

Mass changes of least auklets *Aethia pusilla* during the breeding season: evidence for programmed loss of mass

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Summary

1. Patterns of seasonal variation in body mass by adult and sub-adult least auklets (*Aethia pusilla*, Pallas) were investigated at St Paul Island, Alaska using electronic balances to evaluate whether mass changes during the breeding season resulted from reproductive stress, or from a programmed response to increased flight demands during chick-rearing.

2. Male and female auklets did not differ significantly either in mass or in the pattern of mass change.

3. Sub-adults (2-year olds) were significantly lighter in mass than adults. Among adults, breeders that reached the chick provisioning stage were significantly heavier than failed breeders and non-breeders.

4. Overall, the pattern of mass variation during the breeding season was non-linear, with mass increasing during the prelaying period, stable or increasing during incubation, and declining somewhat by chick rearing.

5. Breeding adult least auklets experienced an abrupt mass loss of 6 g (7% of mean body mass) in 1988 and 3 g (4% of body mass) in 1989 that coincided with the hatching of their chick, afterwards mass stabilized. These mass losses were predicted to reduce flight costs by about 10% (1988) and 4% (1989).

6. The brooding period was not associated with abruptly increased energetic expenditure compared with incubation, because the brooding parents spent less time in the nesting crevice and alternated time at the nest more frequently than during incubation.

7. These patterns are consistent with the hypothesis that mass loss is a programmed response to increasing flight demands, rather than a consequence of reproductive stress.

Key-words: mass changes, anorexia, stress, incubation, Alcidae, *Aethia pusilla*, least auklet, seabird.

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Introduction

Loss of body mass experienced by adult birds during the breeding season has been proposed to be the result of the physiological stress related to reproductive effort (Ricklefs 1974, 1983; Nur 1984; De Laet & Dhondt 1989), or alternatively, to represent programmed mass loss related to changes in physiological demands during the breeding season (Freed 1981; Norberg 1981; Moreno 1989). The latter hypothesis has been referred to as 'adaptive' mass loss because the pattern of mass change is supposed to result from a program favoured by natural selection. I refer to this hypothesis as the programmed anorexia hypothesis (PAH). Rather

than losing mass as a consequence of the stresses imposed by energetic costs of reproduction, PAH suggests that individuals facultatively adjust their body mass to maximize reproductive success. Specifically, Norberg (1981) invoked a need to reduce wing loading during chick provisioning, when flight demands must increase, as a factor favouring programmed loss of mass.

Testing these hypotheses has been somewhat difficult because they are not fully mutually exclusive. Energetic stress during breeding would be expected to lead to mass loss whether or not the usual pattern of mass change results from programmed anorexia. However, the stress hypothesis (SH) would seem to predict a pattern of gradual mass loss over the

breeding season as the energetic costs of reproduction accumulate, while PAH predicts an abrupt adjustment of body mass when practical needs dictate. Croll, Gaston & Noble (1991) suggested that this could involve an abrupt loss of body mass about the time of hatching, when adults' flight demands increase, but Ricklefs (1983) pointed out that an abrupt loss of mass would occur if parental duties during brooding of the chick are unusually stressful.

To evaluate these mass loss hypotheses, I studied least auklets (*Aethia pusilla*, Alcidae), small (75–100 g) monogamous seabirds that congregate at dense breeding colonies on talus slopes and boulder-strewn shorelines of remote islands in the Bering Sea. The sexes are similar in appearance, the clutch size is one, and both parents equally share incubation and provisioning of their chick in the nesting crevice before it departs from the colony (Piatt *et al.* 1990; Roby & Brink 1986). During the incubation stage, a breeding auklet's activities alternate between continuous 24-h incubation shifts and 24-h off-duty periods when it has the opportunity to forage at sea (Roby & Brink 1986). During chick rearing, which lasts about 4 weeks, each breeding auklet makes 1–4 deliveries of food to the chick each day (Roby & Brink 1986; I.L. Jones unpublished data), each delivery representing a round trip of 10–30 km or more (Roby & Ricklefs 1986; I.L. Jones unpublished data). Thus, least auklet flight demands increase drastically (2–3 times that during incubation) when the chick hatches, so an abrupt reduction in mass at this time could provide significant energy savings (Freed 1981; Croll *et al.* 1991). Because least auklet body mass can be monitored throughout the breeding season, which lasts about 12 weeks with stages that potentially place different energy demands on breeders, and because both breeding and non-breeding birds attend the colony simultaneously, this species provides an excellent opportunity for investigating questions about mass changes. Furthermore, least auklets nest at high densities so large numbers of individually marked breeders and non-breeders can be monitored simultaneously at a single site using remote electronic balances.

In summary, the objectives of this study were to: (1) investigate the seasonal pattern of mass change in least auklets, and how this relates to sex, age and breeding status, as well as inter-seasonal effects; and (2) to test predictions of the reproductive stress and programmed loss of mass hypotheses.

Methods

Mass changes of breeding and non-breeding auklets were monitored at a colony of more than 10 000 least auklets near Tolstoi Point, St. Paul Island, Pribilof Islands, Alaska (57°08'N 170°17'W) during May to August of 1987, 1988 and 1989. At this site, auklets

nest among sparsely vegetated beach boulders and in adjacent cliff crevices. Mass measurements were made at one 150 m² study plot on a talus slope about 5 m above sea level, where about 150 pairs of auklets nested (Jones 1992a). Mass measurements were obtained when birds were captured for ringing early in the season, and later using four electronic balances (Ohaus D1000 LA[®], accurate to ±1 g) set on the study plot. Each balance was equipped with a 20 × 20-cm square plexiglas platform, painted gray, set on the pan. Cables from each balance were connected to a central display in an observation hide adjacent to the study plot and mass records were entered manually, together with the auklet's colour ring combination (if ringed), age (adult or sub-adult) and whether or not the bird had food in the throat pouch. The balances could be tared remotely after each reading when necessary. Each balance was calibrated daily using a known mass (80 g). Auklets readily perched on these platforms long enough for a stable mass reading. Mass measurements were made on days with winds of less than 20 km/h at the plot surface, because air turbulence caused the balance readings to fluctuate. Balances were not used on days with heavy rain. Fortunately, the study area was sheltered from prevailing winds (NE) and precipitation was usually light. Mass records were obtained on 62 days in 1988 and 40 days in 1989. In 1987, all mass records were from birds captured on the study plot and adjacent area (13 different days). All mass records were obtained during the daily peak of auklet activity on the surface (12:00–16:00 hours ADT; Jones 1992a). Mass measurements of auklets delivering food in their throat pouch were excluded from this analysis.

To monitor individuals, a color-ringed population of about 200 regularly attending birds was maintained at the study plot. With the help of field assistants I captured 248 auklets (219 adults, 29 sub-adults) in 1987, 369 (306 adults, 63 sub-adults) in 1988, and 145 (all adults) in 1989 (Jones 1990; Jones & Montgomerie 1992). To minimize disturbance, ringing on the study plot was restricted to the pre-laying and early incubation periods, ringing was carried out only every fourth day, auklets were ringed, measured and released as quickly as possible after capture, and their crevice nest sites were left entirely undisturbed. Capture and handling did not affect auklet reproductive performance or likelihood of returning to the study area in following years (Jones 1992b). Each auklet was given a numbered USFWS stainless steel ring and a unique combination of three plastic color rings. Upon capture, mass was measured to the nearest 1 g using a Pesola spring scale.

In this study, subadults (probably all 2 years old) were distinguished by their brown foreheads with restricted nuptial plumes, worn flight feathers and spotted throats (Bédard & Sealy 1984; Jones 1992a).

Least auklets are virtually sexually monomorphic and sex could not be reliably distinguished by measurements or appearance in the hand. However, the sex of many ringed birds was known because males could be identified by their distinctive vocal advertising behaviour, a regularly repeated chattering vocalization, performed only by males (Jones 1989). Mates of known males were assumed to be females (Jones & Montgomerie 1991).

Disturbance of auklet nesting crevices reduces reproductive success significantly (Roby & Brink 1986; Piatt *et al.* 1990), so breeding performance and phenology were monitored by observing the chick-provisioning behaviour of colour-ringed auklets. Marked adult auklets that delivered food to chicks on at least two occasions were classified as active breeders, those that were never seen delivering food were classified as non-breeders. The term 'active breeder' thus implies success at least to hatching of the chick, while 'non-breeders' include adult birds whose nesting attempt failed during incubation (<15% of breeders, Roby & Brink 1986; Piatt *et al.* 1990) as well as non-breeders (unpaired adults and members of pairs that never produced an egg). Successful breeding was inferred for marked auklets that delivered food on 25 or more consecutive days, a minimum requirement for fledging success (Roby & Brink 1986; Piatt *et al.* 1990; Jones & Montgomerie 1992). Hatching dates were estimated from the date of first appearance with a food load (members of mated pairs invariably delivered food for the first time on the same day). For each year, the population median date of hatching was estimated from the approximate hatching dates of marked auklets. To evaluate seasonal mass variation of the overall adult and sub-adult populations, comparisons were made with dates standardized in relation to this population median date of hatching. To evaluate mass changes of marked active breeding auklets, dates were standardized in relation to each individual's exact

chick hatch date, data that were available only for 1988 and 1989.

Patterns of variation in mass among years and within each breeding season were examined by analysis of covariance (ANCOVA) using sequential sums-of-squares, with mass as the dependent variable, date as the covariate and sex, age (adult versus sub-adult) and status (breeder versus non-breeder) entered as factors. Sums of squares were entered hierarchically (i.e. only preceding effects were accounted for). The sequential sums-of-squares method provides the best model accounting for interaction terms between covariates and categorical effects. A total of 1631 mass records from 880 individual birds (457 sub-adults and 423 adults) were used in the analysis. The residual degrees of freedom and sum of squares were adjusted for each analysis to account for birds weighed more than once ($df = \text{number of individuals included} - 1$). This resulted in an unbalanced design, but no individual bird accounted for more than 1% of the mass records, and ANCOVA, and repeated-measures ANOVA produced similar results, so only the former are presented. Analysis was performed using the Statistical Package for the Social Sciences (SPSS).

Results

To examine the effect of date, age and year, I performed ANCOVA including individuals of both adult and subadult age groups. Males and females did not differ detectably in mass, so males, females and birds of unknown sex were included in the analysis. For example, there was no detectable difference in mean mass between pair members (paired *t*-test, $t = 0.75$, $P = 0.5$, $n = 27$ pairs) and no detectable differences in mass of males and females during prelaying and incubation (Table 1). No difference between the sexes in mass was detected for the week following laying (Table 1), so females were

Table 1. Mass of breeding males and females during prelaying, laying, incubation and chick rearing

Stage of the breeding season*	Year	Mean male mass (g) \pm SE [<i>n</i>]	Mean female mass (g) \pm SE [<i>n</i>]	<i>t</i>	<i>P</i>
Prelaying	1988	86.2 \pm 0.5 [46]	86.0 \pm 0.6 [37]	0.12	0.9
	1989	86.9 \pm 0.6 [49]	87.3 \pm 1.0 [44]	0.36	0.7
Post-laying	1988	88.0 \pm 1.3 [6]	87.4 \pm 2.0 [5]	0.26	0.8
	1989	86.6 \pm 0.8 [13]	87.5 \pm 2.0 [8]	0.47	0.6
Incubation	1988	89.8 \pm 0.7 [34]	87.5 \pm 0.8 [12]	1.76	0.1
	1989	87.8 \pm 0.6 [78]	86.6 \pm 0.9 [40]	1.22	0.2
Chick-rearing	1988	85.0 \pm 0.8 [33]	84.9 \pm 1.1 [19]	0.03	0.9
	1989	86.6 \pm 0.8 [46]	86.6 \pm 1.1 [37]	0.15	0.9

* Prelaying, 70–33 days before hatching; post-laying, 32–26 days before hatching (the first week of incubation); incubation, 32–1 day(s) before hatching; chick-rearing, 0–30 days after hatching. All birds in this analysis were colour-ringed breeding adults with known hatch date.

apparently able to rapidly readjust for any loss of mass related with egg production and laying. Subsequent ANCOVA with sex included as a factor indicated no significant effect. Failure to find significant differences in mass between males and females does not absolutely indicate there is no mass difference (Forbes 1990), but with the large sample of mass records analysed even small differences should have been detectable.

Body mass of adults (breeders and non-breeders) and subadults (2-year-olds) fluctuated during the breeding season (Fig. 1). The best fit between mass and date was a polynomial relationship, suggesting that the pattern of mass variation through the entire breeding season was best described by a curve (Table 2). ANCOVA indicated a significant year effect — least auklets had the highest mean mass in 1987 and were lightest in 1988. Adults were significantly heavier than subadults (Table 2, Fig. 1). Both age and breeding status independently related to mass, because both were statistically significant factors regardless of the order they were entered into the sequential analysis of covariance. The shape of the curve did not differ significantly between all adults and subadults (date² by age term was not significant), indicating that although subadults were lighter in mass, their pattern of mass change was not significantly different from combined breeding and non-breeding adults. When they first arrived at the colony, subadults averaged about 10 g or 12% lighter in mass than adults. In 1987 and 1989, subadults increased continuously in mass throughout the period they frequented the colony (Fig. 1). In 1988, a poor year for reproduction when food availability may have been low (Jones & Montgomerie 1992), subadults remained at a relatively constant mass. Although adults (≥ 3 years old) were clearly heavier than subadults (2-year-olds), there was no evidence that mass increased with age within individual adults. For example, a sample of individually colour-ringed adults weighed in both years tended to lose mass between 1987 and 1988 (paired *t*-test, $t = 5.47$, $df = 77$, $P < 0.0001$) and a similar sample did not change detectably between 1988 and 1989 (paired *t*-test, $t = 0.83$, $df = 94$, $P = 0.4$). Mass variation within individuals weighed in both 1988 and 1989 was less than variation between individuals, because repeatability of mass was significant and greater than

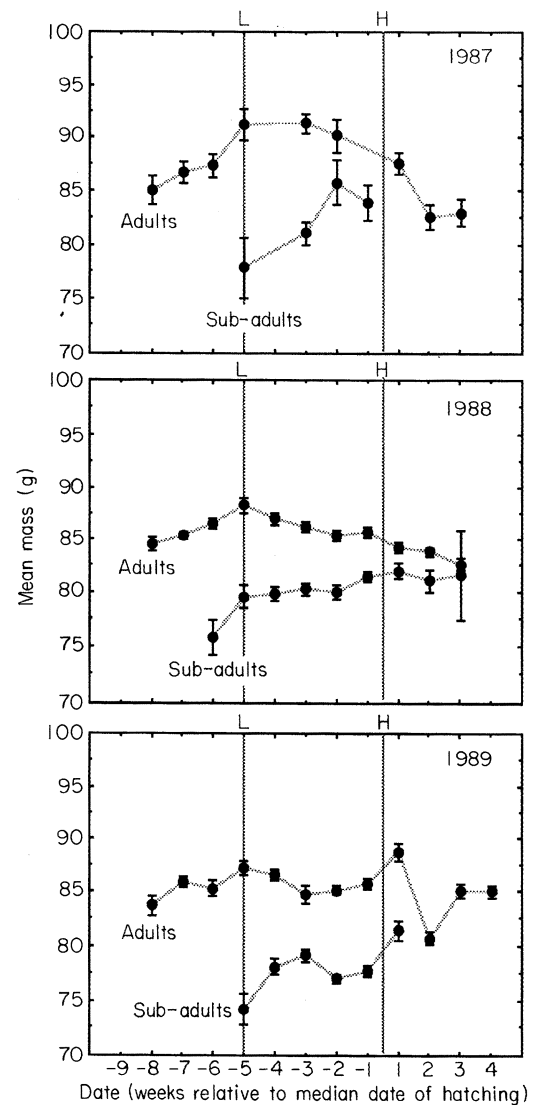


Fig. 1. Patterns of body mass variation of all adults and subadult (2-year-old) least auklets during three breeding seasons. Points indicate weekly (7-day) mean mass, plus or minus standard error. All dates were standardized in relation to the peak of hatching (July 1 in 1987, July 4 in 1988 and 1989).

zero ($r_I = 0.50 \pm 0.05$, $F_{109,413} = 5.61$, $P < 0.0001$, see Zar 1984, pp. 323–325).

To further investigate the effect of sex and breeding status, I performed a second ANCOVA including only adult birds in the analysis, with dates standardized in relation to the population median hatch dates

Table 2. Analysis of covariance of seasonal mass variation of adult and sub-adult least auklets

	SS	df	MS	F	Significance
Date	135.2	1	135.2	4.7	0.03
Date ² *	580.0	1	580.0	20.2	<0.0001
Year	969.3	2	484.7	16.9	<0.0001
Age (adult versus subadult)	1893.0	1	1893.0	66.0	<0.0001
Status (breeder versus non-breeder)	567.4	1	567.4	19.8	<0.0001
Date ² by status	131.7	1	131.7	4.6	0.03
Residual	24997.8	873	66.1		

Table 3. Analysis of covariance of seasonal mass variation of adult least auklets

	SS	df	MS	F	Significance
Date	123.6	1	123.6	4.3	0.04
Date ²	519.6	1	519.6	18.1	<0.0001
Year	342.9	2	171.4	6.0	0.003
Status (breeder versus non-breeder)	271.6	1	271.6	9.5	0.002
Residual	12037.8	421	130.5		

(Table 3). Active-breeders were heavier than non-breeders (combined non-breeding adults and failed breeders; Fig. 2) and this effect of breeding status was highly significant (Table 3). However, the shape of the mass curves did not differ significantly between these groups. Overall then, the pattern of mass variation of non-breeders was essentially similar to that of active breeders.

The relationships between date and mass were further confirmed by a third ANCOVA including only active breeding auklets from 1988 and 1989, and with dates standardized in relation to individuals' hatch dates (Table 4, Fig. 3). Again, sex was not found to be a significant factor. There was only a barely significant effect of year for this sample — despite the differences in overall breeding success

Table 4. Analysis of covariance results for seasonal mass variation of breeding least auklets (dates corrected for individuals' hatch dates)

	SS	df	MS	F	Significance
Date ²	644.0	1	644.0	22.9	<0.0001
Year	212.5	2	106.2	3.8	0.02
Residual	8306.9	300	64.7		

between 1988 and 1989, active breeders were similar in mass. Breeding adults increased in mass during the incubation period in 1988 (regression of mass on date, $r = +0.25$, $r^2 = 0.06$, $P < 0.0001$, $n = 266$), but remained stable in 1989 ($r = +0.08$, $r^2 = 0.01$, $P = 0.2$, $n = 234$; Fig. 3) although a sudden drop in mean mass followed a storm in early June of that year.

Breeding least auklets exhibited an abrupt loss of mass corresponding to the date when their chick hatched. The abruptness of this mass loss is not apparent with dates left unstandardized in relation to individuals' chick hatch dates (Fig. 2), although it is apparent that loss of mass did take place late in the breeding season. However, the sharp decline in mass corresponding to hatching is apparent in the pattern of mass variation of colour-ringed breeding birds with dates standardized for individuals' chick hatch dates (Fig. 3). Breeding auklets lost about 6 g

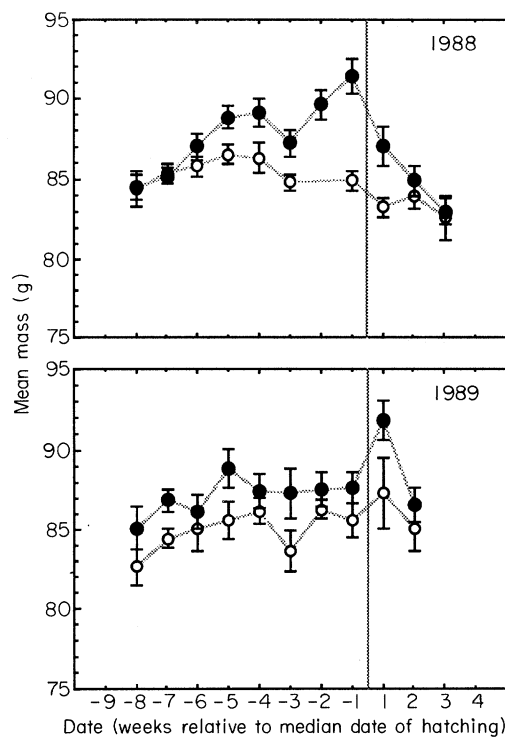


Fig. 2. Patterns of body mass variation of adult active breeding and non-breeding least auklets during the 1988 and 1989 breeding seasons. Points represent 7-day mean masses, plus or minus standard error. Solid points indicate active breeders, unfilled points indicate non-breeders and failed breeders combined. Vertical line indicates population median date of hatching. Note that mass change of breeders is uncorrected for each individual's chick hatch dates (see Fig. 3).

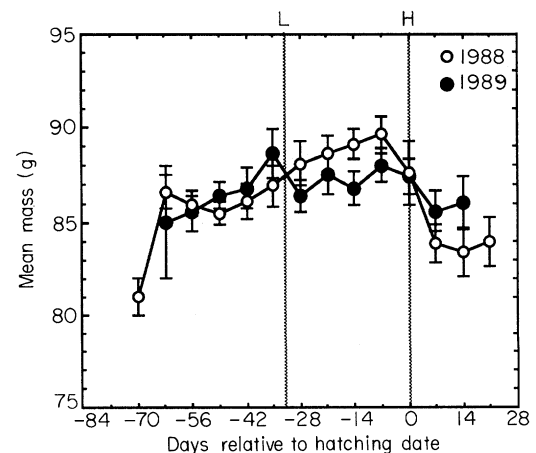


Fig. 3. Patterns of body mass variation of active breeding least auklets during 1988 and 1989. All dates were standardized relative to each individual's chick hatch date. Points represent 7-day mean masses, plus or minus standard error. Vertical lines indicate dates of egg laying and hatching.

(7% of their body mass before hatching) in 1988 and about 3 g (4% of their body mass before hatching) in 1989, at the hatch of the chick (Fig. 3). Breeders lost a roughly equivalent amount of mass to the mass of one meal delivery to a chick (Jones & Montgomerie 1992; Roby & Brink 1986). In both years the difference in mean mass between the week preceding hatching and the week following hatching was statistically significant (1988: $t = 3.99$, $df = 50$, $P = 0.0002$; 1989: $t = 2.22$, $df = 59$, $P = 0.03$). Mass then stabilized for the remainder of chick rearing. For example, there was no change in breeders' mass between the first and second weeks following hatching (1988: $t = 0.13$, $df = 77$, $P = 0.1$; 1989: $t = 0.23$, $df = 39$, $P = 0.2$) and no decline in mass through chick-rearing in either 1988 (regression of breeders' mass on individually hatch-corrected dates during chick-rearing, $r = +0.01$, $r^2 < 0.01$, $P = 0.96$, $n = 83$) or 1989 ($r = +0.04$, $r^2 < 0.01$, $P = 0.8$, $n = 50$). Non-breeders showed no indication of mass loss at the time of the breeders' peak of hatching (Fig. 2).

There was no evidence that adults suddenly increased energy expenditure when their chick hatched (i.e. that the brooding period was energetically more stressful than incubation; Ricklefs 1983). From inspections of nesting crevices and observation of marked individuals, it was apparent that: (1) least auklet chicks received minimal provisioning (possibly as little as one feed per day from each parent) in the first few days after hatching; (2) adults exchanged places more frequently during brooding of the chick than during incubation (up to two times per day) and chicks were left alone as much as 15% of the time during days 1–5. Thus, there was no indication that the brooding period was extraordinarily stressful, because the parents had marginally more opportunity to feed themselves and more flexibility in the timing of their foraging trips. There is probably less stress on parents during the brooding period compared to later in chick rearing because chick's total food demand at this time is relatively low.

Using the equations of program 1 from Pennycuik (1989) and estimates of wing span, flight distances and food load size for least auklets in the Pribilofs, it is possible to estimate the energy savings that result from this loss of mass. For these calculations I assumed that least auklets that were feeding chicks made three round-trips between the nesting crevice and foraging area per day (Roby & Brink 1986; Jones and Montgomerie 1992), that each trip involved a total flight distance of 30 km, that the average mass of a food load was 8 g (Jones and Montgomerie 1992) and I calculated for an 89.5 g auklet that lost 6 g (1988) and an 88 g auklet that lost 3 g (1989). If these estimates are correct, least auklets at Tolstoi would have spent about 1.9 hours day^{-1} flying at maximum range speed at a cost of 70.0 kJ (1988) or 73.6 kJ (1989) during chick-rearing. The estimated

energy savings due to the loss of mass amounted to about 10.3% of the cost of flight in 1988 and 3.5% of the cost of flight in 1989. These calculations are only a rough estimate, but they do suggest that the observed loss of mass could lead to significant energy savings.

There were differences in colony attendance and reproductive performance among years that are important in interpreting inter-year differences in mass. Although the timing of breeding differed little among years, the 1988 breeding season was a poor year for both reproduction and colony attendance compared to other years of the study (Jones 1992a; Jones & Montgomerie 1992). For example, the daily maximum number of birds on the Tolstoi study plot from mid-June to mid-July differed significantly among years (Kruskal-Wallis ANOVA, $H = 30.4$, $P < 0.0001$, $df = 2$). Maximum daily counts in 1987 (median = 103 birds, $n = 21$ days sampled) and 1989 (107 birds, $n = 36$) were both significantly different from 1988 (72 birds, $n = 37$; $P < 0.05$ in each case) using non-parametric multiple comparisons (see Zar 1984, pp. 199–201). The proportion of auklets that attempted to breed also differed significantly among years. In 1987, 83% (203/242) of the marked adults attending the plot attempted breeding, whereas a significantly lower proportion attempted breeding in 1988 (52%; 123/236, log-likelihood ratio test, $G = 10.67$, $P < 0.01$), and 1989 (61%; 109/180, $G = 4.49$, $P < 0.05$). A smaller proportion of birds bred in 1988 than 1989, but the difference was not significant ($G = 0.83$, $P < 0.05$).

Discussion

Breeding least auklets experienced an abrupt loss of mass at the time of hatching and showed no further mass loss during chick rearing. This pattern of mass change is not consistent with the hypothesis that mass loss is related to reproductive stress. It is more consistent with the idea that mass change is a programmed response to the requirement to lose mass during the period when lowered wing loading is advantageous — when breeding adults commence provisioning their chick (Croll *et al.* 1991). When chicks hatch, breeding auklets gradually change their activity from single foraging trips alternating with 24 h incubation stints to a much more active routine later in chick rearing, involving extensive flying between the colony and foraging area (up to four trips per day, for up to 30 days; Roby & Brink 1986; Piatt *et al.* 1990). Energetic calculations have shown that loss of 4–7% of body mass at the point when chick rearing begins could result in energy savings amounting to a biologically significant proportion of daily energy expenditure (this study; Norberg 1981; Croll *et al.* 1991).

Further observations are also consistent with the PAH: breeding auklets either gained mass or

remained at relatively constant mass during incubation, indicating that reproductive stress at least did not lead to mass loss during this period. Breeders and non-breeders exhibited a similar pattern of mass change during the incubation period. This observation is more consistent with the PAH because the SH predicts that breeders should lose mass during incubation (Freed 1981; Norberg 1981; Moreno 1989) and do so at a faster rate than non-breeders (because breeders are engaging in 24-h incubation shifts, while non-breeders are freed from this costly activity).

Some other observations suggest that breeding least auklets were able to maintain their body mass at a stable level, rather than suffering mass loss due to the energetic stresses of reproduction. For example, females were able to produce an egg weighing about 17 g or 20% of their body mass (Roby & Brink 1986) without this causing their mass to differ detectably from males. Females must have rapidly recovered any loss of mass associated with egg production while they were briefly absent from the colony following laying, because no difference in mass was recorded between males and females during the early incubation period (Table 1). This suggests that females were able to regain lost body mass when necessary. Female ancient murrelets (*Synthliboramphus antiquus*) show a similar tendency to recover lost mass after laying (Gaston & Jones 1989).

If a rapid adjustment of body mass is advantageous at the commencement of chick rearing, then this raises the question of why auklets were carrying around extra mass earlier in the season. Breeding least auklets gained mass in the weeks before incubation began, remained at relatively high (stable or increasing) mass through incubation and then lost mass abruptly at the commencement of chick rearing. A possible explanation for this pattern is that the extra mass during incubation (representing additional lipid reserves) is held as an 'insurance policy'. Least auklet incubation shifts (averaging 24 h, occasionally to 36 h; Roby and Brink 1986) are shorter than those of some other alcids (e.g. 72 h in ancient murrelets), but incubators still risk emerging from their nesting crevice after an incubation shift to find weather conditions or other factors have made food unavailable. A probable example of this phenomenon, and an exception to the general stability in mass during incubation, occurred in early June 1989. Early in incubation breeders suffered an abrupt decline in body mass from which they never recovered (Fig. 3) after a period of poor feeding conditions and low colony attendance due to a storm. Extra lipid reserves laid down early in the breeding season could act as a buffer against events such as this.

There is now some evidence from several bird species that mass changes during the breeding season

are related to programmed mass loss rather than reproductive stress. Work on two other alcid species has supported the PAH. Based on the observation that despite varying at the time of clutch completion, ancient murrelet adult mass converged to a constant level following hatching over a 5-year study, Gaston & Jones (1989) concluded that mass loss during incubation better fit the expectations of the PAH. A study of Brünnich's guillemots (*Uria lomvia*; Croll *et al.* 1991) demonstrated that mass loss by breeders involved a rapid change at the onset of chick-rearing and stabilized for the duration of chick rearing, also consistent with the PAH, but less so with the SH.

It may rarely be possible to completely and unequivocally separate these hypotheses, because they often share many predictions. For example, if the early part of the nesting cycle is the most energetically costly for parent birds, as suggested by Ricklefs (1983), even an abrupt loss of mass at this critical period could occur due to stress. However, observations of behaviour during this period suggest that it was not a period of abruptly increased energetic expenditure in least auklets at St Paul Island. After hatching, the chick is brooded most of the time by the parents during the first 5 days (Roby & Brink 1986), but because parents exchanged places frequently and the chick was left alone for part of the time, I believe that energetic stress during the early brooding period cannot explain the abrupt loss of mass experienced by breeding least auklets.

Norberg (1981), Freed (1981) and other authors have referred to loss of mass that provides apparent benefits to birds feeding nestlings as 'adaptive'. However, an adaptation may be best defined as a derived character that evolved in response to a specific selective agent (Harvey & Pagel 1991). To determine whether programmed mass loss is an adaptation (in the narrow sense) in alcids, it would be necessary to investigate the pattern of evolution of this trait using a comparative approach, to show whether alcids evolved from ancestors that lack this trait. Ancient murrelets (chicks fully precocial with colony departure at 2 days of age), Brünnich's guillemots (partly-grown semiprecocial chicks depart colony at 2–4 weeks of age) and least auklets (fully-grown semiprecocial chicks depart colony at 4 weeks of age) represent the complete range of chick-development modes in the alcids, and there is evidence for programmed mass loss in each of these species. Furthermore, these three species belong to separate well-diverged tribes within the sub-family Alcinae (Sibley *et al.* 1988; Strauch 1985). Thus, the presently available data are consistent with the idea that programmed mass loss is an ancestral trait among alcids. Programmed mass loss may indeed be an adaptation in Alcinae, since the extraordinary energetic demands of flight in this sub-family could provide much greater selective advantages for the

trait in alcids compared to their close relatives the gulls (Larinae).

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