

The effect of egg size on post-hatching development in the Razorbill: an experimental study

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A recent experimental study reported that Thick-billed Murre *Uria lomvia* chicks that hatched from large eggs grew their wing feathers more quickly than did small-egg chicks. There is little evidence of this (or any other) egg-size effect on post-hatching development in other birds. Thick-billed Murres are marine birds of the family Alcidae that employ the unique “intermediate” developmental strategy: chicks go to sea after 15–30 days at the nest site, at < 30% of adult mass, accompanied by their male parent. Rapid feather growth during the brief nestling period is critical to enable chicks to make the transition from life at the nest site to life at sea quickly and safely. At the Gannet Islands, Labrador, Canada, in 1996 and 1997, I tested whether egg size has the same effect on wing-feather growth in the Razorbill *Alca torda*, another of the intermediate auks. To control for underlying correlations between egg size and other parental attributes, eggs were switched randomly among pairs. As in other birds, egg size strongly predicted hatchling mass, and to less extent hatchling size (tarsus length), but had no effect on the rate at which nestlings gained mass. However, egg size had the same effect on wing growth in Razorbills as in Thick-billed Murres: the wings of large-egg chicks began rapid, linear growth sooner, indicating that early development of wing feathers was enhanced in large-egg chicks. Differences in wing length established in this manner persisted through the nestling period. Egg-size effects on feather growth have not been detected in experimental studies on other birds, suggesting that effects of the magnitude seen in Razorbills and Thick-billed Murres might reflect evolutionary priorities in the post-hatching development of intermediate auks.

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Egg size has been widely studied in the context of life-history theory because it can be highly variable, even within populations, and yet studies on a variety of taxa have shown that egg size can affect both parental and offspring fitness (reviewed in Bernardo 1996, Azevedo et al. 1997). Interestingly, studies of the relationship between egg size and offspring quality in birds have produced somewhat equivocal results (Williams 1994). In studies that controlled for potentially confounding factors (parental quality, within-clutch egg-size variation, laying sequence), egg size sometimes affected hatching success (Croxall et al. 1992, Magrath 1992, but see Reid and Boersma 1990, Smith et al. 1995), and early nestling survival (Ankney 1980, Bolton 1991, but see Ollason and Dunnet 1986, Meathrel et al. 1993). Egg size always affected hatchling mass and size,

but this effect weakened as nestlings aged, and egg size had no overt effect on the rate of post-hatching development (e.g. Amundsen et al. 1996). However, a recent experimental study reported that egg size positively affected early wing-feather development in the Thick-billed Murre *Uria lomvia*, a marine bird of the family Alcidae, and that egg size-induced differences in wing length persisted until nest departure (Hipfner and Gaston 1999a).

The Alcidae is unique among bird families in including species that exhibit a wide range of post-hatching developmental strategies (Sealy 1973, Gaston 1985). At one extreme, young precocial auks *Synthliboramphus* spp. (terminology follows Sealy 1973) are not fed at the nest and depart to sea at 2–4 days of age, still covered in down, and accompanied by both parents. At the

other extreme, young semi-precocial auks (e.g. puffins *Fratercula* spp.) are fed at the nest for 25–75 days, but are independent of their parents after they depart to sea, fully feathered, and at 50–100% of adult mass. The genera *Uria* and *Alca* employ a developmental strategy that is “intermediate” between the extremes and unique to the auks: the young are fed at the nest site for 15–30 days before going to sea at <30% of adult mass, accompanied by their male parent. At nest departure, intermediate auks are covered in a transitional, mesoptile plumage; growth of the large flight feathers (rectrices and remiges) begins once the chick is at sea (Bédard 1969).

No previous experimental study has detected an effect of egg size on post-hatching feather growth such as that seen in Thick-billed Murres, suggesting that an effect of that magnitude is not widespread. Hipfner and Gaston (1999a) proposed that it might reflect evolutionary priorities in the post-hatching development of intermediate auks. Rapid wing-feather growth during the brief nestling period is critical to enable intermediate auks to make the transition from life at the nest site to life at sea quickly and safely (Birkhead 1977, Hipfner and Gaston 1999b).

In this paper, I examine the effect of egg size on post-hatching development in the Razorbill *Alca torda*, an intermediate auk of Arctic and boreal Atlantic waters. Because egg size may be correlated with other female attributes that could affect how quickly her chick grows, such as her age (Lloyd 1979) or foraging skill (Lack 1968), I switched eggs among pairs to disengage such phenotypic correlations. The two main objectives of the paper are to test: (i) whether egg size has the same effect on early wing-feather development in Razorbills as in Thick-billed Murres; and (ii) whether females that initially lay large eggs will raise fast-growing chicks, i.e., whether egg size will reflect other aspects of female quality.

Methods

The study took place at the Gannet Islands, Labrador, Canada (53°56' N, 56°32' W), in 1996 and 1997. This colony is situated in the low-Arctic oceanographic zone (Nettleship and Evans 1985).

For conciseness, I use the following definitions: *Initial Volume* is the volume index of the eggs initially laid by the experimental females; *Foster Volume* is the volume index of the eggs that the experimental pairs received after eggs were switched; *Mass Growth* and *Wing Growth* are the changes in chick mass and wing length between 2 and 14 days of age; *14 d Mass* and *14 d Wing* are chick masses and wing lengths at 14 days of age; and *Departure Mass* and *Departure Wing* are chick masses and wing lengths on the last check before nest departure.

Just prior to the start of hatching, 60 (1996) and 50 (1997) Razorbill nest sites were found and numbered with paint on a nearby rock. The length and maximum breadth of each egg was measured (± 0.1 mm) with calipers, and the eggs were then redistributed randomly among nests. As a measure of egg size, I used an egg volume index ($\text{length} \times \text{breadth}^2$) that has a strong linear relationship with fresh egg mass in Razorbills ($r = 0.912$, Birkhead and Nettleship 1984). Both Initial and Foster volumes were known for each pair.

Nest sites were checked at 2-d intervals (rather than daily, to reduce disturbance), except for occasional 1-d delays, and one 2-d delay, due to bad weather. Eggs that were pipped on day (i) and had hatched on day (i + 2) were assumed to have hatched on day (i + 1), unless the chick was wet or the down still matted (indicating that it had hatched early on the same day). On all visits, each chick was weighed (± 1 g) with a 300 g spring balance, and the right wing measured (± 1 mm) from the carpus to the tip of the longest feather with the wing held flat and straight along a ruler. Measurements at 2 days old were interpolated from measurements at days 1 and 3 for chicks not measured at 2 days. Because three chicks were considered to be 3 days old when first found, sample sizes for Mass Growth and Wing Growth, which require day 2 measurements, are slightly smaller than are those for other parameters. Some chicks were difficult to catch in enclosed nest sites. In the analyses, I included only chicks that were measured on all visits, and that survived to at least 15 days of age, the minimum age at which undisturbed chicks departed the nest site (Hipfner and Bryant 1999).

In addition, a sample of undisturbed Razorbill nest sites was watched daily for hatching in both years. At these sites, I measured mass and tarsus length (with dial calipers, ± 0.1 mm) of chicks that were still wet or that had matted down when found. I also measured tarsus length on experimental chicks that were wet or matted.

Data were analysed using SPSS (version 7.5) statistical software. All residuals were plotted and found to adequately meet the normality and equality of variance assumptions of parametric statistical tests. Data relating hatchling mass, hatchling size, and measures of chick growth to a measure of egg size were analysed using analysis of covariance, with egg volume as continuous independent variable, and year as grouping variable. In none of these ANCOVAs were the year or interaction terms statistically significant (all $F \leq 1.53$, all $P \geq 0.22$), so data from the two years were pooled. All reported probability values are two-tailed.

Results

Inter-year differences and experimental protocol

Both Initial and Foster volumes, as well as all measures of growth in mass and wing length, were similar in the two years (Table 1). There was little correlation between Initial and Foster volumes for individual pairs ($r_{54} = -0.13$, $P = 0.33$), indicating that egg-switching had the desired effect of randomizing the relationship between the sizes of eggs laid and fostered.

Because nest sites were not checked daily around hatching, there are potential errors associated with the estimates of chick age. However, in order for this to drive the results, the errors in age estimation would have to be related systematically to Initial or Foster volumes. In fact, there was little difference in either Initial ($F_{2,52} = 1.72$, $P = 0.20$) or Foster volumes ($F_{2,52} = 0.69$, $P = 0.51$) for chicks estimated to be 1, 2, or (in three cases) 3 days of age when first measured.

Egg size effects on hatchling mass and size

In a sample that included both undisturbed and experimental chicks, egg volume index explained most of the variation in hatchling mass ($r^2 = 0.71$, $F_{1,36} = 89.87$, $P < 0.001$, slope = 0.39 g cm^{-3} ; Fig. 1a), and a significant proportion of the variation in hatchling tarsus length ($r^2 = 0.30$, $F_{1,36} = 16.40$, $P < 0.001$, slope = 0.04 mm cm^{-3} ; Fig. 1b).

The relationship between chick growth and foster volumes

Foster Volume had no effect on Mass Growth, and showed only weak, positive relationships with both 14 day Mass and Departure Mass (Table 2, Fig. 2a). Although Foster Volume had no effect on Mass Growth,

Table 1. Comparisons (mean \pm SD) of egg size and growth of the Razorbill chicks in the two years. None of the between-year differences were significant (all $t \leq 0.72$, all $P \geq 0.48$). Coefficients of variation (CV) are reported with the two years combined.

	1996 (N = 30)	1997 (N = 26)	CV, %
Initial Volume (cm ³)	178.1 \pm 16.0	180.8 \pm 14.1	8.4
Foster Volume (cm ³)	177.1 \pm 15.4	178.4 \pm 18.1	9.3
14 day Mass (g)	180.4 \pm 27.6	184.7 \pm 22.8	13.9
Departure Mass (g)	187.9 \pm 25.8	187.1 \pm 23.4	13.1
14 day Wing (mm)	62.2 \pm 7.2	63.4 \pm 4.7	9.7
Departure Wing (mm)	74.4 \pm 6.0	75.1 \pm 6.6	8.3

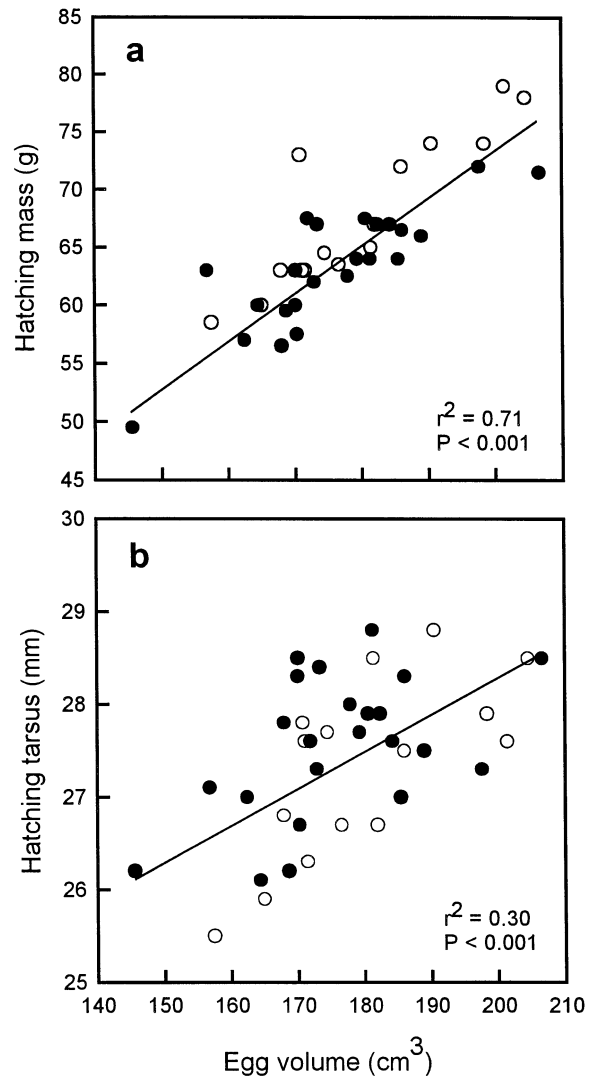


Fig. 1. Scatterplots showing the relationship between egg size and (a) hatchling mass, and (b) hatchling tarsus length, for Razorbill chicks. Data points from 1996 are open circles (N = 15), those from 1997 are filled circles (N = 23).

all measures of growth in wing length increased with Foster Volume (Table 2, Fig. 2b).

To investigate the nature of this egg-size effect on Razorbill wing growth, I plotted wing length against chick age for chicks that hatched from the largest one-third of eggs, and from the smallest one-third of eggs (the largest eggs averaged 19.9% larger than the smallest). Mass Growth differed very little between chicks that hatched from the largest and smallest eggs ($t_{34} = 0.45$, $P = 0.66$). Wing lengths of large-egg and small-egg chicks differed by $< 1 \text{ mm}$ on average at 2 days of age. The differences in wing length increased slowly to 6 days of age, then began to increase rapidly in favour of large-egg chicks, levelling off at 4 mm by 9 days of age (Fig. 3). This is equivalent to about 1 day's growth in wing length.

Table 2. Relationships between Foster Volume and growth of the Razorbill chicks. Data from 1996 and 1997 were pooled.

	N	r ²	Slope	F	P
Mass Growth	53	<0.01	-0.01	<0.01	0.96
14 day Mass	56	0.04	0.34	2.25	0.14
Departure Mass	56	0.06	0.38	3.21	0.08
Wing Growth	53	0.10	0.12	5.50	0.02
14 day Wing	56	0.13	0.15	8.19	0.006
Departure Wing	56	0.13	0.15	8.16	0.006

The relationship between chick growth and initial volume

Initial Volume showed very little relationship with any measure of growth in mass or wing length (all $r^2 < 0.01$, all $F \leq 0.60$, all $P \geq 0.44$, sample sizes as on Table 2).

Discussion

Egg size and post-hatching development in Razorbills

Egg size explained most of the variation in hatchling mass (71%) in Razorbills, but less than half as much of the variation in hatchling tarsus length (30%). These values are similar to those reported for other species of birds (Williams 1994). Egg size typically affects hatchling mass more strongly than it affects hatchling size in birds, because the main effect of egg size lies in the mass of the residual yolk sac that the chick retains at hatching (Williams 1994). This has been demonstrated previously in Razorbills (Birkhead and Nettleship 1984).

Egg size had no effect on the rate at which nestling Razorbills gained mass, consistent with experimental studies on a variety of other species (e.g. Amundsen and Stokland 1990, Reid and Boersma 1990), and suggesting that this is the norm for birds. Conversely, the rate of post-hatching wing growth increased with egg size, the main effect occurring between 6 and 9 days of age. This is the period during which the primary coverts (the longest feathers on the wings of nestling Razorbills) burst from their sheaths, and the wings begin rapid, linear growth (Bédard 1969). Consequently, it appeared that egg size affected early feather development in Razorbills. Moreover, the resulting differences in wing length persisted, so that large-egg chicks had a one-day advantage in wing length by 14 days of age.

Because the main effect of egg size at hatching lies in the mass of the yolk sac in Razorbills (Birkhead and Nettleship 1984), this is likely to be the main cause of any egg size-related differences in post-hatching development. In some species of birds, yolk size (Murphy 1994), and rates of feather growth in moulting adults (Murphy and King 1992), are limited by the availability

of the sulfur amino acids. Large yolk sacs provide hatchlings with large supplies of yolk protein (and perhaps the sulfur amino acids in particular), which the chick uses to grow feathers (Romanoff and Romanoff 1949). The advantages of hatching from a large egg may be most important when feeding conditions are

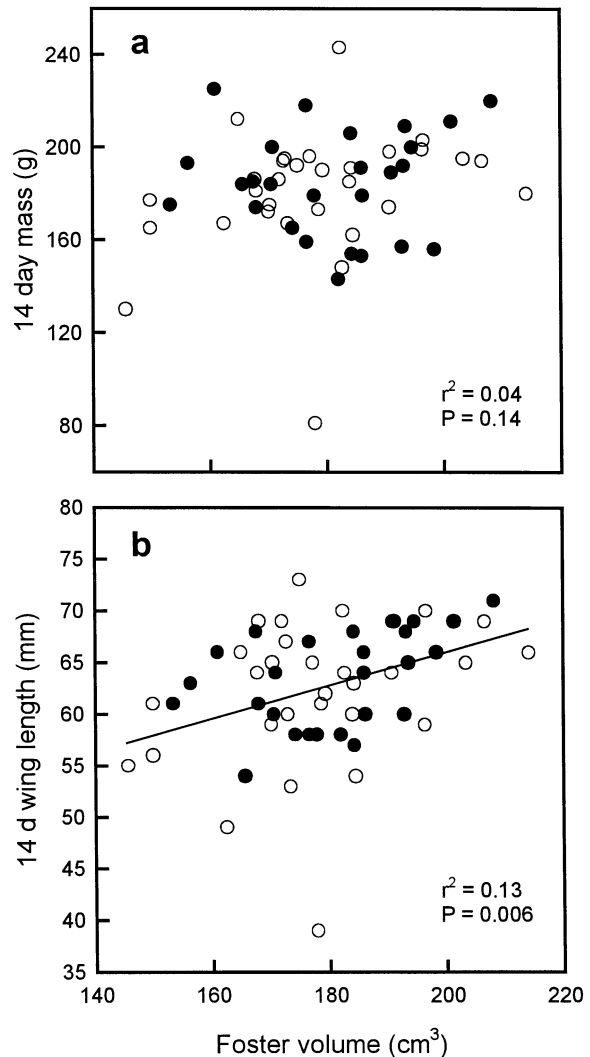


Fig. 2. Scatterplots showing the relationship between Foster Volume and (a) 14 day mass, and (b) 14 day wing length, for Razorbill chicks. Data points from 1996 are open circles (N = 30), those from 1997 are filled circles (N = 26).

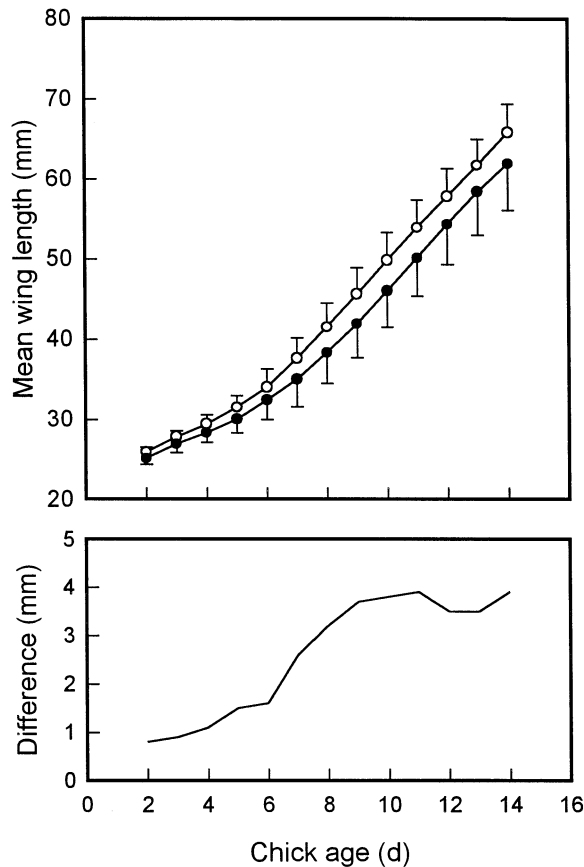


Fig. 3. Wing length (mean \pm SD) in relation to age for Razorbill chicks that hatched from the largest one-third of eggs (open circles), and the smallest one-third of eggs (both $N = 18$). The bottom figure shows the difference in mean wing lengths between the two groups.

unfavourable, and exogenous protein for feather growth is in short supply to the developing chick.

Evolutionary implications

Might this egg-size effect on feather growth reflect evolutionary priorities in the post-hatching development of intermediate auks? Egg size affected Razorbill wing feather growth in the same manner as in the Thick-billed Murre, another of the intermediate auks (Hipfner and Gaston 1999a). No experimental study on other species has detected such an effect, suggesting that effects of the magnitude found in these two species are not widespread. The most striking feature of the intermediate strategy is the short time that chicks spend at the nest site before departing to sea. However, chicks need to complete sufficient development during this brief stay to enable them to make the transition from life at the nest site to life at sea. At nest departure, intermediate auk chicks typically glide down from the

nest site, often located high on a cliff, to enter cold, Arctic or boreal oceans. The primary coverts provide the principal planing surface (Gaston and Nettleship 1981). Many chicks die on the trip from nest to sea (Greenwood 1964), often because they plummet too steeply, and strike ledges or rocks. This can cause direct mortality (Harris and Wanless 1988), can cause chicks to become separated from their attending male parent (Gilchrist and Gaston 1997), or result in chicks having to walk across beaches where predators congregate (Williams 1975). Consequently, there may be an evolutionary premium on rapid feather growth, and perhaps wing-feather growth in particular, during the brief stay at the nest (Birkhead 1977). Thick-billed Murre chicks with longer wings at 14 days of age tend to depart to sea sooner, and this was true of Razorbills in one year of this study (Hipfner and Gaston 1999b).

The intermediate auks probably evolved from a semi-precocial ancestor, perhaps in response to their low potential for growth at the nest site, and the vulnerability of their chicks to predators at open-topped nest sites (Ydenberg 1989, Gaston and Jones 1998; see Gaston 1992 for a discussion of the evolution of the precocial strategy in the auks). Although the evolution of the intermediate strategy appears not to have involved any major adjustments in developmental mode (Ricklefs and Starck 1998), there are a number of subtle adaptations that might explain why egg-size effects on post-hatching feather growth are readily detectable in these birds. Intermediate auks hatch with much less down than do semi-precocial auks (Barrett 1984, M. Hipfner unpubl.), and they hatch with larger, more protein-rich yolk sacs (Duncan and Gaston 1988, M. Hipfner unpubl.). In evolutionary terms, the intermediate auks might have foregone down growth in the egg in favour of retaining protein to use to grow feathers after hatching. The cost involved may be a delay in the onset of thermoregulation (Barrett 1984). A second change, unique to the intermediate auks, is the delay in the growth of the large flight feathers until after the chick has departed to sea. This might enable chicks to channel limited protein, including yolk protein, into growing only the smaller feathers that are immediately critical for a timely transition from nest site to sea. As a result of both of these adaptations, yolk protein should constitute a larger proportion of the total protein required for feather growth in nestling intermediate auks, which should make egg-size effects on feather growth easier to detect.

Does egg size reflect female quality?

Initial Volume was a poor predictor of the growth of the fostered chicks. This suggests that egg size and chick growth did not both positively reflect measures of female quality. The same result was found in several

previous studies (e.g. Smith et al. 1995, Amundsen et al. 1996), although in others, a female's original egg size predicted her foster chick's growth more strongly (Amundsen and Stokland 1990, Reid and Boersma 1990). Hipfner and Gaston (1999a) offered a number of potential explanations for the lack of relationship seen in Thick-billed Murres. Of these, the most plausible for Razorbills in this study is that the experimental sample was biased towards older and more experienced, and therefore more capable, birds. This might have occurred because young birds are more likely to fail soon after laying (e.g. de Forest and Gaston 1996), whereas eggs were switched just prior to hatching. As a result, even the small-egg experimental Razorbill pairs might have been composed of capable birds; in Thick-billed Murres, egg size varies considerably even among older, more experienced females (Hipfner et al. 1997).

Conclusions

To summarize, egg size had the same positive effect on early wing-feather growth in Razorbills as seen previously in Thick-billed Murres. To date, this effect has been detected only in these two intermediate auks, suggesting that an effect of this magnitude might reflect evolutionary priorities in the post-hatching development of this group. More research is needed to confirm or refute this, and I suggest that studies of the relationship between egg size and post-hatching development in semi-precocial auks might be particularly revealing. More generally, the results of this study again raise the question of how variation in egg size can persist in bird populations, especially in those that lay one-egg clutches. If egg size positively affects fitness, as seems likely from the results of this study, despite having a heritable, genetic component (Boag and van Noordwijk 1987), we would expect natural selection to drive populations towards a ubiquitous, optimal, large egg size. This paradox has been discussed frequently (e.g. Amundsen et al. 1996); future research should examine the consequences of egg size for the fitness of both adults and their offspring.

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