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Changes in body mass and body reserves of breeding Little Auks (*Alle alle* L.)

ABSTRACT: Changes in body mass and body reserves of Little Auks (*Alle alle*) were studied throughout the breeding season. Body mass loss after chick hatching was analyzed with respect to two hypotheses: (1) mass loss reflects the stress of reproduction, (2) mass loss is adaptive by reducing power consumption during flight. Body mass of both males and females increased during incubation, dropped abruptly after hatching, and remained stable until the end of the chick-rearing period. These changes were largely due to change in mass of fat reserves. Body mass, fat, and protein reserves, when corrected for body size, did not differ between sexes at the end of incubation. Female size-corrected body mass at that time was correlated with peak body mass of chicks. The estimated energy savings for flight due to the decline in adult body mass after chick hatching were small compared with the total energy expenditure of adults feedings chicks, which did not support hypothesis (2). The contribution to chick feeding was not equal; the ratio of females to males caught with food for chicks was 1.8. Size-corrected body mass during chick-rearing was lower in females, proportional to their higher chick feeding effort compared with males. Females, in contrast to males, lost protein reserves during chick-rearing. Digestive tract mass of adults increased by half throughout the breeding period. These findings supported elements of hypothesis (1). Despite high energy expenditure rates, both sexes had about 10 g of fat reserves at the end of chick feeding. Body mass of both sexes was constant during the greater part of the chick-feeding period. It was suggested therefore that mass loss is regulated with respect to lower fat reserves required during chick-rearing.

Key words: Arctic, Spitsbergen, Little Auk, body reserves, body composition, foraging.

Introduction

Changes in body mass of adult birds during the breeding season have been studied for over half a century (Baldwin and Kendeigh 1938), but recently there has been disagreement over the proximate and ultimate (evolutionary) factors effecting these changes.

The loss of mass by breeding birds, observed especially during the nestling period, has usually been attributed to the physiological stress or strain imposed by reproduction (Ricklefs 1974). Several studies have demonstrated that birds rearing experimentally enlarged brood-sizes show increased rates of mass loss compared with birds rearing natural brood-sizes (Hussell 1972, Askenmo 1977, Nur 1984, Lessells 1986, Hegner and Wingfield 1987, Reid 1987), but many authors have failed to find such a relationship (e.g., De Steven 1980, Finke, Milinkovich and Thompson 1987). Evidence that body mass loss during breeding influences subsequent survival is sparse (Bryant 1979, Nur 1984, Reyer 1984, Reid 1987).

Freed (1981) argued that body mass loss in chick-feeding passerines does not reflect the cost of reproduction, but instead is beneficial to the parents. Freed (1981) and Norberg (1981) suggested that this mass loss may reduce power consumption in flight and therefore increase energy available for foraging and for feeding chicks. This saving, together with the use of energy from previously stored reserves, may result in more fledged chicks (Norberg 1981). Adaptive hypothesis has been used to explain body mass loss in two species of alcids feeding their chicks (Croll, Gaston and Noble 1991, Jones 1994). Alcids use their wings for diving, and selection to increase swimming efficiency has led to a reduction in size of their wings and high wing loading. This makes flight energetically costly in these birds (Pennycuick 1987), and energy saving due to mass loss may be potentially very beneficial. Gaston and Jones (1989) and Jones (1994) associate body mass loss in alcids with programmed anorexia. Under this hypothesis, body mass is lost even when food is very abundant and birds have sufficient time to forage.

Although the two hypotheses are not mutually exclusive (loss of mass induced by stress will lead to savings on energy expended on flight), they yield different predictions about the timing of mass loss. If loss of mass reflects a physiological cost or stress of breeding, one would expect the loss to be directly related to the cumulative level of effort. The mass should decline throughout the breeding period, the most rapidly during the period of highest demand (presumably during the period of highest chick food demand). If loss of mass is adaptive to maximize flight efficiency, one would expect an abrupt adjustment of body mass about the time of hatching, when adult's flight demands increase (Freed 1981, Ricklefs and Hussell 1984, Croll, Gaston and Noble 1991, Jones 1994). Furthermore, to properly interpret patterns of mass loss, it is necessary to determine the organs and biochemical components involved.

The aim of this paper is to evaluate factors governing the body mass changes, and underlying changes of body reserves (lipids and proteins), in Little Auks (*Alle alle*) throughout the breeding season, with special emphasis on the chick-rearing period. The Little Auk is a small Arctic alcid that lays single-egg clutches. Little Auk is particularly intersting as a subject for such study, because it has extremely high rates of energy expenditure when feeding chicks (Gabrielsen *et al.* 1991) and feeds on food very rich in lipids (Taylor and Konarzewski 1992). It has been previously suggested that the sexes do not share equally in provisioning chicks (Roby, Brink and Nettleship 1981). Because body mass and nutrient reserves should be related to activity level, the relative contribution of the two sexes to chick feeding was also investigated.

Materials and methods

Field work was carried out at the Little Auk breeding colony located on the slopes of Ariekammen, Hornsund, South Spitsbergen (77°00'N, 15°22'E).

Contribution of the sexes to chick feeding

To evaluate the relative contribution of the sexes to chick feeding, Little Auks were mist-netted in the colony during the chick rearing period between 30 July and 14 August 1987. A total of 237 birds with food for chicks in their throat pouch was caught. Food was removed from the throat pouch and weighed to the nearest 0.1 g. Diet composition will be described elsewhere. The birds were weighed (± 1 g) and four external measurements were taken: (1) wing length (maximum flattend chord); (2) head length (maximum distance from the bill tip to the posterior extremity of the occipitalis process); (3) bill depth (with mandibles closed, the greatest dorsoventral distance at the posterior edge of nares); and (4) bill length (tip to proximal end of sheath). All measurements were made to the nearest 0.1 mm with calipers, except wing length which was measured to the nearest 1 mm with a flat ruler.

Some of the captured birds were collected for body composition analysis. The sex of 195 birds which were not collected was determined by the discriminant analysis. All 132 birds collected at five breeding stages (see below), whose sex was known from gonadal inspection, were measured as described above and used to derive the disciriminant functions. The measurements were subjected to stepwise discriminant analysis using the STEPDISC procedure of SAS (SAS Institute 1985). The analysis revealed that bill length and bill depth were the two most discriminating variables. Next, the crossvalidation option of the DISCRIM procedure of SAS system was used to evaluate the performance of derived functions. DISCRIM classified each observation in the data set using a discriminant function computed from the other observations in the data set, excluding the observation being classified. The analysis revealed that the functions classified 89.5% of females and 84.0% of males correctly. These functions were subsequently used to determine the sex of birds caught in the colony.

Birds were also mist-netted between 10 and 15 August 1986, when the age of an "average" chick was between 25 and 30 days. These birds were sexed by gonadal inspection.

Body mass during incubation

To evaluate the potential relationship between Little Auk energy reserves stored before the chick rearing period and chick body mass, both parents were weighed in 66 nests: (1) within 2 days after egg laying, (2) midway through incubation, and (3) when the egg was pipped. The birds were measured and ringed during the first weighing, and sexed by discriminant analysis combined with inspection of the cloaca (the shape of cloaca in females was very changed soon after laying). The chicks were weighed in these nests at the age of 7 and 21 days post-hatch. The complete data were collected from 32 nests.

Adult body mass was corrected for body size using principal component analysis (PCA). PCA of the correlation matrix for the three morphological measures (head and bill length, bill depth) for each adult was performed for males and females separately. The first principal component (PC1) described a positive correlation in the measures. PC1 accounted for 78% and 74% of the three total original variation in males and females, respectively. The PC1 score for each bird was used as a measure of its body size, with positive values indicating larger than average body size and negative values indicating smaller than average body size. Next, body masses of males and females were regressed on their PC1 scores separately for each of the three stages of incubation. All regressions were significant at $P<0.05$. Residuals from these regressions were used as a measure of male and female body mass corrected for body size (condition indices) in multiple regression analysis relating chick body mass to body masses of both parents.

Body composition

Birds were collected for carcass analysis under the permission of the Governor of Svalbard SMS 1111/86 a512.7 and SMS 919/87 a512.41. The Little Auk is one of the most numerous bird species in the Arctic, and the most abundant species in Spitsbergen (Croxall, Evans, Schreiber 1984). In 1987 birds were collected at five different stages of the breeding season:

Prelaying. Birds mist-netted in the colony on 31 May and 2 June, i.e. three weeks before the peak of egg laying. The latter date was calculated by subtracting 29 days (average incubation period in Little Auks; Stempniewicz 1981) from the median date of hatching, 20 July, which in turn was determined by daily inspection of 197 nests in different parts of Ariekammen colony.

Postlaying. Birds collected from their nests usually within 24 hrs (up to 40 hrs) after egg laying. The nests were inspected twice daily, and both members of a pair were collected in nearly all cases.
Hatching. Birds collected from their nests just prior to chick hatching, when the egg was pipped. Pipped eggs were also collected for another study.
Chick peak body mass. Birds feeding chicks, mist-netted in the colony with food in gular pouch on 7 and 8 August. At that time the "average" chick, hatched on the median date of hatching, was 19 and 20 days old, e.i., at the age of their maximum body mass before fledging, (Stempniewicz 1980, Konarzewski and Taylor 1989). The age of all chicks in Ariekammen colony is similar on a given date, as hatching is very synchronized. Seventy-eight percent of the chicks hatched within a period of 6 days in 1987.
Fledging. Birds collected as in the stage of chick peak body mass, on 14 August (i.e., one day before peak of fledging).

Birds collected for carcass analysis in 1986 fell into one of two categories: postlaying and hatching.

I belive that collected birds' chicks were successfully raised to fledging by the remaining parent. In the other study (Gębczyński, Taylor and Konarzewski, submitted), in order to increase food demands in Little Auk nests, *n* chicks were rotated over *n/2* nests, producing equivalent of two chicks per nest. Adults can fledge two chicks, although at body mass lower than that in control fledglings, and on average few days later. The experiment started with 7-day-old chicks. Consequently, I expect that one adult can rear one 19—20 day old chick to fledging (on average at 27 days post-hatch in nonmanipulated chicks [Stempniewicz 1980, Konarzewski and Taylor 1989]), prolonging its parental care if necessary. Moreover, the chicks have very large fat reserves (Taylor and Konarzewski 1989), which should tide them over potential period of food shortage. Little Auk chicks fledge at two-thirds of adult body mass (Stempniewicz 1980), and presumably also lighter chicks can catch up with body mass when foraging at the sea.

Upon capture, birds were immediately killed by chloroform inhalation, weighed to the nearest 0.1 g, and all four external measurements described above were taken. The flight muscles *pectoralis major* and *supracoracoideus* were dissected out on both sides of the keel. Keel length was measured as the distance between the anterior edge of the keel and the posterior ossified edge of the sternum. Liver, gizzard, intestine, and gonads were removed after separation of mesenteric fat, which was replaced in the body cavity. Food and ingesta were removed from the digestive tract and body mass reported herein does not include ingesta mass. All dissected organs and the remainder of the carcass (with feathers) were dried separately in an oven at 70°C. Water content was calculated from the difference in mass before and after drying. Body components, except gizzards, intestines and gonads, were homogenized in an electric mill. Aliquots of 3 to 4.5 g of flight muscles and carcasses, as well as other organs in total, were extracted in petroleum ether in Soxhlet extractors, re-dried, and the lipid content calculated from the mass lost during extraction. The remaining residue was nonlipid dry mass consisting mainly of protein.

Structural body size is an important source of variation not only in body mass, but also in the size of a bird's protein reserves (e.g., Alisauskas and Ankney 1987). When comparing body mass and reserves in Little Auks collected throughout the breeding season, I attempted to account for this variation. PC1 scores from PCA of the four morphometric variables (head length, bill length, bill depth, and also keel length) were used as a measure of body size. PC1 accounted for 70% of the total original variation in all birds. Body masses and body reserves were compared within and between sexes using analysis of covariance with PC1 scores as covariate whenever the scores were significantly correlated with parameters under comparison. Wing length was not used in the set of measurements in PCA, because it caused interactions in some ANCOVA comparisons.

Means ± standard error are reported throughout the paper. All interactions in ANCOVA's and ANOVA's reported below were nonsignificant ($P>0.05$).

Results

Contribution of the sexes to chick feeding

The numbers of male and female Little Auks caught in the colony with food for their chicks in 1987 revealed that the contribution of the sexes to feeding was not equal (Fig. 1). Of 218 adults caught up to the time when "typical chicks" (hatched at median hatching date) attained their peak mass (i.e., by 8 August), 145 were females and 73 were males (sex determined by discriminant analysis; the sample also included adults that were collected and sexed by dissection). The ratio of females to males was 2.0:1 and was significantly different from 1 (χ^2 test, $p<0.001$). The numbers of males and females were also corrected for performance of discriminant functions used for sex classification, assuming that 10.5% of females and 16.0% of males were not classified correctly (see Methods). Resulting numbers were 140 females and 78 males, a ratio of 1.8:1, still different from 1 (χ^2 test, $P<0.001$). The corrected numbers are presented in Fig. 1. The observed pattern did not depend on time of day. Seventy-one males and 126 females were caught during the day (10:00 to 19:00), while 7 males and 14 females were caught at night (21:30 to 2:00 on 1/2 August; corrected numbers). The difference between day and night was not significant (χ^2 test with Yates correction, $P>>0.05$).

The data also indicate that females ceased chick feeding shortly before chicks fledged. Three females and 16 males were caught at that time (Fig. 1; sex

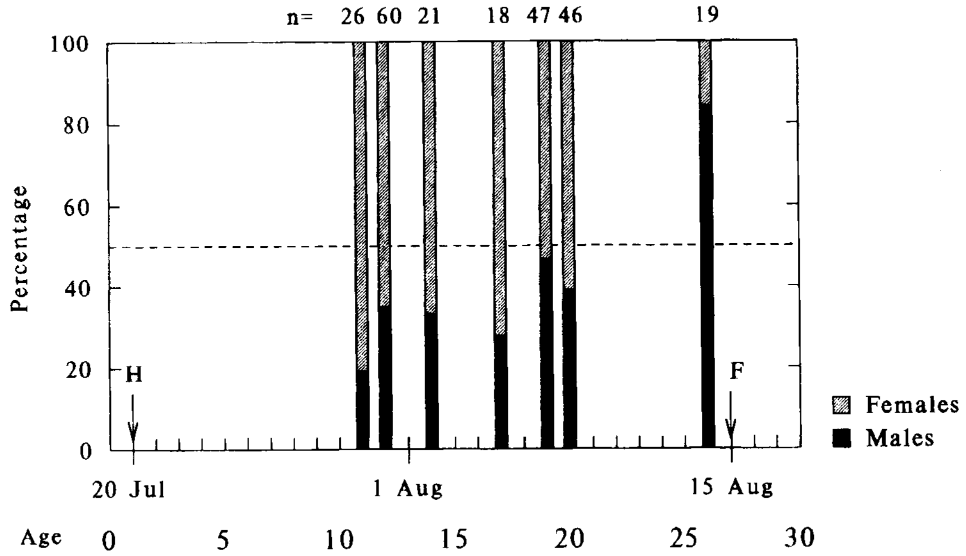

Fig. 1. Proportion of Little Auk males and females caught in the colony with food for chicks. Total number of adults caught on a given day are given at the top of the diagram. Horizontal dashed line indicates 50%. Median dates of chick hatching (H) and fledging (F), as well as the age of a chick hatched on the median date of hatching, are given.

of 17 of 19 adults was determined by dissection). Similarly, 5 females and 34 males were caught just before chicks fledged in 1986. The ratio of males to females was 6.25:1 in the combined 1986 and 1987 samples and was different from 1 (χ^2 test, $P<0.001$). In 1986, 26 males and 4 females were caught during the day and 8 males and 1 female were caught at night.

Adult body mass before chick hatching

Little Auk body mass before and just after egg laying did not differ in either males or females (t-test, $P>0.05$), and increased markedly during the incubation period ($P<0.001$, t-test; Fig. 2). Males and females gained on average 13.1 g and 10.6 g body mass during incubation, attaining 182.4 ± 1.7 g ($n = 50$) and 174.4 ± 1.4 g ($n=49$) by chick hatching, respectively.

Weighing individual adults in the colony during incubation revealed that the increase in body mass during the first half of incubation did not differ from that in the second half for either sex (paired t-test, $P>0.05$; Fig. 2). Body mass of these adults prior to chick hatching, when corrected for body size, was positively correlated with body mass of their chicks. Multiple regression analysis of body mass of 7-day-old chicks on body mass of both parents indicated a significant relationship with male body mass, but not with female mass. The simple correlation coefficient (r) between chick and male body mass

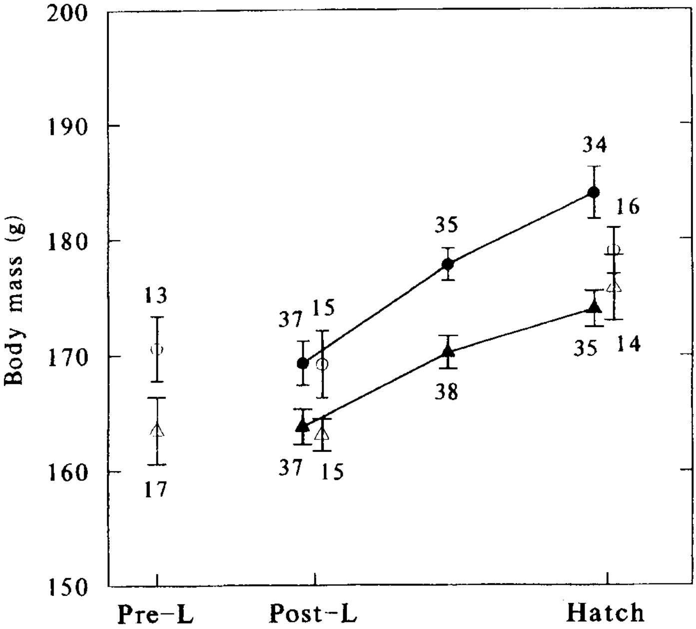

Fig. 2. Mean (± SE) body mass of breeding males (circles) and females (triangles) during the prelaying period (Pre-L), just after laying (Post-L), midpoint of the incubation period, and just prior to hatching (Hatch); see Methods section for description of breeding stages. Solid symbols denote individuals weighed in the colony at the three stages of incubation, open symbols are birds collected for body composition. Numbers are sample sizes.

was 0.56 ($P < 0.001$, $n = 32$). When body mass of 21-day-old chicks (the age of maximum body mass) was regressed, the opposite was true, i.e., only female body mass was significant ($r = 0.36$, $P < 0.05$, $n = 32$). There was no relationship between chick body mass and size-corrected mass of parents at the start or at the mid-point of incubation, or the increase in parental body mass during incubation.

Adult body mass after chick hatching

Body mass of adults (both sexes) declined after chick hatching (Fig. 3). Fig. 3 shows body masses of adults of both sexes caught with food for chicks from 30 July until the end of feeding duties, which continue longer for males (Fig. 1). There was no dependence of body mass on the date of capture throughout the catching period; either in males or females, as revealed by regression analysis ($P > 0.05$, Fig. 3).

Body masses of a given sex pooled over the entire catching period were significantly lower than mean body mass of the same sex at the end of incubation (t-test, $P < 0.001$ in both cases, Fig. 3). This, in combination with the

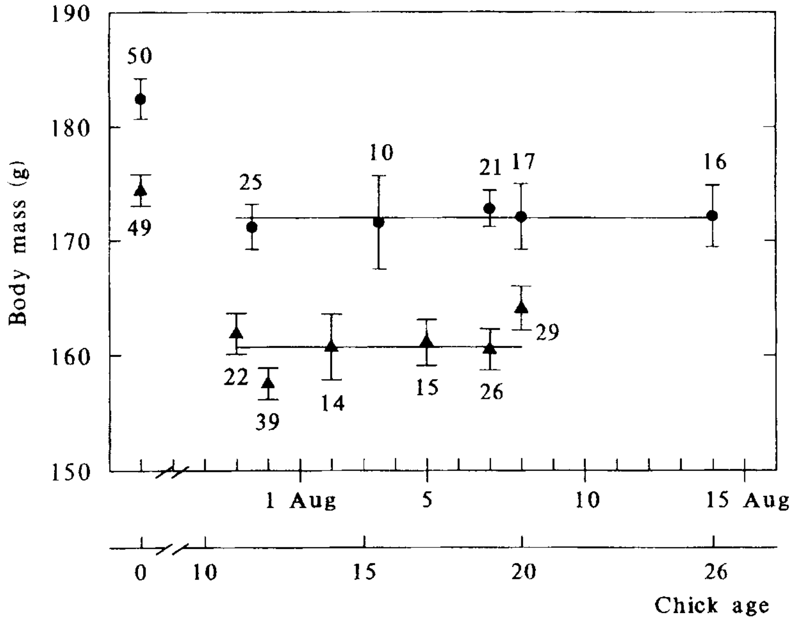

Fig. 3. Body mass of Little Auk adult males (circles) and females (triangles) that were caught with food for chicks during chick rearing against date and age of chick hatched on the median date of hatching. Masses of the two sexes just before hatching (chick age = 0) are given for comparison. Means (± SE and sample sizes). Some body masses from adjacent days were combined to increase sample size.

constancy of body mass after July 30, indicates that body mass loss in breeding Little Auks was completed earlier, within the first one-third of the chick-rearing period.

Body mass corrected for body size was significantly greater in males than in females during chick-feeding (ANCOVA with PC1 score as a covariate; $P < 0.01$). The majority of birds caught in the colony with food for chicks was sexed by discriminant analysis. Therefore, it was assumed that 10.5% of females and 16.0% of males (see Methods) having the lowest probability of correct sex classification were not classified correctly, and the above comparison was performed again. Body size-corrected masses of males and females were still different ($P < 0.05$). This difference between sexes found in chick-feeding adults was the only difference in size-corrected body mass throughout the breeding period; no such differences between sexes were found during incubation or before egg-laying.

A positive correlation was found between size corrected-body mass of adults and the mass of adults and the mass of food carried by them for chicks, in the sample of males and females caught at the time of peak chick body mass ($n = 25$, $r = 0.48$, $p < 0.05$; corrected body mass was calculated as residuals from the regression of body mass on PC1). ANCOVA with corrected body mass as a covariate indicated no difference in the food load between sexes in these birds.

Comparisons of body mass during four periods (pre-laying, early incubation, late incubation, and chick-rearing) using ANCOVA and Tukey tests at $P = 0.05$, for males and females separately, yielded the same results for both sexes: body mass during late incubation was significantly different from the three other means, with no differences among the latter three means.

Body composition

The course of body mass change throughout the breeding season (Fig. 4a) was largely a reflection of changes in fat mass of adults (Fig. 4b). Total ether-extractable body lipid content increased significantly by 103% and 72% during incubation in males and females, respectively, attaining on average 23.2 ± 1.4 g and 24.6 ± 1.8 g of fat (Fig. 4b; equal to 31.2% and 33.2% of dry body mass). The significant decline in fat reserves took place during chick rearing, and both sexes contained less fat at the end of their chick-rearing duties than before breeding (ANOVA and Turkey test, $P < 0.05$). Body fat at the end of chick-rearing did not differ between sexes (t-test, $P > 0.05$). The only intersexual difference in body fat occurred after egg laying, when males had significantly less fat reserves (Fig. 4b).

The LDM of pectoral muscles, which is considered a source of protein reserves, varied throughout the breeding seasons with conspicuous declines in females during chick rearing, but not in males (Fig. 4c). Body size-corrected pectoral LDM of females at the time of peak chick mass was lower than in males at that time, and lower than in males at chick fledging (ANCOVA of pectoral LDM with PC1 as a covariate, $P < 0.02$ and $P < 0.005$, respectively).

One of the most striking changes in internal organ mass was observed for the digestive tract. LDM of intestine, stomach, and liver increased dramatically between the time of egg-laying and the time of chick maximum body mass (Fig. 4d, e, Appendix 1). Intestine LDM increased by 46% in males and by 49% in females, stomach LDM by 69% and 45%, and liver by 48% and 31%, respectively. The percentage increase in wet mass and dry mass of these three organs was similar (Appendix 1).

Body composition of the two sexes during chick rearing is of special interest because of very high energy expenditure rates in adults at that time (Gabrielsen *et al.* 1991), a decline in body mass after incubation, higher chick provisioning rates by females, and significantly lower size-corrected body mass of females during chick rearing. The latter difference could not be attributed to lower fat reserves (Table 1). At the end of female's feeding duties, females had not only significantly smaller pectoral muscles than males, but also body size-corrected carcass LDM (total LDM diminished by LDMs of pectoral muscles, digestive tract, and gonads) was lower (Table 1). Size-corrected carcass LDM of females was also significantly smaller than that of males at the end of their feeding

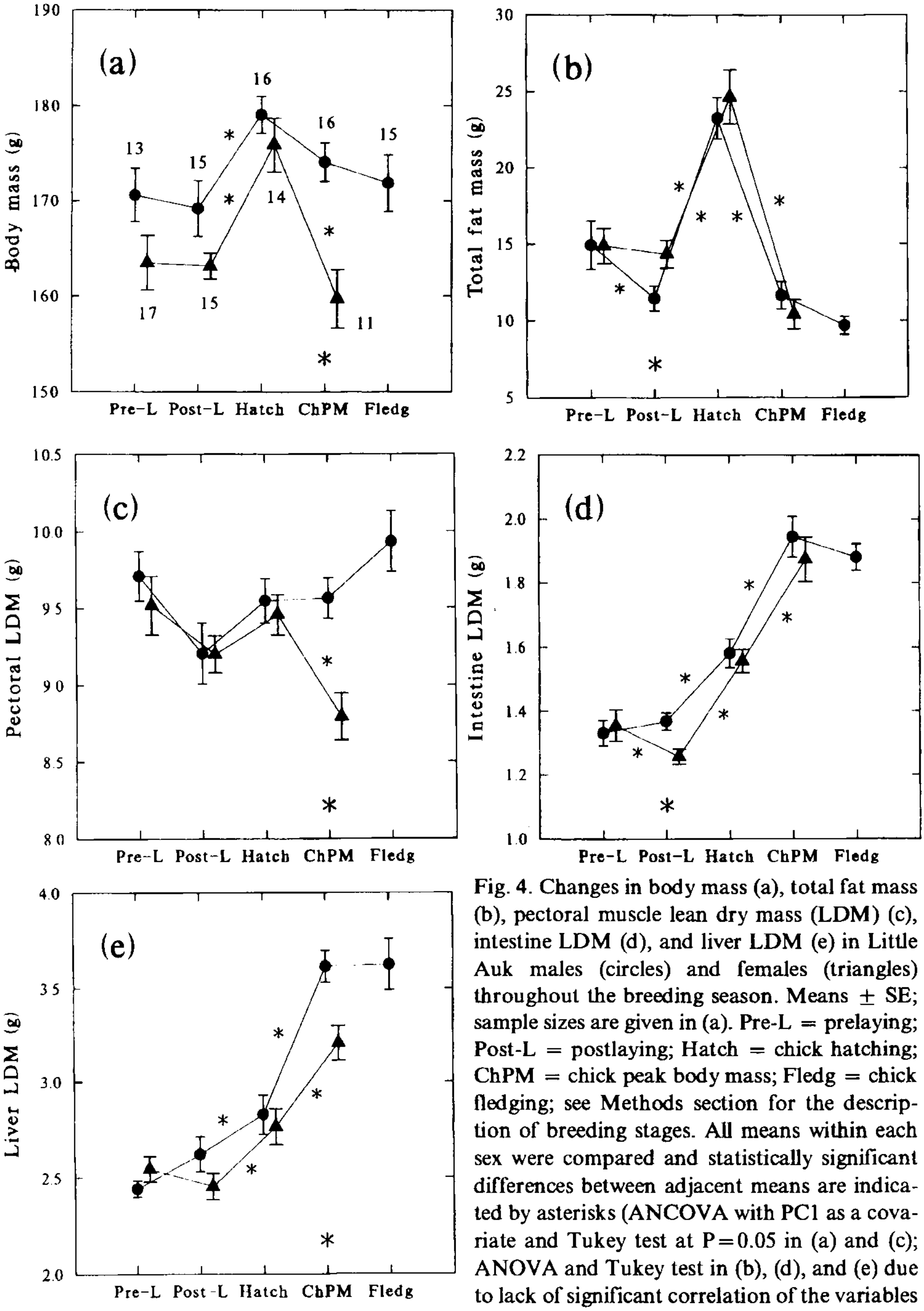

Fig. 4. Changes in body mass (a), total fat mass (b), pectoral muscle lean dry mass (LDM) (c), intestine LDM (d), and liver LDM (e) in Little Auk males (circles) and females (triangles) throughout the breeding season. Means ± SE; sample sizes are given in (a). Pre-L = prelaying; Post-L = postlaying; Hatch = chick hatching; ChPM = chick peak body mass; Fledg = chick fledging; see Methods section for the description of breeding stages. All means within each sex were compared and statistically significant differences between adjacent means are indicated by asterisks (ANCOVA with PC1 as a covariate and Tukey test at P=0.05 in (a) and (c); ANOVA and Tukey test in (b), (d), and (e) due to lack of significant correlation of the variables with PC1). Also, the pairs of male and female mean body masses (a) and pectoral LDM's (c) were compared controlling body size, by ANCOVA/PC1, and significant differences are indicated close to x-axis; other inter-sex comparisons (in (b), (d), and (e)) by t-test (no significant correlation with PC1).

Table 1

Comparison of body component masses corrected for body size in the two sexes at the end of chick-feeding by females (in the period of chick peak body mass; ChPM males and ChPM females), and at the end of chick-feeding by both sexes (Fledg males and ChPM females). Probability levels that two means do not differ; NS = $P>0.05$. Mean values corrected for body size were always lower in females when the difference between sexes was statistically significant

body component	ChPM males /ChPM females[1]	Fledg males /ChPM females[2,3]
body mass	$P<0.05$	NS
total LDM	$P<0.01$	$P<0.05$
digest. syst. LDM	$P<0.05$	NS
pectoral m. LDM	$P<0.05$[4]	$P<0.01$
the rest	$P<0.01$	$P<0.05$
fat	NS	NS[5]
total water	$P<0.01$	NS
digest. syst. water	NS	NS
pectoral m. water	$P<0.05$[4]	$P<0.05$
the rest	$P<0.01$	NS

[1] PC1 scores were not significantly correlated with variables under comparison, except for indicated cases; hence the values of each individual were divided by its skull length, and means compared by Mann-Whitney test.

[2] ANCOVA with PC1 scores as covariates, except one indicated comparison.

[3] Two tests: Mann-Whitney test on the values divided by the skull length, and ANCOVA with PC1 scores, both performed at $P=0.05$, gave the same results except for the water in carcass (significant difference from the latter test).

[4] ANCOVA with PC1 scores as covariates.

[5] Values divided by skull length and compared by Mann-Whitney test.

duties (Table 1), but no such difference was detected during the prelaying or incubation periods.

In general, the pattern of body mass and fat mass increase during incubation that was found in 1987 was also found in 1986 (Table 2). However, the body mass increase in 1986 females was not statistically significant. Both during the post-laying and chick-hatching periods there was no significant difference in size-corrected body mass or fat mass between the two years and sexes (Table 2).

To assess the importance of adult protein reserves during chick feeding, the body size-corrected pectoral muscles LDM of adults caught at the time of peak chick body mass (i.e., at the end of female feeding duties) was compared with the mass of meals brought by them to their chicks. Corrected LDMs were calculated as residuals from the LDMs of the two sexes regressed on their common PC1 scores. The residuals were positively correlated with food loads ($r=0.56$, $P<0.005$), i.e., adults with larger size-corrected pectoral muscle LDMs brought larger food loads (Fig. 5). Size corrected-carcass LDM (calculated by the same method; carcass defined as above) was also correlated with food load ($r=0.64$, $P<0.001$). At the same time, ANCOVA indicated no

Table 2

Body mass and total fat mass (means ± SE, grams) of Little Auk males and females just after egg laying (Post-L) and at chick hatch (Hatch) in 1986 and 1987 breeding seasons[1]

	Males		Females	
	1986	1987	1986	1987
Body mass				
Post-L	168.7 ± 3.3^{a2}	169.2 ± 2.9^{a}	161.9 ± 2.7^{a}	163.1 ± 1.4^{a}
Hatch	176.4 ± 2.9^{b}	179.0 ± 2.0^{b}	168.3 ± 3.1^{a}	175.8 ± 2.8^{b}
Fat mass				
Post-L	11.59 ± 0.84^{a}	11.44 ± 0.82^{a}	11.55 ± 0.85^{a}	14.33 ± 0.91^{a}
Hatch	21.48 ± 1.29^{b}	23.25 ± 1.36^{b}	22.11 ± 1.78^{b}	24.65 ± 1.79^{b}
Sample size				
Post-L	12	15	10	15
Hatch	15	16	15	14

[1] The two-factor (year and sex) Model I ANCOVA of body mass, with keel length as a covariate to control body size, revealed no differences between the two factors, both in Post-L and Hatch periods. The same results were obtained for fat mass from the two-way ANOVA (ANOVA was performed because keel length was not significantly correlated with fat mass). Keel length was used, not PC1 scores to correct body mass, because not all morphometric measurements were taken in 1986 birds.

[2] Two means for a given sex and year sharing the same letter are not significantly different (at $P = 0.05$), based on the ANCOVA with keel length as a covariate in body mass, and on the t-test in fat mass.

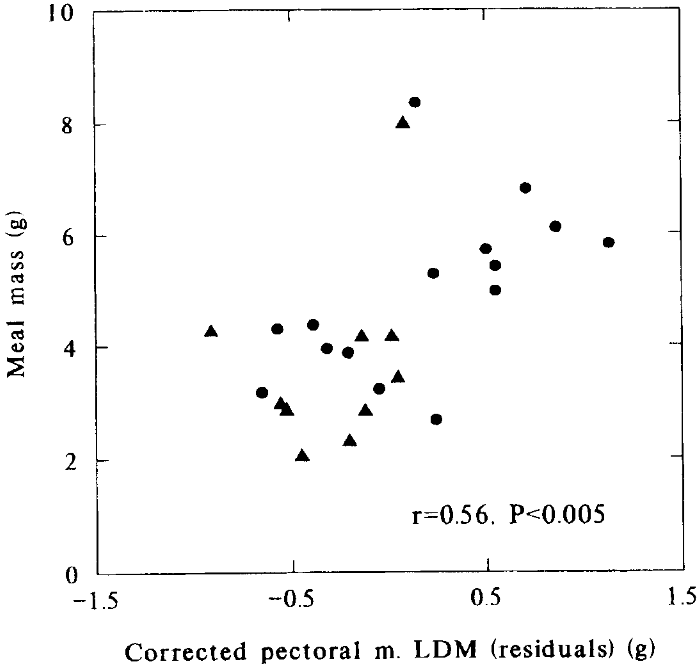

Fig. 5. Relationship between the mass of chick meals and the body size-corrected pectoral muscle LDM in adult Little Auks (see text for further explanation). Circles: males, triangles: females.

significant differences in food load between sexes, when the corrected pectoral muscle LDM or corrected carcass LDM was used as a covariate. There was no correlation between food load mass and total fat mass in the collected adults.

Discussion

Body mass and nutrient dynamics before chick hatching

Body mass, fat mass, and pectoral LDM of females after egg laying, as compared with the pre-laying period, revealed that laying a single-egg clutch was not a burden for females. In contrast, fat reserves of males declined during the same period (Fig. 4 b). Although very little is known about the pre-laying biology of Little Auks, it is likely that this decline is related to female-guarding by males. Common Guillemot (*Uria aalge,* Little Auks' closest relative) males remain at the breeding colony almost continuously throughout the pre-laying period, performing forced extra-pair copulations, guarding their own mates, and defending them from other males. Thus males have much reduced opportunities for feeding. Females are in the colony only infrequently at this period, and mainly forage at the sea (Birkhead, Johnson, Nettleship 1985). Extra-pair copulations have also been recorded in Little Auks (P.G.H. Evans in Birkhead 1985).

The increase in body mass of Little Auks during incubation is rather an exception among birds (Moreno 1989), but similar increase has been observed in some years in other alcids (Gaston and Perin 1993, Jones 1994). The body mass increase in Little Auks was due almost solely to fat deposition (Fig. 4 a, b), and was associated with a very high lipid content of the diet (Taylor and Konarzewski 1992). Also, Little Auk chicks deposit very large fat depots during the nestling period (Taylor and Konarzewski 1989). Lack of differences between the two sexes in body and pectoral muscle mass when corrected for body size, as well as in fat mass at the end of incubation (Fig. 4 a, b, c) are in agreement with the equal contribution of the sexes to incubation reported by Stempniewicz and Jezierski (1987).

The correlation of chick body mass at the age of peak body mass (21 days) with female, but not male, condition (body mass corrected for body size) at the end of incubation corresponds well with the nearly two times higher chick meal delivery rate by females (Fig. 1). The decline in body mass of adults shortly after chick hatching and the constant body mass thereafter (Fig. 3) reflect the abrupt loss of fat reserves down to much lower levels. This suggests that the use of previously stored reserves by the female when feeding the chick is not an explanation for the correlation between female condition at chick hatching and the chick's body mass close to fledging. A more likely interpretation is that females which were more efficient in energy management during incubation were also more efficient during chick feeding.

It is more difficult to interpret the correlation between chick body mass at age 7 days (shortly after attaining homeothermy) and male condition at the end of incubation, as nothing is known about the relative roles of the sexes in early chick-rearing.

Relative contribution of the sexes to chick feeding

Inter-sexual differences in body mass and composition during chick-rearing (Table 1, Fig. 4 a, c; discussed in detail in the next section) correlate well with the unequal division of labour at this stage of the nesting cycle (Fig. 1). Females provide most of the meals for chicks until chicks attain their peak body mass. Then they abandon the chick for the last week of its stay in the nest, leaving feeding to the male, or at least their role is negligible at that time. The few females caught at the colony close to chick fledging were probably birds feeding late broods. Also, of 95 adults caught with food during 17 days late in the chick-rearing period in Greenland, 60 were males and 35 were females (Roby, Brink and Nettleship 1981). The long sampling period could have been responsible for the high proportion of females in this sample. Harris and Birkhead (1985) have hypothesized that unequal contribution of sexes could result from sexual differences in diurnal activity patterns, but present findings do not support this. Feeding of the nearly fledged chick by only the male coincides with (1) a significant decline in the number of meals received by chicks per day (Stempniewicz and Jezierski 1987), (2) a decline in total food consumption of chicks (Konarzewski, Taylor and Gabrielsen 1993), (3) a recession in chick body mass (Stempniewicz 1980), and (4) a decline in chick fat reserves (Taylor and Konarzewski 1989).

Body mass and nutrient reserves dynamics after chick hatching

The pronounced decline in adult body mass of Little Auks after hatching (Fig. 3, 4a) is typical of nidicolous birds in general (Moreno 1989), and alcids in particular (Harris 1979, Barrett *et al.* 1985, Harris and Wanless 1988, Croll, Gaston and Noble 1991, Jones 1994).

Detailed studies of Brünnich's Guillemot (*Uria lomvia*; Croll, Gaston and Noble 1991, Gaston and Perin 1993), and Least Auklet (*Aethia pusilla*; Jones 1994) show abrupt declines in adult body mass after hatching and levelling off thereafter, as in Little Auks. The authors of these studies have argued that the observed pattern of body mass change supports the adaptive hypothesis (adaptive programmed loss reducing costs of flight when provisioning chicks): the abrupt adjustment of body mass occurs when practical needs dictate. The stress hypothesis would predict a gradual decline in mass throughout the breeding season, the most rapid during the period of highest demand (presumably during the period of highest chick food demand; Freed 1981, Croll, Gaston and Noble 1981, Jones 1994).

It may be argued however, that an abrupt decline in body mass may reflect stress if the period of chick brooding is more energetically demanding than the incubation period. According to Ricklefs (1983) the greatest energy requirement relative to the ability of the parents to provide food occurs during the chick brooding period because parents can feed only half time yet must support both themselves and their chick at the nest. Energy requirements of Little Auk chicks increase rapidly after hatching and approach maximum values by day 10 post-hatch (Konarzewski, Taylor and Gabrielsen 1993).

It might be expected that body mass loss would reduce daily energy expenditure in Little Auks, considering their high wing loading and frequent distant flights for food when feeding chicks. The cost of flight in Little Auks, calculated using Pennycuik's (1989) computer program [with 39 cm wing span (A. Magnan in Greenewalt 1962, Taylor and Konarzewski, *unpubl. data*), and basal metabolic rate = 2.06W (Gabrielsen *et al.* 1991)], is high. For females, providing almost 2/3 of meals to chicks, the calculated cost is equal to 23.5 W, i.e. 175% of the flight cost of the "average" bird of the same body mass using flapping flight (wing span = 56 cm; Viscor and Fuster 1987). A decline in adult body mass after hatching resulted in 11% and 7% energy savings in calculated cost of flight for females with empty gular pouches, and adults carrying an average chick meal of 4.4 g (Konarzewski and Taylor, *unpubl. data*), respectively. The energy savings in flight costs for females translate into a 4% saving of total daily expenditure during chick-rearing, assuming 4 foraging trips a day (Norderhaug) and a 25 km foraging range. Thus the savings are not as large as might be expected.

Similarly, Jones (1994) has calculated by the same method that Least Auklets over two seasons saved 10.3 and 3.5%, respectively, of the cost of flight due to body mass loss after chick hatching. Assuming average daily energy expenditure by Least Auklets of 358 kJ/day (Roby and Ricklefs 1986), these savings translate into a reduction in DEE by 2.2 and 0.7%, respectively. This brings into question Jones' (1994) conclusion that "the observed loss of mass could lead to significant energy savings".

It is problematic whether body mass loss in Little Auks is adaptive in reducing daily energy expenditure, although it may be argued that any saving is beneficial. On the other hand, utilizing energy from fat depots may substantially facilitate shift by adults from incubation to brooding and chick feeding. The metabolism of 14.2 g fat in females and 11.6 g in males provides the energy equivalent of 18 and 15 hours, respectively, at average adult energy expenditure rates during chick-rearing (assuming 1 g fat = 38 kJ).

Other findings also do not support the adaptive mass loss hypothesis. Positive correlation in adults between their size-corrected body mass and the mass of meal carried by them for chicks is more consistent with stress than with adaptation. Much higher mass of adult digestive organs during chick-rearing compared with incubation (Fig. 4 d, e) indicates higher food consumption rates (Gross, Wang and Wunder 1985, Dykstra and Karasov 1992). Such an increase in intestine mass is not consistent with adaptative anorexia.

Comparison of changes in body mass nad body composition for the two sexes may indicate stress. Apparently body mass is negatively correlated with chick-feeding effort. Body mass corrected for body size is lower in females that provision their chicks at higher rates (Fig. 1). This inter-sexual difference in body mass was found only during the chick-feeding period, and not during incubation when parental effort is similar. Lower size-corrected body mass in females is not an adaptive compensation for higher working levels. The estimated savings to females in flight costs due to body mass loss below male body mass is only 1% of daily energy expenditure. Lower female body mass was due to lower protein reserves (Fig. 4c, Table 1), and was only observed during the chick-feeding period. A decline in LDM reserves (Fig. 4c) may result from stress, as birds with less protein reserves in pectoral (flight) muscles and in carcass bring smaller meals to their chicks (Fig. 5). Food load was also positively correlated with size-corrected body mass in birds caught at the time of peak chick mass. A negative correlation (light birds bring large food loads) would be expected in the case of adaptive mass loss.

It is not clear whether loss of protein from pectoral muscles in females can impair their flight capability during chick feeding. Kendall, Ward and Bacchus (1973) have pointed sarcoplasm as a labile source of protein that can be mobilized without contractile function of muscles being impaired. On the other hand, Swain (1992) found a significant reduction in protein-specific glycolytic capacity of flight muscle tissue in starving birds, which suggested that their flight performance was affected in some way. Irrespective of whether flight capability of females is impaired, the loss of protein reserves in females corresponds well with their earlier cessation of chick feeding.

Differences in foraging effort may also explain variation in body mas of Brünnich's Guillemots during chick-feeding. After an abrupt decline after chick hatching, body mass of adults stabilized at lower level in a year when food was scarce and adults spent more time foraging (Croll, Gaston and Noble 1991). Also, Least Auklets stabilized their body mass at lower level in a poor reproduction year, when food was probably less available (Jones 1994).

The constancy of Little Auk body mass during the greater part of the chick-feeding period and large fat reserves at the end of this period are not consistent with the stress hypothesis. Adults, even when working hard, do not allow reserves to drop below some critical level. Both sexes have about 10 g fat reserves at the end of female chick-feeding, i.e., lipid index (fat mass/total lean dry mass) = 0.22. This lipid index falls near the upper end of the range of minimum indices observed in other bird species during the breeding period (0.08 – 0.25; Pinowska 1979, Raveling 1979, Ankney and Scott 1980, Reinecke, Stone and Owen 1982, Jones 1987, and others). Ten is also much more than the average body fat (1.1 ± 0.4 g, n = 9) of starved Little Auks found in Farsund, Norway, in winter 1990/91 (T. Anker-Nilssen and J.R.E. Taylor, *unpubl. data*). The average body mass of Little Auks during chick-feeding does not differ from body mass before or just after egg-laying, indicating that adults are not excessively stressed at that time.

Constant average body mass of Little Auks during the greater part of the chick-feeding, combined with considerable fat reserves, suggests some sort of regulation. One possible explanation for this constancy is that birds modulate their chick-feeding effort in response to changes in endogenous reserves. This interpretation is supported by the results of an experiment (Gębczyński, Taylor and Konarzewski, *submitted*) in which food demands at Little Auk nests were increased by rotating a number of hungry chicks over a smaller number of nests, and adults refused to substantially increase their chick-feeding rate.

In summary, the evidence was found that body loss in Little Auks shortly after chick hatching is not purely adaptive by reducing power consumption during flight. Protein reserves loss in females proportional to their higher feeding frequency as compared to males, the dramatic increase of the digestive tract mass, and the positive correlation between body mass/protein reserves and meal mass for chicks supported elements of the stress hypothesis.

The explanations for mass loss after hatching all focus on why lower fat reserves are either required during chick rearing (adaptation) or necessary (stress). But the question may be asked: why are larger fat reserves required or necessary during incubation? Adults must subsist on fat reserves during incubation bouts that last on average 12.5 hrs in Little Auks, and may be as long as 33 hrs (Stempniewicz and Jezierski 1987). Large reserves during incubation, especially late incubation (Figs 2, 4b) when investment is higher and cooling tolerance of embryo lower, may be beneficial as insurance against being forced to abandon the egg. Once brooding is over, large reserves are no longer adaptive, and adults may shed the surplus of fat.

The results indicate that body mass changes in Little Auks during chick-rearing result from shifting trade-offs between opposing pressures. Body mass may decline due to foraging effort increased chick hatch, as indicated by the marked increase of intestine mass in this period (Fig. 4d). The decline is proportional to the foraging effort. On the other hand, the decline should not be so large as to lower the safety margin for fasting endurance.

I suggest that body mass, after the initial decline, is regulated (maintained constant) with respect to lower fat reserves required during chick-feeding.

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Appendix 1

Change in digestive organs mass in Little Auks throughout the breeding season. The lowest means (±SE) (before laying, Pre-L, in males, and just efter laying, Post-L, in females) and the highest means (at chick age of peak body mass, ChPM) are shown. Sample sizes as in Fig. 1

	males			females		
	Pre-L	ChPM	%	Post-L	ChMP	%
intestine						
wet mass	5.89±0.17	9.00±0.33	53[1]	5.78±0.15	8.54±0.34	48
dry mass	1.49±0.05	2.16±0.07	45	1.41±0.03	2.07±0.07	46
stomach						
wet mass	1.05±0.03	1.88±0.07	79	1.11±0.03	1.71±0.11	54
dry mass	0.33±0.01	0.54±0.02	65	0.33±0.01	0.48±0.03	43
liver						
wet mass	8.64±0.21	12.74±0.30	48	8.77±0.27	11.42±0.37	30
dry mass	2.62±0.07	3.86±0.10	47	2.54±0.08	3.45±0.09	36
total						
wet mass	15.58±0.36	23.62±0.46	52	15.67±0.36	21.67±0.76	38
dry mass	4.43±0.11	6.55±0.11	48	4.29±0.09	6.00±0.17	40
LDM	4.07±0.08	6.07±0.10	49	4.02±0.08	5.53±0.16	38

[1] Percentage difference between the two means. The means of each pair are significantly different (t-test, $P<0.001$).

Streszczenie

Badano zmiany masy ciała i rezerw energetycznych u traczyka lodowego (*Alle alle*) na Spitsbergenie w trakcie całego sezonu lęgowego. Spadek masy ciała po wykluciu pisklęcia analizowano w kontekście dwóch hipotez: (1) spadek masy ciała odzwierciedla stres związany z reprodukcją, (2) spadek ten jest adaptacyjny, gdyż zmniejsza energetyczne koszty lotu. Masa ciała samców i samic wzrastała w czasie inkubacji, spadała gwałtownie po wykluciu pisklęcia, i pozostawała stała do końca okresu karmienia pisklęcia. Zmiany te były spowodowane głównie zmianami otłuszczenia. Masa ciała, tłuszczu i rezerw białkowych, korygowana o wielkość ciała, nie różniła się między płciami w końcowym okresie inkubacji jaj. Masa ciała samic w tym okresie, korygowana o wielkość ciała, była skorelowana z maksymalną masą piskląt. Oszacowany zysk w kosztach lotu, związany ze spadkiem masy ciała po wykluciu pisklęcia, był mały w porównaniu z całkowitymi wydatkami energetycznymi traczyków karmiących pisklęta, co nie potwierdziło hipotezy (2). Udział dwóch płci w karmieniu pisklęcia nie był równy. Stosunek ilości samic do samców złapanych z pokarmem dla piskląt wynosił 1,8:1. Masa ciała samic korygowana o wielkość ciała była w czasie karmienia niższa niż u samców, zgodnie z większą częstotliwością karmienia przez samice. Samice, w przeciwieństwie do samców, zużywały w tym okresie zapasy białkowe. Masa przewodu pokarmowego wzrastała u traczyków o połowę w trakcie sezonu lęgowego. Fakty te potwierdzały pewne elementy hipotezy (1). Mimo wysokich wydatków energetycznych, obie płcie miały około 10 g tłuszczu z końcem karmienia piskląt. Po spadku, masa ciała obu płci była stała do końca okresu karmienia. Sugeruję więc, że masa ciała traczyków jest regulowana w okresie karmienia piskląt zgodnie z mniejszymi niż w czasie inkubacji wymaganymi zapasami tłuszczowymi.