

FOOD SUPPLY AND THE CONSEQUENCES OF EGG SIZE IN THE THICK-BILLED MURRE¹

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Abstract. We examined the effect of egg size on post-hatching development in the Thick-billed Murre (*Uria lomvia*), an Arctic seabird that lays a one-egg clutch, at a colony where food availability during chick-rearing was low (Digges Island, Nunavut, Canada). We compared our results to those of a previous study conducted at a colony where food availability was higher (Coats Island, Nunavut). To control for underlying phenotypic correlations between egg size and parental quality, we switched eggs at random among pairs. Egg size positively affected the rate of early wing-feather growth, but contrary to prediction, the advantage enjoyed by chicks from large eggs over those from small eggs at Digges Island (1.6 days' feather growth on average) was no greater than at Coats Island (2.0 days). Egg size had no effect on the rate at which chicks gained mass at Digges Island, but young from large eggs tended to remain heavier than those from small eggs. At Coats Island, this occurred only in a year in which chicks grew relatively slowly, offering some support for the hypothesis that a large egg confers greater advantage when feeding conditions are unfavorable. Adults at Digges Island invested heavily in provisioning their chicks, but there was no evidence of a trade-off between egg size and provisioning. As costs associated with large eggs have not been detected in Thick-billed Murres, the existence of considerable variation in egg size, beyond that associated with female age or experience, remains unexplained.

Key words: chick growth, egg size, food supply, Thick-billed Murre, *Uria lomvia*, wing-feather growth.

Disponibilidad de Alimento y Consecuencias del Tamaño de Huevo en *Uria lomvia*

Resumen. Estudiamos el efecto del tamaño de los huevos en el desarrollo posterior a la eclosión en *Uria lomvia*, un ave marina ártica que presenta una nidada de un solo huevo. Realizamos el estudio en una colonia donde la disponibilidad de alimento durante la cría de polluelos fue baja (Isla Digges, Nunavut, Canadá). Comparamos nuestros resultados con los obtenidos en un estudio previo en una colonia en que la disponibilidad de alimento era mayor (Isla Coats, Nunavut). Para controlar la subyacente correlación fenotípica entre el tamaño de los huevos y calidad parental, los huevos fueron cambiados al azar entre parejas. El tamaño del huevo afectó positivamente la tasa de crecimiento temprano de plumas del ala. Contrariamente a las predicciones, en la Isla Digges la ventaja de los polluelos provenientes de huevos más grandes sobre aquellos provenientes de huevos más pequeños (media de 1.6 días para crecimiento de plumas) no fue mayor que en la Isla Coats (2.0 días). El tamaño del huevo no tuvo efecto sobre la tasa a la cual los polluelos ganaron peso en la Isla Digges, sin embargo los polluelos provenientes de huevos grandes presentaron una tendencia a permanecer con mayor peso que aquellos provenientes de huevos más pequeños. En la Isla Coats esto ocurrió sólo durante un año en el cual los polluelos crecieron relativamente lento, apoyando la hipótesis que huevos grandes confieren una mayor ventaja cuan-

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do las condiciones de alimentación son desfavorables. Los adultos en la Isla Digges invirtieron fuertemente en el aprovisionamiento de sus polluelos, pero no hubo evidencia de un compromiso entre el tamaño de los huevos y el aprovisionamiento. Debido a que el costo asociado con huevos de mayor tamaño no ha sido detectado en *U. lomvia*, la existencia de una gran variabilidad en el tamaño de los huevos, mas allá de la asociada a la edad o experiencia de la hembra, permanece inexplicada.

INTRODUCTION

Egg size is an important life-history trait because it can simultaneously affect the fitness of both parents and their offspring (Mousseau and Fox 1998). Effects on adult females can be direct, if the extra resources invested in large eggs reduce those available for self-maintenance, or indirect, if there are trade-offs between egg size and clutch size (Stearns 1992). In many taxa, offspring that hatch from large eggs have advantages over those from small eggs (Azevedo et al. 1997), but the relationship between egg size and offspring fitness is not necessarily straightforward. In particular, advantages of hatching from a large egg may be magnified when food availability is low, which could cause the magnitude, or even the direction, of selection on egg size to fluctuate with environmental conditions (Semlitsch and Gibbons 1990, Hutchings 1991). For example, brown trout (*Salmo trutta*) that hatched from large eggs grew more quickly than did those from small eggs, but differences in growth rate decreased as food availability increased (Einum and Fleming 1999). These authors suggested that in favorable environments, female trout maximize fitness by producing small eggs, because this allows them to lay more eggs; in unfavorable environments, the better strategy is to lay fewer, larger eggs (Hutchings 1991).

For birds, it is often suggested that the advantages of hatching from a large egg are more pronounced when feeding conditions are unfavorable. Young from large eggs hatch with large yolk reserves that might tide them over periods of food shortage soon after hatching (Parsons 1970). In addition, differences in hatchling mass established by egg size may be more persistent when chicks grow slowly, so that fledglings from large eggs will be more likely to survive because they are heavier (Styrsky et al. 1999). Fluctuating selection on egg size in relation to environmental conditions might explain why this inherited trait, widely thought to affect fitness, shows such extreme variation in many bird populations (Ankney and Bissett 1976). How-

ever, as in other taxa (Einum and Fleming 1999), few avian studies have examined the consequences of egg size across a range of feeding conditions (Martin 1987, Smith and Bruun 1998). Moreover, few studies on birds have unequivocally demonstrated that egg size affects offspring performance (Williams 1994).

Thick-billed Murres (*Uria lomvia*) are colonial, cliff-nesting seabirds of Arctic waters that lay a single-egg clutch. Feeding conditions vary markedly among colonies, as evidenced by a strong, inverse relationship between chick growth rate and colony size; large aggregations of murres probably deplete food supplies in nearby waters (Gaston 1985). Research at a small colony of 30 000 pairs at Coats Island, Nunavut, Canada, where chicks grew quickly, showed that egg size varied markedly among females (Hipfner et al. 1997). Moreover, young murres that hatched from large eggs developed a 2-day (ca. 7-mm) advantage in wing length over those from small eggs by 12 days of age, apparently because the primary coverts burst from the sheaths earlier on chicks from large eggs (Hipfner and Gaston 1999a). To survive the descent to the sea from nest sites located high on cliffs, at >14 days of age, Thick-billed Murre chicks require wings that are long enough to enable them to avoid plummeting into ledges or rocks below. At some colonies, it is also important that chicks glide a sufficient distance that they reach the sea directly, rather than landing on a beach where predators congregate (Hipfner and Gaston 1999b). Young Thick-billed Murres that hatched from large eggs at Coats Island also tended to remain heavier than those from small eggs in a year of slower growth, but not in a year of faster growth. However, the variation in growth rate between years at the same colony is very small compared to the variation found among colonies (Gaston et al. 1983).

Here, we examine the consequences of egg size for Thick-billed Murres at East Digges Island, Nunavut, Canada. The Digges Sound region supports about 300 000 breeding pairs of Thick-billed Murres. Adult murres, and their

eggs, are similar in size to those at Coats Island, but chicks grow much more slowly at Digges Island (Gaston et al. 1983). As in the Coats Island study, we switched eggs among pairs to disengage underlying correlations between egg size and phenotypic attributes of adult females. Our main goal was to examine whether feeding conditions affect the relationship between egg size and wing-feather growth. Nestlings use protein from the yolk sac (in addition to that from feedings) to grow feathers after hatching (Romanoff and Romanoff 1949), and the size of the yolk sac is largely determined by egg size (Birkhead and Nettleship 1984). Where chicks grow their feathers slowly, this yolk protein might constitute a greater proportion of the total protein in the feathers at any given age. We therefore predicted that egg size would have a more pronounced effect on wing-feather growth at Digges Island than at Coats Island.

METHODS

STUDY AREA AND EXPERIMENTAL PROTOCOL

Fieldwork was conducted at East Digges Island, Nunavut, Canada (62°33'N, 77°50'W) during July and August 1999. East Digges Island (hereafter, Digges Island) is situated 200 km east of Coats Island (62°57'N, 82°00'W), and the two colonies experience very similar summer climatic conditions.

For clarity, and for consistency with the Coats Island study, the following definitions are used: *volume index* is the product of an egg's length times its maximum breadth squared ($l \times b^2$), a measure of egg size that has a strong linear relationship with fresh egg mass in Thick-billed Murres ($r = 0.971$, Hipfner, unpubl.); *initial volume* is the volume index of the eggs that the experimental females laid, prior to egg-switching (the independent variable that measures how the growth of the experimental chicks is affected by the quality of the parents that raise them, while controlling for effects of the size of the egg from which they actually hatch); *foster volume* is the volume index of the eggs that experimental pairs received after egg-switching (the independent variable that measures how the growth of the experimental chicks is affected by the size of the egg from which they hatch, while controlling for effects of the quality of the parents that actually raise them); *mass growth* and *wing growth* are the changes in the experimental

chicks' masses and wing lengths between 2 and 14 days of age; and *14-day mass* and *14-day wing* are chick masses and wing lengths at 14 days of age.

Just prior to the start of hatching, we mapped and numbered the locations of sites occupied by 85 breeding pairs on an accessible plot situated near the top of the colony. Every egg was marked with its site number in permanent ink, and the length and maximum breadth measured to the nearest 0.1 mm using vernier calipers. The eggs were redistributed randomly among sites after being measured, so that for each pair we knew both initial volume and foster volume.

Sites were checked at 2-day intervals (rather than daily, to reduce disturbance), but occasionally at 3-day intervals when weather conditions forced a delay. Eggs that pipped on day i and hatched on day $i + 2$ were assumed to have hatched on day $i + 1$, except for three chicks that were still wet when found, and had obviously hatched earlier the same day. When checks were 3 days apart, new chicks with wing lengths ≥ 27 mm were assumed to have hatched 2 days previously (based on our previous work; see Results for an analysis of this potential bias). Each chick was marked with a binary code of nail clipping, and banded when large enough. On all visits, chicks were weighed to the nearest 1 g with a 300-g spring balance, and the right wing measured to the nearest 1 mm from the carpus to the tip of the longest feather with the wing held flat and straight along a ruler.

Larger samples were available for 2-day-old than for 1-day-old chicks because 2-day measurements could be estimated from measurements at 1 and 3 days using linear interpolation. Therefore, we used 2-day measurements as estimates of initial size. Only chicks that survived > 14 days ($n = 53$) were included in the analyses because 15 days is the youngest age at which Thick-billed Murre chicks are known to depart the nest site of their own volition (Gaston and Nettleship 1981). Because some chicks were first measured at 3 days of age, sample sizes for parameters that require 2-day measurements (i.e., mass growth and wing growth) are smaller ($n = 37$). For chicks lacking 14-day measurements, we used linear interpolation between the two ages closest to 14 days.

STATISTICAL ANALYSES

Data were analyzed using SYSTAT (version 8.0) statistical software (SPSS Inc. 1998). All resid-

TABLE 1. Measures (mean \pm SD) of Thick-billed Murre egg size and chick growth at Digges Island and Coats Island (Coats Island data from Hipfner and Gaston 1999a).

	Digges Island (<i>n</i>)	Coats Island (<i>n</i>)	
		1994	1995
Initial volume (cm ³)	203.3 \pm 18.5 (53)	201.3 \pm 18.3 (33)	208.7 \pm 16.1 (27)
Foster volume (cm ³)	205.1 \pm 14.7 (53)	206.2 \pm 15.4 (33)	209.4 \pm 14.9 (27)
Mass growth (g)	51.6 \pm 14.1 (37)	116.8 \pm 19.3 (30)	103.8 \pm 20.0 (27)
14-day mass (g)	125.9 \pm 24.7 (53)	199.0 \pm 19.6 (33)	182.7 \pm 21.1 (27)
Wing growth (mm)	19.8 \pm 4.6 (37)	28.1 \pm 4.2 (30)	28.1 \pm 4.4 (27)
14-day wing (mm)	45.5 \pm 8.0 (53)	54.7 \pm 4.5 (33)	53.4 \pm 4.7 (27)

uals were plotted and found to adequately meet the normality and equality of variances assumptions of parametric statistical tests.

We examined the effects of initial volume (parental effects) and foster volume (egg-size effects) on measures of chick growth using multiple linear regression. The effects of foster volume on wing growth were compared between Digges and Coats Islands in two ways: (i) we regressed 14-day wing against foster volume, and tested for differences in the slopes of the lines at the two colonies using analysis of covariance (ANCOVA), and (ii) following Hipfner and Gaston (1999a), we plotted mean wing length against chick age for chicks from the largest and smallest one-thirds of eggs in the sample. We then calculated the mean difference in 14-day wing between the two groups, and estimated the number of days it would take for each of the small-egg chicks to make up that difference based on its own rate of wing growth between 12 and 14 days of age. By 12 days of age, all chicks have started the linear phase of wing growth (pers. obs.). We also used ANCOVA to test for differences in the slopes of the lines relating 14-day mass to foster volume at Digges Island and Coats Island. As the slopes for mass differed significantly in both slope and elevation at Coats Island between 1994 and 1995 (unlike those for wing length, which were similar in both respects), comparisons with the Digges Island sample were made separately for each of the two years from Coats.

All references to observations from Coats Island are to data in Hipfner and Gaston (1999a); references to previous observations from Digges Island are to data in Gaston et al. (1983) and Gaston et al. (1985). A significance level of $\alpha = 0.05$ is used throughout, and all probability values are two-tailed. Values are reported as means \pm SD.

RESULTS

There was no correlation between initial and foster volumes ($r_{51} = 0.01$, $P > 0.9$), indicating that egg-switching randomized the relationship between the sizes of eggs laid and fostered by individual pairs. Hatching spanned 7 days, but none of initial volume, foster volume, 14-day mass, or 14-day wing were significantly related to hatching date (all $r^2 \leq 0.04$, all $F_{1,51} \leq 2.40$, all $P > 0.1$), so seasonal trends in egg size and chick growth rate probably were unimportant. Finally, neither initial volume (independent $t_{48} = 1.07$, $P > 0.2$) nor foster volume (independent $t_{48} = 0.52$, $P > 0.5$) differed significantly between chicks estimated to be 2 and 3 days of age when first found. Therefore, it is unlikely that errors in age estimation had overt, systematic effects on the analysis of growth in relation to either of these independent variables.

Eggs at Digges Island were similar in size to those laid there in previous years, and similar in size to those laid at Coats Island (Table 1). Chicks grew very slowly at Digges Island in 1999, so that both 14-day mass and 14-day wing were lower than in other years there, and much lower than at Coats Island (Table 1). Although 14-day wing was lower at Digges Island, chicks at that colony exhibited considerably more relative variation in 14-day wing (CV = 17.6%, $n = 53$) than was found among chicks at Coats Island (CV = 8.5%, $n = 60$).

In multiple regressions, initial and foster volumes combined explained little of the variation in mass growth (Table 2). Despite this, these variables explained a significant proportion of the variation in 14-day mass; however, only the positive effect of foster volume was statistically significant (Table 2). This indicates that differences in nestling mass, established by egg size, tended to persist, and that the size of egg a fe-

TABLE 2. Multiple regressions relating measures of the growth of Thick-billed Murre chicks to initial volume (the parental effect) and foster volume (the egg-size effect).

Measure of growth	Multiple regression			Initial volume		Foster volume	
	<i>n</i>	<i>F</i>	<i>R</i> ²	<i>t</i>	Slope/trend	<i>t</i>	Slope/trend
Mass growth	37	1.09	0.06	1.35	+	0.52	+
14-day mass	53	3.33*	0.12	0.99	+	2.36*	0.38
Wing growth	37	4.67*	0.22	1.50	+	2.57*	0.11
14-day wing	53	6.43**	0.21	1.54	+	3.22**	0.14

* $P < 0.05$; ** $P < 0.01$.

male laid was not a good predictor of the growth of the chick she fostered. The slope of the line relating 14-day mass to foster volume at Digges Island (0.38 g cm^{-3}) differed little from that at Coats Island in 1995 (0.59 g cm^{-3} ; ANCOVA, $F_{1,76} = 0.52$, $P > 0.4$), the year of slower growth at Coats Island; the slope at Digges Island differed more, although not statistically significantly, from that at Coats Island in 1994 (-0.10 g cm^{-3} ; ANCOVA $F_{1,82} = 3.21$, $P > 0.05$), the year of faster growth there.

In multiple regressions, initial and foster volumes combined explained significant proportions of the variation in both wing growth and 14-day wing, but in both cases, only the positive effects of foster volume were statistically significant (Table 2). The plot of mean wing length

against age for chicks from the largest and smallest eggs at Digges Island showed that the effect of egg size was the same as at Coats Island: the wings of large-egg chicks began the linear growth phase sooner after hatching than did those of small-egg chicks. This indicates that foster volume affected early wing-feather development (Hipfner and Gaston 1999a). The slope of the line relating 14-day wing to foster volume at Digges Island was similar to that at Coats Island in the two years of study there (Fig. 1). At 14 days of age, Digges Island chicks from the largest one-third of eggs had wings that averaged 3.9 mm longer than those from the smallest eggs. This amounted to a 1.6 ± 1.0 day advantage in wing growth, not significantly different than the 2.0 ± 1.0 day advantage enjoyed by large-egg chicks at Coats Island (independent $t_{35} = 1.55$, $P > 0.1$).

DISCUSSION

Thick-billed Murre chicks grew extremely slowly at Digges Island in 1999. The mean 14-day mass (126 g) was the lowest yet recorded at this large colony noted for slow growth rates (Gaston et al. 1983 reported means of 134–156 g in 3 years using similar weighing schedules). Apparently, feeding conditions during chick-rearing were particularly unfavorable at Digges Island in 1999. This is supported by the observation that 16 incubating adult Thick-billed Murres averaged 123 g heavier than 43 chick-rearing adults (Hipfner, unpubl.); a much larger difference than occurs at Coats Island (differences of 45–86 g in 5 years, Gaston and Perin 1993), or at the Gannet Islands, Labrador, Canada (differences of 24–68 g in 4 years, Birkhead and Nettleship 1987, Bryant et al. 1999), two small Thick-billed Murre colonies where adults are similar in size to Digges Island birds but where feeding conditions are more favorable.

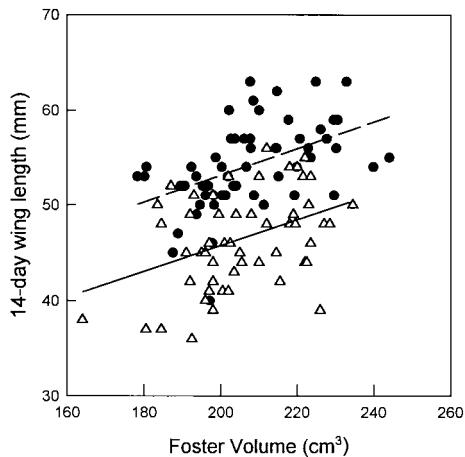


FIGURE 1. Scatterplot showing the relationship between 14-day wing length and egg size for Thick-billed Murre chicks at Digges Island (open triangles) and Coats Island (filled circles). The slope ($\beta \pm \text{SE}$) of the line at Digges Island ($0.14 \pm 0.04 \text{ mm cm}^{-3}$) was similar to that at Coats Island ($0.15 \pm 0.04 \text{ mm cm}^{-3}$; ANCOVA, $F_{1,109} = 0.02$, $P = 0.9$). Coats Island data from Hipfner and Gaston (1999a).

Egg size had a positive effect on the rate of increase in wing length in Thick-billed Murre chicks at Digges Island, as observed previously at Coats Island (Hipfner and Gaston 1999a). Gaston and Nettleship (1981) reported strong, positive correlations between 2-day mass and 14-day wing length at Prince Leopold Island in two years, probably also largely due to this egg-size effect. The length of a murre chick's wings is an important factor affecting whether it survives the descent from the nest site, often located high on a cliff, to the sea (Birkhead 1977). In previous studies at Digges Island, chicks that had longer wings at 14 days of age tended to depart to sea when younger than those with shorter wings (Hipfner and Gaston 1999b). Consequently, there is likely to be a fitness advantage for murre chicks in hatching from a large egg, because a large-egg chick will be developmentally prepared to leave the nest early, and therefore in synchrony with others. Synchronous departure is important for a number of reasons. First, it can reduce the mortality risk for individual chicks at nest departure through predator swamping (Daan and Tinbergen 1979). Second, it lessens the amount of time that late-hatched chicks spend at the nest site after most other chicks have gone, when the risk of predation may be especially high (Hatchwell 1991). Early departure itself also might be advantageous, as it has been associated with increased post-departure survival in Common Murres (*Uria aalge*; Harris et al. 1992), although there was no evidence of this in Thick-billed Murres at Coats Island, when the quality of the parents of early and late-departing chicks was controlled (Hipfner 2000). However, contrary to prediction, a large egg size provided no more time-saving advantage for nestling murre chicks growing feathers at Digges Island than at Coats Island, despite the marked differences in chick growth rates. To explain this will require research into the proximate basis for the effect of egg size on post-hatching feather growth.

Thick-billed Murre chicks that hatched from large eggs tended to remain heavier than did those from small eggs at Digges Island, similar to the effect seen at Coats Island in the year of slower growth (Hipfner and Gaston 1999a). Common Murres that departed the nest heavier survived for longer without food (Hatch 1983), so there may be an advantage for murre chicks in hatching from a large egg in terms of survival

after departure from the colony. Moreover, results of this study and the one at Coats Island suggest that any survival advantage this egg-size effect confers may be more important when food is less available, because differences in hatching mass may be more persistent under these conditions (Styrsky et al. 1999). In other species, large eggs also may confer survival advantages soon after hatching, because chicks from large eggs hatch with large energy reserves that tide them over short-term food shortages (Parsons 1970, Rhymer 1988). Our methods were not well suited to examining the effects of egg size on nestling survival; however, even at Digges Island, where food availability appeared to be very low, 93% ($n = 46$) of chicks observed daily from a distance survived to the age of nest departure (15 days). There was no evidence that any of those that did not had starved to death at the nest site (Hipfner, unpubl.). Death through starvation appears to be a rare occurrence for nestling Thick-billed Murres.

What about the consequences of egg size for adult Thick-billed Murres, a species in which there is substantial female-specific variation in egg size (Hipfner et al. 1997)? The existence of so much variation appears paradoxical, because there is a genetic component to egg-size variation in birds (Boag and van Noordwijk 1987), yet egg size probably affects offspring fitness. Therefore, assuming that egg size confers sufficient advantage (it is possible that it does not), we would expect directional selection towards a ubiquitous, optimal, large egg size. In that case, the persistence of substantial variation in egg size suggests that there may be costs associated with large eggs that counteract any fitness benefits they confer (Ankney and Bissett 1976). Thick-billed Murres that lay larger eggs do not take longer to form them than do birds that lay smaller eggs (Hipfner et al. 1997), and egg size has only weak to non-existent effects on length of incubation (Hipfner et al. 2001). Consequently, the time saving associated with hatching from a large egg is not wholly counteracted by increases in either of these phases of breeding. Moreover, when parental quality is controlled, Thick-billed Murres that lay larger eggs are as likely to replace lost eggs as are those that lay smaller eggs, and birds that lay larger eggs take no longer to re-lay (Hipfner et al. 1999). This suggests that within-season trade-offs between

egg size and egg number are unimportant for more capable birds.

Life-history theory predicts that in species with high annual survival rates and low annual fecundity rates (like murre), adults should be unwilling to jeopardize their survival, and future reproductive potential, by investing too heavily in any single breeding episode (Clutton-Brock 1988). Consequently, the costs associated with trade-offs in breeding should be borne largely by offspring (Mauck and Grubb 1995). However, even though adult murre appeared to invest heavily in chick rearing, apparently at the expense of their own body condition, there was no suggestion of a trade-off between egg size and chick provisioning.

Egg size increases with female age in Thick-billed Murres (Hipfner et al. 1997), and chicks raised by older, more experienced parents tend to grow more quickly (de Forest and Gaston 1996). This age effect will tend to produce positive relationships between egg size and chick growth, which could override trade-offs occurring among older, more experienced females. However, this seems unlikely in our study, because most young Thick-billed Murres lose their eggs soon after laying (de Forest and Gaston 1996), and long before we switched eggs, so that the vast majority of females in our sample probably were older, more experienced birds. Egg size varies markedly even among older birds (Hipfner et al. 1997).

Even if there is a trade-off for adult females between egg size and survival (in effect, a trade-off between egg size and egg number that operates across years), the effect probably would be very difficult to detect in a species with such a high annual survival rate (ca. 90% at Coats Island, Gaston et al. 1994). While studies on other avian species have detected trade-offs between clutch size and provisioning (Heaney and Monaghan 1995, Monaghan et al. 1998), and between clutch size and female health (Oppliger et al. 1996), no study has detected any such trade-offs involving egg size (Smith et al. 1995). Consequently, the existence of so much female-specific variation in egg size in Thick-billed Murres, and other birds, remains unexplained.

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