

Adult Brünnich's Guillemots *Uria lomvia* balance body condition and investment in chick growth

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To investigate the covariation of adult body condition and nestling growth, we weighed adult Brünnich's Guillemots *Uria lomvia* rearing chicks at Coats Island, Nunavut, Canada, each year between 1988 and 2002. We estimated chick mass at 14 days for a sample of chicks reared in the same years. Adult mass and chick mass at 14 days were highly correlated, suggesting that, as feeding conditions deteriorate, adults compromise by reducing their own body reserves, while at the same time delivering less food to their offspring. We compared the prediction of the least-squares regression for the Coats Island data with observations made at Digges Island, a much larger colony about 300 km away, where birds are similar in linear body measurements to those at Coats Island and have a similar body mass while incubating. Adult mass at Digges Island averaged 11% less during chick-rearing than during incubation, compared with only a 5% difference at Coats Island. Mean chick mass at 14 days at Digges Island was lower in all years than was observed for chicks at Coats Island in any year. The observed 14-day chick masses at Digges Island in two years were close to values predicted by adult mass and somewhat lower in two other years (those when chick growth was slowest). At Digges Island, the distribution of mass for brooding adults was right skewed and suggested a lower threshold at 800–850 g, below which Brünnich's Guillemots terminate breeding. We conclude that the correlation between adult and chick mass represents a dynamic equilibrium in which adults simultaneously adjust their own energy reserves and their delivery rate to the chick. This compromise must be based on behavioural choices made by individual birds and is unlikely to be a passive consequence of fluctuating conditions.

Theories of life-history strategy suggest that, in iteroparous organisms, the investment in reproduction in a given year should be adjusted to the likelihood of future survival (Ricklefs 1977, Partridge & Harvey 1988). In annually breeding seabirds, among the slowest-reproducing organisms, a negative relationship between reproductive investment and survival has been detected in the Wandering Albatross *Diomedea exulans* (Weimerskirch 2000), European Shag *Phalacrocorax aristotelis* (Harris *et al.* 1998) and Black-legged Kittiwake *Rissa tridactyla* (Golet *et al.* 1998). In all cases the effect detected was a lowering of survival among birds that succeeded in rearing chicks (Kittiwake, Shag), or reared larger chicks (Albatross), compared with those that either did not do so or reared small chicks.

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Presumably the effort involved in chick-rearing observed in these studies resulted in a lowering of body condition that caused higher subsequent mortality. Hence, 'reproductive investment' can be partitioned into the effort invested in offspring (including provisioning rate of food delivered) and the loss of condition accepted in order to make that investment. Among species, the optimization of life-history may involve very different partitioning of feeding effort and loss of condition, depending on the likelihood of survival to, or the effect on, future reproductive attempts (Ricklefs 1977).

For birds with high annual survival rates, detecting adjustments involving adult survival rates may be difficult, because the variation in survival needed to balance a given variation in reproductive investment may be too small to be detected with the sample sizes available. Adjustments involving changes in body

condition (mass) provide a more readily accessible measure of investment. A number of studies have reported the relationship between parental body condition and reproductive output (number of chicks, or chick growth rates) for individuals in a given population (Chastel *et al.* 1995, Lorentsen 1996, Wernham & Bryant 1998, Wendeln & Becker 1999, Tveraa & Christensen 2002). However, within species, the partitioning may vary among individuals in relation to age, sex and individual tactics (Pugesek 1981, 1983, Phillips & Furness 1997). Hence, the effects of variation in effort can only be assessed when controlled for ability (i.e. age, experience, individual quality).

Three scenarios can be envisaged for breeders adjusting their effort to variations in the availability of food: (1) body condition is kept constant, resulting in all variation in food availability being expressed as variation in chick provisioning rates; (2) feeding rates are kept constant while environmental variation is expressed as variation in adult condition; (3) a compromise is developed in which both adult condition and feeding rates are adjusted. Clearly, there is a lower limit to provisioning rate at the point where chick survival is severely compromised and a lower limit to adult condition below which the subsequent survival is similarly compromised. Moreover, *ad libitum* feeding by adults, resulting in extreme obesity, is unlikely. Time budgets have been shown to switch from feeding to resting when food availability exceeds a certain threshold (Burger & Piatt 1990, Gill & Hatch 2002).

Previous work on the relationship between adult condition and chick growth has concentrated on the ability of adults to respond to changes in chick condition. Experimental manipulations of chick age through switching nestlings among sites have shown that many Procellariiform seabirds feed at a rate appropriate to the age of their own chick (Ricklefs 1987, 1992, Hamer & Hill 1994, Mauck & Grubb 1995, Weimerskirch *et al.* 1997, Bradley *et al.* 2000; but see Tveraa *et al.* 1998 for a contrary example). Similar manipulations for puffins (*Fratercula*, *Cerorhinca* spp.) suggest that parents adjust their feeding effort to the age of their chick, apparently as a result of communication from the chick (Harris 1983, Erickstad *et al.* 1997, Wernham & Bryant 1998, Johnsen *et al.* 1994, Bertram *et al.* 1996). However, the presence or absence of an ability to assess and adjust to chick condition has no implications for the three scenarios outlined above.

Regardless of the presence or absence of communication regarding the condition of the chick, deci-

sions concerning provisioning rates are made by the parent. The decision point comes when the parent breaks off feeding and returns to the colony, and presumably depends on the bird's assessment of its own nutritional status, on the ease with which food can be obtained in future (its assessment of feeding conditions) and its knowledge on the chick's condition. The last may be based solely on intrinsic factors relating to the time from hatching, or modified by communication from the chick. However, information provided by the chick is simply additional data to be weighed in the eventual decision – it cannot determine the outcome. Consequently, throughout this paper, we assume that outcomes are determined by parental behaviour.

Another approach to the problem of detecting a compromise between body condition and reproductive output is to observe the reactions of a given population to variation in environmental conditions, assuming that mean ability within the population remains constant over time (e.g. Weimerskirch *et al.* 2001). This can be done by comparing mean productivity with mean parental body condition over a number of years.

In this paper, we use records of adult body mass and chick growth for Brünnich's Guillemots *Uria lomvia* at Coats Island, Nunavut, Canada, over 15 years to examine whether there is an interaction between parental condition and chick growth. For these comparisons, we have attempted no correction for individual body size, assuming the average to be constant among years. Moreover, adult Guillemots brooding chicks normally empty their stomachs before returning to the colony (birds collected while brooding have nothing in their stomachs, our pers. obs.). Hence, we have assumed that most inter-year variation is related to the amount of stored fat and have treated body mass as a direct measure of body condition. Values for Coats Island are compared with values for the nearby colony at Digges Island, Nunavut, where adult linear measurements are similar to those for birds at Coats Island (Gaston & Hipfner 2000).

The colony at Coats Island consists of two sub-colonies totalling about 30 000 breeding pairs in 1990 (Gaston *et al.* 1993). The colony at Digges Island was estimated at 180 000 pairs in 1980, with an additional 120 000 pairs on nearby Cape Wolstenholme, Quebec (Gaston *et al.* 1985). Coats and Digges islands experience similar Low Arctic climates and sea-ice regimes in summer (see Gaston & Hipfner 1998). The difference in size between the colonies is thought to create greater competition for food around Digges Island,

resulting in birds flying further to feed and provisioning their chicks less frequently than those at Coats Island (Gaston *et al.* 1983). Hence, inclusion of measurements made at Digges Island should extend the range of feeding conditions covered by our results.

METHODS

Adult mass

Adult Brünnich's Guillemots were captured at Coats Island, Nunavut, Canada, for a variety of research purposes during the breeding seasons of 1988–2002. The colony was described by Gaston *et al.* (1993). Catching extended throughout the period from the start of hatching to the start of chick departures (roughly 20 July–15 August). From 1989 onwards, if birds were not being captured as part of other research projects, a sample of ten birds was captured every 7 days throughout the study period, except during the first 2 weeks when seven birds with eggs and seven with chicks were captured every 7 days. 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 day) from its size and feather development. All birds were weighed on a Pesola spring balance (± 1 g) at each capture. Only birds with chicks were included in the present analysis. Yearly sample sizes ranged from 36 to 133 (mean 84).

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 1995, 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, as we now know, males (K. Woo & A.J.G. unpubl. data). Previous studies of Brünnich's Guillemots have shown no systematic difference in mass between the sexes (Gaston & Nettleship 1981, Gaston & Hipfner 2000). Consequently, we have ignored sex in the present analysis.

The mean mass of all birds brooding chicks captured before the median date of chick departures was used as an index of adult body condition for each year. Because adult mass generally shows a decline during the chick-rearing period (Gaston & Hipfner in press), means were adjusted by ANCOVA, using date as a covariate, to correspond to those at the covariate mean, using the least-squares method of STATISTICA 6.1 (Statsoft 2003).

Chick mass

Each year, prior to hatching, a group of 30–60 eggs was selected and checked for hatching every 2 days. Little inter-year variation in egg size was observed (our unpubl. data), but, regardless, egg size has little effect on rate of mass gain in Brünnich's Guillemots (Hipfner & Gaston 1999a). Once hatched, chicks were weighed (± 1 g) on a 300-g Pesola spring balance. Subsequently, they were weighed at 2- or 3-day intervals until departure (see Hipfner & Gaston 1999b). As chicks may begin to leave the colony as young as 15 days, we used the mean mass at 14 days (extrapolated by linear interpolation for chicks not weighed on day 14) as a measure of chick growth rate in a given year. The sample of adult birds weighed did not include parents of the chicks for which growth was measured. Yearly sample sizes for chicks reaching 14 days ranged from 19 to 51 (mean 41).

Previous work suggested that chicks of inexperienced breeders hatch later and grow more slowly than those of experienced birds (de Forest & Gaston 1996, Hipfner & Gaston 2002). Because eggs were sometimes lost during our weighing operations, and because these losses were more likely to occur for late-hatched eggs, our samples could have been biased towards early-hatched chicks. Consequently, we examined the relationship between date of hatching and chick mass at 14 days to develop a method to minimize this potential source of bias. In order to combine data from different years, hatching dates were expressed in terms of 'relative hatching date' (days \pm the median date of hatching for the population in the year in question: for methods of estimating timing of breeding, see de Forest & Gaston 1996). Mass at 14 days was found to be relatively constant over most of the range of relative hatching dates, but fell sharply after about 90% of chicks had hatched (see Results). Consequently, chicks hatching after this point of inflection (5 days after median hatch) were omitted from calculations of annual mean 14-day mass.

Although our visits to weigh and measure chicks caused some parent birds to leave the cliff, and some consequent egg-loss (up to six eggs in a given year), the whole operation took less than 30 min, during which only a proportion of our study birds were affected. Given that visits were made only every 2–3 days, disturbance occurred for only about 1% of the time. We do not feel that this level of disturbance is likely to have affected overall food delivery rates to chicks.

Procedures used in determining chick mass have been approved, since 1995, by the Animal Care Committee of the National Wildlife Research Centre, Ottawa, operating under the guidelines of the Canadian Council for Animal Welfare.

Comparison with Digges Island

Data from Digges Island were available for three years within the period of the Coats Island study (1992, 1994, 1999), as well as for 1981 (latter data from Gaston *et al.* 1985). In 1981, 1994 and 1999, chick mass was measured as at Coats Island. In 1992 chick mass at 14 days was estimated by linear regression of mass on age for a sample of 108 chicks weighed once only at 8–16 days, for which age was estimated from wing-length (based on data for 1981 from the same colony from Gaston *et al.* 1985). Although wing-length varies somewhat with the nutritional condition of the chick (Hipfner & Gaston 1999a), the relationship of chick mass to wing-length was similar in 1981 and 1992. Hence, our extrapolation should be unbiased. All chicks, including those weighing less than 130 g, were included.

Adult Guillemots were not captured systematically at Digges Island, but were taken opportunistically during 12–19 August in 1992, 26 July–23 August in 1994 and 27 July–12 August in 1999. Birds incubating eggs were captured only in 1994 and 1999. The method of weighing was the same as used at Coats Island.

RESULTS

Hatch date and 14-day mass

At Coats Island, chick mass at 14 days ranged from 109 to 269 g, but very few chicks weighed less than 130 g (< 1%, $n = 602$). Some of these very light chicks subsequently starved and they may have been deserted by one of their parents (which may have died), or may have fallen from their natal ledge and been sheltered, but not fed, by non-parents (Gaston *et al.* 1995). We omitted chicks weighing less than 130 g at 14 days from subsequent analyses. When the remaining data were plotted by relative hatching dates, mass was constant until 5 days after median hatch, after which it fell sharply, but returned to earlier levels after 11 days (Fig. 1). To improve comparability among years (reduce noise), inter-year comparisons of 14-day mass excluded chicks with relative hatching dates > 5 days after the median date of hatch for the population (8% of chicks reaching 14 days).

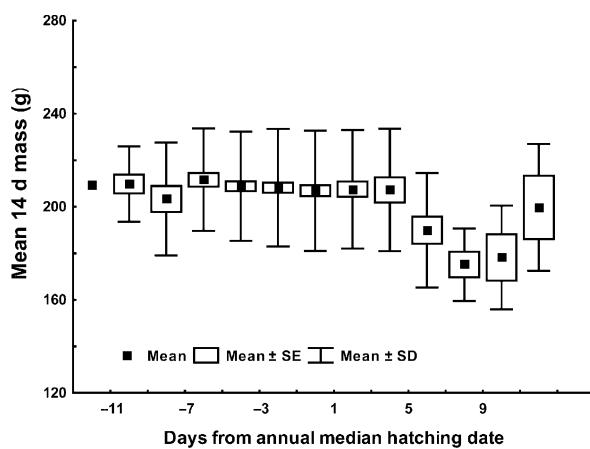


Figure 1. Brünnich's Guillemot chick mass at 14 days in relation to the relative hatching date (days \pm the annual median).

Adult mass and 14-day chick mass

The mean (\pm sd) adult mass of incubating birds at Coats Island in all years combined was 1014 ± 64 g ($n = 1324$) and of birds brooding chicks was 967 ± 63 g ($n = 1234$) with 95% confidence intervals of 865–1070 g. There was no correlation between the mass of incubating and chick-rearing birds in a given year ($R^2 = 0.09, P = 0.31$). Annual means of birds rearing chicks varied from 956 to 994 g. Mean 14-day chick mass varied from 178 to 227 g. Both adult mass and chick mass at 14 days varied significantly among years (Table 1). There was a significant positive correlation between mean adult body mass during chick-rearing and mean chick mass at 14 days ($r_{14} = 0.79, P < 0.001$, Fig. 2).

The mean (\pm sd) adult mass during incubation at Digges Island (years 1994 and 1999 only, combined) was 1031 ± 65 g ($n = 26$), not significantly different from the mean mass of incubating birds at Coats Island ($t_{25} = 1.34, P = 0.19$). During chick-rearing in 1994 and 1999, mean adult mass was 919 ± 56 g ($n = 113$). Mean masses of chick-rearing adults in 1981 and 1992 were similar (906 and 901 g, respectively, Table 1). There was no significant variation among years ($F_{3,171} = 1.79, P = 0.15$). Chick 14-day masses were 134, 141, 123 and 126 g in 1981, 1992, 1994 and 1999, respectively (Table 1): all consistently lower than those measured at Coats Island. The values for 1981 and 1992 were close to the least-squares regression line for the Coats Island data (predicted chick 14-day mass for a mean adult mass of 900 g = 138 g), while the mass of chicks in 1994 and 1999 fell at (1994) or below (1999) the 95% confidence interval predicted by the Coats Island regression.

Table 1. Mean mass of brooding adult and nestling Brünnich's Guillemots at Coats and Digges islands. Adult mass is corrected for date. Chick mass excludes chicks hatched more than 5 days after the median date of hatch for the year. ANOVA results for inter-year variation at Coats Island: adult mass, $F_{13,940} = 2.23$, $P = 0.007$; chick 14-day mass, $F_{13,512} = 13.25$, $P < 0.001$.

Colony	Year	Adult mass			Chick mass at 14 days		
		mean	se	n	mean	se	n
Coats Island	1988	980.6	5.9	100	215.2	3.2	48
	1989	974.4	8.2	51	205.3	3.2	46
	1990	965.0	12.3	23	208.9	3.6	39
	1991	969.3	9.2	41	209.0	3.4	41
	1992	977.8	8.5	48	204.3	3.4	43
	1993	993.6	7.0	70	218.6	4.2	27
	1994	979.8	12.4	23	208.8	2.8	57
	1995	956.5	7.3	66	188.8	2.9	56
	1996	985.5	5.6	110	218.8	3.7	33
	1997	973.9	6.7	78	211.1	3.5	37
	1998	956.0	6.8	79	178.5	4.9	20
	1999	957.7	6.4	84	188.8	3.1	50
	2000	980.8	9.7	37	205.4	4.0	29
	2001	976.5	5.8	103	226.8	3.2	48
	2002	972.9	7.9	136	214.2	4.1	28
Digges Island	1981	905.6	8.7	48	134.0	2.6	53
	1992	896.3	7.8	31	141.0	5.2	8
	1994	912.0	6.9	71	122.5	4.6	15
	1999	930.2	7.8	42	125.9	3.4	53

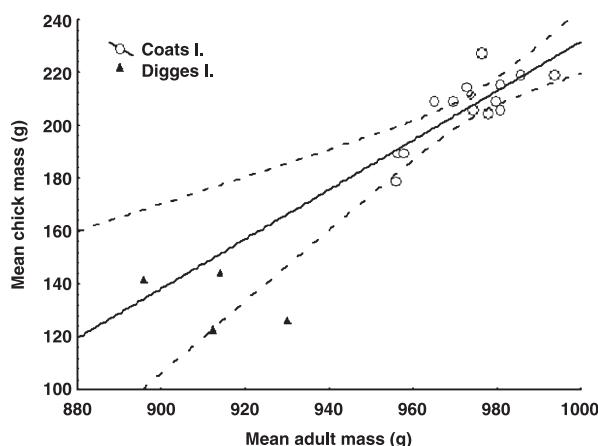


Figure 2. Brünnich's Guillemot chick mass at 14 days in relation to mean mass of brooding adults, Coats Island, 1988–2002 (regression: chick mass [g] = $-701.4 + 0.933$ adult mass [g]) and Digges Island in 1981, 1992, 1994 and 1999.

The distributions of adult mass at Coats and Digges islands (all years combined) were both somewhat right-skewed (Fig. 3). However, the mass of birds at Digges was more strongly truncated (skewness = 0.31) than at Coats Island (skewness = 0.11). This result is

consistent with the existence of a threshold mass below which birds will not allow themselves to fall.

DISCUSSION

The lowest mean 14-day chick mass observed at Coats Island was well above the lowest observed at Digges Island. Similarly, the mean adult body mass at Coats Island in all years was greater than the means observed in four years at Digges Island, where birds are similar to those at Coats Island in linear body measurements (Gaston *et al.* 1985, Gaston & Hipfner 2000) and where the mass of incubating birds did not differ. The mass difference between incubating and chick-rearing birds at Coats Island was 47 g (5% of incubating mass), while at Digges Island the difference was 112 g (11%).

The mean 14-day mass of Brünnich's Guillemot chicks at Coats Island in the years when growth was most rapid was close to the highest recorded for the species, while the mean mass of chicks recorded at Digges Island in the years with the lightest chicks was close to the lowest on record (Gaston *et al.* 1983, Gaston & Hipfner 2000). Presumably the difference in growth observed between the two colonies

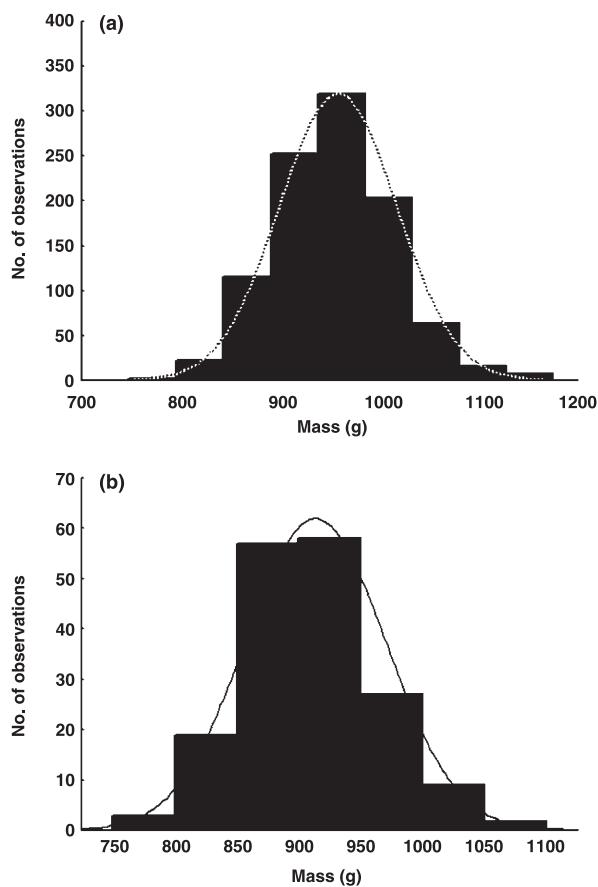


Figure 3. Mass distribution of adult Brünnich's Guillemots rearing chicks at (a) Coats Island in 1988–2002 and (b) Digges Island in 1992, 1994 and 1999.

reflects a large difference in feeding conditions. Brünnich's Guillemot chicks that weigh less than 100 g at 14 days show impaired feather development and do not normally survive to fledge (our pers. obs.). As a result, Figure 3 is likely to represent most of the range of response exhibited by the species. Clearly, observations at a single colony, even over a 15-year period, will not necessarily provide evidence of responses to the full range of conditions with which the species can cope.

The significant inter-year variation in both adult and chick mass at Coats Island probably related to the timing of ice break-up and dispersal in surrounding marine waters. The three years of slowest chick growth (1995, 1998 and 1999) were all among the four years of lowest summer ice extent in Hudson Bay (Gaston & Hipfner 1998, Gaston *et al.* 2005). The cause of the persistently lower nestling growth rates at Digges Island is unknown, but may relate to intraspecific competition, as the Digges Island colony

is roughly ten times as large as that at Coats Island (Gaston *et al.* 1983, Cairns 1992).

The strong correlation between adult mass during chick-rearing and chick mass at 14 days shows that Brünnich's Guillemots exhibit our type 3 strategy: as feeding conditions deteriorated, parents compromised by reducing their own body condition while simultaneously reducing provisioning rates to chicks. This result supports the flexible investment hypothesis of Johnsen *et al.* (1994). Findings by Erickstad *et al.* (1997), based on within-year manipulations of Atlantic Puffins *Fratercula arctica*, point to a similar conclusion.

The Yellow-nosed Albatross *Diomedea chlororhynchos* exhibits a similar correlation between adult mass and chick growth (Weimerskirch *et al.* 2001), but in that species adults adjust their body condition in relation to chick growth only over a relatively narrow range of conditions when they are good. Some other species of seabirds have shown no sign of adjusting body mass when deteriorating conditions or experimental manipulations forced changes in provisioning rates (e.g. Atlantic Puffin, Barrett & Richardson 1992; Leach's Storm Petrel *Oceanodroma leucorhoa*, Mauck & Grubb 1995; Antarctic Prion *Pachyptila desolata*, Weimerskirch *et al.* 1999). Our results show no sign of an asymptote in chick growth, suggesting that faster growth continues to benefit the chick over the entire range observed.

As we expected, a positive correlation between chick mass at 14 days and the likelihood of returning to the colony as an adult was found at Coats Island for chicks reared during 1987–96. This relationship was still maintained when chicks weighing less than 130 g were excluded (U. Steiner unpubl. obs.). Hence, the observed variation in chick growth rates could have affected subsequent recruitment of chicks. Whether adult survival was affected by observed variation in mass during chick-rearing is unknown.

The 14-day mass of chicks at Digges Island in two years (1981, 1992) fell close to that predicted by the least-squares regression for the Coats Island data. In the other two years it was somewhat lower. This suggests that in 1994 and 1999 (the years of lowest chick mass), some adults rearing chicks at Digges Island were approaching the point (apparently about 800 g) where they were unwilling to reduce their own body condition further. If some birds had actually terminated breeding because of the adverse conditions, then our samples in those years may have been biased towards better-quality birds – we have no evidence on this point, although general observations suggest

that the majority of breeding birds were still active during our visit.

The regression of chick 14-day mass on adult mass predicts a mean adult mass of 840 g for a chick 14-day mass of 100 g: below the lower bound of the 95% confidence interval for the mass of all chick-rearing adults at Coats Island. At Digges Island, the distribution of mass for chick-rearing birds was somewhat truncated between 800 and 850 g. Both this truncation and our deduction from the adult/chick mass relationship at Digges Island in 1994 and 1999 suggest that the masses of the lightest birds measured at Digges Island were close to a threshold below which birds are reluctant further to reduce their mass. Emaciated Brünnich's Guillemots collected in winter weighed less than 750 g (A.J.G. unpubl. obs.), indicating that birds at 800 g probably still retain substantial reserves.

The possibility that the relationship between adult and chick mass that we describe is the result of passive reaction to varying environmental conditions is unlikely. Many studies have demonstrated changes in adult time budgets in relation to changes in environmental conditions (lower feeding rates, shorter resting periods, etc.; Gaston & Nettleship 1982, Burger & Piatt 1990, Hamer *et al.* 1993, Hill & Hamer 1994, Gill & Hatch 2002, Tveraa & Christensen 2002, Davoren & Monteverchi 2003). Such changes in time budgets can only be the result of decisions about when to switch from one behaviour to another (i.e. from self-feeding to chick-provisioning to resting or socializing). Either of scenarios 1 and 2 could originate through passive reaction to environmental change, based on fixed intrinsic rules, but not scenario 3, which can only develop as a result of birds using information about their own and their chick's condition to adjust their behaviour towards a compromise. Their information on the chick's condition may or may not include direct communication from the chick. Whether adult provisioning rates are affected by communication from the nestling is not known for *Uria*.

We conclude that Brünnich's Guillemots at the two colonies we investigated adjust their body mass and presumably energy reserves in relation to environmental conditions, carrying smaller reserves when the rate at which they provision their chicks is lower. Hence, the correlation between adult and chick mass represents a dynamic equilibrium in which adults simultaneously adjust their own energy reserves and their delivery rate to the chick. We assume that the balance struck has evolved in response to how their

condition affects the subsequent survival probabilities of chicks and adults and future reproductive success. This compromise must be based on behavioural choices made by individual birds and is not a passive consequence of fluctuating conditions. In addition, our findings show that in Brünnich's Guillemots both adult mass and chick growth may be useful as indicators of food availability, but that they are not independent of one another. Their strong correlation suggests that, for a given population, one measurement may be used as a surrogate for the other.

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