658 J. MARK HIPFNER ET AL.

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

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 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 = 34years 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 Other data were obtained from unpublished government reports or from our unpublished observations.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).

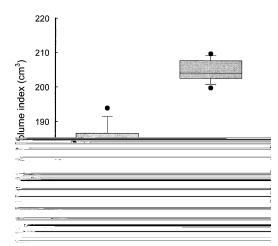
At Coats Island, the timing of breeding in each year was taken to be the median laying date determined from daily observations on study plots. In each year, a random sample of eggs was measured just prior to the start of hatching (n = 65-101).

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

660 J. MARK HIPFNER ET AL



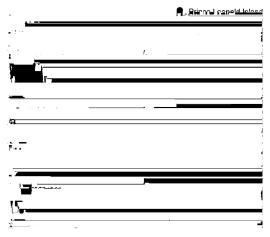


FIGURE 4. Relationship between mean egg volume index and median laying date at 2 breeding colonies in the High Arctic (filled symbols; 16 colony-years in total) and at 2 colonies in the Low Arctic (unfilled symbols; 20 colony-years).

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 cm³ 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

662 J. MARK HIPFNER ET AL.

these four years (Nettleship et al. 1984). This

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 repro-