

VARIATION IN EGG SIZE AND LAYING DATE IN THICK-BILLED MURRE POPULATIONS BREEDING IN THE LOW ARCTIC AND HIGH ARCTIC

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Abstract. We used data collected across 28 years (1975–2002) to compare how timing of laying and egg size respond to environmental variability in two low-arctic and two high-arctic Thick-billed Murre (*Uria lomvia*) populations. Ice conditions strongly affect food availability to marine birds in the Arctic, and the percentage of the sea's surface covered by ice within 300 km of the breeding colony varied more among years near the start of laying at our high-arctic study colonies (Prince Leopold and Coburg Islands, Nunavut, Canada) than at our low-arctic study colonies (Coats and Digges Islands, Nunavut). However, mean values differed little. These results indicate that Thick-billed Murres breeding in the High Arctic experience more variable ice conditions, but not necessarily more severe ice conditions, during the period of egg formation. In response, both median laying date and mean egg size varied more among years at high-arctic than at low-arctic colonies. Several lines of evidence suggested that the variation was a result of within-female effects, i.e., phenotypic plasticity rather than different individuals breeding in years in which environmental conditions differed. Previous studies have shown that Thick-billed Murres lay eggs later in years of heavier ice coverage, especially in the High Arctic where ice conditions can be severe, and only in the High Arctic was later laying associated with reduced egg size. The relationship tended towards a negative asymptote suggesting that each female may have her own minimum egg size. Our results show that Thick-billed Murres that inhabit a more variable environment display greater variability in life-history traits. More generally, they offer insight into mechanisms linking environmental heterogeneity to phenotypic variation in life-history traits.

Key words: egg size, environmental conditions, laying date, plasticity, Thick-billed Murre, *Uria lomvia*.

Variación en el Tamaño del Huevo y la Fecha de Puesta en Poblaciones Reproductivas de *Uria lomvia* en el Ártico Bajo y el Ártico Alto

Resumen. Empleamos datos colectados a lo largo de 28 años (1975–2002) para determinar cómo el ajuste temporal de la puesta y del tamaño del huevo responde a la variabilidad ambiental en dos poblaciones del Ártico bajo y dos poblaciones del Ártico alto de *Uria lomvia*. Las condiciones del hielo afectaron fuertemente la disponibilidad de alimentos para las aves marinas en el Ártico. El porcentaje de la superficie del mar cubierta por hielo a menos de 300 km de la colonia reproductiva varió más entre años cerca del inicio de la puesta en nuestras colonias de estudio del Ártico alto (Isla Prince Leopold y Coburg, Nunavut, Canadá) que en nuestras colonias de estudio del Ártico bajo (Isla Coats y Digges, Nunavut). Sin embargo, los valores medios difirieron poco. Estos resultados indican que los individuos de *Uria lomvia* que crían en el Ártico alto experimentan condiciones de hielo más variables, pero no necesariamente más severas, durante el período de la formación del huevo. Como respuesta, tanto la fecha mediana de puesta y la media del tamaño del huevo variaron más entre años en las colonias del Ártico alto que en las del Ártico bajo. Varias líneas de evidencia sugirieron que esta variación fue el resultado de variaciones propias de las hembras (i.e., plasticidad fenotípica) y no de variación entre individuos diferentes que criaron en años en los cuales las condiciones ambientales difirieron. Estudios previos han mostrado que *Uria lomvia* realiza su puesta más tarde en los años de mucha cobertura de hielo, especialmente en el Ártico alto, donde las condiciones de hielo pueden ser severas, y sólo en el Ártico alto la demora de la puesta se asoció con una reducción del

Manuscript received 22 July 2004; accepted 29 March 2005.

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tamaño del huevo. La relación tendió hacia una asíntota negativa, sugiriendo que cada hembra podría tener su propio tamaño mínimo del huevo. Nuestros resultados muestran que los individuos de *Uria lomvia* que habitan un ambiente más variable muestran mayor variabilidad en los rasgos de historia de vida. De modo más general, nuestros resultados ofrecen información sobre los mecanismos que vinculan la heterogeneidad ambiental con la variación fenotípica en los rasgos de historia de vida.

INTRODUCTION

Environmental conditions can vary dramatically across the breeding ranges of species distributed widely over latitude or altitude. As a result, geographically segregated populations often display marked differences in the mean values of their life-history traits (Berven and Gill 1983, Fleming and Gross 1990). The extent of variation in environmental conditions can also differ across a species' range, with conditions often being less variable at low latitudes and altitudes. As a result, segregated populations can also differ in the amount of variation they exhibit in their life-history traits (Blackenhorn 1997, Laurila et al. 2002). Consequently, key demographic parameters such as age and size at recruitment, timing of breeding, and number and size of offspring, may show little variation in a population that inhabits an environment in which conditions vary little from one breeding season to the next, yet vary markedly in a population that experiences more variable, and occasionally harsh, conditions (Ferguson and Talent 1993, Seigel and Ford 2001).

Studies that compare how segregated populations respond to local conditions can provide strong insight into mechanisms linking environmental heterogeneity with life-history variation. The manner in which life-history traits vary in response to environmental conditions has been well studied within avian populations (Boyce and Perrins 1987, Oro et al. 1999). In addition, among-population (i.e., geographic) variation in the mean values of life-history traits has received considerable attention (Ricklefs 1980, Encabo et al. 2002). However, few avian studies have compared the variability exhibited in life-history traits among populations in relation to heterogeneity in local environmental conditions (Nager and van Noordwijk 1995).

Thick-billed Murres (*Uria lomvia*) are highly colonial, cliff-breeding seabirds that dominate, in terms of biomass, over much of the Arctic Ocean in summer (Gaston and Hipfner 2000). In eastern Canada, the breeding range of the Thick-billed Murre extends from near the southern lim-

its of the low-arctic oceanographic zone at Bird Rocks, Gulf of St. Lawrence, Québec (47°51'N, 61°12'W), far into the high-arctic oceanographic zone at Coburg Island, Nunavut (75°48'N, 79°25'W). The low- and high-arctic oceanographic zones in eastern Canada are characterized by a variety of features including ice coverage, water temperature, salinity, and faunal affinities. The High Arctic is dominated by polar water of low salinity, with surface temperatures remaining close to 0°C and pack ice persisting through the summer; the fauna is comprised exclusively of arctic species. Low-arctic waters include a mixture of polar and warmer, more saline Atlantic waters, with an ice-free season of several months, and support a mixture of Atlantic and Arctic species (Dunbar 1968). Seasonal sea-ice break-up in both oceanographic zones begins in May, but is much more prolonged and unpredictable in the High Arctic, where in some years pack ice over large areas may not clear at all (Markham 1986, Parkinson 2000).

During the early spring prior to and during egg formation, Thick-billed Murres forage preferentially at interfaces between ice and open water (Bradstreet 1980). As a result, ice conditions strongly affect food availability during this critical period, and reproduction in Thick-billed Murres and other arctic seabirds can be affected by the timing and extent of sea-ice clearance (Brown and Nettleship 1981; Gaston et al., in press). Differences in the variability and predictability of environmental conditions in the Low Arctic and High Arctic provide an ideal framework within which to examine links between environmental heterogeneity and phenotypic variation in life-history traits. Here, we: (1) examine how two key avian life-history traits, timing of laying and egg size, respond to inter-annual variation in ice conditions, using data collected at two high-arctic (more variable ice conditions) and two low-arctic (more consistent ice coverage) Thick-billed Murre breeding colonies in Canada's eastern Arctic over 28 years (1975–2002), and (2) compare patterns of co-variation between egg size and laying date at colonies in these two oceanographic zones.

METHODS

INTERANNUAL VARIATION IN ICE CONDITIONS

To illustrate the nature and extent of interannual differences in ice conditions in the Low Arctic and High Arctic, we used maps provided by the Canadian Ice Service. We measured the percentage of the sea's surface covered by ice within in 3° latitude by 8° longitude (Low Arctic) or 3° latitude by 10°longitude (High Arctic) blocks centered on four Thick-billed Murre study colonies: Prince Leopold Island (74°02'N, 90°00'W, which supports 100 000 breeding pairs) and Coburg Island (75°48'N, 79°25'W, 160 000 pairs), Nunavut, in the High Arctic; and Coats Island (62°33'N, 77°50'W, 30 000 pairs) and Digges Island (62°33'N, 77°50'W, 180 000 pairs), Nunavut, in the Low Arctic. Information was available at ca. 7-day intervals, and we used the data from the period nearest in date to 18 June, the difference being no more than 3 days in any year. That date was chosen because it approximates the start of egg laying in early years at colonies in both oceanographic zones. We used ice data for the period 1971 to 2004 ($n = 34$ years for all colonies).

THICK-BILLED MURRE BREEDING PARAMETERS

Information on egg size and timing of laying was available from populations on Prince Leopold Island in 1975–1978, 1984, 1987, 1988, 1993, and 2000–2002; from Coburg Island in 1979, 1987, and 1997–1998; from Coats Island in 1990–1999 (excluding 1993); and from Digges Island in 1980–1982, 1985, 1994, and 1999. We used data published in the primary literature where available (Gaston and Nettleship 1981, Birkhead and Nettleship 1981, Gaston et al. 1983, Gaston et al. 1985, de Forest and Gaston 1996). Other data were obtained from unpublished government reports or from our unpublished observations. Exact methods used varied somewhat among colonies and years, depending on the timing and length of visits to the colony, as discussed below.

At Prince Leopold Island, we determined timing of breeding from median laying dates observed on breeding plots in 1975–1977, 2001 and 2002, median hatching dates observed on breeding plots in 1978, 1988 and 2000, and median hatching dates estimated from egg densities in 1984 and 1987. We used median dates, rather

than mean dates, because egg laying in most years follows a right-skewed pattern (de Forest and Gaston 1996). At Coats Island, estimates of median laying dates based on egg densities differed by no more than 1 day when compared with observed dates of laying for the years 1988–1995 (AJG, unpubl. data). To estimate annual median laying dates from annual median hatching dates, we subtracted 33 days, the mean incubation period in Thick-billed Murres, as incubation period varies little in this species (Birkhead and Nettleship 1987, Hipfner et al. 2001). We used calipers to measure the length and maximum breadth of eggs between the peak of egg laying and the start of hatching in all years ($n = 29$ –265). As a measure of egg size, we used the annual mean egg-volume index (length \times maximum breadth²), which has a strong linear relationship with fresh egg mass in Thick-billed Murres ($r > 0.95$; Birkhead and Nettleship 1981, Hipfner et al. 2001).

At Coburg Island, timing of breeding was determined using the median laying date observed on breeding plots in 1979, the median hatching date estimated from egg densities in 1987, and the median hatching date of chicks measured at 2-day intervals on growth plots in 1997 and 1998. In all years, a sample of eggs was measured after peak laying ($n = 23$ –198).

At Coats Island, the timing of breeding in each year was taken to be the median laying date determined from daily observations on study plots. In each year, a random sample of eggs was measured just prior to the start of hatching ($n = 65$ –101).

Finally, at Digges Island, the timing of breeding was determined from median hatching dates of chicks used in growth studies. A sample of eggs was measured just prior to the start of hatching. Because there was slight but significant variation in egg size among study plots at Digges Island in 1980–1982 (Gaston et al. 1985), we used values for Plot S in each year, because eggs were measured there or on nearby plot J in all years ($n = 79$ –127).

STATISTICAL ANALYSES

Variation in environmental parameters (ice coverage) and breeding parameters (egg size, lay date) were compared between low-arctic and high-arctic colonies with Levene's tests, after first testing for differences in means between colonies within each zone, using *t*-tests. We used

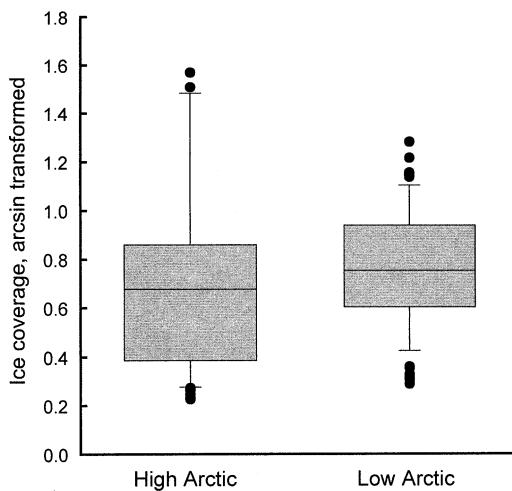


FIGURE 1. Interannual variation in the percentage of water covered by ice over a 34-year period (1971–2004) at two Thick-billed Murre breeding colonies in the High Arctic (Prince Leopold and Coburg Islands) and in the Low Arctic (Coats and Digges Islands). Box plots show outliers, median, and the 10th, 25th, 75th, and 90th percentiles.

first and second order least squares regressions to examine relationships between mean egg size and median laying date. All data were analyzed using Statistica v. 6.1 statistical software.

RESULTS

VARIATION IN ICE CONDITIONS

The percentage of the sea's surface covered by ice within designated blocks centred around each Thick-billed Murre breeding colony varied more among 34 years at two colonies in the High Arctic than at two colonies in the Low Arctic (Levene's test, $F_{1,34} = 9.6$, $P = 0.002$; Fig. 1). Note, however, that the means differed little ($t_{67} = 0.7$, $P = 0.51$). That result suggests that the distances that female birds must fly to find good feeding conditions at that time of year are not necessarily any greater in the High Arctic than in the Low Arctic, only that there is more variation among years in the High Arctic.

VARIATION IN TIMING OF LAYING AND EGG SIZE

Thick-billed Murres laid eggs later at Digges Island than at Coats Island in the Low Arctic ($t_{15} = 5.3$, $P < 0.001$). Therefore, to standardize data across all colonies, we assigned the earliest median laying date at each colony a value of 1.

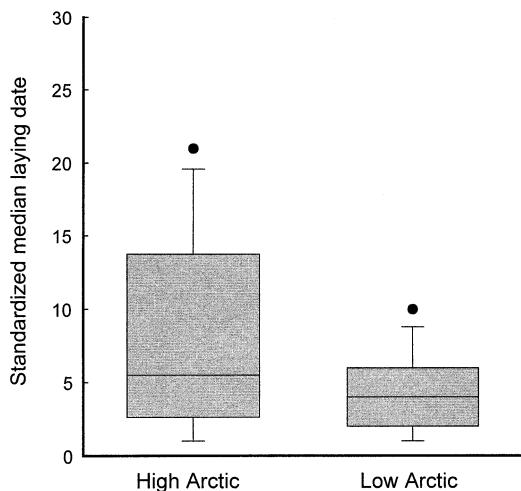


FIGURE 2. Interannual variation in median laying dates at 2 breeding colonies in the High Arctic (16 colony-years in total) and at 2 colonies in the Low Arctic (15 colony-years in total), standardized at each colony to earliest median date. Data are depicted as in Figure 1.

In this analysis, median laying dates varied more among years in the High Arctic than in the Low Arctic (Levene's test, $F_{1,29} = 18.4$, $P < 0.001$; Fig. 2).

Likewise, using the same sets of years as those used for laying dates, there was much more interannual variation in mean egg-volume index at high-arctic than at low-arctic colonies (Levene's test, $F_{1,29} = 7.3$, $P = 0.01$; Fig. 3). We attribute the overall difference in egg size between low-arctic and high-arctic populations to differences in body size. Thick-billed Murres at our study colonies in the High Arctic tend to be smaller in mass and linear dimensions than birds at our study colonies in the Low Arctic (Gaston et al. 1984, Gaston and Hipfner 2000).

COVARIATION OF EGG SIZE AND LAYING DATE

Mean egg size was unrelated to median laying date at colonies in the Low Arctic (linear regression, $r^2 = 0.05$; Fig. 4). In contrast, in the High Arctic, there was a strong tendency for eggs to be smaller in years of later laying (quadratic, $r^2 = 0.80$, $F_{2,13} = 25.2$, $P < 0.001$; Fig. 4). Two things stand out: first, even very small delays in laying date were associated with reductions in egg size at colonies in the High Arctic (i.e., the negative relationship between egg

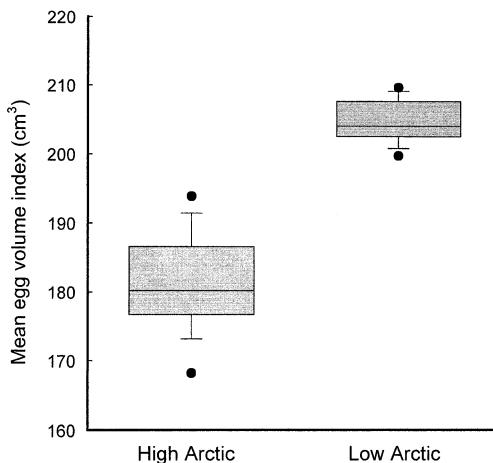


FIGURE 3. Interannual variation in mean egg volume indices at 2 breeding colonies in the High Arctic (16 colony-years in total) and at colonies in the Low Arctic (15 colony-years in total). Data are depicted as in Figure 1.

size and laying date was established across the earliest seasons); and second, in the High Arctic, egg sizes tended towards a minimum value of just over 175 cm^3 in the years of latest laying; only 1993, a relatively late year, had a smaller mean egg size.

DISCUSSION

VARIATION IN ICE CONDITIONS, LAYING DATE, AND EGG SIZE

The timing and extent of sea ice clearance in northern Canada is more variable in the High Arctic than in the Low Arctic (Markham 1986). Consistent with that fact, we found that the extent of sea surface area covered by ice varied more among years on the same date within about 300 km around Thick-billed Murre breeding colonies in the High Arctic, although mean values were similar. Ice conditions affect food availability for arctic seabirds, which tend to feed at interfaces between ice and open water early in the season (Bradstreet 1980, McLaren 1982). Consequently, Thick-billed Murres breeding at high-arctic colonies will encounter greater interannual variation in feeding conditions during the period of egg formation, although not necessarily less favorable feeding conditions, compared to birds breeding at low-arctic colonies. The energetic costs of having to search widely for food are likely to be especially high in murres, which have extremely high wing-loading (Gaston and

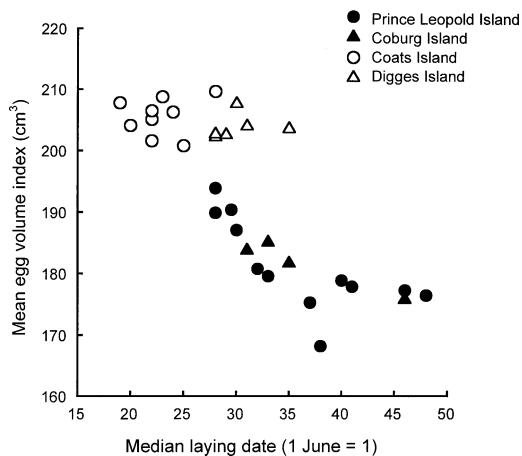


FIGURE 4. Relationship between mean egg volume index and median laying date at 2 breeding colonies in the High Arctic (filled symbols; 16 colony-years in total) and at 2 colonies in the Low Arctic (unfilled symbols; 20 colony-years).

Jones 1998). Not surprisingly, heavier ice coverage results in delayed laying (Gaston and Hipfner 1998), and that effect is particularly marked in the High Arctic (Gaston et al., in press).

In response to the differences in environmental heterogeneity, we found that Thick-billed Murres breeding in the High Arctic exhibited greater interannual variation in median laying date and mean egg size than did those breeding in the Low Arctic. Variation in these life-history traits could be a result of phenotypic plasticity (i.e., within-individual variation across years), or alternatively, it could result from different individuals of the same population laying in years in which environmental conditions differ. While we do not have enough information on egg size and laying dates of individual females across years to rigorously test for plasticity in these traits, several lines of evidence lead us to believe that the variation did result from plastic responses of individual females.

First, Thick-billed Murres have a high annual adult survival rate of over 90%, and exhibit strong mate and nest-site fidelity (Gaston and Hipfner 2000). At Prince Leopold Island, the years 1975 to 1978 spanned virtually the entire range in ice conditions, laying date, and egg size (only the mean egg size in 1993 fell outside the range), yet the number of birds breeding on delineated plots differed by less than 3% across

these four years (Nettleship et al. 1984). This suggests that the same females laid eggs, despite markedly different ice conditions. Second, more young females recruit in years in which the population lays early (Hipfner et al. 1997; AJG, unpubl. data), and these recruits lay small eggs after the population peak (Hipfner et al. 1997, Hipfner et al. 2003). Thus, in the absence of adjustments in egg size and laying date by all laying females, and specifically the more experienced females that comprise the bulk of the population, we would expect a larger mean egg size in a later year, not a smaller mean egg size. Third, with reduced numbers of first-time breeders, we would expect less overall variation in egg size in a later year, yet the coefficient of variation in egg size was higher in the latest year, 1978 (11%), than in any year between 1975 and 1977 (7.6%–8.8%). Finally, the extent of within-individual variation in egg size (25–30 cm³ of volume index) and laying date (15–20 days) that can be attributed to female age and experience at low-arctic colonies (Hipfner et al. 1997) is similar to the extent of variation detected among annual means and medians in the High Arctic. Thus, female Thick-billed Murres display considerable plasticity in both life-history traits early in their breeding lives, even in environments in which the capacity is rarely, if ever, exhibited later.

COVARIATION OF EGG SIZE AND LAYING DATE

The strong, negative relationship between egg size and laying date in the High Arctic indicates that in years in which feeding conditions are unfavorable due to heavy ice coverage, females produce smaller eggs after an extended period spent accruing additional reserves. In contrast, in the Low Arctic, where conditions are rarely severe, female murres are consistently able to produce large eggs in a timely manner. Large eggs are beneficial in that they speed the offspring's posthatching development (Hipfner and Gaston 1999), while having little effect on incubation period (Hipfner et al. 2001). Because the amount of time required for murres to form eggs varies on a scale of days (Hatchwell and Pellatt 1990, Hipfner et al. 1997), a delay in laying on a scale of weeks is more likely a result of delayed initiation of egg formation, rather than an extended period of egg formation. This also appears to explain late laying among young,

inexperienced Thick-billed Murres (Hipfner et al. 1997).

That egg size and laying date were negatively related across the years of earliest laying in the High Arctic suggests that there may be particularly tight physiological constraints on egg production in the High Arctic. At the same time, egg size tended towards a negative asymptote suggesting that each female has her own minimum egg size, and that she will not lay an egg smaller than that irrespective of her laying date. Consistent with the existence of a threshold below which eggs will not be laid, the mean egg size in the latest years in the High Arctic (175–180 cm³) closely matched the mean egg size of recruits in the Low Arctic (Hipfner et al. 1997, 2003).

Most theoretical models of optimal maternal investment predict that eggs will be larger when conditions for offspring growth or survival are less favorable, because offspring then require the additional resources available in larger eggs (Parker and Begon 1986, McGinley et al. 1987). That idea is well supported by empirical observations on a variety of taxa (Landa 1992, Sinerivo et al. 2000). Although female birds generally show little capacity to modulate egg size (Christians 2002), individuals in some species that lay multi-egg clutches do produce fewer, larger eggs later in the season (Styrsky et al. 1999).

Why then do female Thick-billed Murres lay smaller eggs in later years, but only in the High Arctic? One possibility is that delayed laying and reduced egg size are simply passive consequences of poor feeding conditions affecting adult body condition (Gonzalez-Solis et al. 1999), and that these effects are particularly acute during severe years in the High Arctic. Studies on Tengmalm's Owls (*Aegolius funereus*) have shown that the relationship between clutch size and laying date can vary, even within the same population: the ubiquitous negative relationship weakens when feeding conditions are favorable, indicating that food supply can play a mediating role (Korpimaki and Hakkarainen 1991). The same effects occur with egg size, which tends to decline more strongly with later laying in years of low food availability (Valkama et al. 2002). Food availability during the period of egg formation, as a direct, proximate factor, may similarly influence the relationship between egg size and laying date in Arctic-breeding Thick-billed Murres.

Alternatively, there could be some benefit in reducing egg size, especially in a highly seasonal environment where the window of opportunity for successful breeding closes fast. For example, a female murre's fitness is likely to be affected more strongly by her own survival than by that of any one of her individual offspring. Therefore, she might opt to minimize her reproductive costs by investing less in a late offspring, if it has little chance of surviving. In addition, by spending fewer days forming a smaller egg, the female may be able to complete the breeding cycle earlier (Murphy 1995). Reducing egg size and thus advancing laying, could also potentially benefit offspring (Birkhead and Nettleship 1982). However, any time-saving advantage obtained by reducing egg size in a late year would be countered, at least in part, by an associated increase in offspring development time (Hipfner and Gaston 1999). In addition, the idea that offspring fitness declines with date of laying has been consistently contradicted by experimental studies in which parental effects were controlled at low-arctic colonies (de Forest and Gaston 1996, Hipfner et al. 1999, Hipfner 2001). Nonetheless, it is possible that date effects are more pronounced in the High Arctic, and that Thick-billed Murres breeding in these harsh environments have adapted with a more flexible breeding strategy.

ACKNOWLEDGMENTS

David Nettleship originated seabird colony monitoring in Canada's eastern Arctic. Most of this research was funded by the National Wildlife Research Centre of the Canadian Wildlife Service, with contributions from Natural Sciences and Engineering Research Council of Canada, the Offshore Labrador project of Petro-Canada, the Northern Studies Training Programme and the Atlantic and Prairie and Northern regions of the Canadian Wildlife Service. Birgit Braune was very helpful in organizing and funding the visits to Prince Leopold Island in 1993 and 1998. None of this work would have been possible without logistical support of the Polar Continental Shelf Project of Natural Resources Canada and the Nunavut Research Institute (formerly the Iqaluit Laboratory of the Department of Indian and Northern Affairs). We thank Richard Chagnon and John Falkington of the Canadian Ice Service of Environment Canada for supplying us with ice-cover data. We are most grateful to all those who assisted with observations of murres over the years. Special thanks to Thomas Alogut and Josiah Nakoolak, who kept us safe from polar bears. The manuscript benefited from comments by Charles Francis, Ed Murphy, and an anonymous reviewer.

LITERATURE CITED

BERVEN, K. A., AND D. E. GILL. 1988. Interpreting geographic variation in life history traits. *American Zoologist* 23:85–97.

BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1981. Reproductive biology of Thick-billed Murres *Uria lomvia*: an intercolony comparison. *Auk* 98:258–269.

BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1982. Adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. *Ecology* 63: 300–306.

BLACKENHORN, W. U. 1997. Altitudinal life history variation in the dung flies *Scathophaga stercoraria* and *Sepsis cynipsea*. *Oecologia* 109:342–253.

BOYCE, M. S., AND C. M. PERRINS. 1987. Optimizing Great Tit clutch size in a fluctuating environment. *Ecology* 68:142–153.

BRADSTREET, M. S. W. 1980. Thick-billed Murres and Black Guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. *Canadian Journal of Zoology* 58: 2120–2140.

BROWN, R. G. B., AND D. N. NETTLESHIP. 1981. The biological significance of polynyas to arctic colonial seabirds, p. 59–65. *In* I. Stirling and H. Cleator [EDS.], *Polynyas in the Canadian Arctic*. Canadian Wildlife Service, Ottawa, Canada.

CHRISTIANS, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biological Review* 77:1–26.

DE FOREST, L. N., AND A. J. GASTON. 1996. The effect of age on timing of breeding and reproductive success in the Thick-billed Murre. *Ecology* 77: 1501–1511.

DUNBAR, M. J. 1968. *Ecological developments in polar regions: a study in evolution*. Prentice Hall, Upper Saddle River, NJ.

ENCABO, S. I., E. BARBA, J. A. GIL-DELGADO, AND S. MONROS. 2002. Geographical variation in egg size of the Great Tit *Parus major*: a new perspective. *Ibis* 144:623–633.

FERGUSON, G. W., AND L. G. TALENT. 1993. Life history traits of the lizard *Sceloporus undulatus* from two populations raised in a common laboratory environment. *Oecologia* 93:88–94.

FLEMING, I. A., AND M. R. GROSS. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. *Ecology* 71:1–11.

GASTON, A. J., AND J. M. HIPFNER. 1998. The effects of ice conditions in northern Hudson Bay on breeding by Thick-billed Murres. *Canadian Journal of Zoology* 76:480–492.

GASTON, A. J., AND J. M. HIPFNER. 2000. Thick-billed Murre (*Uria lomvia*). *In* A. Poole and F. Gill [EDS.], *The birds of North America*, No. 497. The American Ornithologists' Union, Philadelphia, PA.

GASTON, A. J., AND I. L. JONES. 1998. *The Auks*. Oxford University Press, Oxford.

GASTON, A. J., AND D. N. NETTLESHIP. 1981. The Thick-billed Murres of Prince Leopold Island. Canadian Wildlife Service Monograph Series, No. 6.

GASTON, A. J., G. CHAPDELAINE, AND D. G. NOBLE. 1983. The growth of Thick-billed Murre chicks at

colonies in Hudson Strait: inter- and intra-colony variation. Canadian Journal of Zoology 61:2465–2475.

GASTON, A. J., G. CHAPDELAINE, AND D. G. NOBLE. 1984. Phenotypic variation among Thick-billed Murres from colonies in Hudson Strait. Arctic 37: 284–287.

GASTON, A. J., D. K. CAIRNS, R. D. ELLIOT, AND D. G. NOBLE. 1985. A natural history of Digges Sound. Canadian Wildlife Service Report Series No. 46.

GASTON, A. J., H. G. GILCHRIST, AND J. M. HIPFNER. In press. Climate change, ice conditions, and reproduction in an arctic-nesting seabird: Brünnich's Guillemot. Journal of Animal Ecology.

GONZALEZ-SOLIS, J., P. H. BECKER, L. JOVER, AND X. RUIZ. 1999. Intraindividual seasonal decline of egg-volume in Common Tern *Sterna hirundo*. Acta Ornithologica 34:185–190.

HATCHWELL, B. J., AND J. PELLATT. 1990. Intraspecific variation in egg composition and yolk formation in the Common Guillemot *Uria aalge*. Journal of Zoology 220:279–286.

HIPFNER, J. M. 2001. Fitness-related consequences of relaying in an arctic seabird: survival of offspring to recruitment age. Auk 118:1076–1080.

HIPFNER, J. M., AND A. J. GASTON. 1999. The relationship between egg size and posthatching development in the Thick-billed Murre. Ecology 80:1287–1296.

HIPFNER, J. M., A. J. GASTON, AND L. N. DE FOREST. 1997. The role of female age in determining egg size and laying date of Thick-billed Murres. Journal of Avian Biology 28:271–278.

HIPFNER, J. M., A. J. GASTON, D. L. MARTIN, AND I. L. JONES. 2001. Seasonal declines in replacement egg-layings in a long-lived arctic seabird: costs of late breeding or variation in female quality? Journal of Animal Ecology 68:988–998.

HIPFNER, J. M., A. J. GASTON, D. L. MARTIN, AND I. L. JONES. 2001. Seasonal declines in incubation periods of Brünnich's Guillemots *Uria lomvia*: testing proximate causes. Ibis 143:92–98.

HIPFNER, J. M., A. J. GASTON, G. R. HERZBERG, J. T. BROSNAN, AND A. E. STOREY. 2003. Egg composition in relation to female age and relaying: constraints on egg production in Thick-billed Murres. Auk 120:645–657.

KORPIMAKKI, E., AND H. HAKKARAINEN. 1991. Fluctuating food supply affects the clutch size of Tengmalm's Owl independent of laying date. Oecologia 85:543–552.

LANDA, K. 1992. Adaptive seasonal variation in grasshopper offspring size. Evolution 46:1553–1558.

LAURILA, A., S. KARTTUNEN, AND J. MERILA. 2002. Adaptive phenotypic plasticity and genetics of larval life histories in two *Rana temporaria* populations. Evolution 56:617–627.

MARKHAM, W. E. 1986. The ice cover, p. 110–116. In I. P. Martini [ED.], Canadian Inland Seas. Elsevier, Amsterdam.

MCGINLEY, M. A., D. A. TEMME, AND M. A. GEBER. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. American Naturalist 130:370–398.

MCLAREN, P. L. 1982. Spring migration and habitat use by seabirds in eastern Lancaster Sound and western Baffin Bay. Arctic 35:88–111.

MURPHY, E. C. 1995. Seasonal declines in duration of incubation and chick periods of Common Murres at Bluff, Alaska, in 1987–1991. Auk 112:982–993.

NAGER, R. G., AND A. J. VAN NOORDWIJK. 1995. Proximate and ultimate aspects of phenotypic plasticity in timing of Great Tit breeding in heterogeneous environment. American Naturalist 146:454–474.

NETTLESHIP, D. N., T. R. BIRKHEAD, AND A. J. GASTON. 1984. Breeding of Arctic seabirds in unusual ice years: the Thick-billed Murre *Uria lomvia* in 1978. Bedford Institute of Oceanography Review 84:35–38.

ORO, D., R. PRADEL, AND J.-D. LEBRETON. 1999. Food availability and nest predation influence life history tactics of Audouin's Gull, *Larus audouinii*. Oecologia 118:438–445.

PARKER, G. A., AND M. BEGON. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. American Naturalist 128:573–592.

PARKINSON, C. E. 2000. Variability of arctic sea-ice: the view from space, an 18 year record. Arctic 53: 341–358.

PRINSBERG, M. 1986. On the physical oceanography of Foxe Basin, p. 217–236. In I. P. Martini [ED.], Canadian Inland Seas. Elsevier, Amsterdam.

RICKLEFS, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38–49.

SEIGEL, R. A., AND R. B. FORD. 2001. Phenotypic plasticity in reproductive traits: geographical variation in plasticity in a viviparous snake. Functional Ecology 15:36–42.

SINERVO, B., E. SVENSSON, AND T. COMMENDANT. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406: 985–988.

STYRSKY, J. D., K. P. ECKERLE, AND C. F. THOMPSON. 1999. Fitness-related consequences of egg mass in nestling House Wrens. Proceedings of the Royal Society of London Series B 266:1253–1258.

VALKAMA, J., E. KORPIMÄKI, J. WIEHN, AND T. PAKKANEN. 2002. Inter-clutch egg size variation in kestrels *Falco tinnunculus*: seasonal decline under fluctuating food conditions. Journal of Avian Biology 33:426–432.