

THE EFFECTS OF PARENTAL QUALITY AND TIMING OF BREEDING ON THE GROWTH OF NESTLING THICK-BILLED MURRES¹

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Abstract. In the Thick-billed Murre *Uria lomvia*, an Arctic seabird that raises a single chick annually, late-hatched chicks often grow slowly and depart the nest lighter in mass than early-hatched chicks. At Coats Island, N.W.T., Canada, in 1994 and 1995, I examined whether the seasonal declines in growth were caused by timing of breeding (the "seasonal deterioration" hypothesis), or by late breeding of less capable pairs (the "parent quality" hypothesis). I removed the single egg from early-breeding pairs, inducing them to relay, and compared the growth of chicks from these replacement eggs to that of chicks of unmanipulated pairs. Growth rate and mass at nest departure correlated negatively with hatching date in the general population. However, in both years the experimental chicks grew as well as the chicks of unmanipulated early-breeding birds, and departed at similar mass. The experimental chicks also grew more quickly than unmanipulated chicks that hatched later in the season, in one of two years. These results support the parent quality hypothesis, but not the seasonal deterioration hypothesis. I suggest that the late breeding of less capable birds is the likely proximate cause of many of the seasonal declines in success reported frequently in the Alcidae.

Key words: Alcidae, growth, parent quality, Thick-billed Murre, timing of breeding, *Uria lomvia*.

INTRODUCTION

Perrins (1970) proposed that the timing of egg-laying in birds results from an interaction between the evolutionary advantages of early breeding and physiological constraints acting on individual females during the period of egg formation. In this view, early breeding is advantageous because conditions for raising young deteriorate late in the season. However, some birds cannot produce their eggs early, and consequently raise their young when conditions are unfavorable. In many species, young, inexperienced birds lay their eggs later than older, experienced birds (reviewed by Forslund and Pärt 1995) and reproductive success declines with laying date (reviewed by Perdeck and Cavé 1992).

Because there is a causal relationship between parent quality and timing of breeding, it is difficult to distinguish their relative effects on reproductive success. One approach to this problem is to experimentally induce high quality birds to breed late in the season. In experimental studies, timing of breeding determined success

in some cases (Brinkhof et al. 1993, Norris 1993, Wiggins et al. 1994, Barba et al. 1995), but not in others, after controlling for parent quality (de Forest and Gaston 1996). In others, both timing and quality influenced success (Verhulst et al. 1995). In colonial species, timing relative to other members of the population, rather than calendar date, could determine success (Hatchwell 1991). Finally, even if conditions deteriorate late in the season, high quality birds might be able to compensate for this (Brouwer et al. 1995).

For species that breed in highly seasonal environments, such as the Arctic, the short period of favorable conditions should result in strong selection for early laying. However, it may be difficult for females to acquire sufficient food to produce eggs early in the season. Consequently, Arctic species should provide excellent subjects in which to examine the effects of timing of breeding and parent quality on reproductive success.

Thick-billed Murres (*Uria lomvia*) are colonial, cliff-nesting seabirds of Arctic waters. They lay a single egg and feed their chick at the nest for 15-30 days, at which time the chick departs to the sea at up to 25% of adult mass (Gaston and Nettleship 1981). In agreement with

¹ Received 3 June 1996. Accepted 27 January 1997.

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Perrins' hypothesis, older Thick-billed Murres lay earlier than younger birds (de Forest and Gaston 1996), and reproductive success declines with date (Birkhead and Nettleship 1981, Gaston and Nettleship 1981, de Forest and Gaston 1996). Late-hatched chicks often grow slowly and depart the nest lighter in mass than early-hatched chicks (Gaston and Nettleship 1981, Birkhead and Nettleship 1982, Gaston et al. 1983). The seasonal declines in growth rate most often are attributed to reduced food availability late in the season.

Gaston (1985) listed four other factors that might cause late-hatched Thick-billed Murre chicks to grow slowly: (1) egg size declines with date and this might cause corresponding declines in post-hatching growth (Birkhead and Nettleship 1982), (2) lower temperatures late in the season might increase the maintenance requirements of chicks (Uspenski 1956), (3) fewer daylight hours late in the season might reduce the time available for adult birds to forage, and (4) late chicks, if less likely to survive, might receive less investment from their parents. Hypothesis (1) appears unlikely because growth in body mass is independent of egg size in Thick-billed Murres (Hipfner and Gaston, unpubl. data). Hypotheses (2)–(4), like the reduced food availability hypothesis, are effects of timing of breeding.

In this paper, I examine the causes of the seasonal declines in growth rates and departure masses of nestling Thick-billed Murres. I removed the single egg from early-breeding pairs, inducing them to relay about two weeks later (well past the peak laying period), and compared the growth of chicks from the replacement eggs to chicks of unmanipulated early and late-laying pairs. If timing of breeding causes the seasonal declines in growth (the "seasonal deterioration" hypothesis), then the experimental chicks should grow poorly compared to early unmanipulated control chicks. If the decline is a consequence of the late breeding of less capable birds (the "parent quality" hypothesis), then the experimental chicks should grow as well as early control chicks, and better than control chicks born later in the season.

METHODS

This study was conducted at the Thick-billed Murre colony of 30,000 breeding pairs at Coats Island, N.W.T., Canada (62°57'N, 82°00' W), in

1994 and 1995. In relation to other colonies of the eastern Canadian Arctic, Coats Island is noteworthy for the fast growth rates of chicks (Gaston et al. 1983).

Just prior to the start of hatching, I mapped and numbered ca. 50 sites at which an egg was present on each of two plots near the top of the colony. Every egg was marked with its site number in permanent ink, and egg length and maximum breadth were measured to within 0.1 mm with vernier calipers. Subsequently, all sites were checked at 2–3 day intervals, depending on weather; checks were delayed to 4 days twice in the middle of the chick-rearing period in 1994.

The first time a chick was present at a site, I estimated whether it had hatched that day (day 1) or the previous day (day 2), based on the condition of its down; I assumed it had hatched that day if it was wet or the down was still matted. If I was unsure, chicks with wing lengths < 26 mm were assumed to have hatched that day. When checks were 3 days apart, some chicks were considered to be 3 days of age if they had wing lengths > 27 mm. When first found, each chick was marked with a binary code of nail clipping and banded within a week of hatching. On every visit, each chick was weighed to within 1 g with a 300 g spring balance, and the length of the right wing was measured to within 1 mm with the wing held flat and straight along a ruler. All visits were made between 09:00 and 12:00.

I experimentally delayed a sample of early-breeding birds in both years. I mapped and numbered 25 breeding sites on each of two plots, and then measured and removed the single eggs. This was done on 25 and 26 June (near median laying date at this colony), using different plots in the two years. As the background color and pattern of markings is repeated on eggs laid by the same murre (Southern 1951), Polaroid photographs of these eggs were used to verify that the egg later found at the same site had been laid by the same female.

These plots were rechecked ca. 45 days later, based on periods of 14 days for egg replacement (de Forest and Gaston 1996), and 32–34 days for incubation (Gaston and Hipfner, unpubl. data). At this time, the replacement eggs were measured and the growth of the chicks that hatched from them was monitored using the protocol described above. For comparison, unmanipulated pairs were divided into two categories:

TABLE 1. Inter-year comparisons (mean \pm SD) of chick growth parameters. For growth 2–14 days, $n = 43$ (1994) and 44 (1995).

	1994 ($n = 57$)	1995 ($n = 56$)
Egg volume index, EVI (cm ³)	210.3 \pm 18.8	207.6 \pm 18.8
Hatching date (June 1 = 1)	55.8 \pm 4.5	54.9 \pm 5.0
Growth 2–14 days (g)	121.2 \pm 21.2	111.1 \pm 19.1*
Mass (g) at:		
14 days	208.6 \pm 21.1	189.9 \pm 19.1**
Maximum	232.2 \pm 23.7	219.6 \pm 22.8**
Departure	226.0 \pm 23.7	214.8 \pm 23.8*
Age at departure (days)	21.0 \pm 2.1	22.8 \pm 2.4*

* $P < 0.05$. ** $P < 0.01$, based on t -tests.

(1) early-breeding pairs were those that laid by the egg removal date, i.e., whose chick hatched \leq 28 July (25 June + 33 days incubation), and (2) late-breeding pairs were those whose chick hatched $>$ 28 July.

As a measure of egg size, I used an egg volume index (length-maximum breadth², EVI) that correlates linearly with fresh egg mass in Thick-billed Murres ($r = 0.95$, Birkhead and Nettleship 1984). Measurements at 2 days were used to estimate initial size because larger samples were available for 2-day-old chicks than for 1-day-old chicks (2-day measurements could be estimated by linear interpolation for chicks measured at 1-day). Only chicks that survived \geq 15 days are included in any analysis, because 15 days is the youngest age at which Thick-billed Murres are known to depart the nest of their own volition (Gaston and Nettleship 1981). Consequently, 14 days is the oldest age at which a sample is unbiased by some chicks having departed (Gaston 1985).

The following definitions are used: (1) maximum mass is the heaviest mass recorded for a chick, (2) age at maximum mass is the age of

the chick at this measurement, (3) departure mass is the mass of a chick at last measurement, and (4) departure age is the age at last measurement + 1 day. Linear regression was used to examine variation in growth in relation to hatching date. To compare growth between years, and between control and experimental groups in the same year, I used t -tests and analysis of variance (ANOVA). Where significant differences existed in an ANOVA, Tukey's tests were used to make pairwise comparisons. All reported probability values are two-tailed.

RESULTS

INTER- AND INTRA-YEAR VARIATION IN CHICK GROWTH

The egg sizes and hatching dates of unmanipulated Thick-billed Murre pairs were similar in 1994 and 1995 (Table 1). Chicks gained more mass between 2–14 days of age in 1994 than in 1995, and so were heavier at all developmental stages in 1994 (Table 1). Chicks also reached maximum mass and went to sea about 2 days younger on average in 1994 (Table 1).

For the chicks of unmanipulated pairs, total growth between 2–14 days correlated negatively with hatching date in 1995, but in 1994 the negative correlation was not quite significant (Table 2). In both years, 14-day mass correlated negatively with hatching date (Table 2, Fig. 1). The slopes of the regression lines were similar in 1994 (-1.24 g day⁻¹) and 1995 (-1.18 g day⁻¹) (ANCOVA, slopes $F_{1,111} = 0.01$, $P > 0.5$). Maximum and departure masses declined significantly with date in 1994, but not in 1995. Conversely, age at departure correlated negatively with hatching date in 1995 (a chick that hatched 5 days later than another one went to sea about

TABLE 2. Correlation coefficients between growth measurements and hatching date. For growth 2–14 days, $n = 43$ (1994), and 44 (1995).

	1994 ($n = 57$)	1995 ($n = 56$)
Growth 2–14 days	-0.29	-0.37*
Mass at:		
14 days	-0.27*	-0.29*
Maximum	-0.30*	-0.16
Departure	-0.28*	-0.11
Age at departure (days)	-0.21	-0.41**

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

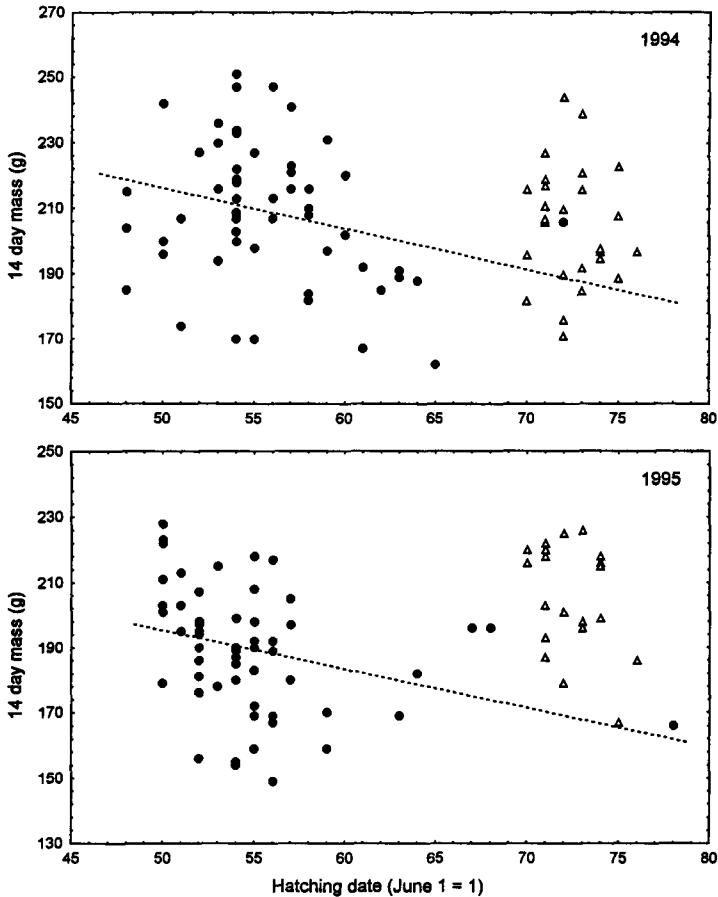


FIGURE 1. Scatter plot showing the relationship between chick mass at 14 days of age and hatching date in 1994 (top) and 1995 (bottom) for unmanipulated pairs (solid circles) and experimental pairs (open triangles). For unmanipulated pairs, the negative correlation between 14 day mass and hatching date was significant in both years (1994, $r = -0.27$; 1995, $r = -0.29$; both $P < 0.05$).

1 day younger on average), but this trend was not significant in 1994 (Table 2).

EGG REMOVAL EXPERIMENT

The egg sizes and hatching dates of early control pairs (mean hatching dates of 23–24 July suggest mean laying dates of 20–21 June) were similar to those of experienced females that were monitored at Coats Island in 1994 and 1995 as part of another study (females ≥ 8 years of age laid eggs with mean volume indices of 212 cm^3 (1994) and 209 cm^3 (1995), and their mean laying dates were 22 June in both years; Hipfner, Gaston and de Forest, unpubl. data) (Table 3). The first eggs of experimental pairs were similar in size to those of early control pairs in both

years (Table 3). This suggests that both groups were composed largely of experienced breeders.

Of the 50 eggs removed in 1994, 31 were replaced and still present when the plots were rechecked. Of these 31 replacement eggs, 26 produced chicks that were included in the analyses because they survived at least 15 days. In 1995, 22 replacement eggs were still present when the plots were rechecked; predation by an Arctic fox (*Alopex lagopus*) caused many losses on one plot. Twenty-one of these chicks reached 15 days of age, but three of these (the only remaining chicks on the fox-predated plot) were excluded from the estimates of maximum and departure mass and age because there was evidence that they were victims of fox predation at

TABLE 3. Comparisons (mean \pm SD) of growth between unmanipulated early chicks and experimental chicks.

Parameter	1994		1995	
	Early (n)	Exp (n)	Early (n)	Exp (n)
Egg volume index, EVI (cm ³)	212.3 \pm 18.2 (45)	214.4 \pm 16.9 (26)	209.1 \pm 18.3 (49)	213.2 \pm 20.3 (21)
Hatch date (June 1 = 1)	54.1 \pm 2.7 (45)	72.5 \pm 1.7 (26)**	53.4 \pm 2.2 (49)	72.5 \pm 1.7 (21)**
Growth, 2–14 days (g)	124.5 \pm 20.1 (37)	121.0 \pm 21.1 (20)	113.1 \pm 18.7 (39)	121.7 \pm 17.6 (17)
Mass (g) at:				
14 days	212.5 \pm 19.9 (45)	205.0 \pm 18.3 (26)	191.7 \pm 20.8 (49)	205.6 \pm 16.5 (21)*
Maximum	235.6 \pm 22.8 (45)	226.7 ^a \pm 18.6 (26)	220.6 \pm 22.9 (49)	226.8 \pm 25.8 (18)
Departure	229.3 \pm 22.5 (45)	228.4 \pm 19.9 (11)	215.4 \pm 23.9 (49)	219.9 \pm 25.7 (18)
Age (days) at:				
Maximum mass	18.0 \pm 2.5 (45)	16.7 \pm 1.6 (11)	19.7 \pm 3.3 (49)	16.7 \pm 1.7 (18)*
Departure	21.0 \pm 2.1 (45)	18.8 ^a \pm 1.5 (18)	23.0 \pm 2.2 (49)	19.6 \pm 1.5 (18)*

^a Probably an underestimate. See text.

* $P < 0.05$, ** $P < 0.01$, based on t -tests or ANOVAs.

14–15 days of age. There was no evidence of fox predation on either plot in 1994, nor on the second plot in 1995. Whereas the growth of unmanipulated chicks was better in 1994 than in 1995 (Table 1), all measures of growth of the experimental chicks were similar in the two years ($0.01 \leq t$ -values ≤ 1.29 ; $0.21 \leq P$ -values ≤ 0.99) (Table 3).

Chicks of experimental pairs hatched 18–19 days later on average than early control chicks in both years (Table 3), and 10 days (1994) and 8 days (1995) later than late control chicks. In 1994, the growth of the experimental chicks between 2–14 days of age was similar to that of early control chicks (Table 3). There were significant differences in the masses at 14 days of age among early control, late control and experimental chicks (ANOVA $F_{2,82} = 4.54$, $P = 0.01$). Tukey's tests indicated that the experimental chicks were similar in mass to early control chicks (Table 3), but unlike early control chicks, the 14 day masses of the experimental chicks did not differ significantly from those of late control chicks either (late control chicks averaged 194.2 ± 19.5 g at 14 days of age, $n = 12$). The masses of the experimental chicks were similar to those of early control chicks at all other developmental stages in 1994 as well (Table 3).

In 1994, 15 of the experimental chicks had not departed when observations ceased; they were 16–22 days of age (mean 18.9 ± 1.8 days) and weighed 177–241 g (mean 217.1 ± 19.0 g) on the day I left. As the maximum mass reported

for the experimental group in 1994 includes all 26 chicks, this mass is a minimum estimate. Nonetheless, this minimum estimate does not differ significantly from that of the early control chicks. The mean age at maximum mass, and the mean departure age and mass of the experimental chicks are for the 11 chicks that had departed when observations ceased. As the remaining chicks were older on average than the mean age at departure of those that left, the difference in mean departure age between the early control and experimental chicks might not be real.

In 1995, the experimental chicks gained slightly more mass between 2–14 days of age than the early control chicks. There were significant differences in 14 day masses among early control, late control and experimental chicks (ANOVA, $F_{2,76} = 6.93$, $P < 0.01$). Tukey's tests indicated that the experimental chicks were significantly heavier at 14 days of age than both early control chicks (Table 3) and late control chicks (late control chicks averaged 176.9 ± 14.8 g at 14 days of age, $n = 7$). Although 14-day mass declined significantly with hatching date (Table 2, Fig. 1), the 14 day masses of early and late control chicks did not differ significantly. The experimental chicks reached maximum mass younger, and departed younger, than early control chicks (Table 3). Both maximum and departure masses were similar in the two groups, possibly because the experimentals departed younger (Table 3).

DISCUSSION

Of the two hypotheses I tested to explain the seasonal declines in the growth rates of nestling Thick-billed Murres, there was no support in either year for the seasonal deterioration hypothesis, whereas the parent quality hypothesis was supported in 1995. Among unmanipulated pairs, growth rates and departure masses correlated negatively with hatching date, as in other studies (Birkhead and Nettleship 1981, Gaston and Nettleship 1981, Gaston et al. 1983). However, the chicks of the experimental pairs grew as well as the chicks of unmanipulated early pairs in both years, which suggests that the seasonal declines in growth rates were not caused by poor late-season feeding conditions. The experimental chicks also grew more quickly than the unmanipulated late chicks in 1995, which suggests that late breeding by less capable parents caused the declines in growth in 1995.

There are two possible explanations as to why timing had no effect on the growth of young raised by high quality pairs: (1) conditions may have been similar early and late in the season, at least in relation to the abilities of high quality pairs, and (2) in response to their lateness, the delayed pairs might have put more effort into provisioning their chicks. In 1995, the chicks of delayed pairs reached similar peak masses at younger ages, and departed younger, than chicks of early control pairs. This suggests that their parents might have worked harder to provision them. There was an indication of this in 1994 as well.

Late-breeding murres could benefit in a number of ways if they can prepare their young to depart early. Early departure might increase the survival of late-hatched chicks by reducing the amount of time they spend at the colony with few neighbors, and consequently under a heightened risk of predation (Hatchwell 1991). Early departure also has been associated with increased post-departure survival in Common Murre chicks *Uria aalge* in some years (Harris et al. 1992). Furthermore, because adult murres molt immediately after breeding (Birkhead and Taylor 1977), late breeders might benefit directly if their young go to sea quickly (Wanless and Harris 1988). Even if environmental conditions do not deteriorate late in the chick-rearing period at the colony, as has been presumed, early

breeding might be favored for these (and other) reasons.

COMPARISONS WITH OTHER STUDIES

Hatchwell (1991) and de Forest and Gaston (1996) conducted similar experiments on murres, and in both studies, experimental chicks grew as well as early chicks. Neither study reported the age and mass at nest departure of experimental chicks. However, Hedgren and Linnman (1979) found that experimental Common Murre chicks grew slowly compared to early chicks. They attributed this to the poor quality of prey available late in the season. Consequently, there may be timing effects on the growth of murre chicks at some colonies and in some years.

Murre colonies might function as "information centers" (Ward and Zahavi 1973). If so, less information may be available about the locations of profitable feeding areas late in the season when few birds are returning to feed chicks. As a result, late pairs in clusters may have an advantage over scattered, naturally late pairs. The experimental pairs in this study were in clusters, which might confound the experiment. However, Thick-billed Murres relieved of brooding duties congregate on the sea below the colony, then fly off in flocks in the direction of incoming birds; those returning to sea after bringing in food for their chicks fly straight back out to sea (Gaston and Nettleship 1981). Consequently, if information transfer occurs, it more likely occurs on the sea, rather than at the nest site (Gaston and Nettleship 1981).

CONCLUSIONS

Three observations suggest that the within-season patterns of food availability differed between 1994 and 1995: (1) while 14 day mass correlated negatively with hatching date in both years, maximum and departure masses did not in 1995. In 1995, departure age correlated negatively with date, so that late-hatched chicks did not achieve masses similar to early chicks by remaining longer in the nest, (2) whereas control chicks grew faster in 1994 than 1995 (suggesting that early in the year conditions were better in 1994), the delayed birds grew equally well in the two years (suggesting that late in the year, conditions were similar), and (3) the 14 day masses of experimental chicks were higher than those of early control chicks in 1995, whereas

they were similar in 1994. The simplest explanation for these observations is that feeding conditions improved late in 1995. Whereas the importance of inter-year variations in food supply for northern seabirds is well documented (e.g., Murphy et al. 1991), intra-year variations have received less attention. The results of this study, and others (e.g., Barrett et al. 1987), indicate that within-year variations also have measurable effects on the growth of nestling alcids.

Research on Thick-billed Murres at Coats Island has indicated that parent quality may be more important than timing of breeding in determining egg size (Hipfner et al., unpubl. data), reproductive success (de Forest and Gaston 1996), chick growth rate (de Forest and Gaston 1996; this study), and departure mass (this study). The breeding of the Alcidae is characterized by seasonal trends that reflect declining offspring quality: egg sizes (Lloyd 1979, Harris 1980, Birkhead and Nettleship 1982), chick growth rates (Nettleship 1972, Sealy 1981, Gaston et al. 1983), and departure masses (Ydenberg 1989) often decline over the season. I suggest that the seasonal declines in offspring quality are due mainly to declines in parent quality and that the putative environmental deteriorations might be of secondary importance. However, exceptions to these trends occur (e.g., masses at nest departure did not decline in 1995), and could be due to within-year variations in food availability.

ACKNOWLEDGMENTS

I would like to thank Josiah Nakoolak for excellent assistance with fieldwork in both years, and Grant Gilchrist for help in 1995. For logistical support, thanks to Lynn Peplinski and the staff of the Science Institute of the Northwest Territories, and the Polar Continental Shelf Project of Energy, Mines and Resources Canada. Funding to conduct this research was provided by the Canadian Wildlife Service, the Natural Sciences and Engineering Research Council of Canada (through a grant to A. J. Gaston), and the Northern Studies Training Program. Comments from Tony Gaston, Grant Gilchrist, and two anonymous reviewers improved an earlier version of this manuscript.

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