ADAPTIVE LOSS OF MASS IN THICK-BILLED MURRES[1]

DONALD A. CROLL[2]
Physiological Research Laboratory, Scripps Institution of Oceanography A-004,
La Jolla, CA 92093

ANTHONY J. GASTON
Canadian Wildlife Service, National Wildlife Research Centre,
100 Gamelin Blvd., Hull, Quebec, Canada K1A OH3

DAVID G. NOBLE
Department of Biology, Queen's University, Kingston, Ontario, Canada

Abstract. Mass loss of breeding Thick-billed Murres, *Uria lomvia*, was examined. Adult breeders lost a significant amount of mass from incubation to chick hatching (0.032 kg in 1988 and 0.063 kg in 1989). Regression of the timing of mass loss during incubation and brooding revealed that body mass was maintained constant during incubation, was lost rapidly soon after chick hatching, and remained constant at the lower level thereafter. Murres made more than twice as many foraging trips per day while feeding chicks than while incubating eggs, and therefore increased the amount of time spent in flight while brooding the chick. The stepwise mass loss is interpreted as adaptive in increasing flying efficiency as murres spend a greater amount of their time in flight during chick brooding. Murres may experience as much as a 25% of BMR per day energetic savings, or a reduction in the mechanical cost of flight of 9.0% to 9.5% by losing the observed 4.4% to 6.2% of incubation body mass. Murre mass loss during breeding was interpreted as adaptive in reducing the energetic cost of reproduction.

Key words: Thick-billed Murre; energetics; reproduction; flight; foraging.

INTRODUCTION

Mass loss during breeding has been interpreted as an indicator of the stress of reproduction (Ricklefs 1974). Among seabirds, stress has been implicated in mass changes observed in Atlantic Puffins *Fratercula arctica* (Harris 1979), Thick-billed Murres *Uria lomvia* (Gaston and Nettleship 1981), and Common Murres *Uria aalge* (Belopol'skii 1956). However, Blem (1976) introduced the alternative hypothesis that mass reduction in birds was adaptive when he concluded that lipid storage levels in birds may be minimized to maintain a low wing loading. Norberg (1981) refined this idea, suggesting that mass loss during breeding may be a means of increasing flight efficiency. This could reduce the energy expended in foraging, and ultimately increase the reproductive success of the parents. This hypothesis has been used to explain seasonal variation in the mass of House Wrens (*Troglodytes*

aedon) (Freed 1981), and female Barn Swallows (*Hirundo rustica*) (Jones 1987).

Although not mutually exclusive (loss of mass induced by stress will lead to savings on energy expended on flight due to reduced wing loading), the two hypotheses yield different predictions about the timing of mass loss. If stress induces mass loss, then mass should decline throughout the breeding period, and should decline most rapidly during the period of highest demand— usually chick rearing. In contrast, if loss of mass is adaptive, the bird may experience an abrupt, or stepwise, decline in mass at (or preceding) the point where mass loss becomes most adaptive, i.e., when flight demand increases. Freed (1981) interpreted the observations that House Wrens lose mass before the period of highest nestling food demand, and that the mass of females stabilizes thereafter, to mean that the mass loss was adaptive rather than stress induced.

The murres and Razorbill (*Uria* spp. and *Alca torda*), which use their wings in diving, have the highest wing loading of any flying bird (Greenwalt 1962). Selection to increase swimming efficiency has led to a reduction in wing size. Pennycuick (1987) calculated the cost of flight in seabirds and found that powered flight efficiency

is negatively correlated with wing loading. Compared to a "standard seabird" of the same mass with longer and broader wings, an auk flies faster, but uses more energy per unit distance flown. We believe that wing loading is an important consideration for murres during chick rearing. Thick-billed Murres make more foraging trips during chick-rearing than during incubation (Gaston and Nettleship 1981, Gaston and Noble 1986). Presumably the advantages of improved flight efficiency are greatest at this time when the birds are doing the maximum amount of flying. Due to their extremely high wing loading, even relatively small changes in the mass of these birds may have a large effect on their flying efficiency and hence their energy budgets.

Because murres carry a single fish to their chicks in their bills, not in their stomachs, their ability to deliver food to the chick is even further constrained. The mean mass of fish delivered to Thick-billed Murre chicks at four colonies in the eastern Canadian arctic averaged less than 1.5% of adult body mass (Gaston and Nettleship 1981, Gaston 1985). Similarly sized procellariiforms (with "standard" wing loading) are capable of delivering a mean food mass that is 15% of adult body mass (Pennycuick 1987). Hence we predict that murres are particularly likely to exhibit adaptive mass loss during breeding. This paper examines patterns of mass loss, and frequency of foraging trips for Thick-billed Murres breeding on Coats Island, Northwest Territories, Canada. Judging from chick growth, the availability of food in the vicinity of this colony appears to be very good compared to other colonies in the eastern Canadian arctic (Gaston et al. 1987). We also examine the probable saving in energy expenditure that may result from observed mass changes.

METHODS

MASS

Thick-billed Murres were captured and weighed on Coats Island throughout the 1988 breeding season, and from late incubation onwards in 1989. Birds were captured on their nest sites using a wire noose, placed in a canvas bag, and weighed to the nearest 0.005 kg using a 1.5 kg Pesola spring scale. We recorded whether the bird was incubating or brooding and made a visual estimate of chick age. We weighed 77 incubating and 102 brooding birds in 1988, and 42 incubating and 100 brooding birds in 1989. In ad-

dition, 18 nonbreeding murres aged 4–7 years were weighed during the 1988 breeding season. Samples were analyzed according to year and breeding stage (incubating or brooding). Linear regressions of date versus mass were calculated for each period and slopes were tested for significance using t-tests. The mean mass of adults for each period was compared using analysis of variance (ANOVA), and multiple comparisons of the means were performed using the Scheffe multiple range test. Stastical procedures were performed using the Statistical Package for Social Sciences (SPSS). Median hatching dates were calculated for 1988 from egg density indices ($n = 128$) using the method described in Collins and Gaston (1987) and in 1989 from regression of wing lengths of chicks ($n = 46$) with age and egg density indices ($n = 43$).

WING SPAN

The wing span of Thick-billed Murres was calculated from the mean of five murres collected off of Newfoundland during the winter of 1988–1989. Band returns have shown that Coats Island murres winter in this area (Richard Elliot, Canadian Wildlife Service, pers. comm.). Wing span was measured as the distance from one wing tip to the other with the wings spread out as far as possible (Pennycuick 1989).

INCUBATION/BROODING SHIFTS

Individual breeding sites were observed continuously for 24 or 48 hr in 1988 to estimate the duration of incubation shifts. One member from each breeding pair was captured prior to the beginning of the monitoring period and a piece of orange nylon ribbon was attached to the crown feathers with cyanoacrylate adhesive, so that the pair could be distinguished easily. Sites were observed from blinds at ranges of 5–15 m. Times of arrival and change-overs were recorded for each pair. Shift durations were calculated from the time of the first exchange of nest duties. After mid-July, darkness precluded the observation of the nests from about 23:00 to 03:00 local time (e.s.t.). However, as birds occupying sites at 23:00 were invariably still present at 03:00, we assumed that no changeovers occurred during darkness. Observations were made of 14 pairs on 29 June–1 July, 10 pairs on 9–10 July, and 17 pairs on 18–19 July. Mean durations were calculated for each period and compared using ANOVA.

TABLE 1. Results of statistical comparisons of adult Thick-billed Murre mass by period and year. Linear regressions were based on plots of mass vs. date for each period. Significance refers to this comparison. Mass difference refers to the difference between brooding and incubation mass within a season.

Period	Regression r^2	Significance*	Mean	SD	Difference	% Difference	n
Incubation 1988	0.08	ns	1,012	53	32	3.2	77
Brooding 1988	0.04	ns	980	70			102
Incubation 1989	0.01	ns	1,031	63	63	6.1	42
Brooding 1989	0.04	ns	968	70			100
Nonbreeding 1988			913	72			19

* Significance of regression of mass vs. date using t-test.

CHICK FEEDING RATES

We recorded the rates at which chicks were fed in 1988 and 1989 by watching an area supporting approximately 108 breeding pairs continuously for 24 hr. Prior to the initiation of the first watch, the positions of eggs and chicks were mapped on a photograph of the plot so that observers could identify the sites where fish were delivered. The number of chicks monitored was different for each watch due to the progress of hatching and losses of chicks as the season progressed. We recorded the time of food deliveries at each site. Mean, median and modal feeding rates were calculated for each watch.

FLIGHT SPEED

Flight speed was measured empirically for use in model estimates of energetic cost of flight. Murres returning to the Coats Island, Cape Pembroke colony routinely flew for some distance parallel to a long sandy beach. Two stations, 200 m apart, were established which sighted perpendicular to the flight path of the murres. The time taken for the lead bird of a flock of murres to traverse the 200 m distance between the stations was recorded using a stopwatch. The average time taken was used to calculate flight speed. Only flocks traveling approximately parallel to the station, flying about 5 m above the water surface, were measured. Measurements were made on a windless day.

RESULTS

MASS

The median date of hatching in both years was 29 July. There were no significant differences between years in the mean mass of either incubating or brooding birds (incubation $t = 1.65$, $P > 0.05$; brooding $t = 0.89$, $P > 0.05$). The average mass of nonbreeding murres on Coats Island dur-

ing the breeding season in 1988 was 0.913 kg, about 9% lower than incubating breeders. In 1988 the mass of incubating birds increased during the season, but the mass of brooding birds fell sharply immediately after the start of hatching (Fig. 1). Results in 1989 were similar over the period of observations. There was no significant linear trend with date for any group (Table 1). After the start of hatching, the mean mass of incubating birds exceeded that of brooding birds by 0.032 kg (3.2%) in 1988 and 0.063 kg (6.1%) in 1989 (Table 1). Brooding birds were significantly lighter than incubating birds in both years (ANOVA, $F = 16.2$, $P < 0.01$).

WING SPAN

Mean ($\pm$SD) wing span of the five murres was 0.723 m ($\pm$ 0.018).

NUMBERS OF TRIPS FROM COLONY TO FEEDING AREA

In 1988 the mean number of incubation changeovers observed per site over 24 hr was 2.12 $\pm$ 0.46 ($n = 41$ pairs), indicating that, on average, each breeder made 1.1 feeding trip each day.

During the chick rearing period, mean daily feeding rates ranged from 4.3–5.0 (mean = 4.73 $\pm$ 0.41, $n = 162$ chicks) feeds/chick in 1988 and from 3.1–3.6 (mean = 3.35 $\pm$ 0.25, $n = 205$ chicks) feeds/chick in 1989 (Table 2). Hence, each adult made an average of 2.4 feeding trips daily in 1988 and 1.7 trips in 1989. In 1988 the number of trips made by breeders feeding chicks was 2.2 times higher than those made by incubating birds.

The difference between years in the rates at which chicks were fed (1.4 more feeds/chick in 1988 than 1989; $t = 37.47$, $P < 0.01$) suggests that food was probably scarcer in 1989 than in 1988. Consequently, incubation shifts may also have been longer in 1989, and the difference be-
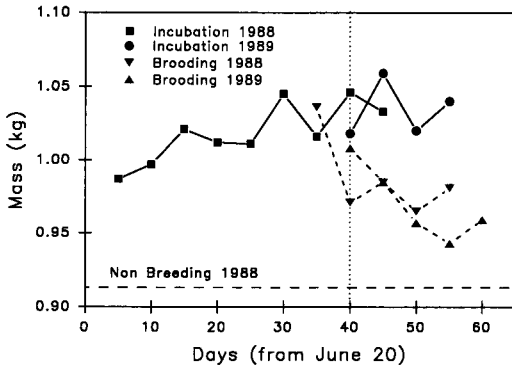
FIGURE 1. Mass of breeding Thick-billed Murres on Coats Island, Northwest Territories, Canada in 1988 and 1989. Dashed line at bottom of graph represents the mean mass of nonbreeding murres measured during the breeding season of 1988. Vertical dotted line indicates the time of median hatch in both 1988 and 1989.

tween incubating and brooding birds in the number of feeding trips made may have been greater than comparison with the 1988 incubation period would suggest.

FLIGHT SPEED

Murres took an average of 9.59 ($\pm$0.52) sec to traverse the 200 m distance. This gave an estimated flight speed of 20.86 m sec^{-1}, or 75.09 km hr^{-1}.

DISCUSSION

Loss of mass has two important effects on flight energetics in birds: a decrease in wing loading, as body mass decreases and wing area remains constant, and a decrease in the body's cross section

tional area as fat reserves are depleted. Through proportionality arguments, Norberg (1981) derived an equation that estimates the energy saving during flight due to these factors. This equation assumes (1) constant flapping flight, (2) that the flight speed remains constant near the maximum range velocity, (3) that mechanical efficiency remains constant, and (4) that mass changes are moderate (<30%). These assumptions probably apply to Thick-billed Murres traveling to and from their colonies. Using Norberg's equation (6) with an exponent of 1.5, and assuming a cost of flight that is 12.5 times basal metabolic rate (BMR, the energy cost at rest in a fasting condition and in the zone of thermoneutrality), we have plotted the energy savings (in % BMR during 24 hr) in relation to mass loss for Thick-billed Murres flying for different lengths of time (Fig. 2). A cost of 12.5 times BMR was chosen as this is the value predicted for the cost of flight of a 1 kg Thick-billed Murre using the equations of Pennycuick (1989) (see discussion below).

We found that Thick-billed Murres on Coats Island lost a significant amount of mass between incubation and brooding (3.2% and 6.1% of the incubation mass in 1988 and 1989 respectively). Given these mass losses, and flying times between 1–4 hr per day (DAC, A.J.G., unpubl.), it is clear that there is a great potential for energy savings (as much as 25% of BMR over 24 hr, Fig. 2).

Alternatively, the power requirements for flight in incubating and brooding murres may be estimated using the equations of program 1a found in Pennyquick (1989). This calculation assumes

TABLE 2. Feeding rates of chicks on Coats Island, Northwest Territories. Estimated duration refers to estimated duration of foraging trips of adult murres feeding chicks.

| Date | No. chicks | Number of feeds chick^{-1} day^{-1} | | | Estimated duration (hr) |
		Mean	Median	Mode	
1988					
24–25 July	53*	4.26	4	4	5.6
5 August	70	5.03	5	4	4.8
12 August	39	4.90	5	5	4.9
1989					
2 August	66	3.11	3	2	7.7
5 August	64	3.17	3	2	7.6
9 August	37	3.49	3	2/4**	6.9
13 August	38	3.63	3	1	6.6

* Due to ambiguities in nest identification, some nests had to be discarded on this date.
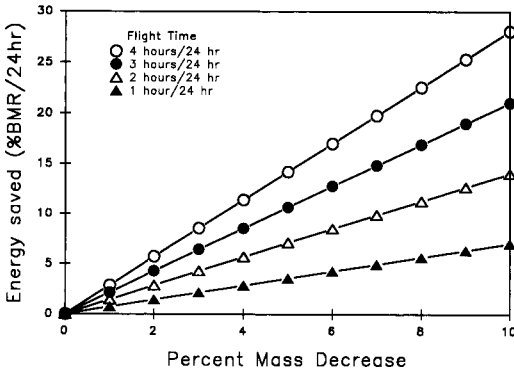** This date showed a bimodal distribution.

FIGURE 2. Theoretical energetic savings for Thick-billed Murres as a function of percent mass loss and amount of time spent flying per day. Lines were derived using the equations of Norberg (1981).

that the bird flies horizontally at a steady speed using aerobic respiration. From these calculations, using a mean wing span for Thick-billed Murres of 0.723 m, and a flight speed of 20 m sec^{-1}, we estimate that the mass losses found in Thick-billed Murres led to a reduction in the mechanical power required for flight of 5.0% and 10.0% in 1988 and 1989, respectively.

Are murres taking advantage of this potential saving? Mass loss in murres during breeding has been examined by several authors (Harris and Wanless 1988, Gaston and Nettleship 1981, Birkhead and Nettleship 1987). In all of these studies, a significant amount of mass was lost between laying and chick-departure. Our results lead us to believe that these mass losses are not induced by stress, but are pre-programmed, through adaptation: (1) Mass loss on Coats Island occurred in a stepwise fashion. Mass was lost rapidly near the median hatch date and leveled off thereafter, and (2) There was no significant negative trend during either incubation or brooding periods.

If the demands of reproduction were imposing a stress during either incubation or brooding, we would expect adult mass to decline continuously. This should be especially true during chick-rearing, as the energy demands of the chick increase as it grows. The fact that mass decline levels off soon after the start of chick-rearing implies that breeders are able to meet the increasing energetic demands of the growing chick without having to utilize their own energy reserves.

The observed mass of nonbreeding murres lends further support to the hypothesis that loss of mass is adaptive. Since these birds are not reproductive, their lower mass cannot be a result of reproductive stress (however, their lower mass could be a result of a lower foraging efficiency). It is interesting to note that the mass of Thick-billed Murres killed off Newfoundland in winter averaged 0.952 kg, about 7% lighter than incubating breeders (Gaston et al. 1983b). The similarity of these masses to those of brooding murres implies that this lower mass may be more energetically efficient.

The energy savings achieved by lowering body mass are proportional to the amount of time spent flying. Cairns et al. (1987) measured the time spent flying during foraging trips by Common Murres. These birds spent about the same amount of time flying per trip during incubation and brooding (9.8% vs. 9.6% over 24 hr). Our data show that murres made more than twice as many foraging trips while feeding chicks as during incubation. If, as the results of Cairns and co-workers suggest, the birds spend the same proportion of time flying per trip, this means a doubling of daily flying time. Similar results have been obtained at other Thick-billed Murre colonies: at Digges Island incubating birds made 0.6 trips/day, while those rearing chicks averaged 1.3 (Gaston and Noble 1986); at Prince Leopold Island the corresponding rates were 0.6 and 2.8 trips/day (Gaston and Nettleship 1981); and at Gannet Island 0.7 and 2.2 trips/day (Verspoor et al. 1987). Thus, it appears that selection to increase flight efficiency by mass loss during chick-rearing may be a general feature of Thick-billed Murre biology.

Several studies have suggested that seabirds may deplete the prey resources around their colonies during the breeding season (Gaston et al. 1983a, Furness and Birkhead 1984, Hunt et al. 1986). Where this occurs, birds will be forced to forage further from the colony as the season progresses. This would serve to further increase flying time, and to increase the advantages of adaptations which lower the energetic cost of flying.

If a lower mass is optimal in terms of flight energetics, why do murres maintain a higher mass during incubation? Nest attendance durations are significantly longer during incubation than during brooding, sometimes exceeding 48 hr (Gaston and Nettleship 1981, Gaston and Noble 1986). The duration of incubation shifts is presumably determined by a trade-off between selection for longer shifts, to reduce the amount of

traveling, and the amount of fat reserves that can be carried. During incubation, the ability of the adult to undertake long incubation shifts is adaptive; parents that can remain on the nest for long durations will raise more offspring than those that, due to their inability to fast, must abandon their eggs to feed (this is occasionally observed in years when food availability is low; A.J.G., pers. obs.). However, once the chick hatches, its metabolic needs require the adults to return to the nest more frequently; adult fat reserves become less important in offspring survival because the chick cannot survive long periods without feeding.

We conclude that loss of mass in breeding Thick-billed Murres occurs as a result of a programmed adaptive response to the transition from incubation to chick-rearing, rather than as a result of stress. Gaston and Jones (1989) similarly concluded that stress was not involved in mass lost by Ancient Murrelets *Synthliboramphus antiquum* during breeding. Changes in the availability of food may modify the pattern of mass loss. During years of low prey availability, adults may lose mass throughout chick-rearing. However, as we observed, the adaptive hypothesis suggests that murres should exhibit some loss of mass between incubation and chick-rearing even when prey is abundant. This is what we observed.

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