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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, sug-

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 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 ± 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).

Adult mass and 14-day chick mass

The mean (±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 ($R^2 = 0.09$, $P = 0.31$).

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The distributions of adult mass at Coats and Digreflects 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 Bay (8505 66.6431 TD ( )Tj 2is07 Tw [(reflecJ6544 Tw 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 & Montevecchi 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

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