

THE RELATIVE IMPORTANCE OF STRESS AND PROGRAMMED ANOREXIA IN DETERMINING MASS LOSS BY INCUBATING ANCIENT MURRELETS

ANTHONY J. GASTON AND IAN L. JONES

Canadian Wildlife Service, National Wildlife Research Centre, 100 Gamelin Boulevard,
Hull, Québec K1A 0H3, Canada, and

Department of Biology, Queens University, Kingston, Ontario K7L 3N6, Canada

ABSTRACT.—We describe changes in the mass of breeding Ancient Murrelets (*Synthliboramphus antiquus*) at Reef Island, British Columbia, during four breeding seasons. Changes are evaluated in the light of two hypotheses that concern mass loss by birds during breeding: that mass loss is a symptom of stress or that it is an adaptive response to optimize mass in relation to the changing demands of breeding activities. We found no differences between sexes in mass or mass changes, and hence samples were combined. Mass at the start of incubation varied significantly among years, but mass at colony departure (ca. 15% lower) did not. Our observations are not compatible with the idea that mass loss during incubation is caused by stress. There was a negative correlation between mean date of laying in a given year and the mean mass of breeders at clutch completion. In one year, there was a negative correlation between the date of laying of individual clutches and the mass of the parent when the chicks hatched. We conclude that variations in the availability of food do not cause the overall pattern of mass change during incubation, but they may be responsible for some inter-year and intra-year variation in adult mass. Received 7 November 1988, accepted 17 May 1989.

Loss of mass by breeding birds during the nesting period occurs in many species and has usually been attributed to the stress imposed by reproduction (Ricklefs 1974). An alternative hypothesis was suggested (Freed 1981) to explain mass loss in female House Wrens (*Troglodytes aedon*) during breeding and was proposed by Norberg (1981) as a general explanation for mass loss among breeding birds. This holds that decrease in mass is an adaptive response which reduces the energy required for flight when this activity is taking up an unusually large proportion of the time-budget. Freed based his rejection of the "stress" hypothesis on the fact that mass loss occurred before the peak rate of chick feeding, that loss did not increase with brood size, and that males did not lose weight, despite feeding the nestlings as much as the females.

The concept of "reproductive stress" has not been rigorously defined. An implicit assumption is that loss of mass during reproduction lowers subsequent survival; hence, lower mass is symptomatic of a fitness cost (Freed 1981). Nur (1984) showed that the subsequent survival of breeding Blue Tits (*Parus caeruleus*) was negatively correlated with mass during chick-rearing. Most other authors have assumed this connection, particularly where they recorded a

negative correlation between brood size and adult mass (Hussell 1972, Askenmo 1977, Bryant 1979, Hails and Bryant 1979, Ricklefs and Hussell 1984). The alternative "adaptive" hypothesis suggests that a decrease does not necessarily have any implications for subsequent survival. Jones (1987) considered that mass loss by female swallows (*Hirundo rustica*) when brooding small chicks was best explained in this way as a form of programmed anorexia, whereas loss of mass by both sexes while feeding larger chicks was probably due to stress.

The two hypotheses are not mutually exclusive. Although average mass may decline during the breeding season (as a programmed response to the need for increased flight efficiency), differences in the extent of mass loss among individuals within the population may be related to stress. The difference between the two hypotheses depends on the mechanism that triggers the loss. Under the stress hypothesis, mass is lost in response to an inability to find food at a sufficient rate. Under the adaptive hypothesis, however, mass is lost in any case (even when food is abundant), presumably through adjustment of the amount of time devoted to, or the intensity of, feeding.

This distinction allows us to make different predictions about how mass should vary both

within and between breeding seasons. If mass loss is triggered mainly by stress, then the change in mass should be greater in years when food is scarce than in years when it is abundant. Likewise, the change in mass of late breeders (presumably lower-quality birds) should be greater than that of early breeders. Conversely, if change in mass is largely an adaptive response, we expect that mass at a given stage in the breeding cycle would be constant from year to year, and among early and late layers, irrespective of the amount of food available, unless adjustments are made in other ways (e.g. clutch size).

We examined changes in mass in the Ancient Murrelet (*Synthliboramphus antiquus*) during breeding. This burrow-nesting seabird has some advantages for studying the relative importance of stress and adaptation in loss of mass, because the young are precocial and leave their natal burrow for the sea within four days. The two parents share incubation duties equally, with most shifts lasting 2–5 days (Gaston unpubl. data). The parents do not feed the chicks in the burrow. After they leave the colony, the family stays together for several weeks, during which time the adults do little or no flying (Sealy 1976). Consequently, mass changes during breeding are unlikely to be related to the need to improve flight performance. In addition, clutch size is virtually constant: 95% of clutches have 2 eggs (Sealy 1976, Gaston pers. obs.). Hence, the energy demands of egg production are not affected by inter-year variation in clutch size.

METHODS

We worked on Reef Island, in the Queen Charlotte Islands archipelago of British Columbia, during the 1984–1988 breeding seasons (see Gaston et al. 1988 for details of the study area). Ancient Murrelets were captured 23 April to 5 June 1984 (median start of incubation: 28 April); 14 April to 15 June 1985 (21 April); 10 May to 13 June 1986 (23 April); 26 April to 15 June 1987 (19 April); 31 March to 15 June 1988 (23 April).

Adult Ancient Murrelets were captured at night, on the forest floor, with long-handled landing nets. Most birds were caught as they arrived, but a few were sitting on the ground. Observations of departure behavior over two seasons showed that most birds did not begin to leave the colony until after 0200 PDT (Jones 1985). As very few birds were caught after 0200, it is likely that practically all birds caught had arrived at the colony that night. Birds caught were examined

for the presence of a brood patch or an egg in the oviduct (in Ancient Murrelets an oviduct egg makes a very conspicuous bulge) and weighed to the nearest 1 g on a 300-g Pesola spring balance. The depth of the bill at the base was measured to the nearest 0.1 mm with vernier calipers. Because of the timing of fieldwork, birds with oviduct eggs were captured only in 1984, 1985, and 1988, and these birds were omitted from the analyses, except where specified.

A sample of burrows was checked each year to determine the timing of laying and hatching. The mass, length, and breadth of eggs found in these burrows were measured. No measurements differed significantly between first and second eggs in any year ($P < 0.05$, Gaston unpubl. data). Hence, all statistics relating to eggs were based on a single egg from each clutch. Where order of laying was known, the first egg was used; otherwise, an egg was selected at random.

All dates were standardized in relation to the median date of clutch completion (7–8 days after the first egg is laid; Sealy 1975, Gaston et al. 1988). In 1984 and 1985, the date was based on the inspection of burrows. In 1986, 1987, and 1988, it was derived by extrapolation from observed dates of chick departure. In 1988, estimates based on burrow inspections and chick departures were identical. We removed, weighed, and replaced birds found brooding chicks. These birds had spent an average of about 36 h in the burrow when weighed. No other birds were removed from burrows because removal during incubation normally leads to desertion in this species (Gaston et al. 1988).

In 1984, 30 breeders were collected and sexed by dissection. Among several external measurements examined, the depth of the bill at the base provided the best discrimination between sexes. Mean bill depth for females was 6.7 ± 0.21 mm ($n = 15$) and for males 7.2 ± 0.22 mm ($n = 15$). Because of the degree of overlap, individual birds could not be sexed with certainty on the basis of bill depth. However, to identify potential differences between the sexes, the sample of birds examined alive was divided into those with a bill depth of <6.9 mm (females) and those with a bill depth of 7.0 mm or more (males).

Breeding Ancient Murrelets develop two lateral brood patches, each 20–25 mm across, which are fully developed at the onset of incubation (Sealy 1976). At Reef Island, in all years, the proportion of trapped birds with brood patches rose to almost 100% by the time 90% of clutches were completed, but then it fell sharply in the middle of the incubation period, as nonbreeding birds began to visit the colony (Gaston and Jones unpubl. data). Consequently, all birds captured before the date at which 90% of clutches were completed were assumed to be breeders. Thereafter, only birds possessing brood patches 20 mm or more across were included. Birds known to have departed with their chicks were never retrapped at the colony

TABLE 1. Regression slopes and intercepts ($\bar{x} \pm \text{SE}$) for the relationship between mass (g) and time (days from median clutch completion) for "male," "female," and combined samples.

Year	Sample	Intercept	Slope	n	r	F	P (slope)
1984	"Male"	229.8 $\pm$ 15.4	-0.38 $\pm$ 0.34	29	-0.205		NS
	"Female"	203.1 $\pm$ 23.1	0.28 $\pm$ 0.51	17	-0.142		NS
	Combined	217.8 $\pm$ 5.2	-0.23 $\pm$ 0.28	47	-0.121	0.7	NS
1985	"Male"	238.8 $\pm$ 6.7	-0.41 $\pm$ 0.14	63	-0.342		<0.01
	"Female"	233.0 $\pm$ 14.5	-0.39 $\pm$ 0.32	13	-0.342		NS
	Combined	230.9 $\pm$ 3.2	-0.51 $\pm$ 0.12	85	-0.416	17.3	0.001
1986	"Male"	246.4 $\pm$ 17.9	-0.66 $\pm$ 0.34	60	-0.244		NS
	"Female"	339.0 $\pm$ 55.5	-2.54 $\pm$ 1.18	15	-0.513		<0.05
	Combined	232.8 $\pm$ 7.6	-0.67 $\pm$ 0.26	84	-0.274	6.6	0.012
1987	"Male"	252.0 $\pm$ 7.2	-0.75 $\pm$ 0.14	65	-0.469		<0.01
	"Female"	252.2 $\pm$ 18.3	-0.85 $\pm$ 0.33	26	-0.336		<0.05
	Combined	238.0 $\pm$ 4.1	-0.85 $\pm$ 0.12	122	-0.540	49.4	0.001
1988	"Male"	232.7 $\pm$ 6.4	-0.43 $\pm$ 0.12	110	-0.335		<0.01
	"Female"	233.2 $\pm$ 11.7	-0.53 $\pm$ 0.22	83	-0.258		<0.05
	Combined	222.0 $\pm$ 3.3	-0.49 $\pm$ 0.10	201	-0.344	23.3	0.001

later in the same year. We believe it unlikely that our sample included any postincubation breeders. A few failed breeders may have been included, although birds known to have deserted were not retrapped at the colony either, and failure due to other causes was rare (<10% in all years, Gaston unpubl. data).

Differences among years in the slope and intercept of the regression of weight on days from the median date of clutch completion were tested using analysis of covariance (GLM procedure of SAS 1985). As all dates were normalized to the median date of clutch completion the standard error (SE) on the intercept was equivalent to the SE on the predicted weight at the start of incubation. All mean values are given ± 1 SE.

RESULTS

Ancient Murrelets trapped before the median date of clutch initiation in 1988 (15 April) had a mean mass of 201.0 ± 1.07 g ($n = 151$). Birds trapped in the same year during the subsequent 15 days (the peak of laying) were significantly heavier ($\bar{x} = 212.9 \pm 3.47$ g, $n = 17$, $t = 3.06$, $P < 0.01$).

For the period from median clutch initiation onwards, there was a negative correlation between mass and date for both sexes in all years except 1984, when there was a nonsignificant positive correlation for females (Table 1). Neither the slope nor the intercept of the regression differed significantly between the sexes in any year. For the combined samples, all correlations were negative, significant, and all slopes differed significantly from zero (except in 1984

when the trend was similar, but not significant) (Table 1; Fig. 1).

Average mass at the median date of clutch completion, estimated from the regression formulae for the combined samples, varied significantly among years ($F = 3.86$, $df = 4$, 529 , $P = 0.004$). Average mass was lowest (217.8 g; Table 1) in the year of latest clutch completion (1984), and highest (238.0 g) in the earliest year (1987). Variation among regression slopes for combined samples approached significance ($F = 2.06$, $df = 4$, 529 , $P = 0.085$). There was a significant negative correlation between the median date of clutch completion and the predicted mass of breeders at that date ($n = 5$, $r = 0.876$, $P < 0.05$, Fig. 2B). There was also a neg-

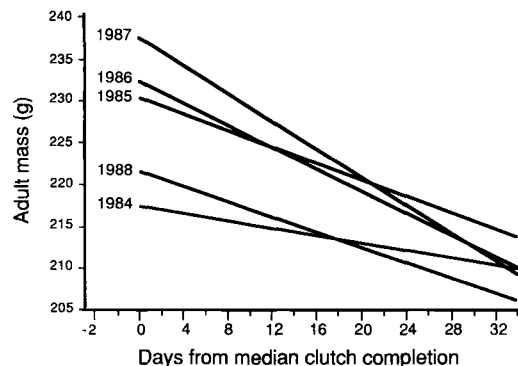


Fig. 1. Regressions of mass on date for breeding Ancient Murrelets trapped at Reef Island (1984-1988). Dates are adjusted to the median date of clutch completion.

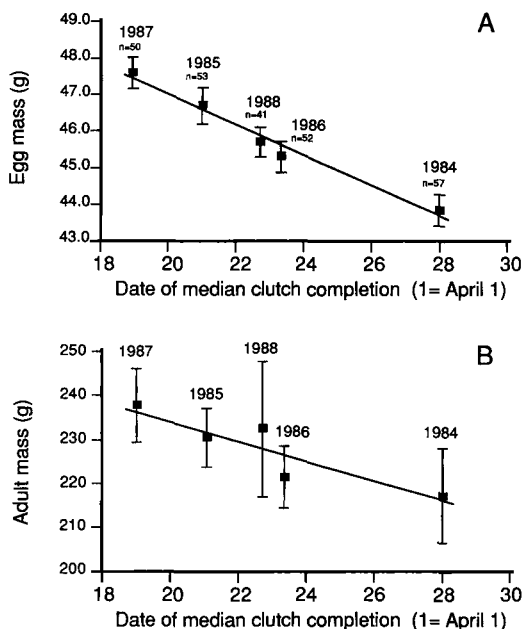


Fig. 2. Mean mass of fresh eggs (A) and adult mass at clutch completion (B) in relation to the median date of clutch completion for each year. Vertical bars give ± 1 SE.

active correlation between the median date of clutch completion and the mean fresh mass of eggs ($n = 5$, $r = 0.984$, $P < 0.001$, Fig. 2A).

The mean mass of females trapped with oviduct eggs minus the mean mass of fresh eggs measured in the same year was 200.7 g in 1984, 204.0 g in 1985, and 202.1 g in 1988 (Table 2). Hence, the mass of these females minus their egg averaged 17.1 g, 26.9 g, and 19.9 g less than the mass predicted by the regressions for the combined samples for the appropriate years. These values fall outside the 95% confidence limits for the estimates of weight at clutch completion for the combined samples. In 1988, the value was close to the mean mass of birds trapped during the prelaying period (see above).

TABLE 2. Mass ($\bar{x} \pm$ SD) of females carrying oviduct eggs, mass of fresh eggs laid in the same year, and estimated mass of females minus eggs. Sample sizes are in parentheses.

Year	Female mass (A)	Egg mass (B)	Difference (A - B)
1984	244.5 $\pm$ 14.0 (30)	43.8 $\pm$ 3.2 (57)	200.7
1985	250.7 $\pm$ 10.3 (22)	46.7 $\pm$ 3.3 (53)	204.0
1988	247.4 $\pm$ 7.1 (16)	45.3 $\pm$ 2.6 (41)	202.1

TABLE 3. Mass ($\bar{x} \pm$ SD) of birds trapped in burrows with newly hatched chicks and correlation of mass with date for the same samples. Sample sizes are in parentheses; NS = not significant.

Year	Mass	r	P
1984	203.9 $\pm$ 9.8 (13)	-0.082	NS
1985	203.7 $\pm$ 9.0 (23)	-0.684	0.01
1986	201.2 $\pm$ 10.8 (19)	-0.340	NS
1987	208.3 $\pm$ 6.6 (31)	-0.078	NS
1988	207.4 $\pm$ 12.1 (40)	-0.043	NS

The mean mass of birds trapped in the burrow after their chicks had hatched ranged from 201.2 g in 1986 to 208.3 g in 1987, with no significant difference among years ($F = 1.177$, $df = 4, 121$, $P > 0.05$). Mass at this point in the breeding cycle had a significant negative correlation with date in 1985, but mass was not correlated with date in 1984, 1987, or 1988 (Table 3).

DISCUSSION

Our finding that breeding Ancient Murrelets at Reef Island normally lost mass during incubation agrees with Sealy's (1976) study at Langara Island, based on birds collected on the feeding sites. Comparison of the "male" and "female" samples provides no evidence of mass differences between the sexes in the Ancient Murrelet, which also agrees with Sealy (1976). The absence of any clear difference between the sexes in the relationship of mass to time from clutch completion is surprising in view of the finding that females with oviduct eggs were lighter (when egg mass was subtracted) than birds trapped at the same time without eggs. Presumably, females quickly regain the mass typical of the rest of the population after laying, and they do not return to the colony until they have done so. Females apparently have little difficulty in adjusting their mass. Similar trends in mass were observed for both sexes, which makes it highly unlikely that mass loss during the incubation period could be explained by a reduction in reproductive tissue (Ricklefs 1974). The mass of male reproductive tissue at laying is less than 5 g (Gaston unpubl. data); much less than the observed difference.

The close correlations between timing of breeding, egg size, and body mass at the start of incubation suggest that these variables are causally linked, presumably via the availability

of food. In early years, females apparently are able to lay large eggs, and breeders begin incubation with a high body mass. Body mass during incubation is probably controlled by immediate environmental conditions, but not all observations support this view.

Although the mass of breeding Ancient Murrelets at the time of clutch completion varied significantly among years, mass at hatching did not. Constant weight at hatching is incompatible with the idea that decrease in mass is caused by stress and requires that, in years of early laying (presumably years when food was readily available), the stress of incubation was greater than in years of late laying. Furthermore, there is no apparent reason why stress should increase during incubation. The length of the daylight period is increasing, which allows more time to feed. Moreover, sympatric Cassin's Auklets (*Ptychoramphus aleuticus*), which feed on similar prey (Sealy 1975, Vermeer 1984, Vermeer et al. 1987), rear their nestlings during the period when most Ancient Murrelets are leaving the colony (Gaston pers. obs.). If the auklets time their breeding so that the nestling period coincides with a peak in the availability of food, then food availability should be increasing during the Ancient Murrelet's incubation period.

Compared with the other Alcidae, Ancient Murrelets have prolonged incubation shifts (Sealy 1976). They exhibit periodic egg neglect during the early part of incubation (Sealy 1976, Gaston and Powell 1989), which suggests that breeders may sometimes experience difficulty in maintaining their incubation schedule. Regular egg neglect throughout incubation, as recorded by Murray et al. (1983) for Xantus' Murrelet (*Synthliboramphus hypoleucus*), does not appear to occur in undisturbed Ancient Murrelets, probably because neglect in the latter species increases the number of days of incubation required (Gaston and Powell 1989). Breeders may therefore increase their energy reserves at the start of incubation to insure themselves against the risk of having insufficient reserves to continue incubation if their mate is delayed in returning to the colony (e.g. because of bad weather affecting feeding conditions). If, as we have argued, conditions are improving during incubation, breeders can afford to reduce their energy reserves progressively. This practice could allow breeding to proceed under less favorable conditions than would otherwise be the case, because the pro-

gressive shedding of energy reserves reduces the total amount of food that must be obtained during incubation (Norberg 1981).

Because mass at hatching was similar in all years, the level of reserves represented by a mean mass (200–210 g) is either necessary for the subsequent needs of chick-rearing and achieved by adjustments to the incubation schedule, or the level of reserves represents a normal optimum mass, reached when the demands of incubation are completed. In either case the mass change occurring during incubation cannot be interpreted as a symptom of stress. In a year when food is readily available and birds begin incubation with large reserves, they should be capable of longer incubation shifts than in a year of poor food availability. In a good year, their mates require less time to replace their reserves than in a bad year, and they are likely to return to the colony sooner. We obtained some evidence of this when we found that incubation shifts observed in 1984 were significantly longer than those observed in the earlier 1985 season (Gaston unpubl. data; these data are only available for two years). The larger reserves carried in more favorable years cannot be regarded as a deliberate response to the prevailing conditions, but must be seen as the accidental result of a general process of mass adjustment during incubation.

We propose that Ancient Murrelets are programmed to lay down energy reserves before starting incubation to reduce the amount of foraging required later. The increase in mass is mediated through an increase in feeding time or effort. In good years, this increase in feeding builds up greater reserves than in bad years, but even in bad years, the reserves are sufficient for most birds to cope with incubation, with some adjustment in the timing of laying. We cannot rule out the possibility that in bad years a proportion of the population does not breed at all, perhaps masking some effects of stress. However, extensive retrap data yield no evidence for nonbreeding among birds that have bred in previous years (Gaston unpubl. data).

One way in which Ancient Murrelets may cope with bad years is to increase the frequency of egg neglect. Murray et al. (1980) found that Xantus' Murrelets neglected their eggs more when food was scarce. Unfortunately, our own activities in disturbing breeding birds probably contributed to the incidence of neglect and we are therefore unable to determine if an increase

in neglect actually occurred (Gaston and Powell in press).

We believe that the sharp increase in mass just before the start of incubation, as well as the subsequent decline during incubation, is an adaptive response by Ancient Murrelets to the demands of breeding. However, inter-year variation in mean mass at clutch completion probably reflects the effect of inter-year differences in the availability of food during the period just before the start of incubation.

ACKNOWLEDGMENTS

We thank all those who assisted with the trapping of adult murrelets at Reef Island: Andrea Lawrence, Pierre Mineau, David Noble, David Powell, Steven Smith, Yves Turcotte, and Louise White. Thanks also to Gary Kaiser and Moira Lemon for advice and assistance with logistics. Timothy Birkhead, James Briskie, Hugh Boyd, Vernon Byrd, George Hunt, David Noble, and Kathy Winnett-Murray made useful comments on the manuscript. The study was funded by the Canadian Wildlife Service.

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ERRATUM

In "Natural incubation, egg neglect, and hatchability in the Ancient Murrelet" by Anthony J. Gaston and David W. Powell (1989, *Auk* 106: 433-438), the degrees of freedom of the Chi-square values on p. 435 should read: " $\chi^2 = 1.01$, $df = 1$, $P > 0.10$ " and " $\chi^2 = 16.4$, $df = 1$, $P < 0.01$."