yet begun nest-building). We weighed and individually color-marked each bird, and measured the tarsus, head-plus-bill, and wingcord lengths of 463 randomly-selected individuals. With PCA we generated weighting coefficients that described positive covariance among the linear measurements. These coefficients had fairly consistent loadings (tarsus 0.41, head-plus-bill 0.43, and wingcord 0.36), and the first principal component accounted for 68% of the variance in the original measures. Standardized measurements were multiplied by these coefficients and added together to produce a PCA factor score (our body size index). By regressing body mass (grams) on the body size index, we developed a least-squares regression ($y = 421.1 + 21.6x$, $n = 463$, $r^2 = 0.25$, $P < 0.0001$) that allowed us to predict the mass of a bird given its size. Although measurements of body size may not always be expected to scale linearly with body mass (Bookstein et al. 1985), we found that the distribution of points about the regression line appeared normal and homoscedastic, and saw no improvement in fit when body mass and body size were log-transformed prior to analyses. In addition to the above regression equation, which was formulated based on analyses of all birds, we developed separate predictive equations for males and females. Because the relationship between body size and mass was not significantly different for males and females, however, we applied the least squares regression listed above (developed from analyses of males, females, and birds of unknown sex) to all experimental birds when characterizing adult condition. Although this equation has relatively low predictive power, it serves as a useful benchmark for comparing mean levels of condition in groups of individuals.

Toward the end of the nestling stage (late July and early August) in 1991–1995 we weighed and measured experimental birds after capturing them with noose poles or monofilament snare traps. In total, 181 experimental adults were captured (all but 5 were first-time captures), 122 from unmanipulated nests, and 59 from manipulated nests (eggs were removed from manipulated nests late in the incubation period, see Golet et al. (1998) for details on the manipulation). Of this total, 133 were of known sex. Sexes were determined based on behavioral observations made during courtship (May and June). Sex-determining behaviors included begging, courtship feeding, standing, and copulating. We calculated the body condition of experimental birds by subtracting the predicted weight of each bird (based on the regression equation) from its actual weight, dividing this difference by the predicted weight, and then multiplying the resulting quotient by 100. This value (our body condition index) represents the percentage by which a bird's measured weight differs from what it was expected to weigh during pre-incubation, given its size. Because our condition index theoretically factors out individual differences that result from linear effects of size, it provides a rough estimate of each bird's level of stored nutrients, which includes both fat and lean mass components (Reinecke et al. 1988).

Assessing fat mass

Before estimating the percent body fat of birds from manipulated and unmanipulated nests, we determined which of several techniques best predicted fat content in a sample of 12 kittiwakes collected from our study site (Appendix). Kittiwakes were collected late in the chick-rearing period, and represented the normal range of body size. Total body fat and TBW were determined through whole-carcass analyses conducted at the Wildlife Habitat Laboratory at Washington State University under the direction of Bruce Davitt. TBW is the proportion of total body mass that is composed of water. Because fat is anhydrous (Blem 1976), TBW can be used to estimate fat-free mass, which can be useful in predicting fat mass when total body mass is known (Degen et al. 1981). Although TBW was determined through carcass analysis in this study, it is can also be measured by isotopic dilution, a noninvasive technique (Degen et al. 1981; Ellis and Jehl 1991). At the Wildlife Habitat Laboratory carcasses were shaved (plucking may remove fats at the follicle), sectioned, freeze dried for 48 h, and then homogenized using a Wiley Mill (Scientific Apparatus, Philadelphia, Penn., USA). A sample of the homogenate was oven-dried at 100°C for 24 h (after which it reached a constant mass) to determine the dry matter (moisture-free basis). Lipids were extracted from an aliquot of 2 g with a Labconco apparatus (Labconco Corporation, Kansas City, Mo., USA) using petroleum ether.

We measured TOBEC of adult kittiwakes with a SA-2 small-animal body composition analyzer (EM-SCAN, Springfield, Ill., USA) late in the nestling phase of 1991. Of a total of 46 kittiwakes measured, 12 were subsequently sacrificed for the development and validation of fat mass models, while the remainder (14 from manipulated nests and 20 from unmanipulated nests) were released unharmed. The SA-2 generates an electromagnetic field, and measures changes in its impedance when subjects are placed within it. Because the electrical conductivity of lipids is only 4–5% that of nonlipid tissues (Pethig 1979), lean mass is the primary determinant of TOBEC (Walsberg 1988). The increased conductivity of lean mass is primarily a function of its higher sodium and potassium ion concentration (Klish et al. 1984). Prior to placing kittiwakes in the measurement chamber of the SA-2, we secured their legs to their primary feathers with a rubber band (thus keeping wings folded, and feet pointing toward the chamber entrance). Birds were then wrapped in a thin clear plastic sheet (C-Line Products, model #80911, DesPlaines, Ill., USA) that held their bills tucked against their chest. The plastic sheeting restricted movement, which can lead to spurious TOBEC readings, and made it easy to slide the birds in and out of the chamber. Finally, wrapped birds were placed on a plexiglass carrier plate (supplied by EM-SCAN), and positioned on their backs with their sternum aligned with the plate's mid point. For each bird, a total of 15 TOBEC measurements were taken, all with the SA-2 set on "peak" mode. We wrapped each bird three times, and took five measurements per wrap. Analyses were based on the mean of the 15 measurements.

To determine which technique best predicted fat content we compared multiple regression models according to methods described by Neter et al. (1989). We considered five independent variables for inclusion in our models: TOBEC, TBW, adult body condition, adult body size (our PC1 score), and adult field mass. Multiple regression models were compared according to the prediction sums of squares (PRESS) procedure of cross-validation. PRESS is a data-splitting technique that predicts each data point from the least squares fitted regression function developed from the remaining $n-1$ data points. Models that have small PRESS values have small prediction errors. In addition, we evaluated models based on the mean square error (MSE), coefficients of determination (r^2), and mean standard error of the predicted values (SEPRED, SYSTAT 1997). In order of relative importance we considered PRESS, SEPRED, MSE, and r^2, when selecting models (as per Neter et al. 1989; Lyons and Haig 1995). Finally, we evaluated the benefit of adding additional independent variables to base regression models for predicting fat mass. This was done by testing the significance of the additional variance explained as the number of independent variables was augmented from k to $k+1$ with an F-statistic (Sokal and Rohlf 1995, p. 627).

Results

Body condition costs of chick rearing

Adult kittiwakes that raised chicks were significantly lighter for their size late in the nestling period than kittiwakes that had their eggs removed (Fig. 1, Table 1). The difference between the two groups was pronounced in all years in which data were collected for both groups (1991, 1992, and 1994). In 1991 adult body condition was significantly lower than in 1994, with both manipulated and unmanipulated adults being in better relative condition in 1994. In all years except 1995, the condition of adults in both the manipulated and unmanipulated groups was reduced relative to the preincubation level of 1991 (our baseline condition level, see Methods). In 1995, the body condition of unmanipulated adults was significantly higher than in all previous years, being approximately equal to the preincubation body condition level of 1991 (no nests were manipulated in 1995). Thus a trend was apparent of increasing adult body condition from 1991–1995.

At the end of the chick-rearing period, females had significantly lower body condition than males (Fig. 2, Table 1). The difference in condition between the sexes

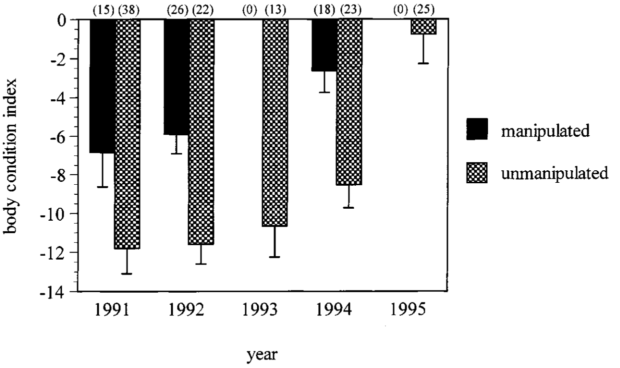

Fig. 1 Body condition (±SE) of adult kittiwakes at manipulated (without chicks) and unmanipulated (with chicks) nests late in the chick-rearing period at Shoup Bay, Alaska. The body condition index is a measure of the percentage by which a bird's body mass differs from what its mass is predicted to be during pre-breeding, given its body size (see Methods). Negative values indicate the percentage by which the observed condition is lower than the predicted condition. *Sample sizes* are given in *parentheses*. In 1993 no adults from manipulated nests were captured, and in 1995 nests were not manipulated

Table 1 Results from multi-way factorial ANOVA to determine the effects of raising chicks, sex, and year on adult kittiwake body condition measured at the end of the nestling period at Shoup Bay, Prince William Sound, Alaska, 1991–1995. All three sources of variance are considered as fixed effects. Significance was determined by examining the variance ratio of the appropriate mean square (MS) over the error MS. *P*-values of significant effects are in *bold type*. Note that all main effects (but no interaction effects) are significant

Model parameters	*df*	*F*-ratio	*P*
Treatment (manipulated vs. unmanipulated)	1, 136	23.6	**< 0.001**
Sex (♂ vs. ♀)	1, 122	13.2	**< 0.001**
Year[a] (1991–1995)	4, 125	14.5	**< 0.001**
Treatment × Sex	1, 128	1.1	0.30
Treatment × Year	2, 136	0.1	0.92
Sex × Year	4, 122	1.3	0.28
Treatment × Sex × Year	2, 95	0.9	0.41

[a] Tukey multiple pairwise comparisons of adult body condition: 1995 > 1991, 1992, 1993 and 1994 ($P < 0.01$ for all); 1994 > 1991 ($P = 0.033$)

was apparent in all years, and apparently arose during the breeding season. Prior to egg laying there was no difference in body condition between the sexes ($F_{1,298} = 1.57$, $P = 0.21$; Fig. 3).

Body composition differences between experimental groups

We predicted the fat content of breeding and non-breeding kittiwakes late in the chick rearing period of 1991 with a multiple regression model that included TOBEC and mass as independent variables. This model best predicted fat mass in the sample of kittiwakes collected for whole-carcass analysis. Adult kittiwakes raising chicks had on average 28% lower body fat content than kittiwakes that had their eggs removed (manipulated: 9.5%, $n = 14$, unmanipulated: 7.4%, $n = 20$, $t = 3.65$, $n = 34$, $P = 0.0009$). No difference in fat content was apparent between the sexes. Males and females raising chicks had a similar percentage body fat (males: 7.6%, $n = 9$, females: 7.5%, $n = 7$, $t = 0.09$, $P = 0.92$), and although there were no males identified in the manipulated group, females had a fat content (9.9%, $n = 8$), which was similar to this group's overall mean.

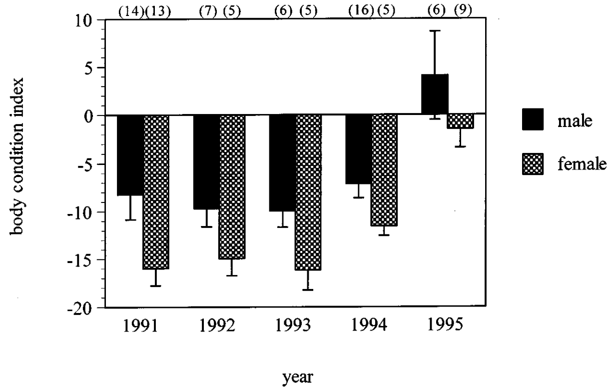

Fig. 2 Body condition (±SE) of male and female adult kittiwakes from unmanipulated nests (with chicks) late in the chick-rearing period at Shoup Bay, Alaska (1991–1995). The body condition index is a measure of the percentage by which a bird's body mass differs from what its mass is predicted to be during pre-breeding, given its body size (see Methods). Negative values indicate the percentage by which the observed condition is lower than the predicted condition. *Sample sizes* are given in *parentheses*. Birds were assigned sex based on behavioral observations (see Methods)

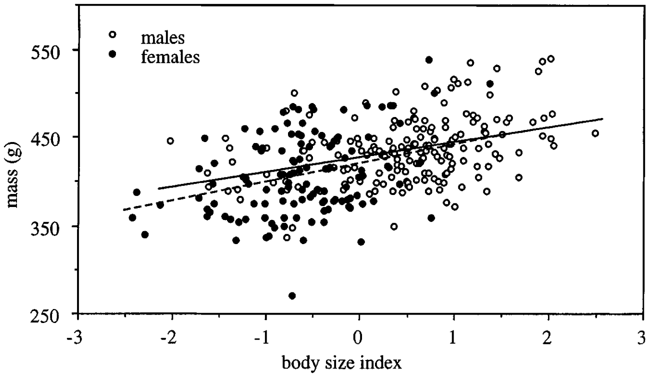

Fig. 3 Relationship between body size and body mass for male ($y = 17.4x + 426.9$, $n = 184$, $r^2 = 0.15$, $P < 0.001$, *solid regression line*) and female ($y = 21.6x + 421.2$, $n = 117$, $r^2 = 0.11$, $P < 0.001$, *dashed regression line*) kittiwakes during pre-breeding at Shoup Bay, Alaska, 1991

Adult body condition and percentage fat (as determined with TOBEC in 1991) were positively correlated [%fat = 10.0 + 17.8 (condition), $n = 52$, $r^2 = 0.33$, $P < 0.001$], demonstrating that differences in fat content among birds explained a substantial portion of the differences in adult kittiwake condition. At all condition levels, however, adults raising chicks had a lower percentage body fat than adults that had their eggs removed [treatment effect adjusted for the covariate (body condition) is significant: $F_{1,30} = 12.3$, $P = 0.001$; Fig. 4].

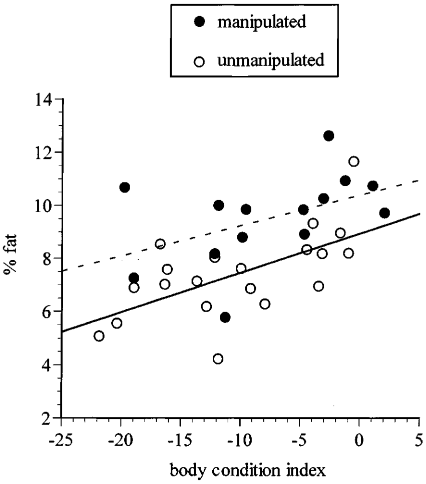

Fig. 4 Relationship between body condition and percent body fat for adult kittiwakes from manipulated (without chicks, $y = 0.11x + 10.4$, $n = 14$, $r^2 = 0.21$, $P = 0.096$) and unmanipulated (with chicks, $y = 0.14x + 8.9$, $n = 20$, $r^2 = 0.38$, $P = 0.003$) nests late in the chick-rearing period at Shoup Bay, Alaska, 1991. Fat content was predicted from model 1,4 [independent variables: total body electrical conductivity (TOBEC) and field mass]

Evaluation of noninvasive methods for predicting fat mass

Although our validation of techniques for estimating fat mass in live kittiwakes was based on a relatively low sample size ($n = 12$ birds), the results are unambiguous. The most parsimonious model for predicting fat mass was based solely on TOBEC and field mass measurements. The selected model, [fat (g) = −68.2 + 0.56(mass) − 0.12(TOBEC)], explained 52% of the variability in fat mass, was statistically significant, and had relatively low PRESS and SEPRED values, indicating reasonable accuracy and precision (Table 2). No models for predicting fat mass were significant without the inclusion of TOBEC, and TOBEC and mass were the only parameters that improved the proportion of variance explained by models lacking individual parameters (Table 3). Neither TBW nor morphometric measurements significantly improved the predictive ability of the models. Fat mass models based on morphometrics alone had high PRESS values, suggesting poor predictive ability, and explained only a small amount of the variance in fat mass (Table 2). Adding TBW to a base models of morphometric measurements produced negligible, and statistically insignificant, increases in the proportion of variance explained (Table 3).

Table 2 Comparisons of models (with different combinations of independent variables, all of which can be determined by non-invasive means) used to predict mass (g) of fat in 12 adult kittiwakes collected at Shoup Bay, Alaska, 1991. Fat mass was determined in the laboratory by chemical extraction. *P*-values of significant models are in **bold type**. Note that no models for predicting fat mass are significant without the inclusion of total body electrical conductivity (TOBEC). Variables 1–5 are defined as follows: *1* TOBEC, *2* body condition index, *3* body size index, *4* field mass (g), *5* total body water (TBW). [*PRESS* prediction sum of squares (Neter et al. 1989), *SEPRED* standard error of predicted values (SYSTAT 1997), *MSE* mean square error]

Independent variables	PRESS	SEPRED	r^2	MSE	*P*
1	590	2.5	0.10	41	0.33
2	551	2.6	0.07	42	0.42
3	458	2.3	0.27	33	0.083
4	493	2.4	0.21	35	0.13
5	569	2.6	0.08	41	0.37
1, 2	695	3.2	0.10	45	0.64
1, 3	475	2.7	0.40	30	0.10
1, 4	470	2.4	0.52	24	**0.036**
1, 5	642	3.3	0.10	45	0.64
2, 5	660	3.3	0.08	46	0.69
3, 4	535	3.0	0.27	36	0.24
3, 5	494	2.9	0.29	35	0.21
4, 5	447	2.8	0.32	34	0.18
1, 2, 5	790	4.0	0.10	51	0.84
1, 3, 5	535	3.2	0.44	32	0.19
1, 4, 5	412	2.7	0.61	22	**0.049**
1, 3, 4, 5	620	3.1	0.63	23	0.10

Table 3 Tests of the significance of the increase in variance explained as additional independent variables are added to base regression models for predicting fat mass (g) in kittiwakes. Numbers presented are *P*-values, and those that are significant appear in **bold type**. Note that only TOBEC and mass significantly improve the base models

Base model	Independent variable added				
	TOBEC	Condition	Body size	Field mass	TBW
TOBEC	–	0.76	0.063	**0.019**	0.76
Condition	0.60	–	–[a]	–[a]	0.76
Body size	0.20	–[a]	–	0.73	0.63
Field mass	**0.038**	–[a]	0.41	–	0.27
TBW	0.67	0.76	0.14	0.11	–

[a] Adult body condition was never included in models with body size and field mass. Body condition can not be considered as independent of these parameters since its definition is based on them (see Methods)

Discussion

Effects of chick rearing on body condition and fat stores

In all years the body condition of adults raising chicks was less than that of adults that had their eggs removed. We interpret this as evidence that body condition can decline in breeding kittiwakes as a short-term cost of reproduction (Bryant 1988). Mass loss during the breeding season has been widely reported in birds, and has often been attributed to the "stress" of reproduction (Hussell 1972; Ricklefs 1974, 1983; Nur 1984). From an energetics standpoint, the reproductive phase of a bird's life cycle is often demanding, nonetheless, it is probably wrong to assume that it is always stressful. Birds have evolved to meet the demands of reproduction, which is, after all, a predictable phase in their life cycle (Wingfield 1994). Recent investigations of body condition in birds have supported an alternative although not mutually exclusive view that body mass during breeding is controlled by intrinsic, often termed adaptive, processes (Blem 1976; Mrosovsky and Sherry 1980; Freed 1981; Norberg 1981; Moreno 1989). This view has become known as the programmed anorexia hypothesis (PAH). The PAH suggests that birds are programmed to automatically lose mass during the chick rearing period to increase their efficiency in transporting prey to their chicks. Compelling evidence in support of the PAH was found in studies of seabirds that abruptly lost mass at the onset of the nestling phase (Jones 1987; Gaston and Jones 1989; Croll et al. 1991; Gaston and Perin 1993; Jones 1994). Although the contribution of these studies to our understanding of how body stores are managed in breeding birds should not be underestimated, it is clear that all mass loss in birds during the breeding season is not caused by intrinsic (programmed) processes. The results of our study and others suggest that interannual differences in body condition of birds at the end of the nestling phase are caused by extrinsic factors, and furthermore, that end-of-season condition may be important in determining how current reproductive efforts translate into future reproductive costs.

Strictly speaking the PAH suggests that the body condition of birds during the breeding season is not influenced by environmental processes, and that body mass at a given stage in the breeding cycle is expected to be constant from year to year (Gaston and Jones 1989). Results from studies of kittiwakes and other birds, however, suggest that this is not the case. We found considerable variability in end-of-season body condition among adults from both manipulated and unmanipulated nests which appeared to reflect interannual differences in foraging conditions. In 1991, when adult body condition was lowest in 5 years of study, foraging conditions appeared challenging for kittiwakes. Foraging trip lengths were longest in 1991, and chick growth rates and brood size at fledging were low (Golet 1999). By contrast, in 1994 and 1995, when foraging conditions appeared better, body condition was higher. These results suggest that body condition in kittiwakes declines more in years when chick provisioning is difficult than in years when provisioning is easier. Reduced end-of-season body condition among kittiwakes has also been documented in Shetland in a year characterized by depressed reproductive success, long foraging trip lengths, and low food availability (Hamer et al. 1993). Studies of other species of birds similarly demonstrate that intrinsic factors alone cannot explain breeding-season body condition and mass loss patterns. For example, among female Tengmalm's owls *Aegolius funereus* body condition was related to vole abundance (Korpimäki 1990); and in green-rumped parrotlets *Forpus passerinus* mass loss was in part explained by territory or mate quality (Curlee and Beissinger 1995). These studies suggest that adult body condition is sensitive to extrinsic forces, and that foraging conditions may play a pivotal role in shaping end-of-season condition in breeding birds.

The PAH also predicts that body condition should not be related to manipulated brood size (Curlee and Beissinger 1995), and that changes in body condition that take place during the breeding season should not affect subsequent survival (Gaston and Jones 1989). Although the evidence from brood manipulation experiments is mixed, these predictions do not appear to be upheld. Numerous studies have shown a negative correlation between manipulated brood size and body condition (see Table 1 in Golet et al. 1998), and among brood manipulation experiments reduced survival was found in a higher proportion of those studies showing body condition effects than in studies lacking such effects (Golet et al. 1998). Thus there is evidence that body condition is influenced by the number of chicks a bird attempts to raise, and further, that variability in end-of-season body condition may be important in shaping long-term reproductive costs. Finally, because both intrinsic and extrinsic factors are likely involved in shaping patterns of mass loss in breeding birds, and because species-specific responses are likely, multi-year comparisons may be necessary before judgements can be made regarding the degree to which the body condition of a population is compromised in any given year.

At all condition levels adults raising chicks had lower fat content than adults from manipulated nests (Fig. 4). Thus it appears that adults that are raising chicks apportion their reserves differently from adults that are working only to meet their own metabolic needs. By having more of their body stores in lean tissue (i.e., muscle) adult kittiwakes raising chicks may be better able to handle the increased energetic load associated with raising chicks (Golet 1999). Adults without chicks likely apportion more of their reserves to fat because this is the most efficient way to store energy (Blem 1990). In summary, we found adults raising chicks to be lighter and leaner than adults from manipulated nests. Although both modifications potentially lower an adult's chances of survival, they appear to be necessary, at least in certain years, if adults are to successfully raise young.

Females appeared to be in worse body condition than males at the end of the breeding season. This does not, however, appear to be indicative of a greater short-term reproductive cost. Late in the chick-rearing period, females were lighter for their size than males in both the manipulated and the unmanipulated groups (Table 1). During much of the year, females may be lighter for their size than males; however, during pre-laying (when the predictive equations were derived for calculating body condition), the relationships between mass and size of males and females were virtually identical (Fig. 3). Prior to laying eggs females accumulate extra reserves, but this mass is lost upon clutch initiation (Barrett et al. 1985). Among kittiwakes studied in Norway, males and females showed parallel fluctuations in mass once the eggs were laid (Barrett et al. 1985), which may be expected given that kittiwake parents contribute equally to raising their chicks (Maunder and Threlfall 1972; Baird 1994).

Predicting fat mass

Our results suggest that fat mass can be predicted with reasonable accuracy for kittiwakes given measures of field mass and total body electrical conductivity (TOBEC). In contrast, measurements of total body water (TBW) and morphometrics appear to be of little utility in predicting fat content in kittiwakes. Initial validation studies similarly suggested that TOBEC was a useful predictor of fat mass. More recent studies, however, have cast doubt on its utility. Early studies partitioned total body mass into components of lean and fat mass according to a two-compartment model, and then focused on the high degree of variability in lean mass explained by TOBEC (Walsberg 1988; Castro et al. 1990; Roby 1991). Given the accuracy in predicting lean mass with TOBEC, it was reasoned that the fat mass could also be accurately predicted (by simply subtracting lean mass from total mass). However, Morton et al. (1991) cautioned that the coefficients of determination for lean mass regressions do not necessarily represent the precision with which fat mass can be estimated. Because fat mass is typically a much smaller component of total body mass than lean mass, the same absolute error in estimating body composition translates to a relatively larger error when estimating fat mass than when estimating lean mass. Later validation studies that adopted more rigorous statistical approaches found TOBEC to be of little use for estimating fat mass (Skagen et al. 1993; Conway et al. 1994; Lyons and Haig 1995; Spengler et al. 1995). All of these studies, however, were conducted on relatively small birds that took up only a small portion of the TOBEC measurement chamber. Asch and Roby (1995) suggested that the precision of the technique may depend upon the size of the study subject relative to the size of the electromagnetic coil which surrounds this chamber. The improved usefulness of TOBEC in our study may be explained, to a large degree, by the greater sensitivity of the SA-2 apparatus to a larger bird. Kittiwakes fit tightly in the SA-2.

TBW has been used successfully to estimate fat content of both mammals (Reilly and Fedak 1990), and birds (Degen et al. 1981; Ellis and Jehl 1991; Groscolas et al. 1991), however it was less useful in our study of kittiwakes. We did, however, find a significant correlation between fat mass (g) and TBW expressed as a proportion of shaved mass [$\text{Fat (g)} = -2.3(\text{TBW}) + 156.7$, $n = 12$, $r^2 = 0.38$, $P = 0.038$]. Apparently the relationship between fat mass (g) and TBW expressed as proportion of field mass was not significant because plumage weight (or perhaps water held in the plumage) was variable among individuals.

Although many studies rely on morphometrics alone to predict fat mass (Bailey 1979; Chappell and Titman 1983; Piersma 1984; Briggs 1989; Briggs et al. 1991), our analyses suggest that such predictions should be made with caution. Within the sample of birds collected for model validation we did not find morphometrics alone to be a reliable predictor of fat mass (Tables 2, 3). Furthermore, within our experimental population, we found that the relationship between fat mass and condition (which is defined based on morphometrics) varied among treatment groups (Fig. 4). Although morphometric measurements other than those employed in our study (e.g., pectoral angle) have, in certain instances, proven useful in assessing fat content (Sibly et al. 1987), van der Meer and Piersma (1994) argued that prevailing methods of predicting fat mass from morphometrics are based on questionable assumptions and should be abandoned. Our analyses suggest that relationships between fat mass and morphometric indices may exist, but that they must be established empirically on a case-by-case basis before they are applied.

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Appendix A1 Body composition, body mass, shaved mass, body size, body condition, and total body electrical conductivity (TOBEC) of 12 kittiwakes collected from Shoup Bay, Alaska during late July and early August 1991

Bird	Body mass (g)	Shaved mass (g)	Fat (g)	Protein (g)	Ash (g)	TBW (g)	TOBEC	Body condition	Body size
1	330	290	33.9	75.0	17.6	163.8	743	−17.2	−1.0
2	326	288	24.0	77.9	20.2	165.9	766	−15.7	−1.6
3	326	284	15.8	79.8	23.9	164.2	784	−16.1	−1.5
4	367	330	26.9	94.5	24.0	184.2	969	−12.4	−0.09
5	371	339	26.7	90.5	24.1	197.4	954	−12.1	0.05
6	375	336	31.5	87.9	29.2	187.1	939	−15.3	1.0
7	337	296	22.8	85.5	24.8	163.6	880	−20.5	0.13
8	303	262	20.4	68.7	18.6	154.3	667	−21.9	−1.5
9	377	330	17.5	92.9	30.0	189.7	995	−12.1	0.35
10	392	339	31.8	94.4	25.9	187.3	1013	−13.0	1.34
11	388	344	35.9	93.9	27.4	186.6	995	−12.5	1.0
12	388	353	25.7	95.4	24.0	208.3	1018	−10.3	0.52

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