EGG PRODUCTION IN THE THICK-BILLED MURRE (Uria lomvia) AND RAZORBILL (Alca torda): A LIFE-HISTORY PERSPECTIVE

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by

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ABSTRACT

A key tenet of life-history theory is that costs of reproduction lead to physiological and evolutionary trade-offs among fitness components. Although avian egg production was a key topic in the development of life-history theory, the significance of egg production costs within the life histories of birds remains poorly understood. Two aspects of egg production that have received considerable attention are variation among females in their capacity to renest following clutch loss, and variation in the size of egg they lay. I examined these aspects of egg production in two pelagic seabirds, Thick-billed Murres *Uria lomvia* and Razorbills *Alca torda*. It is generally thought that egg production costs are relatively low in pelagic seabirds that lay single-egg clutches, but age- and date-specific patterns in renesting capacity and egg size suggest that significant constraints on egg production operate in these birds.

The proportion of Thick-billed Murres that renests following egg loss declines with the date of loss. However, early-laying females that had their eggs removed continued to renest until late in the laying period. First and replacement eggs were similar in crude composition, but replacement eggs had low protein content. Despite this, replacement eggs were no less likely to hatch than were first eggs, and chicks from replacement eggs were no less likely to survive to nest departure, and to recruitment age (4–5 years). I conclude that variation in the egg-production capacity of females that lose their eggs early and late (probably age/experience effects) drives the seasonal declines in renesting rates. Capable females will relay until late in the laying period because, for these birds, the potential fitness payoff from a replacement egg is similar to that from a first egg. It remains to be determined whether there are survival costs associated with the production of replacement eggs for female Thick-billed Murres.

Thick-billed Murre eggs vary considerably in size, and egg size affects offspring performance: chicks from large eggs have their wing feathers grow more quickly than do those from small eggs.

One hypothesis often invoked to explain the existence of variation in egg size in the face of expected directional selection for large eggs is that the optimal egg size varies with environmental conditions; this hypothesis predicts that benefits of hatching from a large egg will be magnified when feeding conditions are unfavourable. I tested this by comparing between colonies that experience favourable (Coats Island) and unfavourable (Digges Island) conditions, using an experimental egg-switching protocol. Contrary to prediction, the effect of egg size on wing feather growth was no greater at Digges Island than at Coats Island.

This effect of egg size on wing-feather growth has not been detected in other birds, suggesting that it might reflect adaptations to the unique "intermediate" developmental strategy employed by murres and Razorbills. To test this hypothesis, I examined the effect of egg size on post-hatching development in the Razorbill using the same egg-switching protocol. Results clearly supported the hypothesis: as in Thick-billed Murres, large-egg Razorbills experienced enhanced early wing-feather growth. There are a number of adaptations in the development of intermediate alcids that might explain why this egg-size effect is readily detectable in these birds. As there was no evidence for a trade-off between egg size and provisioning in either Thick-billed Murres or Razorbills, the existence of considerable female-specific variation in egg size remains unexplained.

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Chapter 1: Introduction and Overview

Research into avian egg production was at the forefront of the development of life-history theory, largely as a consequence of David Lack's early studies of clutch size (Lack 1947). Lack suggested that egg production was not a particularly demanding process for birds, at least in comparison to chick-rearing; this conclusion was based largely on the apparent ease with which many species of birds replaced lost eggs and clutches. For many years afterwards, research into the evolution of avian life-histories concentrated heavily on the reproductive costs associated with chick-rearing, while largely ignoring those associated with egg production (Stearns 1992). However, a number of recent studies have shown that females that produce more than the usual number of eggs subsequently feed their chicks less efficiently (Heaney and Monaghan 1995, Monaghan et al. 1998). Moreover, eggs produced above and beyond the normal number may be of low quality, as indicated by low hatching success (Beintema et al. 1997), or higher-than-expected mortality of the nestlings that hatch from them (Monaghan et al. 1995). As a consequence of new experimental studies, the view that has emerged in recent years is that avian egg production is much more demanding than Lack believed, and that the reproductive costs associated with this stage of the breeding cycle have been important in shaping avian life histories (Monaghan and Nager 1997).

This thesis examines two aspects of avian egg production within a life-history framework: the determinants and consequences of replacement egg-laying among Thick-billed Murres *Uria lomvia* (Chapters 2 -4), and the consequences of egg size for Thick-billed Murres (Chapter 5) and Razorbills *Alca torda* (Chapter 6). Thick-billed Murres and Razorbills are boreal and Arctic-nesting marine birds of the family Alcidae which, like most seabirds, employ high-survival, low-fecundity life-history strategies: both species lay single-egg clutches, and both experience annual adult survival rates of about 90% (Hudson 1985). Species that employ this sort of life-history strategy are expected to invest cautiously in reproduction in any single breeding season, because their maximum reproductive output in any one year represents only a very small proportion of their potential lifetime output, if they survive. While their general life-history strategy is typical of seabirds, murres and Razorbills are unique in employing what Sealy (1973) coined the "intermediate" developmental strategy: their chicks remain at the nest for only about 20 days, before departing to sea with their male parent at <30% of adult mass and covered in a transitional, mesoptile plumage, to complete their growth at sea. The greatly reduced period of development at the colony is thought to reflect the extreme demands of raising young on prey captured far from the colony , and that is unpredictable in space and time (Lack 1968). Constraints on chick provisioning are especially severe for murres and Razorbills, because they have extremely high wing-loading that limits the size of prey that adults can carry back to their offspring at the nest site, and makes trips back and forth from feeding areas to the nest energetically expensive (Pennycuick 1987). As in other marine birds, and perhaps especially for these two species, the single-egg clutch is generally thought to reflect constraints operating at the chick-rearing stage of the breeding cycle, rather than at the egg-production stage. In fact, direct measurements of the energetic content of the yolk relative to the female's standard metabolic rate indicate that, in comparison to other groups of birds, yolk formation may not be a particularly demanding process for murres and most other seabirds (Astheimer and Grau 1990). However, as noted by Monaghan and Nager (1997), the energy content of the final product does not take account of the additional energy expended by the female in foraging to acquire the nutrients to put into the egg. For many pelagic, marine birds, these additional requirements are likely to be considerable. In addition, both Thick-billed Murres (Hipfner et al. 1997) and Razorbills (Lloyd 1979) show age-related trends in egg size that would not be expected if egg-production costs were insignificant.

In Chapter 2, I examine the underlying causes of the seasonal decline in the proportion of Thick-billed Murre pairs that replace lost eggs. This is widely thought to occur because females have little to gain, and much to lose, by renesting late in the season: due to a seasonal reduction in food supply, birds that breed late jeopardize their own survival, while their late-hatched offspring have little chance of surviving. However, birds that lose their eggs late in the season typically are younger, less experienced females, birds whose egg-production capacity (i.e. their ability or "willingness" to invest heavily in producing eggs) is low (Hipfner et al. 1997). Therefore, an alternative hypothesis holds that it is the low egg-production capacity of females that lose their eggs late, rather than the fact that they do lose their eggs late, that makes them unlikely to relay. I use an experimental approach that controls for variation in the quality of birds that breed early and late in the season, to distinguish between these alternatives.

In Chapter 3, I compare survival between colony departure and recruitment age (4-5 yr of age) for Thick-billed Murres that hatched from first and replacement eggs in experimental studies carried out in 1994 and 1995 (Hipfner 1997). Empirical studies (e.g., Birkhead and Nettleship 1981), and theoretical models (Birkhead and Nettleship 1982, Ydenberg 1989), of breeding by Arctic seabirds generally assume that young that depart from the colony late in the season are unlikely to survive. As in Chapter 1, the experimental approach was designed to control for variation in the quality of pairs that breed early and late in the season.

In Chapter 4, I examine characteristics of first and replacement eggs laid by the same early-laying ("high quality") female Thick-billed Murres. A number of studies on other species of birds have compared the characteristics of first and replacement eggs and clutches, and attempted to evaluate whether any differences between them reflected evolutionary strategies that females employ to mitigate the costs of renesting, or were consequences of physiological constraints (e.g., Arnold 1993, Nilsson 2000).

Among Thick-billed Murres, there is a remarkably consistent 5-6% average reduction in egg size between first and replacement eggs. Birkhead and Nettleship (1982) suggested that female murres reduce the size of replacement eggs in order to advance laying ahead of the seasonal reduction in food supply. In support of this, Common Murres *Uria aalge* were found to form replacement eggs more quickly than first eggs (Birkhead and del Nevo 1987), and this appeared to be true for Thick-billed Murres as well (Hipfner et al. 1997). However, the alternative hypothesis, that the small size of replacement reflects constraints on egg production, seems to have been rarely considered. I evaluate the two hypotheses by comparing the size, and crude and biochemical composition, of first and replacement eggs. This chapter also presents data on the amino acid composition of the protein in albumen and yolk in Thick-billed Murre eggs, information that is available for very few species of wild birds.

Chapters 5 and 6 turn to investigations on a second aspect of avian egg production, variation in egg size. In Chapter 5, I test a widely-discussed, but rarely investigated, hypothesis regarding the fitness consequences of egg size for birds: namely, that the advantage(s) of hatching from a large egg is magnified when feeding conditions are unfavourable. In many taxa, offspring that hatch from large eggs enjoy advantages over those from small eggs (Azevedo et al. 1997). However, there are surprisingly few data to support this notion in birds, even though the relationship between egg size and offspring fitness probably has been investigated frequently in birds (Williams 1994). Several researchers have suggested that the lack of evidence for an effect of egg size on offspring fitness may be due to the fact that experimental studies that examined this relationship were carried out in situations in which breeding birds experienced favourable feeding conditions (e.g., Reid and Boersma 1990, Smith et al. 1995). Moreover, it has been suggested that variation in feeding conditions might explain why considerable variation in egg size, an inherited trait thought to affect fitness, persists within bird populations (e.g., Ankney and Bissett 1976). In this view, a range of egg-size genotypes can coexist within a population because the the optimal egg size varies across years, due to variation in feeding conditions. Consequently, in favourable years, the small (or non-existent) fitness advantage that offspring gain by hatching from a larger egg is more than offset by the added fitness cost incurred by the adult female for producing that larger egg. In unfavourable years, a large egg offers sufficient advantage that it outweighs the added costs of producing it. This hypothesis has rarely been tested, because few avian studies have examined the consequences of egg size across a range of feeding conditions. I compare the consequences of egg size for Thick-billed Murres at a colony where feeding conditions during chick-rearing are unfavourable to results of a previous study (Hipfner and Gaston 1999a) carried out at a colony where feeding conditions were more favourable. Thick-billed Murres offer the advantage of being one of very few species for which there is experimental evidence that egg size affects offspring fitness (Hipfner and Gaston 1999a).

Finally, in Chapter 6, I employ an experimental approach to test the hypothesis that the positive relationship between egg size and post-hatching wing-feather growth observed previously in Thick-billed Murres reflects adaptations of "intermediate" alcids (Hipfner and Gaston 1999a). To do this, I carried out an egg-switching experiment in Razorbills. For the intermediate alcids, rapid growth of primary coverts (the longest feathers on the wings of nestling murres and Razorbills) during the brief nestling period appears to be critical to enable the chick to make the transition from life at the nest site to life at sea quickly and safely (Birkhead 1977, Hipfner and Gaston 1999b). This is because these species typically breed high on cliffs, and at nest departure, the chick glides and flutters from the nest to the sea, accompanied by the male parent. Mortality rates are very high on young that fail to reach the sea directly (e.g., Gilchrist and Gaston 1997). There appear to be a number of adaptations in egg characteristics and patterns in the post-hatching development of the intermediate alcids that reflect the urgency of growing long covert feathers. These adaptations are discussed in detail.

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1.2 Co-Authorship Statement

My contributions to the research described in this thesis were: (1) I proposed and developed the research questions, and was primarily responsible for the design of the experiments used to address these questions; (2) I was primarily responsible for carrying out all of the field work described, except for the field work carried out at Coats Island in 1997 (see Chapter 2). The analyses of the biochemical composition of Thick-billed Murre eggs (see Chapter 4) were carried out by, or under the direction of, Drs. J. Brosnan and G. Herzberg, Department of Biochemistry, Memorial University of Newfoundland; (3) I analysed all of the data; and (4) I wrote all of the chapters/manuscripts.

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Chapter 2: Seasonal Declines in Replacement Egg-Layings in a Long-Lived, Arctic Seabird: Costs of Late Breeding or Variation in Female Quality?

2.1. Abstract

In many species of birds, the proportion of females that relays after losing their first clutch varies. Replacement clutches can make important contributions to an individual's lifetime reproductive success, so the decision on whether or not to relay may have significant consequences for fitness. Many studies report that female birds of "high quality" (e.g., older and more experienced) were more likely to relay following clutch loss, and that the proportion of females that relaid declined as the breeding season progressed. High quality females tend to nest early, and may be less likely to lose their clutch. As a result, it is unclear whether few females relay late in the season because there are prohibitive costs associated with late breeding, or because those females that lay and lose their eggs late are of low quality, and therefore incapable of relaying. I examined the roles of date and quality in causing seasonal declines in replacement layings in the Thick-billed Murre *Uria lomvia*, a long-lived, Arctic marine bird that lays a one-egg clutch. At two low-Arctic colonies in eastern Canada in 1996 and 1997, the single egg was experimentally removed from samples of early-laying pairs (presumably those of high quality) at 3 day intervals beginning on the median laying date and ending 12 days later. In the general population, the proportion of pairs that relaid following natural egg loss declined with the date of loss. In contrast, the proportion of experimental pairs that relaid remained high irrespective of the date their egg was removed. These results support the quality hypothesis, but not the date hypothesis. I conclude that seasonal declines in replacement layings occurred primarily because increasing proportions of low quality females lost eggs as the season advanced. The

experimental pairs also suffered no overt reduction in reproductive success as a result of the delay, at least up to the time that their chicks departed to sea. This suggests that timing of breeding had little effect on the immediate success of more capable pairs. These results may have important implications about the seasonality of low-Arctic marine environments, and the life histories of birds that inhabit them.

2.2 Introduction

According to life-history theory, individuals of iteroparous species will attempt to balance the benefits of investing in current reproduction against the costs that reduce their ability to invest in future reproduction in order to maximize their lifetime reproductive success (Stearns 1992). One life-history decision that many birds face during a breeding season is whether to lay a replacement clutch if they lose their first. Replacement clutches potentially make important contributions to an individual's lifetime success, especially in species or populations prone to clutch loss (Martin et al. 1989, Keegan and Crawford 1993). However, many studies report that only a low proportion of female birds that lost their first clutch relaid (e.g., Duncan 1987, Connelly et al. 1993), suggesting that the costs can be prohibitive for many individuals. In several studies, females that relaid following clutch loss were older and more experienced (Wooller 1980, Boekelheide and Ainley 1989, Wheelwright and Schultz 1994), or in better condition (Hegyi and Sasvári 1998), than those that did not relay. Other studies report that females that renested laid more eggs (Rooneem and Robertson 1997) or larger eggs (Sandercock and Pederson 1994) in their first clutches, and that they laid their first clutches earlier in the season (e.g., Kelly and van Horne 1997). These observations suggest that "high quality" females might be more likely to relay. In addition, the proportion of individuals that relays invariably declines with the date of clutch loss (Feare 1976, Parsons 1976, Arnold 1993, Barba et al. 1995). This might reflect the high cost-to-benefit ratio associated with late breeding (Silverin 1980). Consequently, one of the most important evolutionary advantages of early laying for birds might be the increased potential to renest in the event that the first clutch is lost (Hannon et al. 1988).

Thick-billed Murres are colonial, cliff-nesting, marine birds in which annual adult survival is high (c. 90%, Gaston et al. 1994) and annual reproductive output is low (they lay a one-egg clutch). Species with these life-history characteristics, which include many marine birds, are expected to invest cautiously in reproduction in any single year in order to avoid jeopardizing their future reproductive potential. Moreover, Thick-billed Murres breed in the Arctic where the penalties for late breeding are thought to be severe (e.g., reduced reproductive success, Birkhead and Nettleship 1981). It is not surprising then that few Thick-billed Murres replace lost eggs (typically 20-30% of those that lose an egg relay), and that the proportion that replaces declines abruptly with the date of egg loss (Gaston and Nettleship 1981, Birkhead and Nettleship 1987a, de Forest and Gaston 1996). However, many eggs that are lost, and particularly those lost late in the season, belong to young, inexperienced females because these females lay later (Hipfner et al. 1997), and are more likely to lose their eggs than are older, more experienced females (de Forest and Gaston 1996). As a result, it is unclear whether the seasonal declines in the proportion of Thick-billed Murres that lay replacement eggs are caused by date effects *per se*, or by late breeding and late egg loss of low quality females.

In this paper, I examine the roles of date and female quality in causing seasonal declines in replacement layings by Thick-billed Murres. I removed the single egg from early-laying pairs (those that appear to be most capable, de Forest and Gaston 1996) at successively later dates that spanned the interval during which declining proportions of control pairs were replacing lost eggs. If the declines are caused by date effects and are independent of female quality (the *date hypothesis*), then the experimental pairs should follow the population-wide declines. Conversely, if the declines are quality effects and independent of date (the *quality hypothesis*), then the proportion of experimental females that relays should remain high irrespective of the date their egg is removed. I also compare the reproductive success of the experimental pairs to that of early-laying, unmanipulated pairs to investigate whether replacement eggs are less likely to produce fledged chicks than are first eggs for Thick-billed Murre pairs that lay their first eggs early in the season. Finally, I examine causes of variation in the number of days that elapse between removal of the first egg and the laying of a replacement egg (hereafter the relaying interval), and causes of variation in the size of replacement eggs compared to first eggs laid by the same female.

2.3 Study Area and Methods

The study was conducted at the Thick-billed Murre colonies at the Gannet Islands, Labrador, Canada (53°56'N, 56°32'W) in 1996 and 1997, and at Coats Island, Nunuavut Territory, Canada (62°57'N, 82°00'W) in 1997. Both colonies are situated in the low-Arctic oceanographic zone (Nettleship and Evans 1985).

I monitored the breeding chronology and breeding success of Thick-billed Murres using the Type I methods of Birkhead and Nettleship (1980). Experimental pairs were selected from among those pairs that laid by the estimated median laying date for the whole colony. At both colonies in 1997, median laying dates were estimated from plots observed in previous years that held known numbers of breeding pairs. Because 1996 was our first year at the Gannet Islands, the median laying date had to be estimated based on site occupancy on plots observed during the pre- and early-laying periods. These methods proved reliable: the estimated median laying dates were within 1 day of the true median (estimated from laying dates of first eggs for all study pairs) in all samples. In each of the three colony-years of study, the single egg was removed (under permit from the Canadian Wildlife Service) from five to eight experimental pairs on each of five occasions, beginning on the median laying date, and continuing at 3 day intervals up to the median + 12 days. At the Gannet Islands, a total of 30 eggs was removed in 1996, and 25 in 1997; 33 eggs were removed at Coats Island in 1997. Control samples in these three colony-years were 35, 42, and 123 pairs that lost their first eggs naturally. The length and maximum breadth of each removed egg was measured ($\pm$ 0.1 mm) using calipers, and a volume index (length * breadth^2) that has a strong linear relationship with the fresh mass of Thick-billed Murre eggs ($r = 0.952$, Birkhead and Nettleship 1984) was used as a measure of egg size. At Coats Island, where many Thick-billed Murre breeding sites were accessible, most of the experimental replacement eggs were measured. To minimize disturbance, replacement eggs were not measured at the Gannet Islands, where most sites were less accessible.

Wherever possible (see below), the following information was recorded for both control and experimental pairs: (i) laying date of first egg; (ii) date of loss (or experimental removal) of first egg (I attempted to exclude infertile eggs - those that were incubated to full term but failed to hatch - by including only eggs that disappeared <31 days after laying, the minimum incubation period for Thick-billed Murre eggs at both colonies; Hipfner et al. in press); (iii) laying date of replacement egg; (iv) hatching date; (v) date of disappearance of chick. Chicks were assumed to have survived to depart from the colony if they disappeared $\geq$ 15 days after hatching (the minimum age at which Thick-billed Murre chicks are known to depart the nest of their own volition, Gaston and Nettleship 1981); it was assumed that they had died prior to departure if they disappeared at < 15 days of age.

Observations at the Gannet Islands in 1996 continued until all control eggs, and all experimental replacement eggs, had hatched. However, field crews left the islands before all experimental chicks had departed so that fledging success data were unavailable for that year. In addition, the laying dates of few experimental first eggs were known in 1996 (although all were laid by the estimated median laying date). In 1997, observations at the Gannet Islands spanned the entire breeding season, but observations at Coats Island ceased prior to the hatching of all experimental eggs.

2.3.1 *Data Analysis*

Most analyses were conducted using SigmaStat (version 2.0) statistical software, which automatically examines the normality and equality of variance assumptions of parametric statistical tests. Non-parametric tests were used where these assumptions were not met. To analyze variation in the proportion of pairs that relaid in relation to date of egg loss (and other factors, as appropriate), logistic regression analyses were conducted using SPSS (version 7.5) statistical software. I started with logistic regression models that included only the constant and then used a forward stepwise variable selection procedure with all main effects and all interaction terms available. Variable selection was based on the change in the likelihood-ratio that occurred with the variable deleted from the model. Significance levels for entry into the model were set at $P < 0.05$, and at $P > 0.1$ for removal from the model (the default values in SPSS).

To examine natural variation in the incidence of replacement egg-laying in relation to the date of egg loss, the logistic regressions were run first on all control pairs, with date of loss (relative to the median laying date in that colony-year) entered to the exact day. Because eggs were removed at 3 day intervals over a set time period, relaying probability was compared between control and experimental pairs with the data: (i) grouped by 3 day intervals relative to the median laying date in each colony-year, and (ii) limited to the period of overlap between natural egg losses and experimental egg removals (from the median laying date - 1 day, to the median + 13 days, see Fig. 1). All means are reported ± 1 SD, and all reported *P*-values are two-tailed.

2.4 Results

2.4.1 *Timing of breeding*

Timing of breeding by Thick-billed Murres was similar at the Gannet Islands in the two years, with median laying dates of first eggs falling on 26 June (1996) and 28 June (1997). This was similar to the timing recorded in previous years at this colony (Birkhead and Nettleship 1987b). The median laying date at Coats Island fell on 21 June in 1997, which was relatively early in comparison to previous years at this colony (Gaston and Hipfner 1998).

2.4.2 *Date of egg loss and the probability of replacement laying*

Two experimental pairs stole eggs from neighbouring Thick-billed Murres after their own egg was removed at the Gannet Islands in 1996, as did one pair in 1997. In addition, two experimental pairs stole eggs from Common Murre *Uria aalge* neighbours in 1996. These five pairs were removed from all analyses. Two experimental pairs stole eggs at Coats Island, but these eggs were returned by us to their original sites immediately.

In the logistic regression analysis, there was a negative relationship between the relative date of egg loss and the proportion of control pairs that relaid after they lost their first egg (Table 2.1, Fig.

Table 2.1: Results of a forward stepwise logistic regression analysis examining variation in the proportion of control Thick-billed Murre pairs that relaid following natural egg loss ($n = 200$). The constant was entered into the model. Variables available to the model were date of egg loss, colony-year, and the date * colony-year interaction term. Selection of variables was based on the change in the likelihood-ratio with the variable deleted from the model. Variables entered the model at $P < 0.05$, and were removed from the model at $P > 0.1$.

Variable	Change in likelihood-ratio	df	*P*	*R*
Constant		1	<0.001	
Date of egg loss	103.92	1	<0.001	-0.43

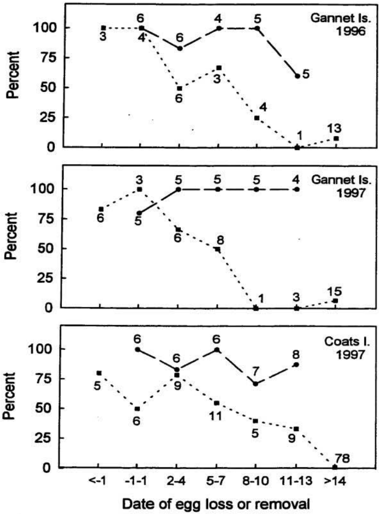

Figure 2.1: Percent of control (dotted line) and experimental (dashed line) Thick-billed Murre pairs that replaced lost eggs in relation to the date of egg loss or removal (grouped by 3 day intervals, in days from the median laying date) in the three colony-years. Sample sizes beside points.

Table 2.2: Results of a forward stepwise logistic regression analysis examining variation in the proportion of control ($n = 79$) and experimental ($n = 83$) Thick-billed Murre pairs that relaid following natural egg loss or egg removal during the period of overlap between the two groups. The constant was entered into the model. Variables available to the model were date of egg loss (grouped by three-day intervals), colony-year, treatment (control and experimental), and all two-way and the one three-way interaction terms. Selection of variables was based on the change in the likelihood-ratio with the variable deleted from the model. Variables entered the model at $P < 0.05$, and were removed from the model at $P > 0.1$.

Variable	Change in likelihood-ratio	df	*P*	*R*
Constant		1	<0.001	
Date of loss * treatment	41.73	1	<0.001	-0.40

three for 15 days. Incubation periods of experimental first eggs that were replaced ranged from 0 to 16 days. During the period of overlap between natural egg losses and experimental removals at the Gannet Islands in 1997 (the only sample in which I had complete data), control pairs had incubated their first eggs for less time before they lost them than had the experimental pairs prior to having their eggs removed (controls: median = 2 days, $n = 21$; experimentals: median = 8 days, $n = 24$; Mann-Whitney test, $P = 0.01$).

2.4.4 *Relaying interval and replacement egg size*

I used multiple regression to examine how relaying intervals were affected by: (i) the date of egg removal, and (ii) the length of time that first eggs were incubated, using data from the two colonies in 1997. The multiple regression was highly significant ($F_{2,54} = 12.52$, $P < 0.001$). However, neither of the independent variables appeared to be important in this analysis (both $P \geq 0.42$), probably because they were strongly intercorrelated ($r_{55} = 0.96$, $P < 0.001$)(see Zar 1996, p. 419). In simple regressions, the relaying interval increased with both the date of egg removal and the number of days that the first egg had been incubated (Table 2.3). The regression lines did not differ significantly in either elevation or slope between colonies (Table 2.3), and Fig. 2.2 shows the relationship between relaying interval and duration of incubation with the two samples combined.

Experimental replacement eggs that were measured at Coats Island averaged 6.1 ± 2.8% smaller than first eggs laid by the same female (first eggs: mean = 211.3 ± 15.4 cm^3; replacement eggs: mean = 198.3 ± 15.3 cm^3, both $n = 27$; paired $t_{26} = 11.89$, $P < 0.001$). The sizes of first and replacement eggs laid by the same female were strongly correlated ($r_{25} = 0.93$, $P < 0.001$). The percent difference in volume index between first and replacement eggs showed little relationship with

Table 2.3: Regressions relating the relaying interval to: (1) the date of removal of first eggs, and (2) the number of days that the first eggs were incubated prior to removal (covariates in the ANCOVAs), for experimental Thick-billed Murres at the Gannet Islands (*n* = 24) and Coats Island (*n* = 33) (grouping variables in the ANCOVAs) in 1997.

					ANCOVA					
	Gannet Islands		Coats Island		Covariate		Colony		Interaction	
Variables	r^2	b	r^2	b	F	P	F	P	F	P
Removal date	0.22	0.18	0.63	0.26	31.70	<0.001	3.26	0.08	0.92	0.34
Incubation period	0.25	0.17	0.57	0.22	30.06	<0.001	1.69	0.20	0.36	0.55

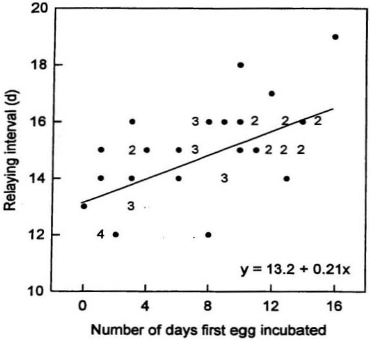

Figure 2.2: Relaying intervals of Thick-billed Murres in relation to the number of days that first eggs were incubated prior to experimental removal. Data from the Gannet Islands and Coats Island in 1997 were pooled.

the date of egg removal ($r^2 = 0.02$, $F_{1,25} = 0.41$, $P = 0.53$), the number of days that the first egg had been incubated ($r^2 = 0.02$, $F_{1,25} = 0.47$, $P = 0.50$), or the relaying interval ($r^2 = 0.01$, $F_{1,25} = 0.24$, $P = 0.68$).

2.4.5 *Reproductive success of experimental pairs*

At the Gannet Islands in 1996, the hatching success of experimental replacement eggs (87%, $n = 23$) was similar to that of first eggs laid by unmanipulated pairs that laid by the date of the first egg removal (93%, $n = 93$; $\chi^2_1 = 0.52$, $P = 0.47$, Yates' correction applied). Hatching success ($\chi^2_1 = 1.47$, $P = 0.23$, Yates' correction applied), fledging success (Fisher's exact test, $P = 0.71$), and reproductive success ($\chi^2_1 = 0.57$, $P = 0.45$, Yates' correction applied), of experimental pairs were similar to those of control early pairs at the Gannet Islands in 1997 (Fig. 2.3).

2.5 Discussion

2.5.1 *Seasonal declines in replacement layings: effects of date or quality?*

As in previous studies (Gaston and Nettleship 1981, Birkhead and Nettleship 1987a, de Forest and Gaston 1996), the proportion of Thick-billed Murres that laid replacement eggs declined with the date of egg loss in the general population. However, the proportion of experimental females that relaid remained high irrespective of the date their egg was removed. Consequently, these results support the quality hypothesis, but do not support the date hypothesis. I conclude that seasonal declines in replacement layings occurred in the general population primarily because increasing proportions of low-quality females lost eggs as the season advanced. A previous study found that young, inexperienced female Thick-billed Murres laid later than older, experienced females (Hipfner et al.

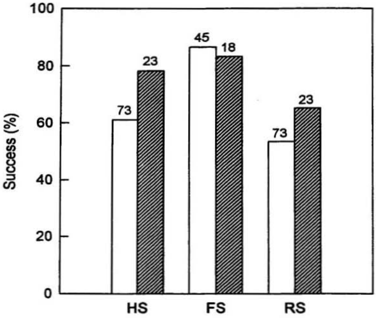

Figure 2.3: Hatching success (HS), fledging success (FS) and reproductive success (RS) of control (open bars) and experimental (hatched bars) Thick-billed Murre pairs at the Gannet Islands in 1997. Control pairs were those that laid by the date of the first experimental egg removal. All measures of success were similar between controls and experimental pairs. Numbers above bars are sample sizes.

1997). Young birds also were less likely to lay a replacement egg, and those that did had long relaying intervals (de Forest and Gaston 1996). These observations indicate that a female Thick-billed Murre's capacity (i.e., her ability or "willingness") to produce a replacement egg increases with her age and/or experience, as does her capacity to produce a first egg (Hipfner et al. 1997). I suggest that the female quality effects documented in this study largely reflect effects of age and/or experience.

Many recent experimental studies, most involving temperate-nesting species, have examined the extent to which date effects and parental quality effects caused avian reproductive success to vary within seasons (e.g., Brinkhof et al. 1993, Norris 1994, Wiggins et al. 1994, Siikimäki 1998). Date effects were more important than parental effects in most studies. For example, experimentally-delayed, early-laying Great Tits *Parus major* were less likely than unmanipulated early-laying females to lay both replacement (Barba et al. 1995) and second (Verhulst et al. 1995, Verboven and Verhulst 1996) clutches. For many birds, there is a highly predictable decline in food availability (e.g., insects) late in the breeding season that is thought to compromise the survival of late-hatched young and late-breeding adults (Perrins 1970, Daan et al. 1988). Late-breeding adults (Gustaffson et al. 1994), and late nestlings (Sorci et al. 1997), may be more susceptible to disease, and late fledglings sometimes fare poorly in competition with those that fledge early (Nilsson 1989, Spear and Nur 1994). In addition, adults that delay their post-nuptial moult might produce a basic plumage of poor quality, which can increase thermoregulatory costs, and reduce overwinter survival (Nilsson and Svensson 1996). Consequently, there often is a high cost-to-benefit ratio associated with late breeding that could strongly influence avian reproductive behaviour. As with seasonal declines in clutch size (e.g., Winkler and Allen 1996) and the proportion of pairs that attempt second broods in the same season

(Verboven and Verhulst 1996), seasonal declines in the proportion of pairs that replace lost clutches might be evolutionary responses to the reduced fitness of late adults and late young in many species of birds (Silverin 1980).

The breeding season is thought to be strictly time-constrained in Arctic environments. Despite this, experimental Thick-billed Murres that laid their first eggs early in the season continued to lay replacement eggs until late in the laying period. This suggests that the evolutionary benefits obtained by relaying and raising young even very late in the season exceed the costs for the more capable members of Thick-billed Murre populations. Life-history theory predicts that species with high survival and low fecundity (like most marine birds, including murres) will invest cautiously in current reproduction because their lifetime reproductive success is influenced more by survival, and therefore the number of breeding episodes, than by annual fecundity (Clutton-Brock 1988). Congruent with this theory, studies on other marine birds often have found that adults faced with experimental trade-offs favoured their own well-being over that of their offspring (Sæther et al. 1993, Mauck and Grubb 1995, Wernham and Bryant 1998; but see Johnsen et al. 1994, Jacobsen et al. 1995). If this is true, then the most important implication of this study is that relaying, breeding late, and departing late from their low-Arctic colonies inflict relatively little additional cost on capable adult Thick-billed Murres. However, this remains to be tested directly.

The reproductive success of the experimentally-delayed Thick-billed Murre pairs was similar to that of unmanipulated early-laying pairs at the Gannet Islands, at least up to the time of departure of their chicks to sea. de Forest and Gaston (1996) obtained the same result in two previous years at Coats Island. In contrast, experimental studies on other bird species often find that replacement eggs follow natural, population-wide seasonal declines in success (Feare 1976, Barba et al. 1995, Verboven and Visser 1998; but see Parsons 1975, Hatchwell 1991). Moreover, Thick-billed Murre chicks raised by early-laying, experimentally-delayed pairs grew as well and were as heavy at nest departure as chicks raised by unmanipulated early pairs in three previous years at Coats Island (de Forest and Gaston 1996, Hipfner 1997). Consequently, it is unlikely that there is a systematic seasonal decline in the availability of food that affects the viability of Thick-billed Murre chicks raised by capable parents, at least at the low-Arctic colonies in this study (chick diets at the two study colonies consist mainly of fish, both pelagic, schooling species and benthic species; Gaston 1985, Bryant et al. 1999). If so, this differs from the situation for many other birds. However, I have no information on food availability after departure from these colonies, nor do I know whether departure date affects post-departure survival of young Thick-billed Murres. In some years, Common Murre chicks that departed late in the season from a temperate colony were less likely to be resighted in the future (Harris et al. 1992; but see Hedgren 1981), but late chicks might have had low survival because they were tended at sea by less capable parents, rather than because they departed late.

Murres also might obtain indirect benefits by laying replacement eggs late in the season if this acts as a signal of the female's-quality to her mate. Many studies have demonstrated the benefits of re-mating with a partner in a subsequent year, and that breeding failure is followed by divorce more often than expected by chance (Rowley 1983). Therefore, a female that relays late in the laying period might benefit through an increased likelihood of remating with her current partner and holding on to her nest site for breeding in a future year. Ainley et al. (1990) suggested that this might partly explain why some female Cassin's Auklets *Ptychoramphus aleuticus* lay second eggs in one season after their first chick fledges.

2.5.2 *Egg size, incubation period, and probability of relaying*

There was little relationship between first egg size and the probability of relaying among the experimental Thick-billed Murre pairs. In contrast, Willow Ptarmigan *Lagopus lagopus* that laid large eggs were more likely to relay following clutch loss, suggesting that both factors reflected a female's capacity to produce eggs (Sandercock and Pederson 1994). By removing the single eggs from pairs that laid early, I excluded most young, inexperienced females, birds that tend to lay small eggs late in the season (Hipfner et al. 1997). However, egg size varies considerably even among older Thick-billed Murres, which tend to lay early, and egg size remains relatively fixed between years for older females (Hipfner et al. 1997). Therefore, even the small eggs removed in this study probably were laid by capable females. If, as I have suggested, age and/or experience largely determines relaying propensity in Thick-billed Murres, then it is not surprising that relaying propensity was not reflected in first egg size among early-laid eggs.

The length of time that first eggs were incubated, like the date of egg removal with which it was highly correlated, also appeared to have little overt effect on relaying probability among the experimental pairs. More importantly, relaying declined with date among control pairs, but not experimental pairs, even though experimental pairs had incubated their first eggs for almost a week longer on average prior to loss. Young Thick-billed Murre pairs typically lay late and lose their egg quickly (de Forest and Gaston 1996), and this tendency was displayed by control pairs. Murphy and Schauer (1994) also found that the duration of incubation had little effect on relaying probability in a non-experimental study of Common Murres.

At Coats Island, Thick-billed Murres usually gain mass over the course of incubation (Croll et al. 1991, Gaston and Hipfner 1998), suggesting that they have little difficulty meeting the energetic demands of incubation at that colony. Therefore, it seems unlikely that a longer incubation period would reduce a female's ability to summon the energy required to produce a replacement egg. However, body mass might not reflect the availability of the more specialized resources required for egg production, which in some species of birds have to be drawn from endogenous reserves laid down before egg production begins (Houston et al. 1995). It is possible that only high quality females will have sufficient reserves to produce both a first and a replacement egg. There was, however, a clear effect of incubation duration on relaying intervals among the experimental females, indicating that physiological changes that affect egg production take place even early in incubation (see below). Such changes likely cause a gradual reduction in the female's egg-production capacity, and this probably contributed to the very low rates of relaying among birds that lost their eggs very late. To investigate the influence of incubation duration on probability of replacement laying in isolation from other, potentially confounding factors (e.g., female quality) will require further study.

2.5.3 *Relaying interval and replacement egg size*

Relaying intervals increased with both the date of egg removal and the number of days that first eggs were incubated prior to experimental removal. I suggest that the first of these positive relationships was caused by the second, as Wooller (1980) suggested for Black-legged Kittiwakes *Rissa tridactyla*. Neither proximate nor ultimate factors seem to explain why relaying intervals should increase as a function of removal date for Thick-billed Murres. Food probably becomes more available through the laying period as sea ice retreats in the summer (Gaston and Hipfner 1998). Therefore, it seems unlikely that relaying intervals would increase due to a decrease in food availability, although simple food availability might not reflect the availability of resources required for egg production.

Moreover, the departure ages of Thick-billed Murre chicks often decline with hatching date (Hipfner and Gaston 1999a), and late Common Murre chicks were more likely to be taken by predators prior to departure in some studies (Hatchwell 1991, Spear 1993). Therefore, it seems unlikely that delaying the laying of a replacement egg would confer an evolutionary advantage on murres.

Where researchers have collected breeding Thick-billed Murres at their colonies, the largest follicle present in the ovary increased in size up to approximately the median laying date, then decreased (Swartz 1966, Gaston and Nettleship 1981). This might reflect an increase in primary follicle size up to laying, followed by atresia of accessory follicles (Common Murres collected with fully-shelled eggs in the oviduct had other follicles developing as well, Murphy and Schauer 1994). Therefore, a murre that loses her egg soon after laying may have a head start in the form of a larger second follicle with which to produce a replacement egg. In conjunction with this, and perhaps more importantly, her hormonal balance might be more favourable for egg production because she has incubated for less time, e.g., perhaps she would have higher levels of follicle-stimulating hormone, and lower levels of prolactin (Wingfield and Farner 1979, Zadworny et al. 1989).

As observed at other Thick-billed Murre colonies (Birkhead and Nettleship 1982), and previously at Coats Island (de Forest 1993, Hipfner et al.. 1997), replacement eggs averaged 6% smaller than first eggs, and the sizes of first and replacement eggs were strongly correlated. None of the factors that I examined influenced the relative change in size between first and replacement eggs. This suggests that replacement egg size, like first egg size (Hipfner et al. 1997), is relatively fixed. Birkhead and Nettleship (1982) suggested that female murres might lay small replacement eggs in order to advance their laying date. A previous study of Common Murres confirmed that the smaller replacement eggs were formed more quickly than first eggs (Birkhead and del Nevo 1987), and indirect evidence suggested that this was true in Thick-billed Murres as well (Hipfner et al. 1997). However, the wing feathers of Thick-billed Murre chicks that hatch from large eggs grow more quickly than do those on chicks from small eggs (perhaps because large-egg chicks hatch with larger yolk reserves, Birkhead and Nettleship 1984), and rapid growth of wing-feathers may enable the chick to go to sea quickly (Hipfner and Gaston 1999 b). Consequently, there might be little time-saving advantage for Thick-billed Murres in producing small replacement eggs. It still is unclear why murres lay small replacement eggs, although time-saving remains a possibility.

To summarize, these results show that Thick-billed Murres that lay early in the season (probably older, more experienced females) have considerable capacity to produce replacement eggs. Laying a replacement egg might confer direct and/or indirect fitness benefits on murres - this warrants further investigation (see Chapter 3). The capacity of high-quality female Thick-billed Murres to produce replacement eggs until very late in the laying period contrasts with observations on some temperate-nesting bird species, and might therefore have important implications about the seasonality of low-Arctic marine environments.

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Chapter 3: Fitness Consequences of Replacement Egg-Laying for Thick-billed Murres: Survival of Offspring to Recruitment Age

3.1 Abstract

In a previous study, female Thick-billed Murres *Uria lomvia* that laid early in the season continued to relay until late in the laying period following experimental removal of their first eggs. This suggests that the fitness benefits obtained by relaying and raising young, even very late in the season, exceed the fitness costs for the more capable members of Thick-billed Murre populations. The most direct fitness benefit would be obtained if young from replacement eggs survived to recruit into the breeding population, but studies on other seabirds indicate that this is unlikely. I compared survival to recruitment age (4-5 yr) of young Thick-billed Murres from first and replacement eggs raised by equally-capable parents from the 1994 and 1995 cohorts at Coats Island, Nunavut Territory, Canada. The proportion of birds from replacement eggs resighted at the colony in 1999 (25%, $n = 44$) was similar to the proportion of first-egg young resighted (19%, $n = 94$). Thick-billed Murres that hatched from replacement eggs were no less likely to survive to recruitment age than were young from first eggs, even though they departed the colony 2-3 weeks later. In other birds, late-fledged young often suffer high mortality soon after they leave the nest because they are unable to compete for limited resources with conspecifics that fledge early. The rapid and widespread dispersal of adult-chick Thick-billed Murre pairs away from the colony may negate intraspecific competition for abundant resources at sea, minimizing the disadvantages of late nest departure.

3.2 Introduction

In many marine birds, offspring that are most likely to survive to recruit into the breeding population are those that fledge heavy in mass (Manx Shearwater *Puffinus puffinus*, Perrins et al. 1973, Black-legged Kittiwake *Rissa tridactyla*, Coulson and Porter 1985, King Penguin *Aptenodytes patagonicus*, Olsson 1997), and those that fledge early (South African Gannet *Sula capensis*, Jarvis 1974, Shag *Phalocrocorax aristotelis*, Harris et al. 1994, Western Gull *Larus occidentalis*, Spear and Nur 1994). Young seabirds that hatch early also often grow more quickly and fledge heavier than those that hatch late, either because feeding conditions are better early in the chick-rearing period (Hedgren and Linnman 1979, Birkhead and Nettleship 1981), and/or because adults that breed early are more efficient at provisioning their offspring (Weimerskirch 1990, Daunt et al. 1999). In addition, young that hatch early tend to remain longer at the nest, which may enable them to develop more fully before they depart to sea (Wanless and Harris 1988, Hipfner and Gaston 1999). As a result, effects of timing of nest departure on subsequent survival can be confounded by other, correlated factors.

Thick-billed Murres *Uria lomvia* are highly colonial, cliff-nesting seabirds of Arctic waters. They lay a single egg, and feed the chick at the nest site for 15-30 days, at which time the chick departs to sea at <30% of adult mass, and covered in a transitional, mesoptile plumage. Upon leaving the nest site, Thick-billed Murre chicks are tended by their male parent at sea for several weeks before they become independent, they first return to the colony at 2-3 yr of age, and all but a very few begin to breed at ≥ 4 yr of age (Gaston et al. 1994). Little is known about the period between departure and the first return to the colony, and of the role that mortality during this time has played in the evolution of their unique "intermediate" developmental strategy (Ydenberg 1998). At Coats Island, Nunavut Territory, Canada (where this study took place), about 20% of chicks die making the trip from nest site to sea (Gilchrist and Gaston 1997), and subsequent mortality rates for chicks that depart successfully are probably highest in the first year (Gaston 1998).

In some years, the survival of young Common Murres *Uria aalge* between nest departure and their first return declined with the date of nest departure from a temperate colony (Harris et al. 1992). However, young, inexperienced murres lay later than older, experienced birds (Hipfner et al. 1997), and late laying by less capable birds, rather than date effects *per se*, largely explains why measures of breeding success decline with laying date at the colony (de Forest and Gaston 1996). As with colony-based measures of breeding success, experimentation is required to distinguish date effects from parental effects on post-departure survival in murres.

In previous studies at two low-Arctic colonies, early-laying Thick-billed Murres that had their eggs experimentally removed continued to lay replacement eggs until late in the laying period, even while the proportion of pairs relaying in the general population was declining sharply (Hipfner et al. 1999; Chapter 2). This suggests that the fitness benefits obtained by relaying and raising young, even very late in the season, exceed the fitness costs for more capable members of Thick-billed Murre populations. Fitness benefits may be indirect, e.g., if relaying increases the probability that individual females retain high quality mates or nest sites for breeding in future years, or they may be direct, if offspring that hatch from replacement eggs recruit into the breeding population. Theoretical models of breeding by Arctic seabirds assume that offspring that hatch late in the season are disadvantaged (Birkhead and Nettleship 1982, Ydenberg 1989), but egg-removal experiments have shown that Thick-billed Murre chicks that hatch from replacement eggs are as likely to survive the nestling period as they would otherwise have been based on their parents' original laying date (de Forest and Gaston 1996, Hipfner et al. 1999). However, it is not known whether Thick-billed Murre chicks from replacement eggs are less likely to survive after they leave the nest.

At Coats Island, Nunavut Territory, Canada, in 1994 and 1995, I experimentally delayed groups of early-laying Thick-billed Murres by removing their eggs, inducing them to relay, to investigate whether the timing of chick-rearing affected growth rates. It did not: in both years, growth rates and departure masses of experimental chicks were similar to those of chicks raised by control groups of early-laying parents (Hipfner 1997). All of these control and experimental chicks were banded, and in 1999, an effort was made to resight them at Coats Island. In this paper, I: (i) describe the natural, seasonal variation in survival between colony departure and 4-5 yr of age (hereafter, recruitment age) for Thick-billed Murres (any trends found in this analysis could be due to date effects and/or parental effects); and (ii) investigate whether chicks from replacement eggs, which departed the nest site 2-3 weeks later than control chicks, were less likely to survive to recruitment age when raised by equally-capable parents (this analysis examines date effects while controlling for parental effects). As there were no demonstrable effects of chick mass, wing length, or age at nest departure on survival in these two years, these factors will not be addressed here.

3.3 Study Area and Methods

The study was conducted at the Thick-billed Murre colony of 30,000 breeding pairs at Coats Island, Nunavut Territory, Canada (62°57'N, 82°00' W). Measuring and banding of chicks took place in 1994 and 1995, while intensive resighting efforts occurred in 1999; however, a few chicks were first resighted in 1997 and 1998.

The methods used to establish control and experimental groups, and to monitor chick growth, are described in detail elsewhere (Hipfner 1997). Briefly, 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 (Z and LF, see Gaston et al. 1994) situated near the top of the colony. Every egg was marked with its site number in permanent ink. Following this initial visit, all sites were checked at 2-3 day intervals from hatching until nest departure. At hatching, each chick was marked with a binary code of nail clipping, and banded within one week with: (i) a year-specific colour band; and (ii) a triangular metal band with the number engraved upright on both sides, making it easy to read (Gaston et al. 1994). Hatching date was taken to be the date midway between when an egg was last present at the site and a chick was first present. On all visits, chicks were weighed to within 1 g with a 300 g spring balance, and their right wings were measured to within 1 mm with the wing held flat and straight along a ruler. Chicks that survived ≥ 15 days at the nest site were considered to have survived to depart the colony, and so were used in the analysis of post-departure survival (15 days is the youngest age at which Thick-billed Murres are known to depart the nest site of their own volition, Gaston and Nettleship 1981). The date of departure was taken to be the date midway between the last check when a chick ≥ 15 days old was present and the first check when it was no longer present.

To establish experimental groups, I delayed samples of early-breeding birds in both 1994 and 1995. I mapped and numbered 25 breeding sites on each of two plots (Z and LF, same areas as the control plots), and then measured and removed the single eggs. This was done on 25 and 26 June (near median laying date), using different areas 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. The experimental plots were rechecked 45 days later, based on periods of 14 days for egg replacement (Hipfner et al. 1999), and 32-33 days for incubation (Hipfner et al. in press). 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 with the experimental pairs, control pairs were considered to be those that laid by the date of the egg removal, i.e., those whose chick hatched on or before 28 July (25 June + 33 days incubation). Fifteen experimental chicks had not yet departed when observations ceased in early September of 1994 (see Hipfner 1997). As all of these chicks were ≥ 16 days of age at last check, for this analysis I assumed that they had departed the colony, on the day after the last check (i.e., they were assigned the earliest possible departure date). Final sample sizes were: 58 first-egg chicks in 1994 (including 50 control chicks), and 57 in 1995 (including 44 controls); 26 experimental chicks in 1994, and 18 in 1995.

In 1999, when birds in these two cohorts were 4 and 5 yr old, watches were carried out at Z and LF from prelaying until the start of hatching to record band numbers. Four and 5 yr old birds are present at the colony throughout the breeding season, irrespective of whether or not they breed in that year (Noble 1990), and young Thick-billed Murres exhibit a high degree of philopatry to the area where they were raised (U. Steiner and A.J. Gaston, pers. comm.). Consequently, it seems likely that a high proportion of birds still alive would have been resighted.

3.4 Results

Timing of nest departure by both first-egg and replacement-egg Thick-billed Murre chicks differed little between 1994 and 1995, and in both years, experimental chicks departed the colony about 2-3 weeks later than control chicks (Table 3.1). Similar percentages of control and experimental chicks raised in 1994 and 1995 were resighted at colony in 1999 (Table 3.1). In addition, all trends relating

Table 3.1: Timing of nest departure in 1994 and 1995 for control ($n = 49$ and 45, respectively) and replacement-egg ($n = 26$ and 18) Thick-billed Murre chicks, and the proportions of these birds resighted at the colony in 1999.

		Year		
Parameter		1994	1995	Inter-year comparisons
Median departure date				
	First-egg	13 Aug	14 Aug	Mann-Whitney test, $P = 0.38$
	Replacement -egg	1 Sep[1]	30 Aug	n/a[1]
Percentage resighted:				
	First-egg	21.1	17.2	χ^2 test, $P = 0.85$
	Replacement -egg	26.9	22.2	Fisher's exact test, $P = 1.00$

[1] A minimum estimate; see text for explanation.

survival to departure dates were in the same direction for chicks raised in the two years. Therefore, I pooled data for the 1994 and 1995 cohorts for subsequent analyses.

For all first-egg chicks, there was only a very weak, negative relationship between departure date and the probability of resighting at the colony (logistic regresssion, Wald $\chi^2_1 = 0.27$, $P = 0.60$, Fig. 3.1). Nestling periods are more variable than incubation periods in murres (e.g., Murphy 1995), so that hatching dates more accurately predict laying dates (i.e., timing of breeding) than do departure dates. For this reason, I reran the logistic regression using hatching dates to test for parental effects. Again, there was only a very weak, negative relationship between hatching date and the probability of resighting (Wald $\chi^2_1 = 0.87$, $P = 0.35$). Therefore, although the trends were in the expected direction, neither departure date nor parental quality could be shown to affect post-departure survival of the control Thick-billed Murre chicks.

The proportion of experimental chicks that were resighted at the colony (25%, $n = 44$; Fig 3.1) was similar to that of control chicks raised by parents that laid by the dates of the egg removals (19%, $n = 94$; $\chi^2_1 = 0.62$, $P = 0.43$). Therefore, chicks from replacement eggs were as likely to survive to recruitment age as were first-egg chicks if raised by parents with similar original laying dates.

3.5 Discussion

Neither the date of nest departure, nor parental quality (as measured by hatching date), had discernible effects on survival to recruitment age (4-5 yr) of Thick-billed Murre chicks from the 1994 and 1995 cohorts at Coats Island. There is a strong relationship between female age and timing of laying in this species: females lay late in their first 2 or 3 breeding attempts (Hipfner et al. 1997). As Thick-billed Murres tend to mate assortatively with respect to age (Gaston et al. 1994), most young females also

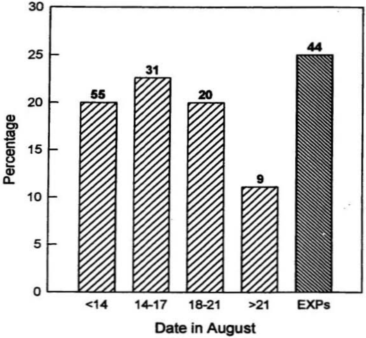

Figure 3.1: Percentage of birds resighted in relation to their date of departure for control chicks, and the proportion of experimental chicks resighted. Sample sizes above bars.

mate with young males. Late laying by these young, inexperienced pairs causes breeding success to decline with date at the colony, mainly through declining hatching success; although their chicks grow more slowly, young pairs that succeed in hatching eggs are not overtly less successful than older, experienced pairs in raising chicks to departure age at Coats Island (de Forest and Gaston 1996). Assuming that the immediate post-departure period is a time of high mortality for murre chicks (Gaston 1998), or that subsequent mortality is affected by the chick's physical condition when it becomes independent (Ydenberg 1989), the results of this study suggest that young, inexperienced males that reach this stage of the breeding cycle are not overtly less capable of tending their chicks at sea than are older, experienced males.

Thick-billed Murres that hatched from replacement eggs and raised by early-laying parents were as likely to survive to recruitment age as early-departing chicks, providing experimental evidence that departure date had little effect on survival. As in previous years (de Forest and Gaston 1996), growth rates of chicks raised by high quality parents were unaffected by timing of chick-rearing at Coats Island in 1994 and 1995 (Hipfner 1997). This suggests that food availability did not decline late in the season to an extent that chicks raised by capable parents were affected; the absence of date effects on nestling survival at Coats Island (de Forest and Gaston 1996) may be largely due to persistent, favorable feeding conditions at this colony (Gaston et al. 1983). Likewise, the weakness of the parental effect, and the absence of a date effect, on post-departure survival suggests that feeding conditions remain adequate after nest departure.

In some other marine birds, late-fledging young suffer high mortality because they fare poorly in competition for limited food resources with those that fledge early (Nisbet and Drury 1972, Spear and Nur 1994). However, in Thick-billed Murres, adult-chick pairs disperse rapidly and widely at sea after they leave the colony (Gaston 1982), so that it is unlikely that intra-specific competition would be a significant factor. In fact, an adequate and predictable food supply for chicks and their moulting, flightless male parents at sea would appear to be a prerequsiste for the evolution of the "intermediate" developmental strategy employed by murres. The tendency for capable Thick-billed Murres to continue to relay until late in the laying period at low-Arctic colonies (Hipfner et al. 1999) may be easily explained by the fact that chicks that hatch from replacement eggs are no less likely to survive to recruitment age. This clearly differs from the situation for many temperate-nesting species of birds (e.g., Sorci et al. 1997).

The fitness benefits of relaying may be obvious, but what about the fitness costs? According to life-history theory, species (like murres) that employ low-fecundity, high-survival life-history strategies should be reluctant to jeopardize their survival, and future reproductive potential, by investing too heavily in any single breeding season (Clutton-Brock 1988). If true, then the costs associated with relaying (including producing an additional egg for the female, and site occupancy and delayed departure from the colony for the male) should not be high. In support of this, I found that females experimentally induced to produce replacement eggs at Coats Island spent as much time incubating, delivered as much food to their chicks, and raised chicks that grew as well as females that laid only one egg (Hipfner et al. *unpubl. data*). Although not expected, it remains to be determined whether adult Thick-billed Murres experience detectable survival costs for relaying.

3.6 Literature cited

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Chapter 4: Composition of First and Replacement Eggs:
Constraints and Strategies for Renesting Thick-billed Murres

4.1 Abstract

A number of studies have examined characteristics of first and replacement clutches in birds. There are nearly always fewer eggs in replacement clutches, but these eggs may be larger, smaller, or the same size, as those in first clutches. The causes and consequences of these relative differences in egg size are unclear. In the Thick-billed Murre, it has been proposed that females facultatively reduce the size of replacement eggs in order to advance laying. As there are no data on the composition of first and replacement eggs, it is unclear whether physiological constraints play a role in limiting replacement egg size. I examined characteristics of first and replacement eggs laid by Thick-billed Murres at Coats Island, Nunavut, in 1998 and 1999. As reported elsewhere, replacement eggs averaged 6% smaller than first eggs laid by the same females, and this was associated with reductions of similar magnitude in the masses of shell, yolk, and albumen. Replacement eggs had significantly lower yolk:albumen ratios, and thinner shells, but the differences were small. The amino acid composition of both yolk and albumen was similar in first and replacement eggs. The reduction in yolk mass was accompanied by roughly similar reductions in protein and lipid content; therefore, replacement eggs contained less yolk, but what yolk there was was of similar quality to that in first eggs. In contrast, the reduction in protein content in the albumen greatly exceeded the reduction in albumen mass. Therefore, replacement eggs contained not only less albumen, but protein-deficient albumen. These results suggest that relaying female Thick-billed Murres face a protein constraint during albumen deposition that might limit the size of replacement eggs, but this does not rule out the possibility that they lay small yolks to advance their laying date.

4.2 Introduction

Avian egg production was a key topic in the development of life-history theory, largely as a consequence of David Lack's work on clutch size (Monaghan and Nager 1997). Lack (1947) believed that egg production was not a particularly demanding process for birds, based largely on the apparent ease with which many birds replaced lost eggs and clutches. However, although replacement clutches can make important contributions to an individual's lifetime reproductive success (Martin et al. 1989, Keegan and Crawford 1993), a number of studies report that either very low, or highly variable, proportions of birds renested after they lost their first clutch (Duncan 1987a, Harris and Wanless 1989). Renesting ability may be proximately constrained by food supply (Eldridge and Krapu 1988), and be more common among older, more experienced females (Wheelwright and Schultz 1994, Wiebe and Martin 1998), and those in better physiological condition (Hegyi and Sasvári 1998). These observations suggest that the costs associated with renesting, due to environmental or physiological factors, can be considerable. In response, renesting females may employ specific strategies in order to mitigate the costs.

A number of studies on a variety of species have compared the characteristics of first and replacement eggs and clutches. Typically, there are fewer eggs in replacement clutches (Brown and Morris 1996, Grand and Flint 1996), which usually is considered to be a strategic adjustment in that the optimal clutch size is smaller later in the season (e.g., Arnold 1993). However, the eggs in replacement clutches may be smaller (Feare 1976, Brown and Morris 1996), the same size (Rohwer 1986, Arnold 1993), or larger (Duncan 1987b, Sandercock and Pederson 1994) than those in first clutches. Not surprisingly, the proximate causes and evolutionary consequences of these inconsistent changes in egg size are unclear. A shift towards larger eggs in replacement clutches could be strategic if larger offspring that hatch with larger reserves have an advantage later in the season, when environmental conditions are less favourable (Nilsson 2000). Alternatively, egg size could increase if food is more available when females are producing replacement eggs (Duncan 1987a). A shift to smaller eggs in replacement clutches also could be strategic if small eggs can be formed more quickly (Birkhead and Nettleship 1982), but egg size also might decrease if, having already produced one clutch, females have fewer endogenous reserves with which to produce a replacement (Houston et al. 1983). Egg production in birds may be limited by the availability of energy (Nager and van Noordwijk 1992), calcium (Beintema et al. 1997), or protein (Robbins 1981), and in the latter case, by specific amino acids (Murphy 1994).

Thick-billed Murres *Uria lomvia* are highly colonial, cliff-nesting seabirds of Arctic waters. They lay a single-egg clutch, and typically about 20-30% of female murres that lose their egg relay, the proportion declining abruptly with the date of egg loss (Gaston and Nettleship 1981, Birkhead and Nettleship 1987). However, experiments indicate that the renesting capacity of Thick-billed Murres is determined more by the "quality" of the female than by the date of loss (Hipfner et al. 1999), and probably her age and/or experience in particular (de Forest and Gaston 1996). For Thick-billed Murres, there is a remarkably consistent 5-6% average reduction in egg size between first and replacement eggs across colonies and years (Birkhead and Nettleship 1982, de Forest 1993, Hipfner et al. 1997, Hipfner et al. 1999). Birkhead and Nettleship (1982) suggested that female murres might facultatively reduce the size of replacement eggs in order to advance laying, ahead of a seasonal deterioration in feeding conditions. In support of this hypothesis, Common Murres *Uria aalge* were found to form the smaller replacement eggs more quickly than they formed first eggs (Birkhead and del Nevo 1987), and there is evidence of this in Thick-billed Murres as well (Hipfner et al. 1997).

However, no study has examined the composition of first and replacement murre eggs, which may shed light on the extent to which physiological constraints, rather than strategic adjustments, limit the size of replacement eggs.

In this study, I compare the composition of first and replacement eggs laid by the same female Thick-billed Murres. To ensure that all eggs were laid by "high quality" females (those most likely to relay), eggs were taken from females that laid prior to the median laying date; typically older, and more experienced females (Hipfner et al. 1997). In the analyses, I consider the crude composition of the egg (the percentage of whole egg mass made up of shell, albumen, and yolk), and its biochemical composition (i.e., lipid content of yolk; and protein content, including amino acid composition, of both albumen and yolk).

4.3 Methods

4.3.1 Field methods

First and replacement eggs were collected within 24 hr of laying at Coats Island, Nunavut Territory, Canada (62°57' N, 82°00' W), during 1998 and 1999. To ensure that all first eggs were laid prior to median laying date, daily observations were made from a blind of birds on a plot that held a known number of breeding pairs, and that was situated close to where I collected eggs. First eggs were collected on or before 21 June in 1998, and on or before 22 June in 1999. At this time, I made sketches of the locations of these breeding sites, and took Polaroid photographs of the first eggs. These plot sketches and photographs were used to verify that the eggs later found at the same sites were replacement eggs laid by the same females. Breeding sites were rechecked beginning 10 days after the removal of first eggs, and continuing until all females had relaid.

4.3.2 Analysis of crude composition

All collected eggs were measured (length and maximum breadth, to within 0.1 mm using vernier calipers; mass to within 0.1 g on an electronic balance). They were then boiled for 12 minutes, allowed to cool, reweighed, and then separated into shell and attached membranes, albumen and yolk. Shell and membrane, and yolk, were weighed (to within 0.1 g on an electronic balance); as water is lost from the albumen through boiling, albumen mass was taken to be the mass of the fresh, pre-boiled egg minus the mass of the shell with membranes, and yolk. For each egg, shell thickness was measured (to within 0.01 mm with a micrometer gauge) at 10 points close to the egg's equator, and the average of these 10 measurements calculated. The components of each egg were then packed into a plastic bag and frozen for biochemical analysis.

4.3.3 Analysis of biochemical composition

From the eggs collected in the field in 1998, seven first and replacement eggs laid by the same females were selected for biochemical analysis. They were selected based on visual inspection of their general condition upon arrival in the laboratory, i.e., the eggs that appeared to be in the best condition after the trip out of the field were used.

Total lipids in egg yolk were determined gravimetrically following extraction with chloroform:methanol (2:1 v:v) as described by Folch et al. (1957). To determine protein content of albumen, a portion of each albumen was powdered in liquid nitrogen and dissolved in 0.1 N NaOH, and its protein content determined using the Biuret method (Layne 1957). To determine protein content of yolk, lipid was removed from a portion of yolk (Brocherhoff and Yurkowski 1965), the remaining protein was dissolved in 0.1 N NaOH and its content then determined by the Biuret method.

Amino acid composition of both albumen and yolk were determined by hydrolyzing 0.5-2 mg samples in 1 ml of 6 N HCl with 0.05% phenol using 16 100 ml culture tubes with teflon-lined screw caps. The tubes were purged for 5 min. with nitrogen before capping. The HCl was removed under vaccuum and the dried sample reconstituted with pH 2.2 lithium citrate buffer 0.2 M Na^+ prior to analysis (Blackburn 1978, Ozols 1990, Carraway et al. 1973, Gehrke et al. 1985).

Because the eggs were boiled and then frozen, and because the eggs experienced temporary periods of thawing on the trip from the field site, absolute measures of amino acid composition may not be completely reliable, for unknown reasons (Kuroda 1963). However, relative measures should be accurate, because all eggs were processed in the same way. Therefore, I concentrate mainly on relative measures, i.e., on comparing the biochemical composition of yolk and albumen between first and replacement eggs, rather than on absolute values.

4.4 Results

4.4.1 Crude composition of first and replacement eggs

The interval between removal of the first egg and the laying of a replacement varied from 12 to 16 days (mean = 13.7 ± 1.0 (SD) days). Data on the crude composition of 24 first and replacement eggs laid by the same females are presented in Table 4.1. The masses of first and replacement eggs were positively correlated, as were masses of all components (Table 4.1, Fig. 4.1).

Replacement eggs averaged 5.9% lighter in mass than first eggs, this overall reduction being associated with reductions in the masses of shell (by an average of 8.7%), albumen (3.8%), and yolk

Table 4.1: Crude composition (mean ± SD) of 24 first and 24 replacement Thick-billed Murre eggs laid by the same females at Coats Island.

	Egg number		Correlations	
Component	First	Replacement	r_{22}	P
Whole egg (g)	110.3 ± 7.6	103.8 ± 7.5	0.73	<0.001
Shell (g)	13.8 ± 1.2	12.6 ± 1.0	0.69	<0.001
As % whole egg	12.6 ± 0.8	12.1 ± 0.9		
Shell thickness (mm)	0.53 ± 0.04	0.51 ± 0.04	0.73	<0.001
Albumen (g)	60.2 ± 5.5	57.9 ± 5.3	0.77	<0.001
As % whole egg	54.5 ± 1.8	55.7 ± 2.5		
Yolk (g)	36.2 ± 2.1	33.4 ± 3.3	0.58	0.003
As % whole egg	32.9 ± 1.7	32.1 ± 2.4		
Yolk:albumen	0.60 ± 0.05	0.58 ± 0.07	0.51	0.01

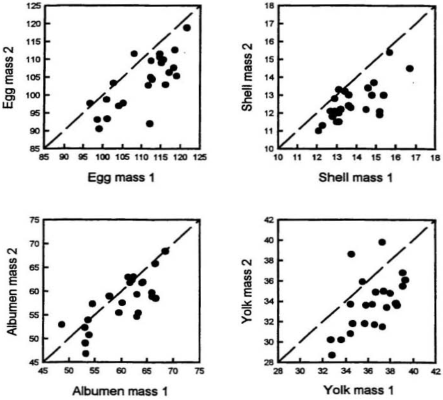

Figure 4..1. Relative masses of whole eggs and egg components for first and replacement Thick-billed Murre eggs. The dashed lines indicate 1:1 relationships.

(7.7%; Table 4.1, Fig. 4.1). Replacement eggs had thinner shells, although the difference was small (on average, 0.02 mm, a 3.8% reduction; paired $t_{23} = 3.48$, $P = 0.002$; Table 4.1). Analyses of covariance (ANCOVA, on log-transformed data), with egg mass as continuous explanatory variable and egg number (first or replacement) as grouping variable, showed that neither the intercepts nor the slopes of the regression lines relating component masses to egg masses differed significantly between first and replacement eggs (Table 4.2). This indicates that replacement eggs were essentially just scaled-down versions of first eggs. However, the difference in elevation approached statistical significance for yolk content ($P < 0.1$; see Table 4.2), and this slight reduction in elevation was associated with a slightly lower yolk:albumen ratio in replacement eggs (paired $t_{23} = 1.96$, $P = 0.06$; but paired $t_{22} = 3.49$, $P = 0.002$ with the one clear outlier removed; Table 4.1, Fig.4.2).

4.4.2 Biochemical composition of first and replacement eggs

The amino acid composition of the protein in the albumen and yolk of seven first and replacement Thick-billed Murre eggs is shown in Table 4.3. Interestingly, the amino acid make-up of the protein in the replacement eggs was considerably more variable than that in first eggs, although much of this added variation was caused by a single one of the seven replacements. There was marked consistency in the amino acid composition of the protein in yolk and albumen; the mean values for the amino acids correlated very strongly ($r = 0.89$) between yolk and albumen in first eggs (Table 4.3).

The masses of each amino acid present in the whole albumen and whole yolk of seven first and seven replacement eggs are shown in Table 4.4. Whereas the amino acid content of the yolks of first and replacement eggs differed little, albumen in replacement eggs had considerably lower masses of all amino acids than did the albumen in first eggs. Based on the data in Table 4.4, there was c. 25% less protein overall in the seven replacement eggs (Table 4.5), although these replacement eggs

Table 4.2: Analyses of covariance (ANCOVAs) relating log component mass to log egg mass for 24 first and 24 replacement Thick-billed Murre eggs laid by the same females at Coats Island.

		Egg mass		Egg number		Interaction	
Component	Model R^2	$F_{1,44}$	P	$F_{1,44}$	P	$F_{1,44}$	P
Shell	0.51	22.65	<0.001	0.77	0.39	0.85	0.36
Albumen	0.85	236.56	<0.001	1.55	0.22	1.44	0.24
Yolk	0.60	38.17	<0.001	2.91	0.09	2.80	0.10

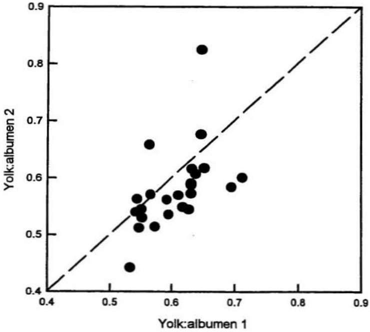

Figure 4.2. Yolk:albumen ratios in first and replacement Thick-billed Murre eggs. The dashed line indicates a 1:1 relationship.

averaged only 3% smaller than the seven first eggs. Most of this reduction in protein content was in the albumen: there was 32% less protein in the albumen of the replacement eggs, although the albumen in replacement eggs averaged only 4% lighter than that in first eggs. In contrast, there was 8% less protein in the yolks of replacement eggs, considerably closer to the 4% overall reduction in yolk mass. Likewise, the reduction in the amount of lipid in the yolks of the replacement eggs (2%, and not statistically significant) was close to the 4% reduction in yolk mass (Table 4.5).

4.5 Discussion

4.5.1 *Composition of Thick-billed Murre eggs*

The crude composition of first eggs laid by early-laying Thick-billed Murres at Coats Island in 1998 and 1999 was very similar to that of eggs laid at the Gannet Islands in 1997 (M. Hipfner unpublished). Their composition was also similar to that of eggs laid by Common Murres *Uria aalge* and Razorbills *Alca torda* (Birkhead and Nettleship 1984, M. Hipfner unpublished), the other two species that employ the same post-hatching developmental strategy (Sealy 1973). Thick-billed Murre eggs show characteristics of relatively precocial species (e.g., a high yolk:albumen ratio), which is consistent with independent measures that place murres well towards the precocial end of the altricial-precocial continuum of avian post-hatching development (Starck and Ricklefs 1998).

As in previous studies (e.g., Birkhead and Nettleship 1982), the 24 replacement eggs averaged c. 6% smaller than first eggs. This overall reduction in egg size was associated with reductions of similar proportions (4-9%) in the masses of shell, albumen, and yolk; the analyses of covariance indicated that, in terms of crude composition, replacement eggs were essentially scaled-down versions of first eggs. However, there were statistically significant differences. Replacement eggs had lower yolk:albumen ratios than did first eggs, although the difference was small (3%), and of unknown

Table 4.3: Amino acid content (mean ± SD, in μm g^{-1} protein) of seven first and seven replacement Thick-billed Murre eggs laid by the same females.

	Albumen		Yolk	
Amino acid	First egg	Replacement	First egg	Replacement
1. Essential amino acids				
Arginine	103 ± 36	78 ± 17	269 ± 29	256 ± 41
Histidine	143 ± 16	173 ± 46	169 ± 17	157 ± 25
Lysine	341 ± 11	369 ± 95	369 ± 37	345 ± 48
Isoleucine	348 ± 5	379 ± 98	356 ± 35	333 ± 50
Leucine	655 ± 19	707 ± 167	612 ± 53	570 ± 80
Valine	504 ± 13	555 ± 153	472 ± 45	442 ± 66
Methionine	231 ± 8	250 ± 64	168 ± 15	157 ± 23
Cystine	14 ± 3	16 ± 2	13 ± 2	12 ± 2
Phenylalanine	331 ± 12	362 ± 100	253 ± 24	235 ± 35
Tyrosine	241 ± 11	269 ± 77	235 ± 21	218 ± 31
Threonine	489 ± 7	535 ± 140	286 ± 26	269 ± 40
Tryptophan	---	---	---	---
2. Nonessential amino acids				
Alanine	479 ± 14	520 ± 153	591 ± 55	549 ± 83
Aspartic acid	596 ± 20	660 ± 173	619 ± 54	576 ± 82
Glutamic acid	823 ± 22	892 ± 215	742 ± 70	692 ± 104
Glycine	433 ± 26	485 ± 139	477 ± 47	441 ± 65
Proline	354 ± 11	390 ± 107	348 ± 33	325 ± 49
Serine	574 ± 11	619 ± 143	365 ± 39	344 ± 57

Table 4.4: Amino acid content (g) of seven first and seven replacement Thick-billed Murre eggs laid by the same females.

	Albumen		Yolk	
Amino acid	First egg	Replacement	First egg	Replacement
1. Essential amino acids				
Arginine	0.20 ± 0.08	0.10 ± 0.02	0.21 ± 0.03	0.21 ± 0.03
Histidine	0.25 ± 0.07	0.19 ± 0.04	0.11 ± 0.02	0.11 ± 0.02
Lysine	0.56 ± 0.16	0.38 ± 0.08	0.23 ± 0.03	0.23 ± 0.03
Isoleucine	0.49 ± 0.14	0.34 ± 0.06	0.20 ± 0.02	0.19 ± 0.03
Leucine	0.94 ± 0.26	0.63 ± 0.11	0.34 ± 0.04	0.33 ± 0.04
Valine	0.63 ± 0.18	0.43 ± 0.08	0.23 ± 0.03	0.22 ± 0.03
Methionine	0.38 ± 0.11	0.26 ± 0.05	0.11 ± 0.01	0.10 ± 0.01
Cystine	0.02 ± 0.004	0.01 ± 0.002	0.01 ± 0.001	0.01 ± 0.002
Phenylalanine	0.60 ± 0.16	0.42 ± 0.08	0.18 ± 0.02	0.17 ± 0.02
Tyrosine	0.48 ± 0.13	0.34 ± 0.07	0.19 ± 0.02	0.18 ± 0.02
Threonine	0.63 ± 0.18	0.43 ± 0.09	0.14 ± 0.02	0.14 ± 0.02
Tryptophan	---	---	---	---
2. Nonessential amino acids				
Alanine	0.43 ± 0.12	0.29 ± 0.06	0.21 ± 0.03	0.20 ± 0.03
Aspartic acid	0.86 ± 0.23	0.59 ± 0.11	0.35 ± 0.04	0.33 ± 0.04
Glutamic acid	1.33 ± 0.37	0.90 ± 0.17	0.47 ± 0.06	0.45 ± 0.06
Glycine	0.31 ± 0.08	0.22 ± 0.04	0.13 ± 0.02	0.13 ± 0.02
Proline	0.43 ± 0.12	0.30 ± 0.05	0.17 ± 0.02	0.16 ± 0.02
Serine	0.63 ± 0.19	0.43 ± 0.09	0.16 ± 0.02	0.15 ± 0.03

Table 4.5: Protein and lipid content (g) of seven first and seven replacement Thick-billed Murre eggs laid by the same females.

	Egg number			Paired t-test	
Component	First	Replacement	% change	t_6	P
Total protein	12.8 ± 2.5	9.6 ± 1.2	-25.1	3.00	0.02
Total lipid	13.0 + 1.7	12.7 + 1.1	-2.3	0.28	0.79

biological significance. The same can be said for the small (4%) reduction in the thickness of the shell. For whole eggs and all components, there were strong correlations between masses in the first and replacement eggs, indicating that there is a strong, female-specific component to egg-production capacity in Thick-billed Murres (see also Hipfner et al. 1997).

While the crude composition of first and replacement eggs was generally similar, this was not entirely true of their biochemical composition. Per gram of protein, the amino acid composition of the protein in seven first and replacement yolks and albumens was generally similar, and, as in other birds, the amino acid composition of yolk and albumen were similar (Murphy 1994). Moreover, the reduction in the overall amount of protein-bound amino acids in the yolks (8%) was of similar magnitude to the overall reduction in yolk size (4%), and this was true of lipid content as well (2% reduction). Consequently, while replacement eggs contained less yolk, what yolk there was appeared to be of roughly similar quality to that in first eggs. Conversely, the reduction in the protein content of the albumen in the replacement eggs (32%) exceeded the reduction in albumen mass (4%) by a factor of eight. Presumably, there was a corresponding increase in the water content of the albumen in replacement eggs. Consequently, replacement eggs not only contained less albumen, but what albumen there was was deficient of protein compared to that in first eggs.

Several studies have found egg production to be limited by the quality and quantity of protein available to the female as she forms eggs (e.g., Bolton et al. 1992). In other birds, some of the amino acids used to produce egg proteins are drawn from endogenous reserves laid down before egg production begins (Houston et al. 1995a,b). In Lesser Black-backed Gulls *Larus fuscus*, a female's ability to replace eggs lost within a single clutch is limited by the size of her protein reserves, but not her lipid reserves (Houston et al. 1983). My results for Thick-billed Murres are consistent with these findings, in that there appeared to be a protein deficit, but not a lipid deficit, in the replacement eggs. Dietary protein also may be important for renesting females; protein-supplemented Northern Pintails *Anas acuta* laid larger eggs in replacement than in first clutches, while non-supplemented birds laid smaller eggs in replacement clutches (Duncan 1987b). Species vary in the extent to which they rely on endogenous and exogenous sources during breeding (Drent and Daan 1980), and we do not know where egg-laying Thick-billed Murres lie along this "capital-income" continuum. However, food is likely to be more available when females at Coats Island are forming replacement eggs, because sea ice typically is retreating in northern Hudson Bay at that time (Gaston and Hipfner 1998). Therefore, it seems unlikely that any protein deficiency is due to a shortage of dietary protein, which implicates a limit on endogenous sources. Endogenous protein reserves may supply specific amino acids that otherwise could limit egg production if birds were relying solely on dietary sources of protein (Murphy 1994, Houston et al. 1995a,b).

The relative reduction in protein content of the albumen in replacement eggs far exceeded the relative reduction in yolk protein content. This suggests that protein constraints were more severe during the period of albumen formation (which occurs over a short period of 2-3 days, Birkhead and del Nevo 1987), than during yolk formation (which occurs over 12-16 days, Hipfner et al. 1997). In Common Terns *Sterna hirundo*, the size of the last-laid egg was determined by the amount of food the female received from the male during the period of albumen formation (Nisbet 1973), while in Lesser Black-backed Gulls, females provided with supplemental, high-quality protein produced larger eggs due to increased yolk protein content, but not albumen protein content (Bolton et al. 1992). These apparent discrepancies among Charadriiforme birds suggest that there is much to be learned about the sources and destinations of the protein required to produce yolk and albumen.

If replacement eggs laid by Thick-billed Murres are of lower quality than first eggs due to a low albumen protein content, a low yolk:albumen ratio, or thin egg shells, we might expect this to translate into low fitness of young from replacement eggs. Thin egg shells, attributed to calcium deficiencies during egg production, have been linked to low hatching success in Black Terns *Chlidonias niger* (Beintema et al. 1997). In Lesser Black-backed Gulls, which normally lay a clutch of three eggs, the mortality rate on nestlings from experimentally-induced fourth eggs was high, apparently because they were lighter in mass (Monaghan et al. 1995). Thick-billed Murre chicks from replacement eggs are lighter in mass than those from first eggs (M. Hipfner unpublished), but there is no evidence that hatching or nestling success (de Forest and Gaston 1996, Hipfner et al. 1999), nestling growth rates (Hipfner 1997), or post-departure survival (M. Hipfner unpublished) are affected. However, both colonies where this research has been carried out (Coats Island, Nunavut, and the Gannet Islands, Labrador) have favourable feeding conditions during chick-rearing (Gaston et al. 1983, Bryant et al. 1999). Consequences of hatching from replacement eggs may be more significant where feeding conditions are less favourable.

4.5.2 Constraints and strategies for renesting Thick-billed Murres

Birkhead and Nettleship (1982) suggested that severe time constraints associated with breeding in the Arctic not only determine whether or not a female Thick-billed Murre will relay, but also the size of her replacement egg. However, experiments suggest that female quality, rather than time constraints, drive the seasonal decline in renesting rates in this species (Hipfner et al. 1999). It has proven far more difficult to determine whether female murres facultatively reduce replacement egg size in order to advance their laying date, or whether physiological constraints limit the size of replacement eggs.

Birkhead and del Nevo (1987) found that the rate of yolk deposition had been faster in replacement eggs laid by Common Murres, but that females ended yolk deposition more quickly, resulting in replacement eggs having smaller yolks; this strongly supports Birkhead and Nettleship's hypothesis.

The results of this study suggest that Thick-billed Murres face a protein constraint while they form replacement eggs, and this would likely limit egg size. However, the protein constraint appeared to affect albumen size more than yolk size, and the period of albumen deposition is small compared to the period of yolk deposition. Therefore, these results do not necessarily contradict the Birkhead and Nettleship hypothesis; Thick-billed Murres may have laid replacement eggs with small yolks in order to advance their laying date. Indirect evidence suggests that, as in Common Murres (Birkhead and del Nevo 1987), Thick-billed Murres form replacement eggs more quickly than they form first eggs (Hipfner et al. 1997). However, it may be that female murres use up finite supplies of endogenous protein reserves during the formation of replacement eggs, and this is why they form these eggs more quickly. In addition, there is no evidence that feeding conditions deteriorate late in the season at Coats Island (de Forest and Gaston 1996, Hipfner 1997), and no evidence of reduced pre- or post-departure survival of late-hatched young (de Forest and Gaston 1996, Hipfner et al. 1999, M. Hipfner unpublished). Moreover, a reduction in yolk size may actually prolong the nestling period, because yolk may supply protein for early wing growth in nestling murres, which could help to reduce the nestling period (Hipfner and Gaston 1999). In sum, it appears that the evolutionary benefits of reducing replacement egg size are questionable in murres, and it may be more profitable to further investigate proximate, physiological constraints.

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Chapter 5: Food Supply and the Consequences of Egg Size For Thick-Billed Murres

5.1 Abstract

It is widely believed that the advantages of hatching from a large egg are more pronounced when food availability is low, but very few studies have examined the consequences of egg size across a range of feeding conditions. At Digges Island, Nunavut Territory, Canada, where food availability during chick-rearing was low, I 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. I compared results to those of a previous study at Coats Island, where food availability was higher. To control for underlying phenotypic correlations between egg size and parental quality, I switched eggs at random among pairs. Egg size positively affected the rate of 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 growth) 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 under unfavourable feeding conditions. 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 producing large eggs have not been detected in Thick-billed Murres, the existence of considerable variation in egg size, beyond that associated with female age/experience, remains unexplained.

5.2 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, e.g., if there are trade-offs between egg size and clutch size (Stearns 1992). In many taxa, offspring that hatch from large eggs appear to have advantages over those from small eggs (reviewed in 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 favourable environments, female trout maximize fitness by producing small eggs, because this allows them to lay more eggs; in unfavourable environments, the best strategy is to lay fewer, larger eggs (see also Hutchings 1991).

For birds, it is often suggested that the advantages of hatching from a large egg are more pronounced when feeding conditions are unfavourable. 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 persist longer 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 (e.g., Ankney and Bissett 1976). However, 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 one-egg clutch. Feeding conditions vary markedly among colonies, as evidenced by a strong, inverse relationship between chick growth rates 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 Territory, Canada, where chicks grow quickly, showed that egg size varied markedly among females (Hipfner et al. 1997). Moreover, young that hatched from large eggs developed a 2 day (c. 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). Successful departure from the nest site (at >14 days of age) requires that Thick-billed Murre chicks have wings of adequate length to enable them to reach the sea on the descent from the nest site (Hipfner and Gaston 1999b). Young Thick-billed Murres that hatched from large eggs also tended to remain heavier than those from small eggs in a year of slower growth at Coats Island, but not in a year of faster growth. However, the inter-year variation in growth rate at Coats Island was very small compared to that found among colonies.

In this paper, I examine the consequences of egg size for Thick-billed Murres at East Digges Island, Nunavut Territory, 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, I switched eggs among pairs to disengage underlying correlations between egg size and phenotypic attributes of adult females. My main objective was to test the hypothesis that egg size would have a more pronounced effect on wing-feather growth at Digges Island, where Thick-billed Murres chicks grow their wing feathers slowly, than at Coats Island, where chicks grow their wing feathers quickly. For example, nestlings use protein from the yolk-sac to grow feathers after hatching (Romanoff and Romanoff 1949); 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, so that variation in the amount of yolk protein might be manifested more strongly in variation in feather length.

5.3 Study Area and Methods

Field work was conducted at East Digges Island, Nunavut Territory, Canada (62°33' N, 77° 50' W) during July and August, 1999. 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 consistency with the Coats Island study, the following definitions are used: *Initial Volume* is the volume index of the eggs that females initially laid; *Foster Volume* is the volume index of the eggs that pairs received after egg-switching; *Mass Growth* and *Wing Growth* are the changes in 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, I 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 within 0.1

mm using vernier calipers. A volume index (length x breadth^2) that has a strong linear relationship with the mass of fresh Thick-billed Murre eggs at the two study colonies (r = 0.971; Hipfner, unpublished data) was used as a measure of egg size. The eggs were redistributed randomly among sites after being measured, so that for each pair I knew both Initial and Foster volumes.

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 were pipped on day (i) and hatched on day (i + 2) were assumed to have hatched on day (i + 1). Three chicks were still wet when found, and had obviously hatched earlier that 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 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 within 1 g with a 300 g spring balance, and the right wing measured to within 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 of age using linear interpolation. Therefore, I used 2 day measurements as estimates of initial size. Only chicks that survived > 14 days, and that were at least this old when field work ended (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 (Mass Growth and Wing Growth) are smaller (n = 37). Linear interpolation was used to estimate 14 day measurements for chicks not measured at exactly this age.

5.3.1 *Data analysis*

Data were analysed using SPSS (version 8.0) statistical software. All residuals were plotted and found to adequately meet the normality and equality of variances assumptions of parametric statistical tests.

I examined the effects of Initial and Foster volumes 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) I 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), I plotted mean wing length against chick age for chicks from the largest and smallest one-thirds of eggs in the sample. I 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 12-14 days of age. By 12 days of age, all chicks have started the linear phase of wing growth. I 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 14 day Mass differed significantly in both slope and elevation at Coats Island between 1994 and 1995 (unlike those for 14 day Wing, 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).

5.4 Results

5.4.1 *Experimental protocol and inter-colony differences*

There was no correlation between Initial and Foster volumes ($r_{51} = 0.01$, $P = 0.92$), 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 $P > 0.12$), so that seasonal trends in egg size and chick growth rates probably were unimportant. Finally, neither Initial (independent $t_{48} = 1.07$, $P = 0.29$) nor Foster volumes (independent $t_{48} = 0.52$, $P = 0.60$) 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.

Data on measures of egg size and chick growth at Digges and Coats islands are presented in Table 5.1. Eggs at Digges Island were similar in size to those laid there in previous years, and similar to those laid at Coats Island. 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. 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%, $n = 60$).

5.4.2 *The relationship between Initial and Foster volumes and chick growth*

In multiple regressions, Initial and Foster volumes explained little of the variation in Mass Growth (Table 5.2). Despite this, these variables had a significant effect on 14 day Mass, explaining 12% of the variation; however, only the positive effect of Foster Volume was statistically significant (Table 5.2). This indicates that differences in mass, established by egg size, tended to persist, and that

Table 5.1: Measures (mean ± 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 (*n*)	Coats Island (*n*)	
		1994	1995
Initial Volume (cm^3)	203.3 ± 18.5 (53)	201.3 ± 18.3 (33)	208.7 ± 16.1 (27)
Foster Volume (cm^3)	205.1 ± 14.7 (53)	206.2 ± 15.4 (33)	209.4 ± 14.9 (27)
Mass Growth (g)	51.6 ± 14.1 (37)	116.8 ± 19.3 (30)	103.8 ± 20.0 (27)
14 d Mass (g)	125.9 ± 24.7 (53)	199.0 ± 19.6 (33)	182.7 ± 21.1 (27)
Wing Growth (mm)	19.8 ± 4.6 (37)	28.1 ± 4.2 (30)	28.1 ± 4.4 (27)
14 d Wing (g)	45.5 ± 8.0 (53)	54.7 ± 4.5 (33)	53.4 ± 4.7 (27)

Table 5.2: Multiple regressions relating measures of chick growth to Initial and Foster volumes at Digges Island. For clarity, significant results are in bold.

	Multiple regression				Initial Volume			Foster Volume		
Measure of growth	*n*	R^2	*F*	*P*	*t*	*P*	slope/trend	*t*	*P*	slope/trend
Mass Growth	37	0.06	1.09	0.35	1.35	0.19	+	0.52	0.61	+
14 d Mass	53	**0.12**	**3.33**	**0.04**	0.99	0.33	+	**2.36**	**0.02**	**0.38**
Wing Growth	37	**0.22**	**4.67**	**0.02**	1.50	0.14	+	**2.57**	**0.02**	**0.11**
14 d Wing	53	**0.21**	**6.43**	**0.003**	1.54	0.13	+	**3.22**	**0.002**	**0.14**

the size of egg a female 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, $F_{1,76} = 0.52$, $P = 0.48$), 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 $F_{1,82} = 3.21$, $P = 0.08$), the year of faster growth there.

In multiple regressions, Initial and Foster volumes 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 5.2). The plot of mean wing length against age for chicks from the largest and smallest eggs at Digges Island showed that the effect 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 (see 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. 5.1). 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 ± 0.1 day advantage in wing growth, not significantly different than the 2.0 ± 0.1 day advantage enjoyed by large-egg chicks at Coats Island (independent $t_{35} = 1.55$, $P = 0.13$).

5.5 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 chick growth rates (Gaston et al.

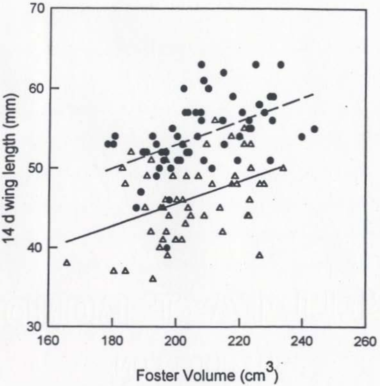

Figure 5.1: Scatter plot showing the relationship between 14 day wing length and egg size for the fostered Thick-billed chicks at Digges Island (open triangles) and Coats Island (filled circles). The slope of the line at Digges Island (0.14 ± 0.04 (SE) mm cm^{-3}) was similar to that at Coats Island (0.15 ± 0.04 (SE) mm cm^{-3}; ANCOVA, $F_{1,109} = 0.02$, $P = 0.89$). Coats Island data from Hipfner and Gaston (1999a)

(1983) reported means of 134-156 g in 3 years using similar weighing schedules). Therefore, feeding conditions during chick-rearing appeared to be particularly unfavourable 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, unpublished data); a much larger difference than occurs at Coats Island (differences of 45-86 g in five years, Gaston and Perin 1993), or at the Gannet Islands, Labrador, Canada (differences of 24-68 g in four 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 appear to be more favourable. Monaghan et al. (1994) estimated that Common Murres *Uria aalge* had to expend twice as much energy while foraging in a year of poor feeding conditions compared to a year of good feeding conditions at a colony in Shetland. Moreover, chick feeding rates were much lower at Digges Island in 1999 than at Coats Island in either 1994 or 1995 (Hipfner, unpublished data).

5.5.1 *Egg size and post-hatching development: comparison between colonies*

Egg size had a positive effect on the rate of increase in wing length among 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. Previous studies at Digges Island have shown that Thick-billed Murre chicks that have longer wings at 14 days of age tend to depart to sea when younger than do those with shorter wings (Hipfner and Gaston 1999b). Consequently, there is likely to be a fitness advantage for offspring in hatching from a large egg, because a large-egg chick will be developmentally prepared to leave the nest early, or to leave synchronously with other chicks. However, contrary to prediction, a large egg size provided no more time-saving advantage for nestling Thick-billed Murres at Digges Island than at Coats Island, despite the marked differences in 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 in mass survived for longer without food (Hatch 1983), so there may be an advantage for murres in hatching from a large egg in terms of survival after departure from the colony. Moreover, results of this study and that 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 hatchling mass may persist more strongly under these conditions (see also Styrsky et al. 1999 for passerines). In other species, large eggs also may confer survival advantages soon after hatching, because chicks from large-eggs hatch with large energy reserves that can tide them over short-term food shortages (Parsons 1970, Rhymer 1988). My methods were not well suited to examining the effects of egg size on nestling survival; however, even in a situation in which food availability appeared to be very low, 93% ($n = 46$) of chicks observed daily from a distance survived to departure age (15 days) at Digges Island in 1999, and there was no evidence that any of those that died had starved to death at the nest site (Hipfner, unpublished data). Starvation of nestling Thick-billed Murres appears to be a rare occurrence.

5.5.2 *Consequences of egg size for adults*

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, one would expect directional selection to drive populations towards a ubiquitous, optimal, large egg size. This has led to the suggestion that there may be costs associated with large eggs that counteract any fitness benefits they confer (e.g., Ankney and Bissett 1976).

Life-history theory predicts that in species with high annual survival rates, and low annual fecundity rates (like murres), 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 such trade-offs should be borne largely by offspring (e.g., Mauck and Grubb 1995), and may have resulted in negative relationships between the size of eggs females initially laid and the growth of the chicks they fostered. However, even though adults appeared to invest heavily in chick rearing, apparently at the expense of their own body condition, all relationships were (non-significantly) positive. Consequently, 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 than do those raised by younger, less experienced parents (de Forest and Gaston 1996). This age effect will tend to produce positive relationships between egg size and chick growth, which could override negative relationships occurring among older, more experienced females. However, few young Thick-billed Murres retain their eggs until late in incubation (de Forest and Gaston 1996), when the eggs were switched, so that the vast majority of females in the sample probably were older, and more experienced; egg size varies markedly even among these birds (Hipfner et al. 1997). Consequently, it seems very unlikely that this age effect could have masked underlying negative relationships among older females.

In fact, rather than facing immediate trade-offs as a consequence of producing large eggs, adult Thick-billed Murres may actually experience a direct, as well as an indirect, fitness benefit by doing so. If the more rapid development of offspring from large eggs enables them to depart to sea earlier, this would reduce the amount of time and energy that adults spend in the costly process of raising nestlings. As these costs appeared to be greater at Digges Island than at either of two small colonies, and because nestling periods are generally longer at slow-growth colonies like Digges Island than elsewhere (Gaston et al. 1983), these direct fitness benefits may be greater at larger colonies.

Even if adult females bear the brunt of any costs associated with producing large eggs, such that there is a trade-off between egg size and survival of adult females (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 (c. 90% at Coats Island, Gaston et al. 1994). Previous studies on the incidence and costs of relaying following egg loss suggest that egg production may not be a particularly demanding process for capable Thick-billed Murres at small colonies (Hipfner et al. 1999 (see Chapter 2), and unpublished data), but I do not know whether this is true at Digges Island. 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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Chapter 6: The Effect of Egg Size on Post-Hatching Development in the Razorbill: An Experimental Study

6.1 Abstract

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.

6.2 Introduction

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 Dunnett 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 differences in wing length that were established by egg size 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.

6.3 Study Area and 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 (length x 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. I used 15 days as a standard because it was 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.

6.4 Results

6.4.1 *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 6.1). 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.

Table 6.1: Comparisons (mean ± 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 (cm³)	178.1 ± 16.0	180.8 ± 14.1	8.4
Foster Volume (cm³)	177.1 ± 15.4	178.4 ± 18.1	9.3
14 day Mass (g)	180.4 ± 27.6	184.7 ± 22.8	13.9
Departure Mass (g)	187.9 ± 25.8	187.1 ± 23.4	13.1
14 day Wing (mm)	62.2 ± 7.2	63.4 ± 4.7	9.7
Departure Wing (mm)	74.4 ± 6.0	75.1 ± 6.6	8.3

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.

6.4.2 *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. 6.1a), 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 $\text{cm}^{-3;}$ Fig. 6.1b).

6.4.3 *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 6.2, Fig. 6.2a). Foster Volume had no effect on Mass Growth, but measures of growth in wing length increased with Foster Volume (Table 6.2, Fig. 6.2b).

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 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

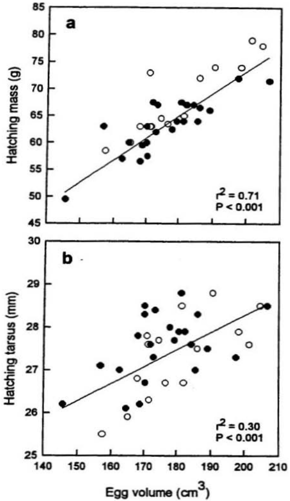

Figure 6.1: Scatterplots showing the relationship between egg size and (a) hatchling mass, and (b) hatchling tarsus length, for Razorbills chicks. Data points from 1996 are open circles (*n* = 15), those from 1997 are filled circles (*n* = 23)

Table 6.2: 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

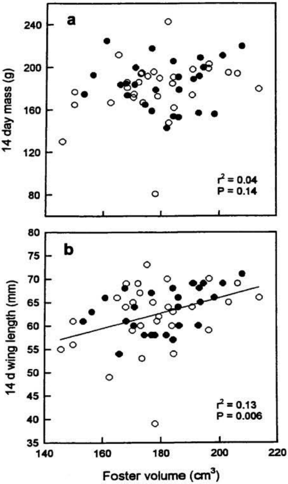

Figure 6.2: Scatterplots showing the relationship between Foster Volume and (a) 14 day mass, and (b) 14 day wing length, for Razorbill chicks. Data points from 1996 are open circles ($n = 30$), those from 1997 are filled circles ($n = 26$).

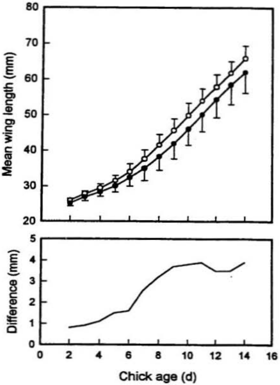

Figure 6.3: Wing length (mean ± SD) in relation to age for Razorbill chicks that hatched from the largest one-third of eggs (open circles), and the smallest one-third of eggs (both $n = 18$). The bottom figure shows the difference in mean wing lengths between the two groups.

of large-egg chicks, levelling off at 4 mm by 9 days of age (Fig. 6.3). This is equivalent to about 1 day's growth in wing length.

6.4.4 *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 $r^2 \leq 0.01$, all $F \leq 0.60$, all $P \geq 0.44$, sample sizes as on Table 6.2).

6.5 Discussion

6.5.1 *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 unfavourable, and exogenous protein for feather growth is in short supply to the developing chick (but see Chapter 5).

6.5.2 *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). However, because one parent must be present at all times to guard the chick at open nest sites, the chick is brooded constantly and this delay may be of minor importance. 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.

6.5.3 *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).

6.5.4 *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), one 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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Chapter 7: Summary

Like most marine birds, Thick-billed Murres and Razorbills employ high-survival, low- fecundity life-history strategies. It is generally believed that the single-egg clutch that is so common among pelagic seabirds has evolved mainly in response to the extreme demands of raising young on distant and unpredictable marine food sources, rather than to the demands of egg production (Lack 1968). For marine birds, the energetic demands of egg production appear to be comparatively low (reviewed in Astheimer and Grau 1990), while the demands of raising even a small number of young at the nest appear to be comparatively high (for species of Alcidae, reviewed in Hodum et al. 1998). While experimental studies have shown that adult seabirds that raise additional young suffer a detecable reduction in survival (Golet et al. 1998), there is no evidence of survival costs associated with producing more eggs in these birds. Because of extremely high wing-loading, which limits the size of food that can be carried back to the nest site and makes flights back and forth between feeding areas and the colony expensive, the demands of raising young at the nest site are especially high for murres and Razorbills (Pennycuick 1987). Constraints n the rate at which adults can feed their young probably have been the most important factors favouring the evolution of the unique "intermediate" developmental strategy (Gaston and Jones 1998), and computer modelling suggests that the long distances birds must commute between feeding areas and the colony may be especially important (Houston et al. 1996). The most striking feature of the intermediate strategy is the greatly reduced period of development at the nest site, the male parent taking the chick to sea within a few weeks of hatching, when the chick is less than one-quarter of final adult size. The chick is taken to the food source early in its development, rather than having the adults continue to take food back to the nest site. In Razorbills and murres, nestling growth rates tend to level off in the few days prior to nest departure (e.g., Hipfner and Bryant 1999), which suggests that the parents become unable to provide enough food for continued growth of a large nestling.

In sum, there is every reason to believe that constraints operating during chick-rearing, rather than those operating during egg production, have been of paramount importance in the evolution of the single-egg clutch, and later, the intermediate developmental strategy. Nonetheless, egg-production constraints also could be significant. In comparison to other Charadriiform birds, the single egg laid by murres and Razorbills is large in comparison to adult size (11-13 % of adult size; see Fig. 6.1 in Gaston and Jones 1998), and their eggs have relatively large yolks, and therefore, a relatively high energy content (see Chapter 4). In addition, for both species, there is likely to be be a selective advantage associated with a large egg (Hipfner and Gaston 1999, Hipfner 2000, see Chapters 5 and 6), but despite this, egg size varies substantially with female age, and also shows marked, and repeatable, variation among older females (Hipfner et al. 1997). Moreover, the effect of female age on egg-production capacity extends also to the capacity to renest following loss of the first egg: young females are less likely to renest, and the few that do have long relaying intervals (de Forest and Gaston 1996). These patterns in egg size and renesting capacity would not be expected if constraints on egg production were insignificant.

Recent studies of two species of inshore marine birds of the family Laridae found that pairs experimentally induced to produce three or four eggs, rather than two or three, subsequently were less successful in raising offspring (Heaney and Monaghan 1995, Monaghan et al. 1995, 1998). The existence of this within-season cost of producing extra eggs suggests that egg production may be a significant component of the total reproductive investment for inshore seabirds that lay multi-egg clutches. However, a subsequent study on one of these species (Lesser Black-backed Gull *Larus fuscus*) showed through continuous egg removals that females were able to lay 9 eggs on average, and some as many as 15, within a single bout (Nager et al. 2000). Therefore, even for these species, there is some doubt about how demanding it is for females to produce extra eggs. It is difficult to compare costs of producing an extra egg within a single clutch (as in the studies cited above) with the costs associated with producing an extra egg within a second clutch (as in species that lay a single-egg clutch), because of the difference in the time period over which the additional eggs are produced. The present study of pelagic Thick-billed Murres has shown that early-laying females have considerable capacity to renest, and that they are willing to continue to do so until very late in the laying period (Hipfner et al. 1999, see Chapter 2). Moreover, pairs in which the female was induced to renest suffered no reduction in reproductive success (Hipfner et al. 1999, see Chapter 2; see also Hatchwell 1991, de Forest and Gaston 1996), and previous studies have shown that replacement-egg chicks grow as well as first-egg chicks if both are raised by high-quality parents (Hatchwell 1991, de Forest and Gaston 1996, Hipfner 1997). Female Thick-billed Murres that renest spend as much time incubating as females that lay only one egg, and they suffer no delay in laying, or reduction in breeding success, in the following season (Hipfner et al. unpublished). In contrast to seabirds that lay multi-egg clutches, overt costs of producing extra eggs have not yet been detected in those that lay single-egg clutches.

For species that employ low-fecundity, high-survival life-history strategies (annual survival rates in murres are about 90%, Gaston et al. 1994), offspring raised in one breeding season represent only a small proportion of an individual's potential lifetime reproductive success. Life-history theory therefore would predict that murres should be unwilling to invest in any one breeding episode to a level that threatens their own survival (Stearns 1992). If true, the results of this study suggest that production of a replacement egg should not be excessively taxing for early-laying females (typically older, more experienced birds, Hipfner et al. 1997). Nonetheless, the comparison of the composition of first and replacement eggs indicated that females faced a protein shortage during production of the replacement eggs (see Chapter 4). In other Charadriiform birds, egg proteins are derived from both exogenous (dietary) and endogenous sources (Houston et al. 1983). As this protein shortage occurred at a time when dietary protein was likely to have been more available than it was during production of the first egg, due to recession of sea ice around the colony in late spring (Gaston and Hipfner 1998), it seems likely that the shortage was of endogenous protein (e.g., that derived from skeletal muscle, Houston et al. 1995; see Chapter 4). One might intuitively expect that there would be a survival cost to the female of expending heavily from her endogenous reserves, although protein may be drawn from specific types of reserves such that muscle function is not impaired (Houston et al. 1995). Clearly, the biggest gap in our knowledge of the life-history implications of replacement egg-laying in Thick-billed Murres, and other long-lived birds, is the across-season effect on female survival. At any rate, the effect would probably be very difficult to detect in a species with such a high survival rate.

Even if the costs of renesting are small, the considerable renesting capacity exhibited by early-laying female murres suggests that they must experience a net fitness benefit. Both empirical studies (Birkhead and Nettleship 1981, Gaston and Nettleship 1981), and theoretical models (Birkhead and Nettleship 1982, Ydenberg 1989), of breeding by Arctic seabirds assume that late-hatched offspring are at a disadvantage because food is less available late in the season. However, experimental studies have shown that parental quality, rather than timing, is the major factor affecting annual productivity and nestling growth rates in Thick-billed Murres; there is no evidence of a seasonal deterioration in feeding conditions (de Forest and Gaston 1996, Hipfner 1997, Hipfner et al. 1999, see Chapter 2).

Gaston (1992) has argued that increased precociality could have evolved in the Alcidae (probably from a semi-precocial ancestor) only if the food supply was predictable and adequate at sea during the period of growth after departure from the colony. In the intermediate alcids, adult males take their flightess chicks to sea and themselves undergo their post-nuptial moult, becoming flightless. As a result, the speed with which these adult-chick groups can search for food is limited to the swimming speed of the chick. If food supplies were declining and hard to find during this time, this would seem to be the worst possible strategy (Gaston 1992). By taking the chick to sea the range of diet items also may be increased; adult murres bringing food to the nest site bring back larger items than they themselves feed on (Gaston and Jones 1998).

As discussed earlier, late-fledging young in other marine birds may suffer high mortality because they fare poorly in competition for limited food resources with those that fledge early (Nisbet and Drury 1972, Spear and Nur 1994). However, in Thick-billed Murres, adult-chick pairs disperse rapidly and widely at sea after they leave the colony (Gaston 1982), so it is unlikely that intra-specific competition would be intense. While it appears counterintuitive for an Arctic-nesting species, in fact it should come as no surprise that the rates of survival to recruitment age differed little between first- and replacement-egg Thick-billed Murre chicks raised by early-laying parents (see Chapter 3). However, it remains an open question as to whether the poor quality of replacement eggs compared to first eggs (see Chapter 4) might have negative fitness consequences at colonies that experience poor feeding conditions and lower chick growth rates.

While much has been learned from this study of the life-history implications of renesting for Thick-billed Murres, the life-history implications of variation in egg size remain less clear. Thick-billed Murre eggs vary substantially in size: at Coats Island, among females that were at least 8 years old and breeding for at least the third time, the largest egg was about 33% larger than the smallest (Hipfner et al. 1997). This marked variation occurs despite the fact that egg size has been shown to affect offspring performance in this species (Hipfner and Gaston 1999). In studies where no positive fitness effects of egg size were found, researchers often mentioned the possibility that the absence of an effect might reflect the fact that their studies were carried out under favourable feeding conditions (Reid and Boersma 1990, Smith et al. 1995). Advantages of hatching from a large egg may be more pronounced where feeding conditions are unfavourable (Williams 1994).

This study found at best only very weak support for that hypothesis: the magnitude of the effect of egg size on the rate of wing-feather growth was no greater at a colony (Digges Island) where both provisioning rates (M. Hipfner unpublished) and chick growth rates were lower than at Coats Island (see Chapter 5). However, there was a suggestion that mass advantages associated with hatching from a large egg persisted more strongly where growth was slower, although we would have expected a more marked effect at Digges Island than was found in the year of slower growth at Coats Island (see Chapter 5). A larger body mass might provide a murre with a survival advantage (Hatch 1983), although there was no clear support for this (see Chapter 5).

If egg size and offspring fitness are positively related, directional selection would be expected to drive bird populations towards a ubiquitous large egg size, because there is a genetic component to egg-size variation (Boag and van Noordwiijk 1981). However, egg size varies substantially in bird populations, and a number of hypotheses have been advanced to explain this paradox. For example, it has been suggested that alleles influencing egg size might be pleiotropically linked to other alleles that influence general metabolic processes (Williams et al. 1993), or that natural selection might not act directly on egg size, but rather on non-heritable environmental effects on egg size that are mediated by female condition (as Price et al. 1988 suggested for laying date). In addition, it has been suggested that small eggs might occasionally be favoured if they can be formed more quickly (Birkhead and Nettleship 1982). It is also sometimes suggested that adult females may face a trade-off between egg size and capacity to invest in other phases of breeding that season.

To date, no study has documented any such within-season trade-offs (Smith et al. 1995). As discussed previously, life-history theory predicts that any trade-offs between egg size and the female's provisioning capacity will be borne mainly by offspring in long-lived species, and if so, should be manifested as death, or reduced growth, of offspring. However, to the contrary, the relationship between the size of egg female Thick-billed Murres originally laid and the growth of the chicks they fostered was positive in direction, rather than negative, and very few chicks died despite poor feeding conditions (see Chapter 5). Consequently, the existence of considerable, female-specific variation in egg size remains unexplained. I suggest that an examination of the relationship between egg size and female survival is required, although as with relaying, a negative relationship between egg size and female survival probably would be very difficult to detect in long-lived Thick-billed Murres.

Much of the foregoing discussion of the life-history implications of egg size applies equally to Razorbills, because the relative variation in egg size in this species is similar to that in Thick-billed Murres (Lloyd 1979, M. Hipfner unpublished). In addition, there was no suggestion of a trade-off between egg size and provisioning among Razorbills (see Chapter 6). However, my main interest in examining the relationship between egg size and post-hatching development in this species was to test the hypothesis that the positive effect of egg size on wing feather growth seen in Thick-billed Murres reflected adaptations to the intermediate developmental strategy. This effect has so far been detected only in this species, which suggests that an effect of that magnitude is not widespread. The results clearly supported this hypothesis (Hipfner 2000, see Chapter 6).

As suggested by Ydenberg (1989), I see the intermediate strategy as having evolved in response to the need to get a nestling that is growing slowly (due to constraints on parental provisioning), and that is vulnerable to predators (due to an open nest site), from nest site to sea as quickly as possible, but with the risk associated with that transition minimized. A key factor is the growth of sufficiently long wings that will enable to the chick to plane rather than plummet on the descent from a cliffside nest site (Birkhead 1977, Hedgren 1981). Therefore, natural selection should favour factors that result in rapid growth of wing feathers. Some or all of the following factors might be involved in producing the observed effect of egg size on feather growth in intermediate alcids: first, the incubation period in murres and Razorbills is briefer than expected for the size of the egg in comparison to semi-precocial alcids (Barrett et al. 1995). This might maximize the mass of the hatchling's yolk sac, and therefore its reserves (Barrett 1984). Duncan and Gaston (1988) showed that the yolk sac comprises about 17% of hatchling mass in Thick-billed Murres, but only 7-9% of hatchling mass in three species of semi-precocial alcids, even though the yolk content in fresh eggs is similar. Laying and incubating on an open ledge, rather than in an enclosed burrow (as most semi-precocial alcids do), may be important, because this increases the gradient in humidity across the egg shell, which could speed the development of the embryo (Rahn and Ar 1974). Next, the amount of down grown during embryonic development is minimized, and the yolk protein that is saved used to grow feathers after hatching; intermediate auks hatch with much less down than do semi-precocial auks in proportion to the size of the hatchling (Barrett 1984, M. Hipfner unpublished). Finally, the growth of the large flight feathers is delayed until after the chick has departed to sea, so that the protein requirements for feather growth are minimized during the period of development at the colony. In that way, the relative contribution from yolk protein to post-hatching feather growth is larger than in other species of birds that undergo growth of all feathers soon after hatching.

This thesis has examined two aspects of egg production in Thick-billed Murres and Razorbills within a life-history framework. As might be expected, more questions were left unanswered than were answered. I suggest that the following might be productive areas for future research:

(1) There is a need to examine the effect of relaying on subsequent female survival, although, as as discussed, any effect would probably be small. Moreover, a long-term dataset, a rare commodity, would obviously be required.

(2) The relaying decision of Thick-billed Murres could be examined under different ecological conditions, such as at a colony where feeding conditions are less favourable than they are at the Gannet Islands and Coats Island, or at a high-Arctic rather than a low-Arctic colony, where time constraints might be more pressing.

(3) The consequences for chick growth or survival of hatching from the lower quality replacement eggs could be examined at a colony where feeding conditions are less favourable, and where chicks grow more slowly.

(4) The relationship between egg size and female survival also could be examined, although the same constraints (and which would probably be more severe) apply here as apply to the examination of the effects of relaying on survival.

(5) The relationship between egg size and post-hatching development could be examined in semi-precocial alcids to either confirm or refute the hypothesis that the effect observed in intermediate alcids does in fact reflect evolutionary priorities in the post-hatching development of this group.

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