

Body mass changes in Brünnich's guillemots *Uria lomvia* with age and breeding stage

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Body mass of Brünnich's guillemots *Uria lomvia* breeding at Coats Island, Canada, was measured during incubation and chick-rearing in 1988–2001. In most years, mass increased during incubation and fell after hatching, leveling off by the time chicks were 18 d old, close to the age at which chicks departed. Mass during incubation increased with age up to about 12 yr, but the mass of birds brooding chicks was not related to age. The trend towards increasing mass during incubation was mainly a consequence of mass increases of young breeders as older birds maintained a constant mass. The variation in adult mass with age during incubation seems likely to reflect age-related variation in foraging ability, but the loss of mass after hatching, being greater for older birds, appears best explained as a response to the demands of provisioning chicks, with older birds transferring their accumulated reserves to their chicks via higher provisioning rates.

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The body mass maintained by birds is known to fluctuate seasonally in response to climate and the demands of migration and reproduction (Newton 1968, Evans 1969, King 1972, Blem 1976, 1980, Blem and Shelor 1986, Rogers 1987). Fluctuations in mass may be affected by programmed mass changes that are independent of environmental factors (i.e. an adaptive strategy), as well as by direct resource limitation (constraint; Freed 1981, Norberg 1981, Lima 1986, Blem 1990, Gosler 1996, Lilliendahl et al. 1996, Holt et al. 2002, Moe et al. 2002). Body mass has been used as an indicator of nutritional status for many species of birds (Gaston 1981, Lehtikoinen 1986, Conway et al. 1994, Wendeln and Becker 1996, Gebhardt-Heinrich et al. 1998). However, the value of body mass as an indicator of nutritional conditions depends on a proper understanding of whatever programmed mass trajectory (in relation to age, season, sex, etc.) is characteristic of the species.

Previous discussions of mass dynamics of breeding birds have tended to centre on the question of how much

mass variation is controlled by intrinsic regulating mechanisms and how much of the variation is a response to external environmental factors, such as food (e.g., Norberg 1981, Freed 1981). The assumption that heavy birds are necessarily of better quality than lighter birds has been challenged recently (Gosler 1996, 2002, Langseth et al. 2001). In the case of the Brünnich's guillemot *Uria lomvia*, a rapid loss of mass by breeders coincides with the hatching of the chick and this has been interpreted as an adaptive response to minimize energetic costs associated with the additional flying required to provision the chick (Croll et al. 1991, Gaston and Perin 1993). A similar loss of adult mass at hatching for the Least Auklet has also been interpreted as a strategic response (Jones 1994). These interpretations are consistent with the idea that mass changes function principally to reduce flight costs (Freed 1981, Norberg 1981). In this paper, we examine the interrelationship between age and body mass in breeding Brünnich's guillemots to assess the relative stress imposed by reproduction on different

age classes. We use this information to further develop arguments relating to the adaptive significance of mass changes to guillemots during breeding and the possible role of stress in contributing to observed variation.

In order to place age-related variation in mass in context, we consider first whether growth plays any part in age-related mass differences. We also describe seasonal mass trends. Age-related variation for our study population is then examined in relation to other factors affecting body mass.

Methods

Adult Brünnich's guillemots were captured at Coats Island, Nunavut, Canada, for a variety of research purposes during the breeding seasons of 1988–2001. The colony is described by Gaston et al (1993). Catching extended throughout the period from the start of egg-laying to the start of chick departures in all years except 1989, 1993, 2000 and 2001. In the latter years, catching began only in late incubation. From 1989 onwards, if birds were not being captured as part of other research projects, a sample of 10 birds (different individuals each time) was captured every 7 d throughout the study period, except during the two weeks immediately after the start of hatching when seven birds with eggs and seven with chicks were captured every 7 d.

More than 1000 Brünnich's guillemot chicks were banded yearly from 1984 onwards, each receiving a metal band and a year-class color band. As a result of this banding effort, a substantial number of the birds we captured were of known age, the oldest being 17 yr. All birds captured that had not been banded as chicks were banded with a metal band and a plastic color band denoting "banded as adult". Birds banded as breeding adults were assumed to be 5 yr old when captured (median age at first breeding, Gaston et al. 1994) and those thus estimated to be 18 yr or older at recapture in 1998 or later were included in analyses by age to extend the age range of the sample. Where possible, the presence of an egg or chick at the site from which the bird was removed was recorded and the age of the chick was estimated (± 1 d) from its size and feather development. Tests of this method suggest that it is accurate within ± 3 d for individual chicks (AJG unpubl. data). All birds were weighed on a Pesola spring balance (± 1 g) at each capture.

For most birds, when captured for the first time, the following measurements were also taken: culmen length, bill depth at gonyx and distance from distal border of nostril to bill tip (all with calipers to ± 0.1 mm) and wing length (from carpus to tip of longest primary, flattened and straightened along ruler). Although the sex of most birds was not known, from 1995 onwards an attempt was made to capture both members of each pair. As a

result, the representation of the sexes in our samples, should have been approximately equal. Prior to that year, our samples probably contained more males than females because most trapping was carried out in the middle of the day, when the majority of birds brooding chicks at Coats Island are known to be males (AJG and K. Woo unpubl. data). Because males and females take equal shares of incubation and chick-rearing and because previous studies have shown no systematic difference in mass between the sexes (Gaston and Nettleship 1981, Gaston and Hipfner 2000) we have ignored sex in the present analysis.

The effects of measurements, year, date and age were analysed using the General Linear Models (GLM) module of STATISTICA v. 6.1 (Statsoft 2003). We used Type 3 models in which all variables are tested. Because breeding Brünnich's guillemots are known to undergo an abrupt loss of mass as soon as their chick hatches (Croll et al. 1991, Gaston and Perin 1993), most analyses were performed separately for birds trapped with eggs and for those trapped brooding chicks. Our data included only a single mass measurement for a given individual each year, but included 1–6 weighings over different years. All data were used to calculate annual means and regressions. However, to avoid lack of independence in statistical analyses, we used only the first capture of each individual where data were combined over years. This applied to all analyses where age was an independent variable. We used the first capture, rather than a randomly selected capture, as the samples sizes for young age classes were small and would have been much diminished if we had not included the first capture.

Results

Mean mass during incubation and brooding

Birds trapped during incubation averaged heavier in all years than those trapped while brooding chicks, the difference being significant in all but one year (1990). The annual differences ranged from 15–74 g (mean = $49.5 \text{ g} \pm 19.3$ (SD); Table 1).

Effects of linear measurements

Significant inter-year variation was found in all measurements except culmen. For depth, only a single year differed significantly, perhaps because of variation in measuring technique, (2001) and this year was omitted from analysis of mass with depth. However, for wing-length and nostril, their relationship with mass was estimated controlling for year, using the GLM procedure. Linear measurements, controlled for year in the case of wing-length and nostril, were all correlated with

Table 1. Mean mass of adults trapped during incubation (years when trapping occurred throughout the incubation period) and chick-rearing.

Year	Mass (g), incubation			Mass (g), chick-rearing			Difference (g)	P
	Mean	SD	N	Mean	SD	N		
1988	1008	59	87	979	64	101	29.1	<0.01
1989				968	71	85		
1990	966	63	91	951	59	70	15.0	0.124
1991	1003	66	120	972	68	97	30.8	<0.01
1992	1013	70	153	960	55	84	52.5	<0.01
1993				985	68	91		
1994	1020	66	120	952	53	39	67.4	<0.01
1995	1020	60	79	946	56	74	74.0	<0.01
1996	1028	58	179	980	53	110	48.1	<0.01
1997	1028	57	103	977	61	89	51.0	<0.01
1998	1017	64	260	959	61	98	57.9	<0.01
1999	1021	63	132	952	62	137	69.1	<0.01
2000				967	75	56		
2001				975	57	103		
All years	1014	64	1324	967	63	1234	47.3	<0.01

mass, both for incubating and brooding birds (maximum R^2 values 0.07). Multiple regression analyses incorporating all measurements gave R^2 values of 0.10 for incubating birds and 0.13 for those brooding chicks. Bill depth alone gave R^2 values of 0.05 for both groups. Only bill depth was found to be significantly correlated with age ($F_{1,239} = 5.84$, $P = 0.016$), the relationship being evident to 10 yr old. Considering the relatively small amount of mass variation explained by linear measurements, the fact that only depth was affected by age, and the fact that some birds were not measured, hence potentially reducing our sample size, we decided to use raw body mass as our dependent variable in subsequent analyses, rather than applying any body size correction.

Seasonal trends

We examined trends in mass on date for incubating and brooding birds separately for all years. Mass tended to increase during incubation in all years except 1994, when

the trend was significantly negative (Table 2). Trends were significantly positive in 7/10 years. In the chick-rearing period, mass decreased with date in all years except 1991, when there was no temporal trend. Trends were significant in 10/14 years. Given the similarity in trends across years, we felt justified in lumping data across years for further analyses.

Combining data for all years when trapping was carried out throughout incubation (1988, 1990–92, 1994–99), the linear regression predicted a mass of c. 1000 g for incubating birds on 22 June, about the median date of laying, rising to c. 1025 g at median hatching, about 25 July (adjusted $R^2 = 0.024$, $F_{1,859} = 21.97$, $P < 0.001$; Fig. 1). A polynomial line of best fit to the data for brooding birds suggested a mass on 25 July similar to that of incubating birds, declining to c. 950 g by 15 August (Fig. 2). Both terms (date and date²) contributed significantly to explaining the variation in mass (adjusted $R^2 = 0.050$, $F_{2,925} = 27.18$, $P < 0.001$).

Plotting the mass of brooding parents against the age of their chicks provided a similar curve to that for mass

Table 2. Seasonal trends in body mass of breeding Brünnich's guillemots at Coats Island.

Year	Incubation			Brooding		
	Regression coefficient \pm SE (g/d)	N	P	Regression coefficient \pm SE (g/d)	N	P
1988	1.06 \pm 0.48	87	0.03	2.11 \pm 1.16	101	0.07
1989				-1.99 \pm 1.10	85	0.07
1990	1.68 \pm 0.53	91	<0.01	-0.62 \pm 1.06	70	0.56
1991	2.35 \pm 0.58	120	<0.01	0.55 \pm 0.95	97	0.56
1992	1.22 \pm 0.42	153	<0.01	-2.58 \pm 0.84	84	<0.01
1993				-4.70 \pm 0.83	91	<0.01
1994	-1.96 \pm 0.40	107	<0.01	-4.88 \pm 1.87	39	0.01
1995	0.84 \pm 0.48	79	0.08	-3.17 \pm 0.87	74	<0.01
1996	2.21 \pm 0.46	179	<0.01	-3.38 \pm 1.06	110	<0.01
1997	0.52 \pm 0.53	103	0.33	-2.18 \pm 0.80	89	<0.01
1998	1.19 \pm 0.36	260	<0.01	-3.06 \pm 0.58	98	<0.01
1999	0.97 \pm 0.47	132	0.04	-2.78 \pm 0.72	137	<0.01
2000				-5.94 \pm 1.00	56	<0.01
2001				-4.54 \pm 1.36	103	<0.01

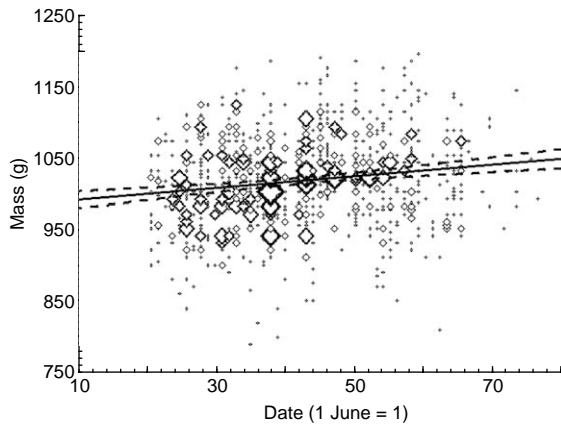


Fig. 1. Mass in relation to date for birds incubating, all years when birds were trapped throughout the incubation period. Linear regression: $\text{mass} = 981.28 + 0.816 (\text{date})$; dashed lines show 95% confidence on regression. Symbol size is proportional to number of records with a range of 1–9.

on date (Fig. 3), showing a decline in mass from 1002 g at hatching to 950 g at 18 d. When date and chick age were entered as independent variables in a multiple regression analysis, only chick age was found to have a significant affect on mass ($R^2 = 0.044$, $F_{2,308} = 8.14$, $P < 0.001$). As most chicks depart by 21 d old, it appears that the relationship between mass and date is created mostly by the intercorrelation between date and chick age.

Age and mass

Plotting mass against age for birds trapped during incubation showed that the relationship was asymptotic, reaching about 1050 g at 12 yr (Fig. 4). When the sample was divided into birds captured before 1995 and those

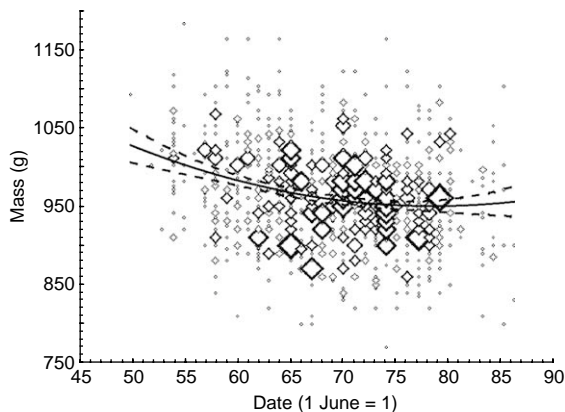


Fig. 2. Mass in relation to date for birds brooding chicks, all years. Best fit polynomial: $\text{mass} = 1533.33 - 14.90 (\text{date}) + 0.095 (\text{date})^2$, dashed lines show 95% confidence on regression. Symbol size is proportional to number of records, with a range of 1–9.

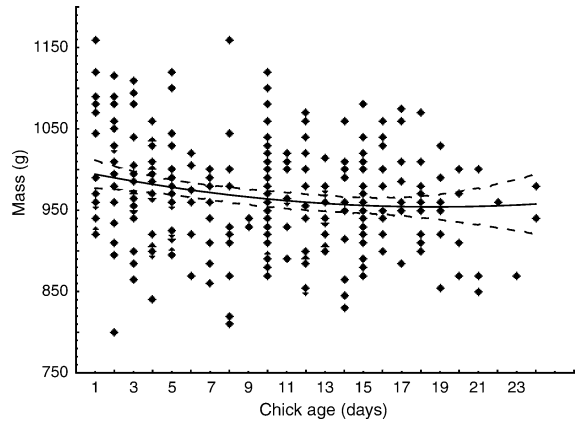


Fig. 3. Adult mass in relation to chick age. Best fit polynomial: $\text{mass} = 1002.4 - 4.91 (\text{age}) + 0.123 (\text{age})^2$. Dashed lines show 95% confidence interval on regression.

captured in later years, both samples showed positive correlations between mass and age (≤ 1994 , $r_{53} = 0.46$, $P < 0.001$; > 1994 , $r_{86} = 0.30$, $P = 0.004$), although the earlier sample contained only birds up to 10 yr old.

Because of the asymptotic affect of age, we combined birds more than 9 years into a single category and analysed mass with age by ANCOVA, treating date as a covariate. Testing for homogeneity of slopes showed that there was a significant interaction of age and date ($F_{15,79} = 3.63$, $R^2 = 0.30$, $P < 0.001$). When birds less than six years old were separated from older birds, the younger group showed a significant increase in mass with date ($F_{1,31} = 6.16$, $R^2 = 0.14$, $P = 0.018$, Fig. 5), while there was no such tendency for older birds ($F_{1,61} = 2.30$, $R^2 = 0.02$, $P = 0.13$).

Controlling for date, using the separate slopes model, mass increased with age from approximately 920 g at 3 yr to more than 1040 g at 10 yr (Fig. 6). For birds captured with chicks, there was no significant relationship

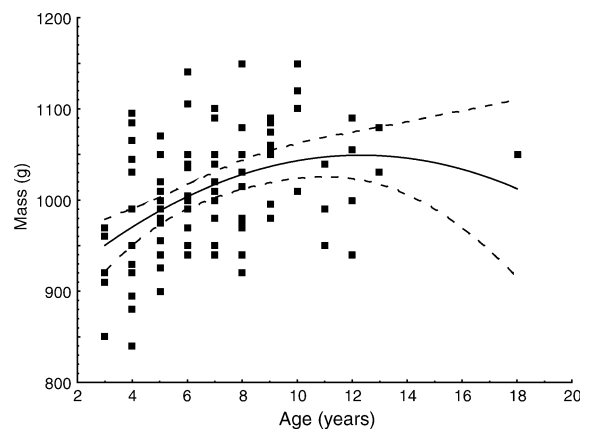


Fig. 4. Mass in relation to age for birds trapped while incubating, all years. Best fit polynomial: $\text{Mass} = 876.50 + 28.05 (\text{age}) - 1.139 (\text{age})^2$. Dashed lines show 95% confidence interval on regression.

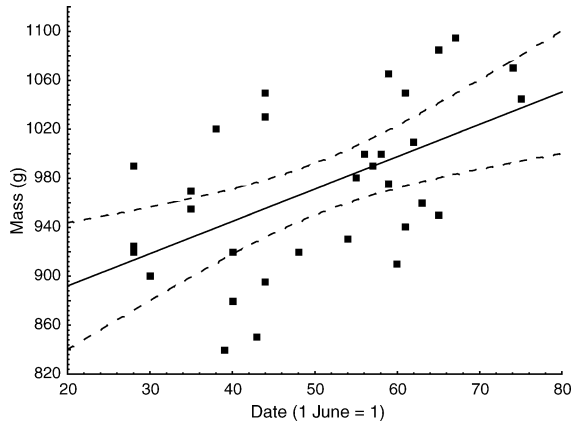


Fig. 5. Mass with date for birds captured during incubation at <6yrs old. Regression formula: $839.3 + 2.64 (\text{date})$. Dashed lines show 95% confidence interval on regression.

between age and mass (Fig. 7), either with or without correction for date (ANCOVA $R^2 = 0.02$, $F_{8,94} = 1.20$, $P = 0.31$). Despite the increase in mass of young birds during incubation, the regression formula predicts a mean mass of 980 g for young birds incubating on 30 July (start of hatching for young breeders in average years), the upper quartile for hatching in this population. That is 60 g less than the mean for incubating birds more than 9 years old (date corrected mean $1041 \text{ g} \pm 16.4 \text{ SE}$, $N = 14$, Fig. 6).

Discussion

Incubating Brünnich's guillemots at Coats Island increased in mass with age up to about 12 yr, the effect

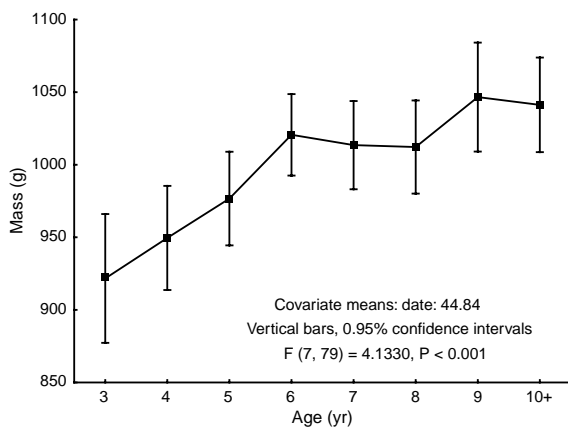


Fig. 6. Mass (least square means) in relation to age for incubating birds (combining ages 10 and older) using the "separate slopes" model of ANCOVA (Statistica 6.1) to control for date.

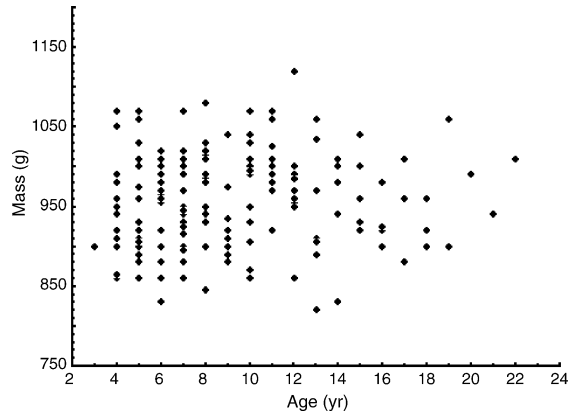


Fig. 7. Mass in relation to age for birds trapped while brooding chicks, all years.

persisting throughout the incubation period. Older birds (>5 yr) kept their mass fairly constant throughout incubation, whereas birds 3–5 yr old increased in mass during the incubation period. An increasing trend for the larger sample, including birds of unknown age, presumably was the result of mass increases by younger birds. Mass differed significantly among years (Gaston and Hipfner in press), but the trend with age cannot have been caused by inter-year variation: there was no tendency for birds to weigh more in later years.

A positive correlation between age and mass in Brünnich's Guillemots was described previously by Noble (1990), but only for pre-breeding birds. The fact that only bill depth showed any increase with age and the relatively weak correlations between measurements and body mass, make it highly unlikely that differences in mass with age were related to growth in size. Young birds tend to lay later than older birds (de Forest and Gaston 1996). However, although the mass of young breeders converges with that of older birds as incubation proceeds, the difference in mass at the start of hatching is still substantial (60 g). Overall, breeding is relatively synchronous both within years (50% of eggs laid within a 7 d period, AJG unpubl. data) and among years (maximum spread of median laying dates during the study 9 d, AJG unpubl. data). Hence none of the observed trends with date can be accounted for by inter-year variation.

At hatching, a slight trend for mass to increase during incubation changed to a decrease in mass that flattened off when chicks reached about 18 d old. Overall, birds were heavier during incubation than during chick rearing: a result that has been observed for several Brünnich's Guillemot populations (Swartz 1966, Gaston and Nettleship 1981, Birkhead and Nettleship 1987, Hipfner and Bryant 1999) and for other seabirds (e.g. Laysan albatross *Phoebastria immutabilis*, Fisher 1967, Antarctic fulmar *Fulmarus glacialis*, Weimerskirch 1990,

cape petrel *Daption capense*, Weidinger 1998, short-tailed shearwater *Puffinus tenuirostris*, Lill and Baldwin 1983, Leach's storm-petrel *Oceanodroma leucorhoa*, Niizuma et al. 2000, black-legged kittiwake *Rissa tridactyla*, Langseth et al. 2001, Moe et al. 2002, common tern *Sterna hirundo*, Wendeln and Becker 1996, Arctic tern *Sterna paradisaea*, Monaghan et al. 1989, least auklet *Aethia pusilla*, Jones 1994, common guillemot *Uria aalge*, Harris et al. 2000). A change in mass for Coats Island Brünnich's guillemots at about the time of hatching has been described previously (Croll et al. 1991, Gaston and Perin 1993).

Our results for Brünnich's guillemots suggest that, at Coats Island, there is an underlying mass trajectory that breeders normally attempt to follow. This involves the accumulation and/or maintenance of reserves during incubation that are then invested in chick-rearing. Younger, less experienced breeders begin incubation at a lighter mass and accumulate lower reserves by hatching. Hence, even if they are capable of foraging as efficiently as older birds, they are likely to rear lighter chicks. The fact that all age classes reach a similar mass during the chick-rearing period suggests that the body mass of approximately 950 g, achieved by the time chicks are about 18 d old, represents the most effective compromise between the needs of the adult and those of the chick. This mass is presumably specific to the particular environment of the Coats Island colony and is not necessarily uniform across the species range.

No effect of age on mass was detected for birds rearing chicks. Consequently, mass loss after hatching was greater among old birds than among young ones. The final mass of adults brooding chicks more than 18 d old (about 950 g) was similar to the mass of the youngest breeders (<6 yr) during incubation. Hence, the magnitude of mass loss after hatching was dependent on mass during incubation, with the heaviest age classes losing the most mass and the lightest not changing in mass at all.

Increase in mass with age has been reported for other long-lived seabirds: Laysan albatross (Fisher 1967), Manx shearwater *Puffinus puffinus* (Brooke 1990), ancient murrelet *Synthliboramphus antiquus* (Gaston and Jones 1998, Gaston 2003), Atlantic puffin *Fratercula arctica* (Harris 1979). In addition, non-breeders weigh less than breeders among most seabirds (for auks, see Gaston and Jones 1998) and some of this difference may be accounted for by age. However, age-specific mass variation among breeders has been reported only for wandering albatross *Diomedea exulans* (Wiemerskirch 1992). In Manx shearwaters (Brooke 1990), little penguins *Eudyptula minor* (P. Dann in Williams 1995) and great skuas *Catharacta skua* (Hamer and Furness 1991) no trend in mass with age was found among breeders.

The increase in mass with age among incubating Brünnich's guillemots can be interpreted according to either the stress hypothesis, or the adaptation hypothesis. Under the adaptation hypothesis, age-related differences in mass during incubation could reflect differences in age-related reproductive strategies. Life history strategy theory predicts that young birds should make a lower investment in reproduction than older birds (e.g. Pugesek 1981, 1983, Reid 1988). However, there is no obvious theoretical reason why carrying less, rather than more, mass would be symptomatic of a lower reproductive investment. Observations on songbirds suggest that birds carry heavier fat deposits in situations where feeding conditions are unpredictable (Lima 1986, Blem 1990). It seems unlikely that feeding conditions would be more predictable for young birds than for old birds: rather, we might expect the reverse if older birds are more experienced.

Under the stress hypothesis, age-related differences in mass during incubation could reflect differences in feeding abilities among age classes, a characteristic that has been observed in several seabirds (Burger 1980). Brünnich's guillemots begin to visit their breeding colonies at 2 yr and begin to breed at 3–7 yr (median 5, Noble et al. 1991, Gaston et al. 1994). The size of eggs laid by young females increases for several years after they begin breeding (Hipfner et al. 1997, Hipfner and Gaston 2002). It seems highly unlikely that their physical abilities at prey capture continue to improve more than marginally after the age at which breeding commences. However, conditions vary considerably from year to year, especially in terms of the extent and position of ice cover around the Coats Island colony (Gaston and Hipfner 1998). It may require several years of breeding before birds have sufficient experience to cope with such variable conditions. Given that there is no obvious theoretical reason why young breeders should choose to carry less mass during incubation than older birds, variation in the ability to find food (i.e. stress), perhaps based on variation in experience, seems the most parsimonious explanation for age-related differences in mass during incubation.

The sample of birds captured during chick-rearing is likely to be biased towards more successful birds, as hatching success at Coats Island has averaged <70% during the years of the study (Gaston et al. 1994 and AJG unpubl. data). In particular, birds <6 yr old have a low hatching success (de Forest and Gaston 1996). Consequently, those young birds that succeeded in rearing chicks may have been of higher quality than usual for their age group. We do not have data to link mass during incubation with hatching success, but it seems possible that those birds that had difficulty maintaining the normal body mass for incubation might have had a lower hatching success.

Once hatching occurred, the mass of brooding adults declined. A similar convergence of mass between heavy and light individuals during the chick rearing period was observed for Arctic terns (Monaghan et al. 1989) and Leach's storm-petrels (Niizuma et al. 2000). Our results suggest that neither mass gain during incubation, when the youngest birds put on mass, nor mass-loss during chick-rearing, when older birds lose mass, can be used as an indicator of stress unless controlled for age.

Irrespective of the cause of age-related mass variation during incubation, the fact that older, more experienced birds lost more mass than young birds during the early part of the chick rearing period and lost more mass in years when mean mass during incubation was higher, suggests that heavy birds deliberately reduced their mass. They may have done so either by reducing their rate of food capture below their potential maximum (i.e. 'programmed anorexia', Gaston and Jones 1989, Jones 1994), or by transferring a greater proportion of the food captured to their chicks. A correlation between chick growth rates and parental age has been observed previously at Coats Island (de Forest 1993, Hipfner and Gaston 2002) and suggests that older birds provide their chicks with more food than young birds. Chicks that are heavier than average at 14 d old have a significantly greater chance than others of surviving to the age of colony return (U. Steiner, AJG and MLH unpubl. data).

Brünnich's guillemots increase their flying during chick-rearing compared with incubation (Gaston 1985, Croll et al. 1991). Moreover, being close to the limit of body mass for their wing area, murrelets may benefit from shedding mass by improving their load-carrying capacity (Croll et al. 1991, Gaston and Perin 1993). Our data included those used by Croll et al. (1991) and the overall change in mass that we found between incubation and chick-rearing (47 g) was similar to that found by the earlier study. Croll et al. (1991) estimated that the mass change between incubation and chick-rearing would save 5–10% of energy expended in flight. By reducing their own intake and committing those resources to feeding their chick, older Brünnich's guillemots may increase their fitness by rearing heavier chicks that have a higher chance of survival after leaving the colony while at the same time increasing their flight efficiency. Both factors may be involved in the mass loss that occurs about the time of hatching.

In the context of Brünnich's Guillemots, assigning mass changes to intrinsic or extrinsic processes seems a sterile exercise. It may be necessary to abandon the paradigm of 'constraint vs adaptation'. Strategic mass adjustments will be apparent only where environmental conditions allow at least part of the breeding population to exercise choice about the amount of reserves to be carried. If conditions are good, the majority of birds presumably will approximate the mass most appropriate

to the particular breeding stage that they are at, based on adaptively determined intrinsic mechanisms. If conditions are bad, mass variation is more likely to be determined by intra-population variation in foraging ability and hence to reflect mainly responses to environmental conditions. Because year to year variation in feeding conditions may affect the proportion of young birds breeding in a given year, age effects are likely to occur in all years. Our observations suggest that: (1) higher mass in old breeders may contribute to higher growth rates of their chicks and (2) in our case, comparisons of mass changes during breeding may be a misleading indicator of nutritional constraint.

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