

EGG SIZE, CHICK DEVELOPMENT, AND THE NEST DEPARTURE DECISION
OF THE THICK-BILLED MURRE

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Abstract

Among long-lived birds which breed in seasonal, time-limited environments, reproductive success usually increases with age, and within seasons, declines with date. However, it can be difficult to determine whether the seasonal patterns are a direct effect of timing of breeding, or are consequences of the late breeding of younger, less capable birds. In addition, some of the patterns may be adaptive responses to breeding in a seasonal environment.

Thick-billed Murres *Uria lomvia* are colonial seabirds of Arctic regions. They lay a one-egg clutch, and the chick leaves the nest, accompanied by the male parent, at a young age and in a partly-developed state to complete its growth at sea. In this thesis, I examine the factors that influence egg size, chick development, and the nest departure decision of young Thick-billed Murres. The study was conducted at a colony of 30,000 breeding pairs at Coats Island, N.W.T., Canada, in 1994 and 1995.

As females increased in age to 8 y (typically the fourth year of breeding), dates of egg-laying decreased while the size of eggs laid increased. Experienced birds initiated egg formation earlier in the season, and deposited more yolk per day, than younger birds. Egg size was negatively correlated with laying date, especially in 1994. I tested two hypotheses advanced to account for the seasonal declines in egg size: (i) the decline is an adaptive response to breeding in a seasonal environment; and (ii) egg size is determined by the abilities of the female, rather than being adjusted to the date of laying. Among experienced pairs, egg size and laying date

were unrelated; eggs laid by young birds at the same time as those of experienced pairs were smaller. These two observations support explanations of the seasonal decline in egg size based on constraint, rather than adaptation.

The consequences of variation in egg size for chick development remain poorly understood in wild birds. In an experiment aimed at separating effects of parent quality from those of egg size, there was a positive relationship between egg size and the rate at which nestling Thick-billed Murres grew their wing feathers. Growth rate in mass was independent of egg size. Chicks with long wings left the nest to go to sea at a younger age than those with shorter wings in one of two years. I conclude that Thick-billed Murre chicks from large eggs have a developmental advantage over those from small eggs, and that this may have life-history consequences. A hypothesis to account for the positive relationship between egg size and the growth rate of the wing feathers is proposed.

In many species of birds, including Thick-billed Murres, young birds lay late and reproductive success declines with date. In an experiment to distinguish between quality and timing effects on the growth of nestling Thick-billed Murres, the chicks of high quality, experimentally-delayed breeders grew as quickly, and departed at similar mass, as those of unmanipulated early-breeding birds. In the general population, growth rate declined with date of hatching. I conclude that the poor quality of late-breeding birds, more than a seasonally-deteriorating environment, causes the declines in growth of nestling Thick-billed Murres at this colony.

Two ubiquitous patterns in the breeding of the Alcidae are that the age and mass of chicks at nest departure relate negatively to hatching date. It is often reported that faster-growing chicks depart at a younger age than slow-growing chicks. Ydenberg (1989) proposed that these patterns are adaptive responses to breeding in a time-limited environment. I tested two main predictions of the Ydenberg model of alcid nest departure for the Thick-billed Murre, which employs a nest departure strategy intermediate within the Alcidae. In inter-colony, intra-colony, and experimental tests, there was some empirical support for the predictions, but more often the results did not support the model. Moreover, in some instances in which the observations did match the predictions, the match might have been spurious. I suggest that there are developmental and behavioural considerations in the nest departure decision of the intermediate alcids not adequately explained by the Ydenberg model. An alternative hypothesis is proposed, which suggests that the strategy centres around getting the chick from the cliff to the sea as quickly as possible, but with the mortality risk involved in making the transition minimized. I discuss the developmental and behavioural implications of this hypothesis.

Resumé

Chez les oiseaux ayant un taux de survie élevé et qui se reproduisent dans un environnement saisonnier soumis à des contraintes temporelles, la réussite de la reproduction augmente avec l'âge, et au cours d'une même saison, diminue avec le temps

qui passe. Cependant, il est difficile de déterminer si les variations saisonnières sont une conséquence directe du moment de l'accouplement ou de l'accouplement tardif des oiseaux les moins aptes. De plus, il se peut que certaines des variations représentent une adaptation de la faculté reproductrice dans un environnement saisonnier.

Les Marmettes de Brunnich *Uria lomvia* sont des oiseaux de mer des régions arctiques, vivant en colonies et nichant à même des falaises. Ils ne pondent qu'un seul oeuf. Le poussin quitte le nid à un jeune âge, accompagné du parent mâle, pour poursuivre sa croissance en mer. Ce travail est consacré à l'étude des facteurs qui conditionnent la taille des oeufs, le développement du poussin, et la décision de quitter le nid chez les jeunes. L'étude a été menée auprès d'une colonie de 30,000 couples à Coats Island dans les territoires du Nord-ouest, Canada en 1994 et 1995.

En vieillissant, jusqu'à atteindre l'âge de huit ans correspond en général à la quatrième année d'accouplement, la fréquence de ponte diminue alors que la taille des oeufs augmente. Chez les oiseaux expérimentés, la formation de l'oeuf commence plus tôt dans la saison, et une plus grande quantité de jaune est déposée chaque jour, par rapport aux jeunes oiseaux. Il y avait une corrélation négative entre la taille des oeufs et la date de ponte, surtout en 1994. Deux hypothèses ont été proposées afin d'expliquer la réduction saisonnière de la taille des oeuf: (i) la réduction est une réponse adaptée à la reproduction soumise à des contraintes temporelles; et (ii) la taille de l'oeuf est déterminée par les

aptitudes de la femme et non pas par la date de ponte. On a trouvé aucune corrélation entre la taille des oeufs et la date de ponte chez les oiseaux matures, et des oeufs pondus par de jeunes oiseaux étaient plus petits que ceux pondus en même temps par des oiseaux matures. Mes résultats appuient la première hypothèse; la réduction de la taille des oeufs est fonction des contraintes plutôt qu'une adaptation.

Les conséquences liées à la taille de l'oeuf sur le développement du poussin chez les oiseaux sauvages, ne sont pas encore bien comprises. Une expérience a été menée pour différencier les effets dûs à l'aptitude parentale par rapport à la taille de l'oeuf. En effet, on obtient une corrélation positive entre la taille de l'oeuf et la vitesse de croissance des plumes des ailes chez les oisillons Marmette de Brunnich. La vitesse de croissance n'était pas liée à la taille de l'oeuf. Les poussins aux ailes longues ont quitté le nid plus tôt que leurs comparses aux ailes plus courtes. J'en conclus que sur le plan du développement, les poussins provenant d'un oeuf de taille supérieure ont un avantage sur ceux provenant d'un oeuf plus petit, ceci ayant des conséquences vitales. Une hypothèse est formulée pour expliquer la relation entre la taille de l'oeuf et la vitesse de croissance des plumes des ailes.

Chez plusieurs espèces d'oiseaux, y compris le Marmette de Brunnich, les jeunes pondent tardivement, le taux de réussite déclinant avec la saison. Du coup, il est difficile de faire la part entre la qualité parentale et la période de l'accouplement sur

ces déclin. Une expérience a été menée dans le but de distinguer entre les effets dûs aux aptitudes parentales et à la date de fécondation sur la croissance des oisillons. Les poussins, nés de parents aptes, dont l'accouplement a été retardé à dessein, se sont développés aussi rapidement et ont quitté le nid au même poids que ceux nés d'oiseaux s'étant accouplés naturellement, plus tôt dans la saison. Dans la population générale, le taux de croissance a décliné en fonction de la date de l'éclosion. J'en conclus que c'est la faible aptitude des oiseaux s'accouplant tardivement, et non pas une détérioration environnementale, qui est responsable du déclin dans la croissance des oisillons Marmette de Brunnich dans cette colonie.

Chez les Alcidae, on constate une corrélation négative entre l'âge et le poids des poussins au moment où ils quittent le nid, et la date d'éclosion des oeufs. On constate que les poussins à croissance rapide sont plus jeunes quand ils quittent le nid que les poussins à croissance plus lente. Ydenberg (1989) explique ceci comme une adaptation de la faculté reproductrice dans un environnement soumis à des contraintes temporelles. Deux prédictions importantes du modèle de Ydenberg ont été testées auprès du Marmette de Brunnich. Que ce soit parmi les différentes colonies, au sein d'une même colonie, ou parmi une population expérimentale certaines des données confirmaient les prédictions, mais dans l'ensemble nos résultats ne validaient pas le modèle. De plus, dans les cas où les données allaient dans le sens des prédictions, les correspondances pouvaient être expliquées

autrement. Une hypothèse alternative est proposée: la stratégie consiste à conduire le poussin de la falaise à la mer le plus tôt possible, tout en minimisant le taux de mortalité durant la transition. Les implications d'une telle hypothèse sur le développement et la comportement de l'oiseau sont soulevées.

Chapter 1: General Introduction

Life-history theory postulates that a trade-off exists between reproduction and mortality. To maximize its fitness, the individual strives to produce as many viable offspring as possible over its lifetime, but each attempt at reproduction lessens the chance that it will survive to reproduce in the future. Consequently, the benefits of current reproduction must be balanced against the costs incurred in terms of reduced future reproduction (Williams 1966).

It is typical in long-lived species of birds that the younger members of the population breed less successfully than the older members (Saether 1990). A number of hypotheses have been advanced to explain this observation. If young birds have higher residual reproductive value than older birds, they should invest less in reproduction (Williams 1966). Alternatively, younger birds might simply lack the experience necessary to succeed (Nur 1984). Finally, both factors could be involved simultaneously: if they find that they are deficient, younger birds should invest little, either because they are unlikely to succeed, or because they might have to invest too much to succeed, and so might incur too high a cost in terms of reduced survival (Curio 1983).

Among species breeding in seasonal, time-limited environments, the timing of breeding also could influence success if conditions for raising young deteriorate late in the season (Perrins 1970). Typically, late-breeding individuals are less successful than those breeding early (e.g., Perdeck and Cave 1992). However, the late-

breeding members of the population tend to be the younger members (Saether 1990). Consequently, young birds, which may lack skill or motivation, also often breed when environmental conditions are worse. As a result, it is difficult to distinguish the extent to which the seasonal declines in reproductive success result from seasonal differences in the age or quality of breeding birds, or from direct effects of timing of breeding (e.g., Verhulst et al. 1995).

The Alcidae show characteristics typical of most marine birds, including high annual adult survival (up to 95% in larger species, e.g. Hudson 1985), deferred breeding (e.g. 7 y median age at first breeding in Common Murres *Uria aalge*, Harris et al. 1994), and a low reproductive rate (most species lay a one-egg clutch) (Lack 1968). In addition, most species breed in seasonal environments. Consequently, they display the features of long-lived birds of seasonal environments: measures of reproductive success increase with adult age and, within seasons, decline with date (e.g., de Forest and Gaston 1996).

Two consistent seasonal trends in the breeding of the Alcidae are: (i) egg size declines with date of laying (Lloyd 1979; Harris 1980; Birkhead and Nettleship 1982); and (ii) chick age and mass at nest departure decline with hatching date (Harris 1980, 1982; Gaston et al. 1983). These declines are most often attributed to direct seasonal effects, for example a reduction in the quality or quantity of available prey late in the season (e.g., Hedgren and Linnman 1979), or to the late laying of young, inexperienced birds

(e.g., Lloyd 1979), so that the trends could result from constraints acting on late-breeding members of the population. Alternatively, mechanisms may have evolved by which birds can minimize the impact of breeding in a seasonal environment, so that the trends in egg size and chick condition at nest departure are actually adaptive responses to this seasonality (Birkhead and Nettleship 1982; Ydenberg 1989).

In this thesis, factors affecting egg size, chick growth and development, and the decision about when to leave the nest for the sea, are examined in the Thick-billed Murre *Uria lomvia*. Thick-billed Murres are Arctic-breeding alcids in which the single chick leaves the nest at a young age in a partly-developed state. Two themes are central to this thesis: (i) the extent to which parental quality or environmental conditions, determine the seasonal patterns of success; and (ii) the extent to which features of the breeding of Thick-billed Murres might represent adaptations to a seasonal breeding environment, or might result from constraints acting on the less capable members of the population. The study was conducted at a colony of 30,000 breeding pairs of Thick-billed Murres at Coats Island, N.W.T., Canada, during 1994 and 1995.

In Chapter 2, the role of female age in determining laying date and egg size is examined; in particular, two hypotheses advanced to explain the decline in egg size with laying date (a widespread, but rarely investigated phenomenon in birds) were tested: one based on the possible adaptive value of the seasonal decline, the other based on constraints limiting egg size among younger, later-laying

birds. In Chapter 3, the consequences of variation in egg size to chick growth and development are examined, controlling for the confounding effects of parental quality. In many species, young birds lay smaller eggs than older birds, and egg size declines with date of laying, but despite much previous research, the effects of egg size variation on offspring fitness remain poorly understood (Williams 1994). In Chapter 4, I examine the causes of the decline in chick growth rates with date of hatching, another widespread phenomenon, to assess the extent to which parental quality and/or environmental conditions determine the seasonal patterns of growth. Finally, in Chapter 5, and by way of summary, I examine the factors that influence the age and mass at which Thick-billed Murre chicks leave the nest. Two predictions of a model of the nest departure decision of alcid chicks developed by Ydenberg (1989) are tested. The central proposition of the model is that the seasonal declines in chick mass and age at nest departure (characteristic patterns in alcids) are adaptive responses to breeding in a seasonal, time-limited environment.

Chapters 2 through 4 are presented as separate manuscripts to be submitted for publication. As a result, there is some overlap in various sections of these Chapters.

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Chapter 2: The Role of Female Age in Determining Laying Date
and Egg Size in the Thick-billed Murre

Abstract.- In many bird species, egg and/or clutch size tends to correlate negatively with laying date. This has been viewed as an adaptive response to breeding in a seasonal environment. At Coats Island, N.W.T., Canada, in 1994 and 1995, I examined the causes of within-year variation in laying date and egg size in the Thick-billed Murre *Uria lomvia*, an Arctic-breeding seabird which lays a one-egg clutch. In particular, two hypotheses advanced to explain the seasonal declines in egg size were tested. The "adaptive" hypothesis proposes that late-laying individuals lay small eggs to minimize the delay in laying; the "constraint" hypothesis proposes that late-laying individuals lay small eggs because they cannot produce larger ones. Laying dates became earlier with increasing female age to 8 y, mainly because older birds initiated egg formation earlier than younger birds. Egg sizes increased with female age to 8 y, possibly because older birds deposited more yolk per day than younger birds. "Individual" effects explained much of the variation in laying date and egg size in both older and younger females. Among experienced breeders (≥ 3 y previous breeding experience), there was no relationship between egg size and laying date, indicating that it is not adaptive for late-laying birds to reduce egg size. Eggs laid by young birds (≤ 6 y) at the same time as those of late-laying experienced birds were smaller. These results support explanations of the seasonal decline in egg size based on constraint, rather than adaptation.

INTRODUCTION

In many long-lived bird species, measures of reproductive success increase with age early in life, and many hypotheses have been proposed to explain this observation (reviewed in Saether 1990; Forslund and Part 1995). For example, life history theory predicts that young birds will invest less in current reproduction than older birds if their residual reproductive value is higher (Williams 1966; Pugesek 1981). An alternative view is that young birds are less successful because they lack the experience of older birds (Nur 1984). Finally, if they lack necessary skills, younger birds should invest little in reproduction, either because they are unlikely to succeed, or because they have to invest too heavily to succeed, and so incur too high a cost (Curio 1983).

In species that breed in seasonal environments, the timing of breeding may also influence reproductive success (Perrins 1970). Individuals that breed early are usually more successful than those breeding late (reviewed in Perdeck and Cave 1992). However, late-laying birds are often the younger, less experienced members of a population, which makes it difficult to distinguish effects of age from those of timing of breeding.

As a group, seabirds are characterized by high annual adult survival and low annual productivity (e.g., Ainley and Boekelheide 1990). Where they breed in seasonal environments, age and timing of breeding are likely to have marked effects on their reproduction. Two measures of reproductive performance that have been examined frequently in seabirds are egg and clutch size. In

species laying multi-egg clutches, egg and/or clutch size typically increases with female age and/or decreases with laying date (Shag *Phalacrocorax aristotelis*, Coulson et al. 1969; Brandt's Cormorant *Phalacrocorax penicillatus*, Boekelheide and Ainley 1989; Great Skua *Catharacta skua*, Hamer and Furness 1991; Herring Gull *Larus argentatus*, Davis 1975, Parsons 1975; Western Gull *Larus occidentalis*, Sydeman et al. 1991; Red-billed Gull *Larus novaehollandiae*, Mills 1979; Black-legged Kittiwake *Rissa tridactyla*, Coulson and White 1958; Common Tern *Sterna hirundo*, Nisbet 1978; Arctic Tern *Sterna paradisaea*, Coulson and Horobin 1976; Black Guillemot *Cepphus grylle*, Cairns 1987). Similarly, in species laying one-egg clutches, egg size typically increases with female age (Wandering Albatross *Diomedea exulans*, Weimerskirch 1992, Croxall et al. 1992; Manx Shearwater *Puffinus puffinus*, Brooke 1978; Northern Gannet *Sula bassanus*, Nelson 1966; Razorbill *Alca torda*, Lloyd 1979) and decreases with laying date (Antarctic Fulmar *Fulmarus glacialis*, Weimerskirch 1990; Northern Gannet, Nelson 1966; Razorbill, Lloyd 1979; Thick-billed Murre *Uria lomvia* Birkhead and Nettleship 1982, Gaston et al. 1985; Atlantic Puffin *Fratercula arctica*, Harris 1980).

Drent and Daan (1980) proposed that the seasonal decline in clutch size observed in many temperate bird species is adaptive: these birds face a trade-off between clutch size (offspring number) and laying date (offspring quality). In this view, individuals in poor condition (such as young, inexperienced birds) delay egg-laying to allow themselves more time to accumulate the reserves

necessary for egg production, increasing their potential clutch size. However, the delay reduces the probability that their offspring will survive to recruitment. These individuals maximize fitness by postponing and laying smaller clutches. The adaptive, time-saving hypothesis of seasonal decline in clutch size has been supported, in particular because declines in clutch size with laying date occur even among experienced birds (e.g. Hamman and Cooke 1989; Hochachka 1990), and in the absence of age effects on clutch size or laying date (Dalhaug et al. 1996).

Species laying only one egg can alter their investment in egg production only through varying the quality of the egg. Birkhead and Nettleship (1982, 1984) proposed that the seasonal decline in egg size observed in the Thick-billed Murre, an Arctic-breeding seabird that lays a single egg, is adaptive: late-laying birds face a trade-off between egg size and laying date. Large eggs and early laying both increase offspring quality, but larger eggs take more time to produce. For birds unable to produce a large egg early in the season (often young, inexperienced birds), the trade-off will increasingly favour earlier laying, and therefore smaller eggs, as the season advances. In support of their model, Birkhead and Nettleship (1982) found that in Thick-billed Murres that lose their first egg and replace it, the difference in size between the first and replacement eggs is very similar to that predicted by the regression of egg size on laying date for the population.

Egg formation may be influenced by other factors as well. The availability of food during the pre-laying period probably affects

all aspects of egg production (Perrins 1970). As a result, laying dates and egg sizes may vary between years due to variations in environmental conditions. Conversely, the qualities of individual females that influence their ability to produce eggs should result in a degree of repeatability between years in these measures (e.g., Croxall et al. 1992; Sydeman and Eddy 1995).

In this paper, I investigate the causes of variation in laying date and egg size among Thick-billed Murres breeding at Coats Island, N.W.T., Canada, in two years. My specific objectives are to examine: (i) the effect of female age on laying date, egg size and the time required to form the yolk; (ii) the repeatability in the laying date and egg size of an individual female, i.e. the "individual" effect; and (iii) the causes of the seasonal decline in egg size. I set out to test the Birkhead and Nettleship (1982) model, comparing it to an alternative hypothesis that proposes the decline results from constraints acting on young, presumably less capable, birds (e.g., Lack 1968). The "adaptive" and "constraint" models are depicted graphically in Figure 1. It is recognized in both models that younger birds lay later, and lay smaller eggs. However, in the "adaptive" model, egg size declines with laying date within age classes; in the "constraint" model, the decline occurs between age classes. The simplest test to distinguish between the two is to examine the relationship between egg size and laying date among experienced birds. If the decline is adaptive, eggs laid by experienced birds should exhibit the decline; if it results from constraints acting on inexperienced birds, there

should be no seasonal decline in egg size among experienced birds.

STUDY AREA AND METHODS

The Thick-billed Murre colony at Coats Island ($62^{\circ} 57'N$, $82^{\circ} 00'W$) consists of two sub-colonies of similar size, separated by 1 km of coastline, which together include ca. 30,000 breeding pairs (Gaston et al. 1993). Since 1984, about 2000 nestling Thick-billed Murres have been banded annually on the west sub-colony, so that a population of breeding birds of known age has been established (Gaston et al. 1994). In addition, about 100 breeding adults have been banded annually. I consider birds banded as breeding adults at least 3 y previously, and therefore breeding for at least the fourth time, to represent experienced breeders (Gaston et al. 1994). A small group of birds (<500 pairs and including many birds banded as adults) occupying the north end of the colony has laid later every year than those on other parts of the colony. This allowed me to examine the effects of laying date on egg size while controlling for age (and vice versa) under natural conditions.

In 1994 and 1995, I observed breeding pairs daily from blinds on a series of six study plots to determine dates of egg-laying to within 24 h, using the Type I methods of Birkhead and Nettleship (1980). I measured the length and maximum breadth of eggs to within 0.1 mm using vernier calipers on accessible areas of four of these plots. As a measure of egg size, I used an index of egg volume ($\text{length} \times \text{breadth}^2$) which is linearly related to fresh egg mass in Thick-billed Murres ($r=0.952$; Birkhead and Nettleship

1984). To minimize disturbance, the plots were visited only once unless they were sufficiently accessible that entering them to take measurements did not cause egg losses.

Effects of age on laying date, egg size, and yolk formation time

To examine the variation in laying dates and egg sizes due to female age, I pooled the samples from the two years (inter-year differences in laying dates and egg sizes among older birds were not significant). The sample sizes within each age class were similar in the two years. In addition to this cross-sectional sample, I also compared the laying dates and egg sizes of the same females in successive years to see whether the pattern observed in individual females matched that of the population sample. Because Thick-billed Murres rarely breed at < 4 y old, and males typically first breed 1 y older than females (Gaston et al. 1994), I assumed that all breeding 3 y olds were female. Other birds were sexed by their position during copulation, but a few were sexed by observing which pair member (the male, Gaston and Nettleship 1981) departed with the chick.

To examine the effects of age on the length of time spent on yolk formation, I collected the first ten eggs laid by pairs in which at least one member was an experienced breeder in an area away from our study plots, and the first nine eggs accessible to me laid by first-time breeding females wherever I could find them. Yolk formation times were estimated using the potassium dichromate staining technique (Grau 1976). The yolks were weighed after being

stained, so the values should not be considered fresh masses.

Individual effects on laying date and egg size

To examine the effect of individual females on laying date and egg size, I compared laying dates and egg sizes of the same females in the two years, analysing older and younger females separately. I also removed the first eggs from samples of birds on 25 and 26 June in both years, inducing them to relay, and then compared the volume indices of the replacement eggs with those of the first eggs. As the background colour and pattern of markings on murres' eggs is repeated on eggs laid by the same female (Southern 1951), I used Polaroid photographs of the first eggs to verify that the egg later found at the same site was laid by the same female.

Intra-year variation in egg size and laying date

To examine variation in egg size with laying date, I measured and weighed (to within ± 1 g with a 300 g spring balance) a random sample of eggs laid by birds of unknown age and breeding history in an area away from our study plots in mid-July of both years (just before hatching began). Laying dates for these eggs were estimated from their densities, as described in Collins and Gaston (1987). To assess the role of age and laying date in determining egg size, I compared laying dates and egg volumes within and between three groups: (i) those in which the female member of the pair was an experienced breeder, or one member of the pair, of unknown sex, was experienced and the other was not a known-age bird < 8 y of age

(EXB); (ii) a naturally late-laying group of experienced breeders, as defined in (i), occupying Plot JB at the extreme north end of the colony (JB EXB); and (iii) those in which the female was < 7 y of age, or one member of the pair, of unknown sex, was banded and < 7 years of age (YNG). While this method is not as rigorous as using only females of known age, I felt it was justified because: (i) Thick-billed Murres tend to mate assortatively with respect to age (Gaston et al. 1994); and (ii) in any case, the only potential bias would be to underestimate the differences between young and experienced pairs by including what were actually YNG pairs in one of the EXB categories (i.e., a pair consisting of an experienced male mated to an unbanded, young female, would be classed as an EXB pair, while a pair consisting of a young male and an unbanded, experienced female would be classed as a YNG pair). Of the YNG pairs used in this sample, at least 67% included a female < 7 y; of the EXB pairs, at least 45% included an EXB female.

RESULTS

Inter-year variation in laying date and egg size

Among older females which laid in both years, neither laying dates nor egg sizes differed significantly between years (Table 1). Among younger females which laid in both years, laying dates were similar but egg sizes larger in 1995 than in 1994 (Table 1).

Effects of age on laying date and egg size

With data from the two years combined, laying dates tended to

decrease with female age to 8 y (Figure 2), and egg volumes tended to increase with female age to 8 y (Figure 3). Laying dates and egg sizes levelled off at > 8 y. The increase in egg size in this cross-sectional sample ($7 \text{ cm}^3 \text{y}^{-1}$) was very similar to that in the sample of young females whose eggs were measured in both years ($8 \text{ cm}^3 \text{y}^{-1}$) (Table 1). The eggs laid by 3 y and 4 y old females were similar in size (Figure 3), probably because all 3 y and most 4 y females were laying for the first time (Gaston et al. 1994). However, 3 y females laid ca. 1 week later on average than 4 y females (Figure 2).

Egg length and breadth followed a similar pattern of increase with age, so that the shape index (length/breadth) of eggs changed very little, and in no systematic fashion, with age (Figure 4).

Effects of age on yolk formation time

Experienced breeders took 12-15 d to form their yolks, while first-time breeders took 13-16 d; the difference between the two groups, <1 d on average, was not significant (Table 2). However, the eggs laid by the first-time breeding females were significantly smaller, and had smaller yolks, than those of experienced pairs. Consequently, although there was little effect of age on the length of time spent on yolk formation, there was a significant effect on the rate of yolk deposition: older birds deposited more yolk per day than younger birds (Table 2). Egg size was independent of yolk formation time for the whole sample, and within the age-classes separately (Table 2). The rings in the yolk of one of the nine

eggs of the young females were indistinct, so the sample size in this group was eight; it included seven 4 y and one 3 y female.

Individual female effects on laying date and egg size

Among older females, both laying dates (Figure 5) and egg sizes (Figure 6) were strongly correlated between 1994 and 1995, with these individual effects explaining 55% and 62% of the variation, respectively. There were similar between-year correlations among young females (laying date: $r=0.57$, $p=0.01$, $N=18$; egg volume index: $r=0.87$, $p<0.001$, $N=11$).

In both years, replacement eggs laid after the removal of first eggs were significantly smaller than the first eggs (by 5-6%), but there were strong correlations between the sizes of the two eggs (Table 3). The size of the first egg explained 58% (1994) and 79% (1995) of the variation in the size of the replacement egg. Both first and replacement eggs were similar in size in the two years (Table 3).

Seasonal variation in egg size: the roles of age and laying date

In the random samples, egg sizes declined with date of laying (Table 4). The decline was steep ($-0.95 \text{ cm}^3\text{d}^{-1}$), and significant, in 1994; in 1995, the decline was less steep ($-0.38 \text{ cm}^3\text{d}^{-1}$), and only marginally significant. The slopes of the declines differed in the two years (Table 4). I probably underestimated the true declines, because young birds lay small eggs late in the season and are more likely to lose eggs than experienced birds (de Forest and Gaston

1996). It is almost certain that some of these small, late eggs would have been lost by the time I took measurements.

There were no seasonal trends in egg size for early- (EXB) or late-laying (JB EXB) experienced breeders in either year (Table 4). In contrast, egg sizes declined with laying date among young (YNG) breeders, although the decline was significant only in 1994. The slopes of the declines in the YNG birds differed between years, and in neither year differed significantly from those in the random samples (Table 4). Using data for females ≤ 8 yr and combining the two years, there was a significant negative correlation between egg volume and laying date ($r=-0.37$, $P=0.007$, $N=51$). However, with age and laying date as independent variables in a multiple regression, only age had a significant effect on egg volume (multiple $r=0.62$, age $P<0.001$, date $P=0.55$).

In both years, late-laying (JB EXB) experienced breeders laid significantly later than early-laying (EXB) experienced breeders, but at the same time as young (YNG) breeders (Table 5). However, the eggs laid by JB EXB breeders were similar in size to those of EXB breeders, and significantly larger than those of YNG breeders in both years (Table 5).

DISCUSSION

Effects of female age on laying date and egg size

The laying dates of Thick-billed Murres decreased with female age, as observed in other species (e.g., Razorbill, Lloyd 1979), to 8 y. Females laying their first eggs took only marginally longer

(<1 d on average) than experienced breeders to form their yolks, but laid ca. 10 d later. Hence, young birds must have initiated yolk formation late, and this was the main reason for their late laying. This is similar to the result of Hatchwell and Pellat (1990), who showed that Common Murres *Uria aalge* took longer to form their yolks in a year of poor food availability (16.1 vs 14.1 d on average), but that the later-laying in that year (by 5 d) was caused more by a delay in the date at which birds initiated egg formation. Similarly, the date of initiation varies in response to environmental conditions during the pre-laying period in Cassin's Auklets *Ptychoramphus aleuticus* (Astheimer 1986).

I can only speculate on why young Thick-billed Murres initiated yolk formation later than experienced birds. The observations on other species suggest the possibility that feeding conditions may have had more effect on young birds than on experienced birds, possibly due to differences in foraging skills. Rowe et al. (1994) suggested that young birds may arrive at breeding grounds later than experienced birds, which is true of both Thick-billed Murres (Noble 1990) and Common Murres (Halley et al. 1995), and that young birds might also arrive in poorer condition. Finally, young Thick-billed Murres may need to spend more time in social behaviour, or pair formation and site retention, than experienced birds breeding at the same colony, which leaves them less time to forage. Hence young birds may have behavioural and/or physical deficiencies compared to birds with more experience (Curio 1983). As 8 y old females are typically breeding for the fourth time (Gaston et al.

1994), this indicates that several breeding attempts are required before Thick-billed Murres reach reproductive maturity.

Egg sizes increased with female age to an asymptote at 8 y of age. A similar pattern has been reported in several species that lay 1-egg clutches, although the age at which the asymptote is reached varies considerably (e.g. 23 y in the Wandering Albatross, Weimerskirch 1992). Murphy (1994) suggested that egg size in birds is limited by the availability of protein. When given a supplemental source of high quality protein, Lesser Black-backed Gulls *Larus fuscus* produced larger c-eggs because the yolk protein content of these eggs was increased (Bolton et al. 1992). In this study, experienced Thick-billed Murres deposited more yolk per day than first-time breeding birds, so that the increase in egg size with age might have resulted from greater efficiency of older birds at acquiring protein during the pre-laying period. Again, this suggests that young birds require several breeding attempts before reaching behavioural and/or physical maturity. The similarity in the rates of increase in egg volume with age in the cross-sectional sample and in the sample of eggs laid by the same young females in the two years, suggests that the increase in egg size results from individual age-related processes, as opposed to being a consequence of higher mortality among females laying small eggs (Curio 1983).

The observation that 3 and 4 y old females (most of which are first-time breeders) laid eggs of similar size, although 3 y birds laid 7 d later on average, suggests that there may be a threshold size below which eggs are not laid.

Egg shape remained constant with age in the Thick-billed Murre. This contrasts with some other species in which the length/breadth ratio of eggs decreases with age (e.g., Manx Shearwater, Brooke 1978; Lesser Snow Goose *Chen caerulescens caerulescens*, Robertson et al. 1994). This tendency, as well as the observation that the first eggs laid by Herring Gulls tend to be thinner than later eggs in the same clutch (Parsons 1976), has been ascribed to an initial inelasticity of the oviduct. Robertson et al. (1994) suggested that inelasticity of the oviduct in young birds results in albumen being deposited preferentially along the length rather than the breadth axis of the egg. The unusual shape of murre's eggs is probably adapted to their nesting habit (Uspenski 1956, Kartaschew 1960). Therefore, little variation in the shape of their eggs might be expected. If inelasticity of the oviduct constricts egg breadth in young murre's, then the shape requirement may dictate the length, and therefore in part determine the overall size of the egg.

Individual female effects on laying date and egg size

Among older females, strong correlations between laying dates in 1994 and 1995 indicate that once they reach full reproductive maturity, older females tend to lay at the same time relative to other experienced females. A similar tendency has been observed in Common Murre's (Wanless and Harris 1988; Hatchwell 1991; Sydeman and Eddy 1995). The significant correlation between laying dates in successive years among young females indicates that an individual

effect also acts in less mature females.

Likewise, there is a strong individual effect on egg size among both older and young females. Once the female reaches full reproductive maturity, the size of the egg remains fixed relative to those of other older females, varying in response to conditions during the period of egg formation. The correlation between egg size in the two years seen in this study (62%) is somewhat higher than that found for Common Murres by Hatchwell and Pellatt (1990) in two years (42%). Individual effects on egg size were also seen within years, as the sizes of the first and replacement eggs were strongly correlated. These correlations (58% and 79%) were similar to those reported by Birkhead and Nettleship (1984) for three species of auks (66-79%).

Seasonal declines in egg size: effects of laying date or age?

In the random samples, egg sizes declined with laying date in 1994 and, to a lesser extent, in 1995. Of the two hypotheses I considered to explain the declines (the "adaptive" and "constraint" hypotheses), my results support only the constraint hypothesis. Egg sizes did not decline with laying date among experienced pairs in either year, indicating that no trade-off existed between egg size and laying date for them. This observation is not consistent with the model of Birkhead and Nettleship (1982). In samples of eggs produced at the same time, those of young birds were smaller than those of experienced birds. This indicates that differences in egg size between young and experienced females were caused by

differences in their egg-producing capacities, or in the optimal size of egg consistent with maximizing their fitness, rather than being adjusted to the time at which they bred. Even the decline in egg size with laying date among females ≤ 8 y old was an effect of age, rather than laying date.

The decline in egg size with laying date was much steeper in 1994 than in 1995 in the random sample, and also among young birds. This between-year difference could have been the result of a number of factors: (i) feeding conditions late in the laying period might have been better in 1995 than in 1994; (ii) egg losses among young birds may have been higher in 1995 than 1994; or (iii) fewer young birds may have laid in 1995 than 1994. I have incidental support for hypothesis (iii) only. On the study plots, eggs were laid at more newly-occupied sites in 1994 than in 1995, and these eggs were similar in size to those laid by females breeding for the first time (unpublished data). This suggests that more young birds laid in 1994 than in 1995. The egg sizes and laying dates of experienced breeders which laid in both years, as well as evidence from chick growth rates (unpublished data), indicated that 1994 may have been a better year than 1995, and a tendency for more young birds to recruit in better years has been seen in other species (Brandt's Cormorant, Boekelheide and Ainley 1989; Western Gull, Spear et al. 1995).

The slopes of the relationship between egg size and laying date in the random samples and the samples of birds ≤ 6 y were similar in both years. Because the population-wide declines result from

increasing proportions of younger birds laying later in the season, they should reflect what occurs among the young birds in the population. Hence I predict that populations experiencing high recruitment are more likely to show a seasonal decline in egg size than those where little recruitment is taking place. Whether young birds laying late in the season lay small eggs because they trade-off between current and future reproduction, as predicted by life-history theory, is yet to be determined.

Conclusions

In species laying multi-egg clutches, declines in clutch size with laying date may be adaptive (Drent and Daan 1980); birds which lay late reduce their clutch size to save time, thus accommodating to reduced food availability for their young late in the breeding season. By doing so, they maximize the production of surviving offspring. I suggest that the seasonal decline in egg size in the Thick-billed Murre is not adaptive in the time-saving manner proposed by Birkhead and Nettleship (1982). The absence of the decline among experienced Thick-billed Murres indicates that these birds produce the optimum-sized egg relative to their capabilities, irrespective of date. For late-laying murres, there may be little advantage in reducing egg size because chicks from larger eggs grow their wing feathers more quickly, which may enable them to depart to sea younger (Hipfner and Gaston in prep.). In any case, timing of breeding seems to have little effect on the reproductive success of experienced murres (Hatchwell 1991; de Forest and Gaston 1996).

Hatchwell and Pellatt's (1990) results also support our conclusion that a reduction in egg size may not be adaptive: in a late year, Common Murres produced large eggs, although two extra days of yolk formation were required. Nonetheless, it remains to be tested directly whether the reduction in the size of replacement eggs is an adaptation to advance laying, as Birkhead and Nettleship (1982) proposed. Assuming a lag of 3.4 d between ovulation and laying (Birkhead and del Nevo 1987), EXB pairs required 16.5 d (13.1 d for yolk formation + 3.4 d lag) on average to form first eggs in 1995. However, EXB pairs which lost their first eggs replaced them in 14.2 ± 0.7 d (N=9). Hence the smaller replacement eggs were laid in ca. 2 d less time, the same difference as seen in Common Murres (Birkhead and del Nevo 1987), and consistent with the Birkhead and Nettleship model.

I suggest that, at the proximate level, the seasonal decline in egg size for Thick-billed Murres at Coats Island results from differences in the egg-producing capacities of individual birds, chiefly mediated by age or experience. Because young birds lay their eggs later than older birds, the proportion of young birds laying, and consequently the proportion of small eggs laid in a given period, increases with date. Although young birds may take slightly longer to form their yolk, most of the difference in date of laying is accounted for by the date at which egg formation is initiated. As murres age and gain experience, their ability to form an egg may improve, which may result in earlier laying and larger eggs. A stable laying date and egg size is reached by 8 y

of age on average, equivalent to the fourth year of breeding.

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Table 1: Mean $\pm$ SD laying dates (LAY, from June 1 = 1) and volume indices (EVI, cm³) of eggs laid by the same older (≥ 9 years or EXB by 1995) and younger (≤ 8 years by 1995) females in 1994 and 1995.

Age	Var	N	Year		Paired t-test	
			1994	1995	t	p
Older	LAY	30	22.9 $\pm$ 3.7	23.8 $\pm$ 4.6	1.75	0.09
	EVI	32	212.4 $\pm$ 13.2	209.4 $\pm$ 15.8	1.74	0.09
Younger	LAY	18	24.0 $\pm$ 5.9	24.5 $\pm$ 7.4	0.33	0.74
	EVI	11	192.7 $\pm$ 23.0	200.3 $\pm$ 19.6	2.19	0.05

Table 2: Mean $\pm$ S.D. laying dates (LAY, from June 1 = 1), egg volume indices (EVI, cm^3), yolk masses (g), and yolk formation times (d) and rates (g/d) of eggs laid by experienced (EXB) and first time (YNG) breeders in 1995.

Age	N	LAY	EVI	Yolk mass	Yolk Formation	
					Time	Rate
EXB	10	19.5 $\pm$ 1.7	210.4 $\pm$ 15.2	35.7 $\pm$ 2.0	13.1 $\pm$ 0.9	2.7 $\pm$ 0.2
YNG	8	29.1 $\pm$ 6.8	183.3 $\pm$ 9.5	31.8 $\pm$ 2.6	13.9 $\pm$ 1.1	2.3 $\pm$ 0.3
		U=80	t=4.36	t=3.33	t=1.65	t=3.32
		p: <0.001	<0.001	0.005	0.12	0.005

Correlations between EVI and yolk formation times:

Whole sample: $r=-0.13$, $p=0.60$, 17 df.

EXB: $r=0.22$, $p=0.54$, 9 df; YNG: $r=0.09$, $p=0.82$, 7 df.

Table 3: Mean $\pm$ S.D. volume indices (EVI, cm³) of first and replacement eggs in 1994 and 1995.

Year	N	EVI		Paired t-test	
		First	Replacement	t	p
1994	31	212.2 $\pm$ 17.1	198.8 $\pm$ 16.1	6.50	<0.001
1995	20	215.0 $\pm$ 15.3	204.0 $\pm$ 13.6	7.14	<0.001
		t=0.60	t=1.19		
		p=0.55	p=0.24		

Correlations between first and replacement EVIs:

1994: $r=0.76$, $p<0.001$; 1995: $r=0.89$, $p<0.001$.

Table 4: Regressions between egg volume index and laying date in 1994 and 1995 for eggs laid by a random sample of birds, early- (EXB) and late- (JB EXB) laying experienced breeders, and young breeders (YNG, ≤ 6 years of age).

Year	Parameter	Sample			
		Random	EXB	JB EXB	YNG
1994	Slope ($\text{cm}^3 \text{d}^{-1}$)	-0.95	-	-	-1.19
	r	-0.35	-0.13	+0.16	-0.45
	p	<0.001	0.53	0.47	0.01
	N	121	26	23	30
1995	Slope ($\text{cm}^3 \text{d}^{-1}$)	-0.38	-	-	-0.59
	r	-0.15	+0.02	-0.13	-0.37
	p	0.06	0.93	0.58	0.12
	N	154	29	20	19

Comparing slopes, at the $p = 0.05$ significance level:

Random 1994 > Random 1995; YNG 1994 > YNG 1995;

Random 1994 = YNG 1994; Random 1995 = YNG 1995.

Table 5: Mean $\pm$ S.D. laying dates (LAY, from June 1 = 1) and volume indices (EVI, cm³) of eggs laid by early-laying experienced breeders (EXB), late-laying experienced breeders (JB EXB), and young breeders (YNG, $\leq$ 6 years) in 1994 and 1995.

Year	Var	Breeding group		
		EXB (N)	JB EXB (N)	YNG (N)
1994	LAY	22.2 $\pm$ 5.5 (26)	26.7 $\pm$ 4.4 (23)	26.8 $\pm$ 6.0 (30)
	EVI	208.7 $\pm$ 17.2 (26)	210.9 $\pm$ 10.6 (23)	192.1 $\pm$ 16.1 (30)
1995	LAY	21.7 $\pm$ 3.9 (29)	27.9 $\pm$ 3.3 (20)	28.8 $\pm$ 8.7 (19)
	EVI	205.3 $\pm$ 17.2 (29)	209.0 $\pm$ 12.7 (20)	186.4 $\pm$ 13.7 (19)

ANOVA for LAY:

1994: $F=6.23$, $p=0.003$; 1995: Kruskal-Wallis $F=23.50$, $p<0.001$;

In both years: EXB < JB EXB = YNG (Tukey's tests (1994), or non-parametric multiple comparisons (1995), at $p=0.05$).

ANOVA for EVI:

1994: $F=12.76$, $p<0.001$; 1995: $F=12.89$, $p<0.001$;

In both years: EXB = JB EXB > YNG (Tukey's tests, at $p=0.05$).

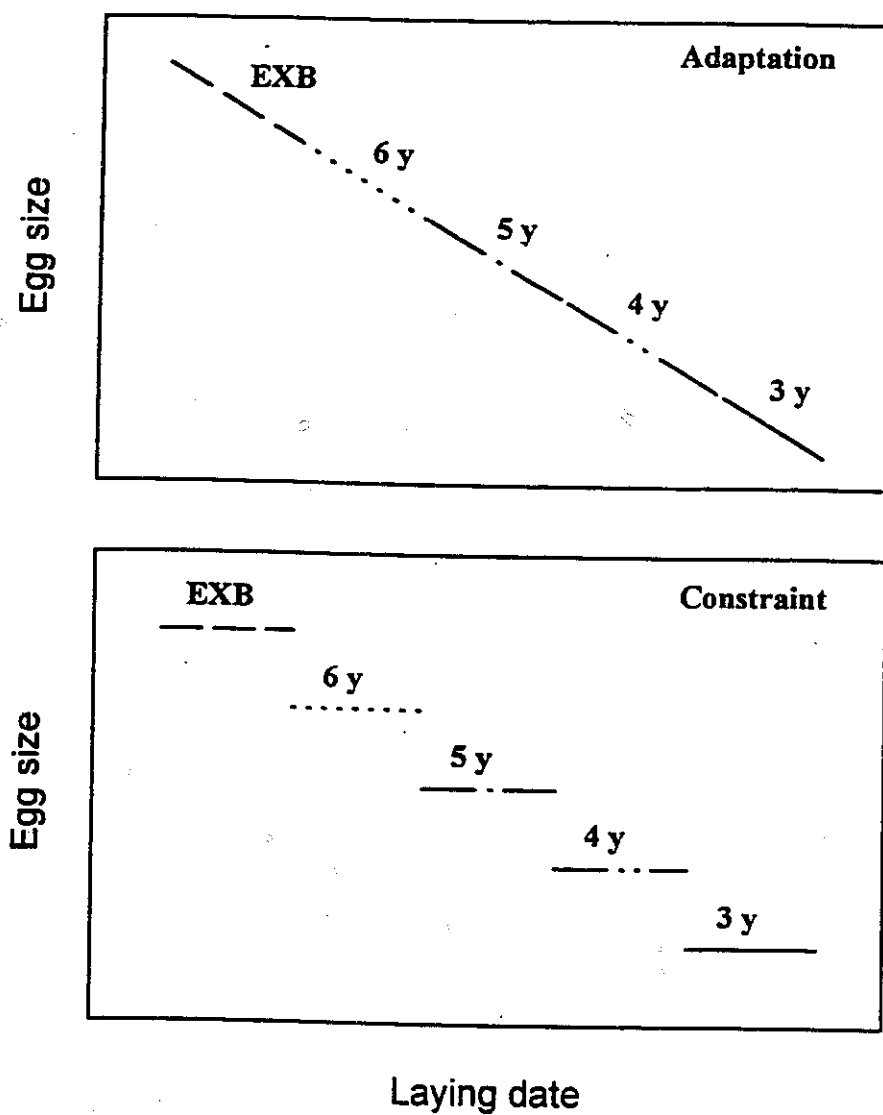


Figure 1: Graphical depictions of the "adaptive" and "constraint" models of seasonal decline in egg size.

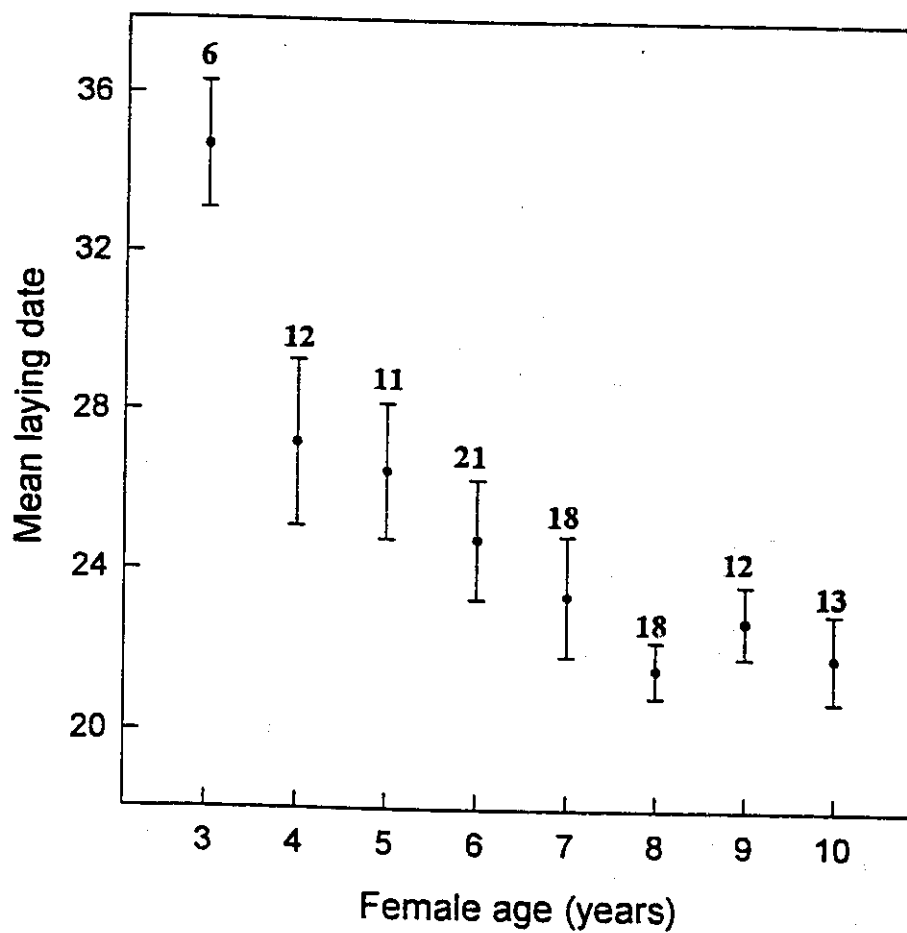


Figure 2: Mean $\pm$ S.E. laying dates (from June 1 = 1) of females of known age in 1994 and 1995.

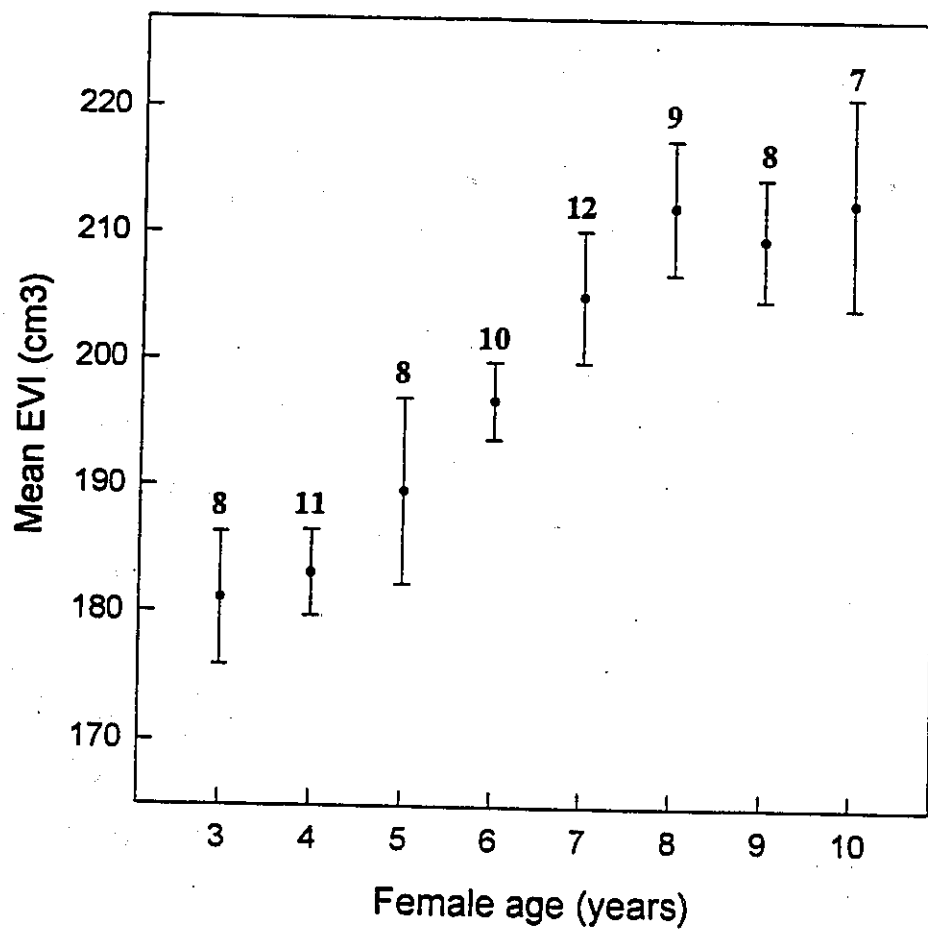


Figure 3: Mean $\pm$ S.E. volume indices of eggs laid by females of known age in 1994 and 1995. Regression equation to 8 y: $b=+6.62x$; $r=0.60$, $p<0.001$, 57 df.

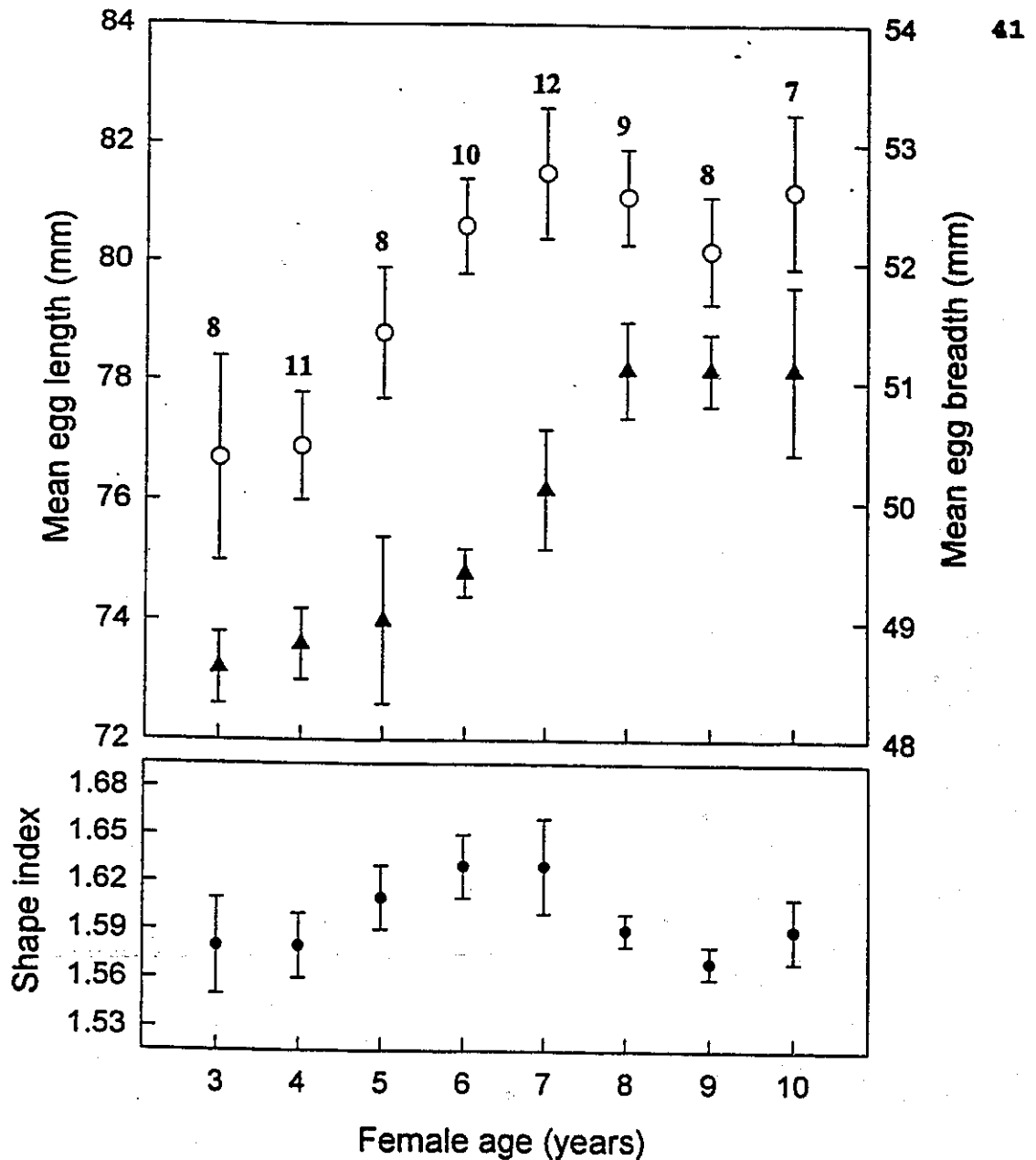


Figure 4: Mean + S.E. lengths (open circles), breadths (closed triangles) (top figure), and mean $\pm$ S.E. shape indices (length/breadth) (bottom figure), of eggs laid by females of known age in 1994 and 1995. Note that the range on the y-axis for egg length is twice that for egg breadth. There are no significant differences in egg shape (Kruskal-Wallis ANOVA, $p = 0.29$).

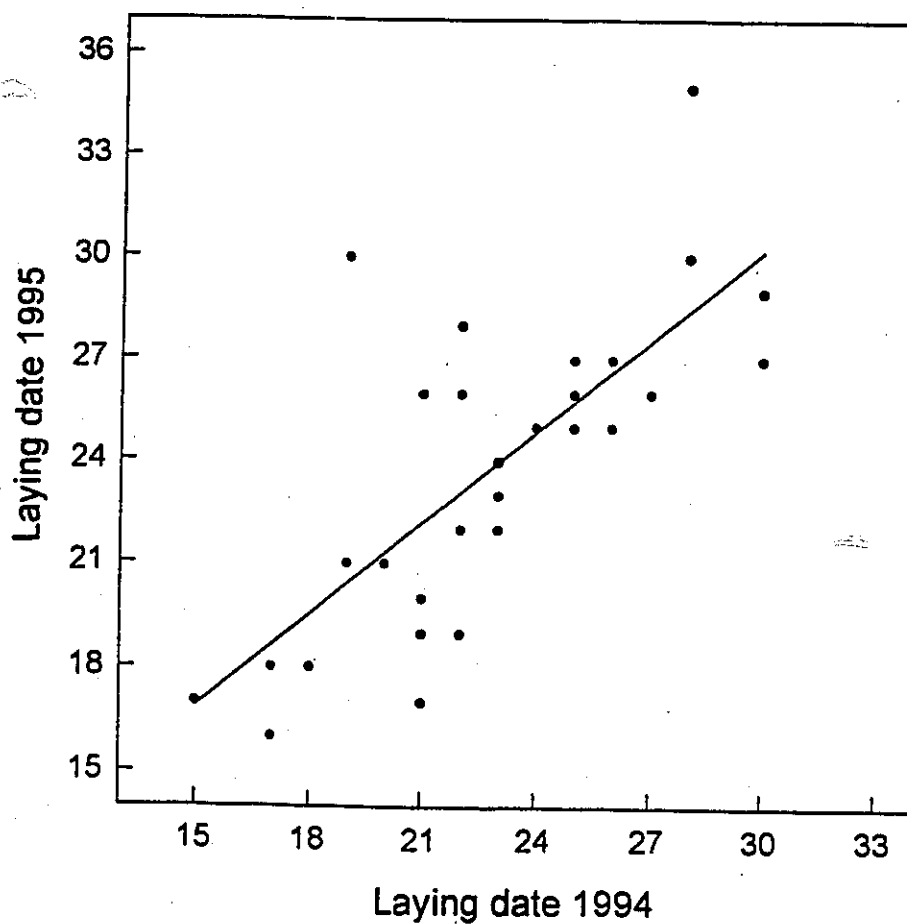


Figure 5: Scatter plot of laying dates (from June 1 = 1) of the same older (≥ 9 y or experienced by 1995) females in 1994 and 1995. Regression equation: $b=0.89x$; $r=0.74$, $p<0.001$, 29 df.

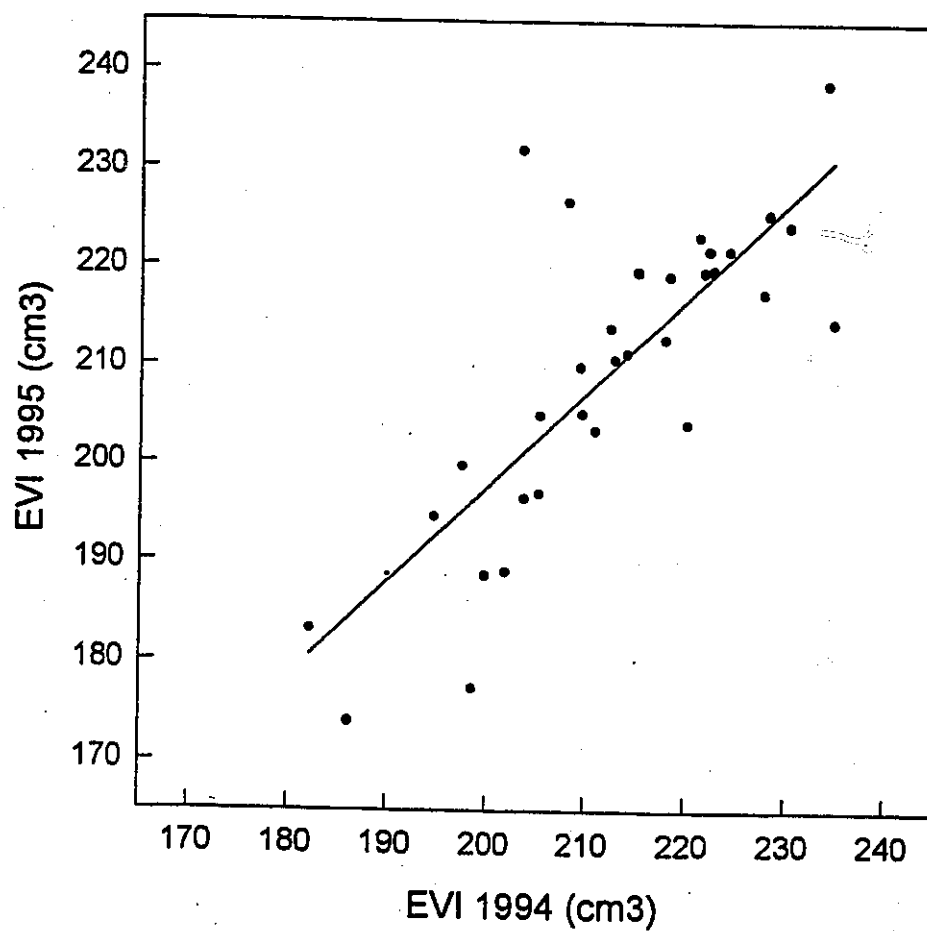


Figure 6: Scatter plot of volume indices of eggs laid by the same older (≥ 9 y or experienced by 1995) females in 1994 and 1995. Regression equation: $b=0.95x$; $r=0.79$, $p<0.001$, 31 df.

**Chapter 3: Consequences of Variation in Egg Size
and Parental Quality to the Growth and Development
of Nestling Thick-billed Murres**

Abstract.- Little unequivocal evidence exists to support the widely-held view that young birds that hatch from large eggs have a developmental advantage over those that hatch from small eggs. I examined the contributions of egg size and parental quality to chick growth in the Thick-billed Murre *Uria lomvia*, an Arctic-breeding seabird in which the single chick leaves the nest in a partly-developed state, in two years of contrasting growth. The relationship between egg quality and parent quality was randomized by switching eggs among breeding pairs; the growth of chicks raised by their own parents was also monitored. I predicted that the growth of the fostered chicks would correlate positively with (i) the size of egg from which they hatched (the egg size effect); and (ii) the size of egg produced by their adoptive parents (the parent quality effect). In both years, the rate at which chicks gained mass was independent of the size of the egg from which they hatched, but the rate of growth in wing length was positively correlated with egg size. In large-egg chicks, the primary coverts, the longest feathers on the wings, burst from the sheaths 2-3 d earlier than in small-egg chicks, and this developmental advantage was maintained until nest departure. Among chicks raised by their own parents, this effect of egg size on wing growth was more pronounced in the year of poor growth. In neither year was growth in mass correlated with the size of egg originally laid by

the adoptive parents, but in the year of better growth, there was a weak but significant positive relationship between wing length at nest departure and the foster parent's egg size. In both years, the rate at which chicks grew their wings was strongly correlated to the rate at which they gained mass. Chicks that grew their wings quickly departed the nest younger, in one of two years. These results indicate that Thick-billed Murre chicks that hatch from larger eggs have a developmental advantage over chicks from smaller eggs, especially when growth is poor. Chicks also benefit if they are raised by parents which produce a large egg, especially when growth is good. The developmental advantage associated with hatching from a large egg, and/or being raised by parents of high quality, has potential life-history consequences.

INTRODUCTION

The relationship between egg quality and offspring quality has been examined frequently in birds (reviewed in Williams 1994). In many studies, positive relationships between egg size and chick survival (e.g. Moss et al. 1981; Galbraith 1988; Grant 1991), and between egg size and chick growth (e.g. Birkhead and Nettleship 1982; Furness 1983) have been demonstrated. However, the potential shortcomings of non-experimental studies are well known (Mueller 1990; Williams 1994). Two common criticisms are: (i) the results may reflect the over-riding effect of parental quality on both egg size and nestling survival and growth; and (ii) females may invest differentially in the eggs within a clutch, such as between the a- and b- versus c-eggs in gulls, which can make it difficult to distinguish between- from within-clutch effects.

Until recently, relatively few studies had examined the effects of egg size on chick survival or growth while controlling for the confounding effect of parental quality. In experimental studies, nestling survival has been shown to relate positively to egg size in the Lesser Black-backed Gull *Larus fuscus*, if the c-egg is included (Bolton 1991), but not in the Fulmar *Fulmarus glacialis* (Ollason and Dunnet 1985) or Short-tailed Shearwater *Puffinus tenuirostris* (Meathrel et al. 1993), which both lay single eggs. In species which show positive relationships between egg size and chick size, any benefits to hatching from a large egg tended to be short-lived; parental quality largely determined the size of the chick late in the nestling period (Amundsen and Stokland 1990; Reid

and Boersma 1990; MacGrath 1992). In his review article, Williams (1994) concluded that there was little unequivocal evidence to support the widely-held view that large eggs increase offspring fitness in birds.

The Alcidae are unique among bird families in that there are three different developmental strategies of the young (Sealy 1973). In the semi-precocial species, the chicks remain at the nest for extended periods, and are independent of their parents when they depart to the sea at 40-100% of adult size. At the other extreme, young of the precocial *Synthliboramphus* murrelets leave the nest at 2-4 d of age without having been fed, accompanied by both parents. Between these two extremes are three intermediate species (*Uria* and *Alca* spp.), whose young remain at the nest for 15-30 d, and depart to the sea accompanied by the male parent at 12-25% of adult size. The semi-precocial strategy is believed to be ancestral within this family (e.g. Gaston 1992), and the evolutionary forces that might have favoured increases in the level of chick precocity have been discussed frequently (Cody 1973; Sealy 1973; Birkhead 1977; Gaston 1985, 1992; Ydenberg 1989).

Thick-billed Murres *Uria lomvia* are colonial, cliff-nesting alcids which, like the other intermediate species, lay a one-egg clutch. The size of the egg tends to increase with female age to about 8 y (Hipfner et al. in prep.), typically the fourth year of breeding (Gaston et al. 1994). Even among experienced females, however, there is substantial variation in the size of egg laid, and females tend to produce eggs of similar size in different years

(Hipfner et al. in prep.). Nestling growth rates vary considerably within and especially between colonies and years, as do chick ages and masses at nest departure (Gaston et al. 1983; Gaston 1985). In general, fast-growing chicks tend to depart to the sea at a young age (Ydenberg 1989). Early departure may lower mortality on late-hatched murre chicks at the nest, because they have fewer neighbours and so may be subject to a greater risk of predation (Hatchwell 1991). In the Common Murre *Uria aalge*, early departure has been associated as well with increased post-departure survival (Harris et al. 1992). Hence, the importance of early nest departure can be seen both in the evolutionary history of this group (departure at a young age and in a partly-developed state has been favoured), and in the behaviour of individual chicks (those departing early might experience increased pre- and post-departure survival).

I examined the contributions of egg size and parent quality to the growth and development of nestling Thick-billed Murres. While Thick-billed Murres can recognize their own eggs, they readily adopt foreign eggs (Gaston et al. 1993). Consequently, eggs were switched among breeding pairs, randomizing the relationship between egg quality and parent quality. At the same time, the relationship between egg size and chick growth was examined under natural conditions. The following predictions were tested: (i) rates of chick growth and/or development relate positively to egg size; and (ii) rates of chick growth and/or development relate positively to the quality of the foster parents, measured as the size of egg they

originally laid. The effects on chick development of variation in rates of food provisioning, an alternate indicator of parental quality measured as the growth in body mass of the chick, were also investigated. The results are viewed within the context of the intermediate developmental strategy employed by the Thick-billed Murre, which requires an increased level of precocity compared to the ancestral semi-precocial strategy.

STUDY AREA AND METHODS

This study was conducted during 1994 and 1995 at Coats Island, N.W.T., Canada ($62^{\circ}57' N$, $82^{\circ}00' W$). The Thick-billed Murre colony there consists of two sub-colonies of similar size, separated by 1 km of coastline, which together include ca. 30,000 breeding pairs (Gaston et al. 1993). Among murre colonies of the eastern Canadian Arctic, Coats Island is noteworthy for the fast growth rates of chicks (Gaston et al. 1983).

On 12 and 17 July in 1994 and 1995 (just prior to the start of hatching), 50 sites at which an egg was present were mapped and numbered on a plot near the top of the colony. Different plots were used in the two years. Every egg was marked with its site number in permanent ink, and its length and maximum breadth was measured to within ± 0.1 mm using vernier calipers. The eggs were then redistributed randomly among sites on the plot. For each breeding pair, both the size of egg they fostered (the "egg size" effect), and the size of egg they produced (the "parent quality" effect), were known. Prior to hatching, the eggs were checked to

ensure that they were still at the sites where they were placed during the switch.

These sites were checked at 2 d intervals, but occasionally at 3 d intervals when weather conditions warranted a delay. On one occasion in the middle of the chick-rearing period in 1995, bad weather forced a delay to 4 d. The first time a chick was present at a site, I estimated its hatching date and marked it with a binary code of nail clipping. When large enough, each chick was banded. On all visits, chicks were weighed to within ± 1 g with a spring balance, and their right wing was measured to within ± 1 mm with the wing held flat and straight along a ruler. All visits were made between 0900 and 1200 h.

The growth of the chicks of a control sample of unmanipulated breeders was also monitored on one (1995) or two (1994) plots near the top of the colony, using the protocol described above.

As a measure of egg size, I used an index of egg volume (EVI, $\text{length} \times \text{breadth}^2$) that relates linearly to fresh egg mass in Thick-billed Murres ($r = 0.952$, Birkhead and Nettleship 1984). The hatching date of a chick was recorded as day 1. Where measurements at a specific age are given, the measurements of any chicks not taken at exactly this age were estimated using linear interpolation (Hussell 1972). Because chicks were measured at 2-3 d intervals, larger samples were available for 2 d than for 1 d old chicks, because measurements at 2 d were estimated from those at 1 d by interpolation. Hence 2 d measurements were used as estimates of initial size. A few chicks were not measured until they were 3 d

old, so that sample sizes for parameters which include a 2 d measurement (growth between 2-14 d), are in some cases smaller than those which do not (e.g. 14 d mass). Only chicks which survived to ≥ 15 d are included in any analysis, because 15 d is the youngest age at which chicks are known to depart the nest of their own volition (Gaston and Nettleship 1981). Consequently, 14 d is the oldest age at which a sample is unbiased by the departure of some chicks (Gaston 1985). The mass of a chick at last weighing was used as an estimate of its departure mass, and the age of a chick at this weighing + 1 d was used as an estimate of its departure age.

RESULTS

There was no correlation between foster chick mass at 2 d and the size of egg originally laid by a breeding pair in either year (both $r = -0.07$, $p > 0.5$), but the correlations between 2 d foster chick mass and foster egg size were significant in both years ($r = +0.57$ and 0.58 , both $p < 0.01$). This indicates that the switches effectively randomized the relationship between parent quality (egg size laid) and egg quality (egg size fostered).

Among pairs that succeeded in raising their foster chick to departure age, the volume indices of eggs laid and fostered were similar in the two years (Table 1). Chicks gained more body mass between 2-14 d of age in 1994 than 1995, and so were significantly heavier at 14 d in 1994. However, chick ages and masses at nest departure were similar in the two years. Despite the faster early growth in mass in 1994, there were no differences between years in

any measures of growth in wing length (Table 1).

Egg size effects on chick growth

In neither year were there significant correlations between the growth in body mass of the foster chick between 2-14 d and the size of the foster egg, indicating that the rate at which chicks gained mass did not depend on the size of the egg from which they hatched (Table 2). In 1994, the year of faster initial growth, there were no relationships between egg size and chick mass at 14 d or at nest departure. In 1995, the year of slower initial growth, there was a significant positive correlation between 14 d chick mass and egg size. As there was no correlation between growth in mass and egg size, this suggests that initial differences in chick mass that resulted from differences in egg size tended to be maintained in that year. When the variation in initial (2 d) mass was controlled using partial correlation, the relationship between 14 d mass and egg size became non-significant ($r = 0.30$, $p > 0.05$). In 1995, as in 1994, chick masses at nest departure were independent of egg size (Table 2).

In both years, there were significant, positive correlations between growth in the length of the wings of foster chicks between 2-14 d of age and foster egg size, indicating that the chicks from larger eggs grew their wings more quickly than chicks from smaller eggs (Table 2). Consequently, there were significant positive correlations between 14 d wing length and egg size in both years (Figure 1), and between wing length at nest departure and egg size,

controlled for variation in age at departure (Table 2).

To examine the relationship between egg size and wing growth in more detail, wing length was plotted against chick age between 2-14 d for chicks that hatched from the largest one-third of the sample of eggs and from the smallest one-third of eggs. As the growth of the wings both of large-egg and small-egg chicks were virtually identical in the two years, and neither the smallest nor largest thirds of eggs differed significantly in size between years (t-tests, p -values > 0.05), data from the two years were combined. The largest one-third of eggs averaged 17% larger in volume index than the smallest one-third of eggs, but growth in body mass between 2-14 d of large- and small-egg chicks was similar (Table 3). The plot of wing length against chick age showed that wing lengths were similar in the two groups up to 6 d of age, at which time the lengths of the wings of chicks from large eggs began to increase rapidly (Figure 2). Six days is the youngest age at which the primary coverts (the longest feathers of the wing in nestling murrelets) burst from their sheaths (Gaston and Nettleship 1981), and this event was delayed by several days in chicks which hatched from small eggs. Consequently, differences in wing lengths between the two groups increased rapidly between 6-10 d of age, and levelled off by about 12 d of age (Figure 2). At 14 d, chicks from small eggs had wings similar in length to those of 12 d old large-egg chicks.

Parent quality effects on chick growth

In neither year were there significant correlations between the growth in mass or wing length of foster chicks between 2-14 d and the size of egg laid by the adoptive parents, indicating that the size of egg a pair produced did not predict their ability to grow a chick (Table 4). Consequently, chick mass and wing length at 14 d was independent of the size of egg produced by the adoptive parents. With variation in age at nest departure controlled using partial correlation, there was likewise no correlation between mass at nest departure and egg size laid in either year, or between wing length at departure and egg size laid in 1995. In 1994, there was a weak but significant correlation between wing length at departure and the size of egg laid by the adoptive parents (Table 4).

An important measure of parent quality is the rate at which the chick is provisioned, which is reflected in its growth rate. To examine the relative contributions of egg size and provisioning to growth in wing length, foster egg size and growth in body mass 2-14 d were entered as independent variables into a multiple regression, with 14 d wing length the dependent variable. In both years, the multiple regressions were significant; together, egg size and growth rate explained 42% (1994) and 47% (1995) of the variation in 14 d wing length. Both egg size and growth in mass contributed significantly to these multiple regressions in both years (all 1-tailed p -values < 0.01).

To examine the relationship between nutrition and wing growth in more detail, wing length was plotted against chick age for the

one-third of chicks that gained the most mass between 2-14 d and the one-third of chicks that gained the least mass, with data from the two years combined. There was no difference in the size of eggs from which the fastest- and slowest-growing thirds of chicks hatched, but the fast-growing chicks gained 51% more mass on average between 2-14 d of age than the slow-growing chicks (Table 5). Differences in wing length with age between the two groups increased slowly but steadily to about 12 d, then began to increase rapidly (Figure 3). Between 12-14 d of age, fast-growing chicks grew their wings at 4.1 mm d^{-1} on average, compared to 3.2 mm d^{-1} in the slow-growing chicks.

Egg size and nutritional effects on growth of control chicks

To examine the relationships between egg size, nutrition, and chick growth under natural conditions, these analyses were repeated for unmanipulated breeders. As in the egg switch experiment, egg sizes were similar in 1994 and 1995 for control breeders, and chick growth was better in 1994 (Table 6); at 14 d of age, chicks in 1994 were ca. 20 g heavier than in 1995. There were very similar weak, but significant, positive correlations of 14 d chick mass on egg size in the two years (Table 6). In multiple regression analyses, egg size and growth in mass between 2-14 d explained 33% (1994) and 35% (1995) of the variation in 14 d wing lengths. However, only growth in mass contributed significantly to the multiple regression in 1994 (1-tailed $p < 0.01$); the effect of egg size was positive, but non-significant (1-tailed $p > 0.1$). Conversely, in 1995, egg

size and growth in mass 2-14 d both contributed significantly to determining 14 d wing length (both 1-tailed p-values < 0.01).

To examine this difference between the two years in detail, the differences in wing length with age between chicks which hatched from the largest and smallest one-third of eggs were plotted, as were the differences in wing length with age between the one-third of chicks which gained the most and the least mass between 2-14 d, in the two years separately. Mean egg sizes and growth in mass 2-14 d for these groups are given in Table 6. In 1994, there was little difference in mean wing length with age between chicks from the largest and smallest thirds of eggs, while the difference in wing length between fast- and slow-growing chicks increased with age, most steeply between 6-12 d of age (Figure 4). In 1995, the differences in wing length with age between large- and small-egg chicks, and between fast- and slow-growing chicks, were apparent: chicks that hatched from the largest third of eggs, and that gained the most mass between 2-14 d, both had better wing growth than the small-egg and slow-growing chicks (Figure 4). Differences due to egg size increased steadily between 5-11 d, similar to the effect seen in the experimental samples, while the differences due to nutrition increased rapidly and steadily after 5 d.

Consequences of variation in chick growth

To examine how the growth or development of the chick affects the age at which it leaves the nest, age at departure was regressed against 14 d body mass and 14 d wing length. Because there is

often a negative relationship between hatching date and departure age in Thick-billed Murres (Gaston and Nettleship 1981; Gaston et al. 1983; Birkhead and Nettleship 1987), variation due to hatching date was controlled using partial correlation. Chick ages at nest departure were negatively correlated with 14 d wing length in 1994 in both the experimental and control samples (Table 7). There was also a weak, but significant, negative correlation of departure age on 14 d body mass in 1994 in the control sample.

DISCUSSION

Egg size effects on growth and development

The results of previous experimental studies suggest that, if present, egg size effects tend to occur earlier, and parent quality effects later, in the nestling period (Amundsen and Stokland 1990, Reid and Boersma 1990; Magrath 1992; Amundsen 1995; reviewed in Williams 1994). Therefore, while egg size might affect the initial size of the chick, and possibly its early survival (Parsons 1970; Bolton 1991), parental quality largely determines the condition of the offspring at nest departure.

In this study, early feather development was enhanced in Thick-billed Murre chicks that hatched from large eggs compared to those that hatched from small eggs. In large-egg chicks, the primary coverts burst from the sheaths 2-3 d earlier, and this advantage was maintained until nest departure. Egg size also influenced the initial mass of the chick, and the egg size-chick mass correlation

was maintained until potential departure age in the year of slower growth. Initial differences in mass disappeared before 14 d of age in the year of better growth. In neither year did the size of the egg affect the rate at which the chick gained mass.

Risk of predation at the nest may be an important factor which has favoured a reduced nestling period in the intermediate alcids, which often nest on exposed sites (Cody 1973; Birkhead 1977; Gaston 1985; Hatchwell 1991). Despite this danger, chicks must remain at the nest until they develop sufficiently to allow them to depart (Birkhead 1977). In this study, Thick-billed Murre chicks with longer wings departed to sea younger than those with shorter wings in one of two years, and this appears to be a general relationship in this species (e.g., Gaston and Nettleship 1981). As early departure might improve a chick's chance of survival (Hatchwell 1991; Harris et al. 1992), and because egg size and wing growth are positively related, there is a potential life-history advantage to producing a large egg.

Nest departure involves a gliding descent from high on a cliff to the sea. In young Thick-billed Murres, the primary coverts act as the principal planing surface for this glide because the growth of the primaries is delayed until after nest departure (Gaston and Nettleship 1981). Mortality at nest departure is high because many chicks fail to unite with their parent at sea, often because they descend too steeply off the cliff and strike ledges below, or land on the beach rather than the sea (Williams 1975; Daan and Tinbergen 1979; Gilchrist and Gaston in press). Consequently, there may be

strong selection for chicks to reach a threshold wing-length or optimal wing-loading while at the nest (Birkhead 1977; Hatch 1983). This may be a critical factor in the departure decision, which is taken primarily by the chick (Gaston and Nettleship 1981), and could explain why chicks with longer wings tend to depart younger. More general plumage development could also be important, because chicks must thermoregulate once on the sea (Gaston and Nettleship 1981). However, at Akpatok Island, N.W.T. in 1993, where chicks departed at exceptionally low weight, many were still covered in down and showed retarded growth of body feathers, although they had wings of normal length (G. Chapdelaine, personal communication; JMH, personal observation).

There was also a negative correlation between mass at 14 d and departure age among control chicks in one of two years (although the correlation with 14 d wing length was stronger in the same sample), and in all experimental and control samples the direction of this relationship was negative. This accords with a theoretical model of nest departure in alcids developed by Ydenberg (1989) and Ydenberg et al. (1995), which predicts that, other factors being equal, large chicks will depart younger than small chicks. Because there was a positive relationship between egg size and chick mass well into the nestling period in one year, this might be another advantage to hatching from a large egg. A large body also might allow a chick to withstand short periods of starvation better, so that large-egg chicks might have a survival advantage. However, I did not test this hypothesis.

Thick-billed Murre chicks from eggs of different size hatch at similar size, but differ in the size of their yolk sacs (Birkhead and Nettleship 1984). Consequently, post-hatching differences in the development of chicks from different-sized eggs are likely to be caused by differences in the size of this yolk reserve. There is indirect evidence that the size of the yolk is maximized in the intermediate species. Duncan and Gaston (1988) showed that Thick-billed Murre hatchlings have a yolk sac twice as large, relative to chick size, as in semi-precocial and precocial species. This may be a consequence of an incubation period that is shorter than expected for the size of the egg, compared to other alcids (Gaston and Jones in prep). However, it is unknown whether this short incubation period is an adaptation to hatch a chick with a large yolk, rather than being a consequence, for example, of differences in nesting habit between open- and hole-nesting species (Rahn and Ar 1974). The results of Hatchwell and Pellatt (1990) also suggest the importance of a large yolk: in a year when feeding conditions during the pre-laying period were poor, Common Murres produced eggs with full-sized yolks although two extra days of yolk formation were required. The mean difference in egg mass between years was equal to the difference in albumen mass.

If differences in feather growth between large- and small-egg chicks are caused by differences in the size of the yolk sac, this poses the question of how yolk reserves influence feather growth? Little is known about how variation in egg composition affects chick development in wild birds (Williams 1994). However, the

availability of the sulfur-containing amino acids may limit the rates both of egg production (Murphy 1994; Houston et al. 1995), and the production of feathers during moult (Murphy and King 1992). Lesser Black-backed Gulls provided with additional, high quality protein produced larger c-eggs because the yolk protein content of these eggs was increased (Bolton et al. 1992). It may be that female Thick-billed Murres that can obtain more protein (and hence the limiting amino acids) in their diet produce larger yolks, and therefore larger eggs, suggesting an advantage to birds with better foraging skills. In agreement with this hypothesis, experienced Thick-billed Murres deposit yolk more quickly than young birds, and produce larger eggs with larger yolks (Hipfner et al. in prep.). As the protein in the yolk is used by the chick to produce feathers (Romanoff and Romanoff 1949), a large yolk sac at hatching might provide a larger reserve of the sulfur-containing amino acids that otherwise may limit feather growth. The protein in birds' eggs is unusually rich in these sulfur-containing amino acids (Houston et al. 1995).

In addition to the chicks, the eggs of the intermediate altricials are, in many respects, intermediate between those of semi-precocial and precocial altricials. Generally, in comparison to more altricial bird families, species in more precocial families produce larger eggs with relatively more yolk and less albumen and water (Carey et al. 1980). In precocial birds, an increase in egg size results in proportional increases in yolk and albumen content, while in more altricial birds, larger eggs have proportionately more albumen and

less yolk (Hill 1995). The intermediate and semi-precocial (e.g. Atlantic Puffin *Fratercula arctica*) alcids produce small eggs with small yolks compared to those of the precocial Ancient Murrelet *Synthliboramphus antiquus* (Sealy 1975; Birkhead and Nettleship 1984; Birkhead and Gaston 1988). However, in intermediate and precocial species, increases in egg size result in proportional increases in yolk and albumen content, while in semi-precocial species, larger eggs have proportionately more albumen and less yolk (Birkhead and Nettleship 1984; Birkhead and Gaston 1988). As well, Thick-billed Murre and Ancient Murrelet hatchlings have similar water content, which is lower than that of semi-precocial hatchlings (Duncan and Gaston 1988). Hence, adjustments have been made in egg composition within the Alcidae similar to those made between more altricial and more precocial families of birds. This indicates the importance of egg composition to post-hatching chick development, and suggests that evolutionary divergences between the three developmental strategies in the alcids depended on changes made concurrently in their eggs.

Parent quality effects on chick development

In this study, the size of egg produced by Thick-billed Murre pairs was a weak predictor of their ability to grow a chick. This result has been seen in some (Smith et al. 1995), but not all (Reid and Boersma 1990), previous studies. However, in the year of better growth, there was a weak but significant relationship between the size of egg laid by an adoptive pair and their foster chick's wing

length at nest departure, and all other correlations had positive directions. Hence, chicks may have benefitted from being raised by parents that produced large eggs in the year of better growth, but there was no indication of this in the year of poor growth.

As there is a strong effect of female quality (age/experience) on egg size in Thick-billed Murres (Hipfner et al. in prep.), some discussion of the weakness of the parental effect, measured by egg size, is warranted. Some possible explanations include: (i) the effect of adult age on chick growth may be weaker than the effect on egg size. However, de Forest and Gaston (1996), despite having a rather small sample size, did find an effect of parental age on chick growth in Thick-billed Murres; (ii) among older females, there is a considerable range in the size of eggs laid (Hipfner et al. in prep.), so that some experienced birds nevertheless lay small eggs; (iii) older birds may have been over-represented in the sample, because they tend to occupy good breeding sites (de Forest 1993), so are more likely than younger birds still to have an egg late in the incubation period (deForest and Gaston 1996), when the eggs were switched; and (iv) if producing a large egg is taxing to the female, then she might later invest less in foraging for the chick. This effect could be more marked when food availability is low, since provisioning the chick is more demanding under these conditions (Monaghan et al. 1994).

Whether or not egg size accurately measures parent quality in terms of chick growth, there was a strong effect of provisioning rate on wing growth. Among experimental chicks, first egg size,

and then nutrition, were important determinants of wing growth. This suggests that early feather production was determined by the size of the yolk reserves, and later by the diet. Among control chicks, a similar effect occurred in the year of slow growth. In the year of fast growth, differences in the rates of provisioning began to affect wing growth soon after hatching, and in that year, there was little effect of egg size. This suggests that when the diet is adequate, the rate of income of the necessary nutrients is sufficient to override disadvantages incurred from a small reserve at hatching. This, and the correlation between egg size and chick mass up to potential departure age in 1995, supports the view that large eggs are particularly advantageous when conditions for raising young are unfavourable (Williams 1994, Smith et al. 1995).

In summary, I suggest that variation in egg size has important consequences to chick development in Thick-billed Murres. Chicks from larger eggs develop their wing feathers more quickly, which potentially prepares them to depart younger, and perhaps increases their chance of survival. Ricklefs (1979) has suggested that post-hatching chick development involves compromises, and that chicks should allocate the limited resources in the manner which maximizes their fitness. In the Giant Canada Goose *Branta canadensis maxima*, nutrients in the yolk sac are allocated preferentially to rapid development of the digestive tract post-hatching, which is critical because the chick's diet is deficient in essential amino acids, and the digestibility is low (Peach and Thomas 1986). The growth of the wing feathers is delayed. This difference between geese and

murres, and the observations on differences in egg characteristics within the Alcidae, indicate that it may be most productive to examine the relationship between egg characteristics and post-hatching chick development in light of the ecology of the species under consideration.

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Table 1: Comparisons between years (Mean $\pm$ SD) of egg volume indices (cm^3), and growth parameters for chicks in the egg switch experiment. In 1994, the sample sizes for growth 2-14 d are 30. Growth measurements are in g (mass) and mm (wing).

Year	N	Laid EVI	Fostered EVI	Growth 2-14 d		Size at 14 d		Size at departure		
				Mass**	Wing	Mass*	Wing	Mass	Wing	Age
1994	33	201.3 ±18.3	206.2 ±15.4	116.8 ±19.3	28.1 ±4.2	199.0 ±19.6	54.7 ±4.5	223.6 ±27.2	77.7 ±7.4	22.0 ±2.6
1995	27	208.7 ±16.1	209.4 ±14.9	104.0 ±20.0	28.1 ±4.4	182.7 ±21.2	53.4 ±4.7	220.1 ±31.5	79.4 ±8.9	22.9 ±2.9

* t-tests, 2-tailed $p < 0.05$; ** 2-tailed $p < 0.01$

Table 2: Correlation coefficients (r) with foster egg volume index for foster chick growth parameters. In 1994, the sample sizes for growth 2-14 d are 30. Departure age was partialled out of the correlations with size at departure.

Year	N	Growth, 2-14 d		Size at 14 d		Size at departure	
		Mass	Wing	Mass	Wing	Mass	Wing
1994	33	-0.29	+0.52**	-0.08	+0.51**	-0.26	+0.33*
1995	27	+0.21	+0.45**	+0.41*	+0.51**	+0.15	+0.52**

* 1-tailed $p < 0.05$; ** 1-tailed $p < 0.01$.

Table 3: Comparisons of foster egg sizes (cm^3) and chick growth (g) (Mean $\pm$ SD) for the one-third of chicks from the largest and smallest eggs, with the two years combined.

Group	Mean egg	Mean growth
	volume index (N)	in body mass, 2-14 d (N)
Largest 1/3	225.9 $\pm$ 7.9 (20)	110.6 $\pm$ 19.8 (19)
Smallest 1/3	191.9 $\pm$ 6.3 (20)	110.7 $\pm$ 19.1 (19)

Table 4: Correlation coefficients (r) with the volume index of eggs laid for foster chick growth parameters. In 1994, the sample sizes for growth 2-14 d are 30. Departure age was partialled out of the correlations with size at departure.

Year	N	Growth, 2-14 d		Size at 14 d		Size at departure	
		Mass	Wing	Mass	Wing	Mass	Wing
1994	33	+0.21	+0.07	+0.24	+0.16	+0.22	+0.30*
1995	27	+0.02	-0.07	-0.02	-0.11	-0.02	-0.11

* 1-tailed $p < 0.05$.

Table 5: Comparisons of foster egg sizes (cm^3) and chick growth (g) (Mean $\pm$ SD) for the one-third of chicks which gained the most and the least mass between 2-14, with 1994 and 1995 combined (both $N = 19$).

Group	Mean egg volume index	Mean growth in body mass, 2-14 d
Most 1/3	204.4 $\pm$ 14.0	132.4 $\pm$ 8.7
Least 1/3	204.7 $\pm$ 16.2	87.5 $\pm$ 11.9

Table 6: Comparisons between years (Mean $\pm$ SD) for chick growth parameters of all control breeders, and for the thirds of chicks that (i) hatched from the largest and smallest eggs, and (ii) grew the most and the least between 2-14 d. Measurements are in cm³ (egg volume index, EVI), and g (growth)

Year	Whole sample ^a			EVI			Growth 2-14 d		
	N	EVI	14 d mass**	N	Largest 1/3	Smallest 1/3	N	Most 1/3**	Least 1/3
1994	57	210.3 ± 18.8	208.6 ± 21.2	19	230.8 ± 12.6	191.1 ± 7.7	14	144.2 ± 11.2	98.2 ± 11.5
1995	56	207.6 ± 18.8	189.9 ± 19.1	19	227.2 ± 7.9	186.2 ± 10.5	15	131.5 ± 9.7	90.7 ± 10.1

** t-tests, 2-tailed $p < 0.01$.

^a Correlations between 14 d mass and EVI: 1994: $r = +0.25$, 1-tailed $p = 0.04$;

1995: $r = +0.26$, 1-tailed $p = 0.03$.

Table 7: Correlation coefficients with age at nest departure for chick growth parameters. Hatching date was partialled out of all correlations.

Sample	Year	N	14 d body mass	14 d wing length
Egg switch	1994	33	-0.19	-0.44**
	1995	27	-0.23	-0.07
Control	1994	57	-0.23*	-0.33**
	1995	56	-0.11	+0.02

* 1-tailed $p < 0.05$; **1-tailed $p < 0.01$.

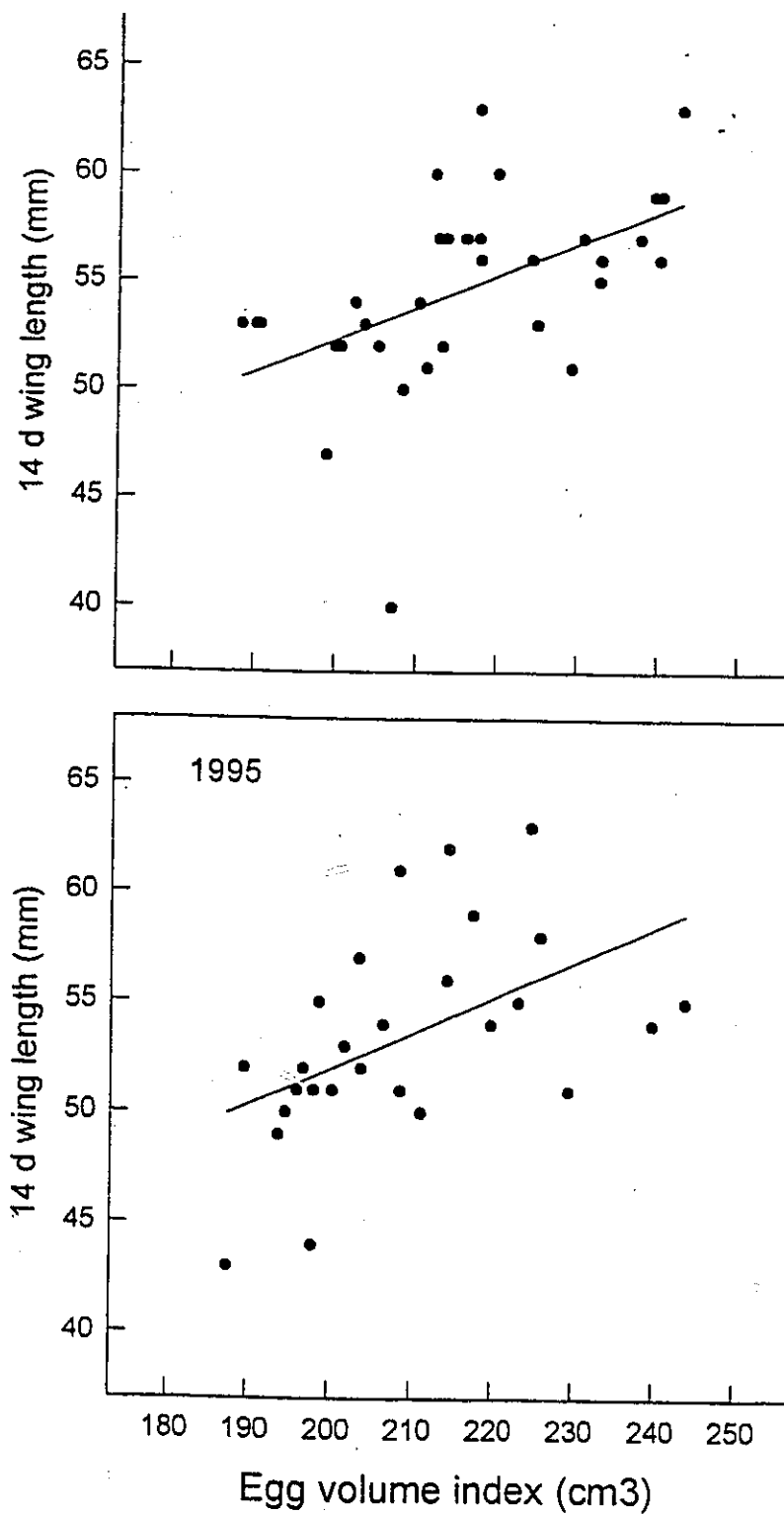


Figure 1: Scatter plots showing the relationship between 14 d wing length and egg volume index of chicks in the egg switch experiment in 1994 (top) and 1995 (bottom).

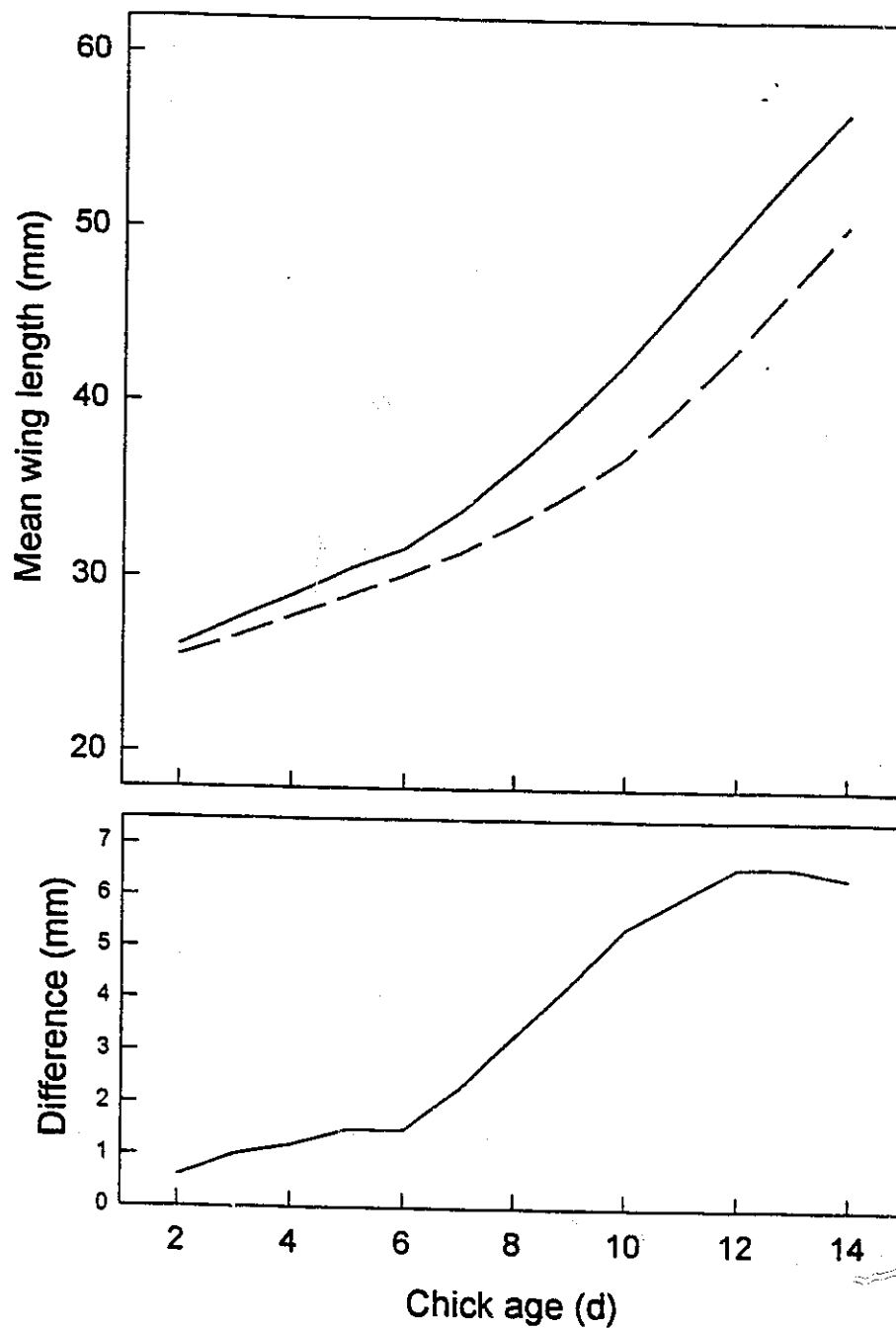


Figure 2: Plot of wing length against age for chicks from the largest one-third of eggs (solid line) and the smallest one-third of eggs (dashed line). The bottom figure shows the difference.

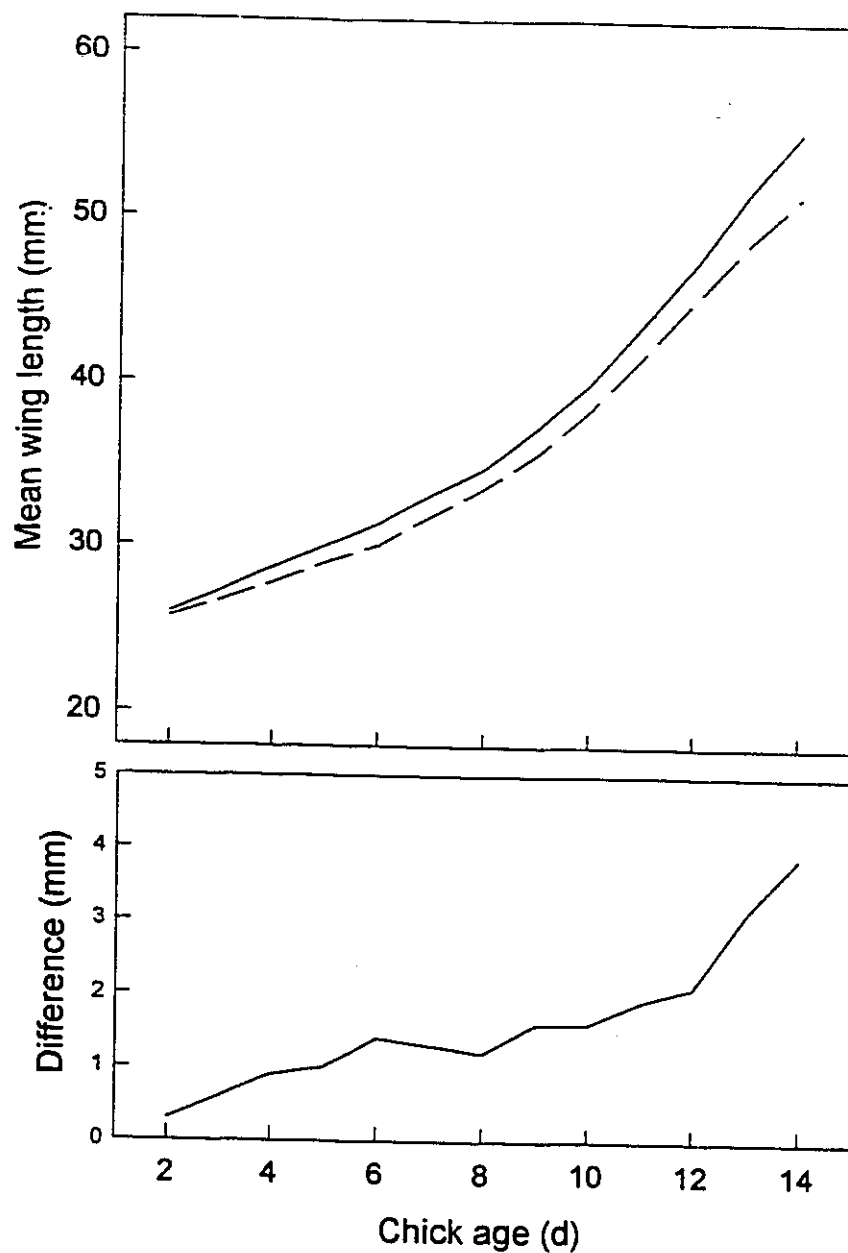


Figure 3: Plot of wing length against age for the one-thirds of chicks that gained the most mass between 2-14 d (solid line) and the least mass between 2-14 d (dashed line). The bottom figure shows the difference.

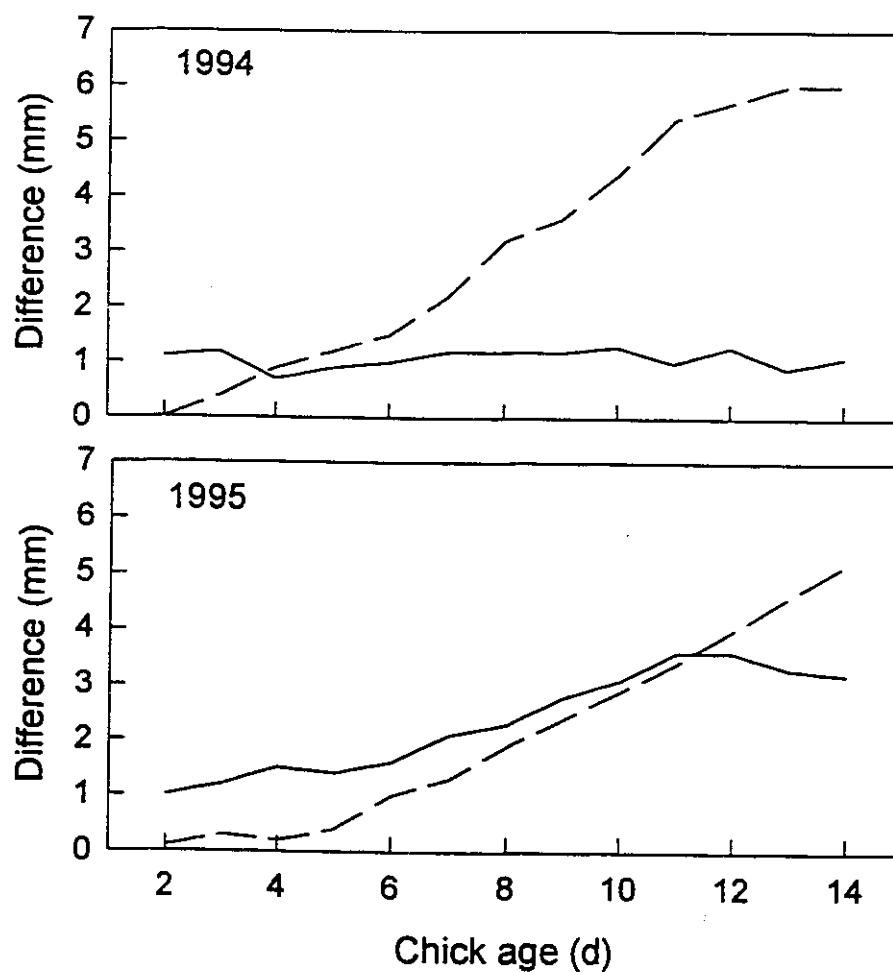


Figure 4: Plots of the differences in wing length with age between chicks from the largest and smallest one-thirds of eggs (solid line), and between the one-thirds of chicks that gained the most and the least mass between 2-14 d (dashed line), in 1994 (top) and 1995 (bottom).

Chapter 4: Effects of Parental Quality
and Environmental Variation on the Growth
of Nestling Thick-billed Murres

Abstract.- Measures of reproductive success decline with date in many bird species. For example, in the Thick-billed Murre *Uria lomvia*, an Arctic-breeding seabird which raises a single chick, late-hatched chicks tend to grow more slowly, and depart the nest lighter, than early-hatched chicks. For Thick-billed Murres at Coats Island, N.W.T., Canada, in 1994 and 1995, I examined whether the decline in growth rate with hatching date was caused by timing of breeding effects (the "seasonal deterioration" hypothesis) or by the late breeding of less capable individuals (the "parent quality" hypothesis). I removed the egg from a sample of early-breeding birds, inducing them to re-lay. The growth of their chicks then was compared with unmanipulated early-breeding birds whose chicks hatched 18-19 d earlier. In both years there were declines in chick growth rate with hatching date among control birds. However, in both years the experimental chicks grew as well as the chicks of unmanipulated, early-breeding birds. This result supports the "parent quality" hypothesis, but not the "seasonal deterioration" hypothesis. I suggest that the late laying of poor quality birds is the likely proximate cause of many of the seasonal declines in reproductive performance associated with the breeding of the Alcidae.

INTRODUCTION

Perrins (1970) proposed that the timing of egg-laying in birds results from an interaction between the evolutionary advantages of early breeding, and physiological constraints acting on individual females prior to and during the period of egg formation. In this view, two factors influence reproductive success: parental quality and timing of breeding. Earlier breeding is advantageous because conditions for raising young deteriorate late in the season. However, poor quality birds cannot produce eggs early and consequently raise their young when conditions are worse. In many bird species, the younger, less experienced members of the population lay later than older, more experienced members (reviewed in Saether 1990), and reproductive success declines with date (reviewed in Perdeck and Cave 1992).

Because of the causal relationship between parent quality and timing of breeding, it can be difficult to distinguish their relative effects on reproductive success. The best way to do this is to experimentally manipulate timing of breeding, for example, by inducing early-laying, high quality birds to breed late in the season (e.g., Verhulst et al. 1995). If the population-wide seasonal declines in reproductive success result from a timing effect, then the success of the experimentally-delayed birds should follow this decline. Conversely, if the declines result from the late breeding of poor quality birds, then the experimental birds should be as successful as unmanipulated early-laying birds, and more successful than late-laying birds. In experimental studies,

timing of breeding determined reproductive success in some cases (Brinkhof et al. 1993; Norris 1993; Wiggins et al. 1994), but not in others, after controlling for parental quality (de Forest and Gaston 1996). In other studies, both timing and quality affected reproductive success (Verhulst et al. 1995). In colonial species, timing relative to others in the population, rather than calendar date, may be important (Hatchwell 1991). Finally, while conditions may decline late in the season, high quality birds can perhaps compensate for this (Brouwer et al. 1995).

For species that breed in seasonal, time-limited environments, such as the Arctic, timing may be critical because the duration of conditions favourable for breeding is short. Hence, there should be strong selection for early laying, and individuals that breed outside of the best period should experience reduced reproductive success. Consequently, Arctic-breeding birds provide excellent subjects for examining the effects of timing of breeding and parent quality on reproductive success.

Thick-billed Murres *Uria lomvia* are colonial, cliff-nesting seabirds of Arctic waters. They lay a single egg, and feed their chick at the nest for 15-30 d, at which time the chick departs to the sea at up to 25% of adult mass (Gaston and Nettleship 1981). In agreement with Perrins' hypothesis, older, more experienced Thick-billed Murres lay earlier than young birds (de Forest and Gaston 1996; Hipfner et al. in prep.), and reproductive success declines with date (Birkhead and Nettleship 1981; Gaston and Nettleship 1981; de Forest and Gaston 1996). Late-hatched chicks

tend to grow more slowly, and depart the nest lighter, than early-hatched chicks, and this most often has been attributed to reduced food availability late in the season (Birkhead and Nettleship 1981, 1982; Gaston and Nettleship 1981). Gaston (1985) suggested that the declines in growth rate with hatching date also could be caused by: (i) declines in egg size with laying date causing corresponding declines in growth rates (Birkhead and Nettleship 1982); (ii) lower temperatures late in the season increasing the maintenance energy requirements of chicks (Uspenski 1956); (iii) fewer daylight hours late in the season reducing the time available for adult birds to forage; and (iv) late-hatched chicks, if less likely to survive, warrant less investment from their parents. Hypothesis (i) is unlikely because recent work has shown that growth in body mass is independent of egg size in Thick-billed Murres (Hipfner and Gaston in prep.). Hypotheses (ii)-(iv), like the food availability hypothesis, are effects of timing of breeding.

I tested whether the declines in growth rate with hatching date in nestling Thick-billed Murres result from a timing effect (the "seasonal deterioration" hypothesis), or from the late-laying of poor quality birds (the "parent quality" hypothesis), by removing the egg from early-breeding birds, inducing them to relay. As the two hypotheses considered are not mutually exclusive, the question addressed in this paper is whether chicks raised by high quality, but late-breeding birds show reduced growth compared to those of early-breeding high quality birds.

STUDY AREA AND METHODS

This study was conducted at Coats Island, N.W.T., Canada ($62^{\circ} 57'N$, $82^{\circ} 00' W$), in 1994 and 1995. The Thick-billed Murre colony there consists of two sub-colonies of similar size, separated by 1 km of coastline, which together include ca. 30,000 breeding pairs (Gaston et al. 1993). Among murre colonies of the eastern Canadian Arctic, Coats Island is noteworthy for the fast growth rates of chicks (Gaston et al. 1983).

Intra-year variation

In mid-July of both years (just prior to the start of hatching) all sites at which an egg was present were mapped and numbered on a series of plots in two areas near the top of the colony. Every egg was marked with its site number in permanent ink, and its length and maximum breadth was measured to within ± 0.1 mm using vernier calipers. Subsequently, all sites were checked at 2-3 d intervals through the season, depending on the weather; on two occasions during the mid chick-rearing period in 1994, checks had to be delayed to 4 d.

The first time a chick was present at a site, I estimated its hatching date and individually marked it with a binary code of nail clipping. Each chick was banded when large enough. At every visit, each chick was weighed to within ± 1 g with a 300 g spring balance, and the length of the right wing was measured to within ± 1 mm with the wing held flat and straight against a ruler. All visits were made between 0900 and 1200 h.

Egg removal experiment

To examine seasonal effects on chick growth while controlling for parent quality, I experimentally delayed a sample of early-breeding birds in both years. I mapped and numbered 25 sites on each of two plots, and then measured and removed the eggs. This was done on 25 and 26 June (ca. median laying date at this colony), using different plots in the two years. As the background colour and pattern of markings is repeated on eggs laid by the same murre (Southern 1951), Polaroid photographs of the first eggs were used to verify that the egg later found at the same site had been laid by the same female.

These plots were rechecked ca. 45 d later (periods of 14 d for egg replacement (deForest and Gaston 1996), and 33 d for incubation (A.J. Gaston unpublished data) are typical). At this time, the replacement eggs were measured, and the growth of these chicks was monitored, using the protocol described above. As a control group, I selected from among the unmanipulated breeders those which would have laid before the date of egg removal, i.e., those where the chick hatched on or before 28 July (25 June + 33 d incubation).

Data analysis

As a measure of egg size, I used an index of egg volume (EVI, length * breadth²) which is linearly related to fresh egg mass in Thick-billed Murres ($r=0.952$, Birkhead and Nettleship 1984). The date of hatching of a chick was recorded as day 1. Measurements at

2 and 14 d were estimated using linear interpolation (Hussell 1972) for those chicks not measured on the exact day. Measurements at 2 d were used as estimates of initial size because larger samples were available than for 1 d old chicks (2 d measurements could be estimated by interpolation for chicks measured at 1 d). Sample sizes that involve a 2 d measurement (growth between 2-14 d) are smaller than those that do not (e.g. 14 d mass) because some chicks were first measured at 3 d. Only chicks that survived to ≥ 15 d are included in any analysis, because 15 d is the youngest age at which chicks are known to depart the nest of their own volition (Gaston and Nettleship 1981). Therefore, 14 d is the oldest age at which a sample is unbiased by some chicks having departed (Gaston 1985). The following definitions are used: (i) maximum mass is the heaviest mass recorded for a chick, and (ii) age at maximum mass is the age of the chick at this measurement; (iii) departure mass is the mass of a chick at last measurement, and (iv) departure age is the age at last measurement + 1 d. All probability values are two-tailed.

RESULTS

Intra-year variation in chick growth

Thick-billed Murre egg sizes and hatching dates were similar in 1994 and 1995 (Table 1). Chicks grew significantly faster over the linear growth phase (2-14 d) in 1994 than 1995, so that masses at all developmental stages were higher in 1994 (Table 1). Chicks reached maximum masses and departed the colony about 2 d younger on

average in 1994 than 1995 (Table 1).

Total chick growth between 2-14 d was negatively related to hatching date in both years, with similar slopes (-1.4 gd^{-1}), although this trend was not quite significant in 1994 (Figure 1). In both years, there were significant negative correlations between 14 d mass and hatching date (Table 2). Maximum and departure masses also declined significantly with date in 1994, but not in 1995. Conversely, age at nest departure was negatively related to date of hatching in 1995 (a chick hatched 5 d later than another departed about 1 d younger on average), but this trend was not significant in 1994 (Table 2).

Egg removal experiment

The egg sizes and hatching dates of the control birds (mean hatching dates of 23-24 July suggest mean laying dates of 20-21 June) matched those of experienced breeders in both years (Hipfner et al. in prep) (Table 3). The first eggs laid by experimentally-delayed birds were similar in size to those of the control birds in both years, which suggests that the two groups were composed of birds of similar quality (Table 3).

Of the 50 eggs removed in 1994, 31 were replaced and still present the day the plots were rechecked. These 31 eggs produced 26 departure-aged chicks. In 1995, 22 replacement eggs were still present when the plots were rechecked; predation by an Arctic fox *Alopex lagopus* caused many losses on one of the two plots. Twenty-one of these chicks reached 15 d of age, but three of these (the

only remaining chicks on the fox-predated plot) were excluded from the estimates of maximum and departure masses and ages because there was evidence that their disappearance at 14-15 d of age was due to the fox. There was no evidence of predation on chicks by foxes on either plot in 1994, nor on the second plot in 1995.

In the control group, egg sizes and hatching dates were similar in the two years (t-tests, p-values > 0.20), but growth was better in 1994 than 1995 (Table 3). Chick masses at all developmental stages were higher, and ages at maximum mass and departure lower, in 1994 compared to 1995 (t-tests, all p-values $\leq$ 0.01). In the delayed group, all growth parameters were similar in the two years (t-tests, all p-values > 0.30) (Table 3).

Chicks of the experimentally-delayed birds hatched 18-19 d later than those of control birds in both years (Table 3). In 1994, growth of the experimental chicks between 2-14 d was similar to that of control chicks (Table 3). Although they hatched from smaller eggs, and so would have been lighter at hatching (Birkhead and Nettleship 1984), the masses of the experimental chicks were similar to those of the control chicks at all stages. In 1994, I left Coats Island before the departure of 15 of the experimental chicks; these chicks were 16-22 d of age (mean 18.9 ± 1.8 d) and weighed 177-241 g (mean 217.1 ± 19.0 g) on the day I left. Because the estimate of maximum mass for the experimentally-delayed group in 1994 includes all 26 chicks, it must be regarded as a minimum. Nonetheless, this minimum estimate does not differ statistically from that of the control group. Age at maximum mass, and departure

age and mass of the experimental chicks are for the 11 chicks which had departed when observations ceased in 1994. As the remaining chicks were, on average, older at last check than the ages at nest departure of those which left, the difference in departure ages may not be real.

In 1995, chick growth between 2-14 d was slightly better in the experimental than the control group (Table 3). At 14 d, the chicks raised by delayed birds were significantly heavier than the control chicks. The experimental chicks reached their peak masses younger, and departed younger, than control chicks. Maximum and departure masses were similar between the two groups, probably due (at least in part) to the fact that the experimentals departed younger.

DISCUSSION

Why did growth rates decline over the season?

Of the two hypotheses I tested which have been proposed to account for seasonal declines in chick growth rates (the "seasonal deterioration" and "parent quality" hypotheses) only the latter is supported by these results. Late-hatched Thick-billed Murre chicks tended to grow more slowly than early-hatched chicks, as in other studies (Birkhead and Nettleship 1981, Gaston and Nettleship 1981, Gaston et al. 1983). However, chicks of experimentally-delayed breeders grew at least as well as those of unmanipulated, early-breeding birds in both years. This indicates that conditions did not decline to below a threshold at which the growth of chicks of late-breeding, but high quality parents was affected. Two

explanations are possible: (i) conditions may have been similar early and late, at least relative to the abilities of high quality birds; (ii) in response to their lateness, delayed birds may have put more effort into provisioning their chicks. In 1995, the chicks of delayed birds reached similar peak masses at younger age, and departed younger, than chicks of control birds. This suggests that their parents might have worked harder to provision them. There was an indication of this in 1994 as well.

Late-breeding murres could benefit in a number of ways if they can prepare their young to depart early. Early nest departure might increase the survival of late-hatched chicks by reducing the amount of time spent at the colony with few neighbours, and consequently under a heightened risk of predation (Hatchwell 1991). Early departure also has been associated with increased post-departure survival in Common Murre chicks *Uria aalge* in some years (Harris et al. 1992). Furthermore, because adult murres moult immediately after breeding (Birkhead and Taylor 1977), there might be direct benefits to the parents of late-hatched chicks if their young go to sea quickly (Wanless and Harris 1988). Regardless of which of the mechanisms was operating, the results indicate that the late-breeding of poor quality birds, rather than timing *per se*, is the primary cause of the seasonal decline in growth rates and departure masses of Thick-billed Murres at this colony.

Hedgren and Linnman (1979) found that experimentally-delayed Common Murres were unable to grow chicks as quickly as a control group. They attributed this to reduced quality of prey late in the

season. However, they removed eggs well after most birds had laid, so their results may not be directly comparable to those presented here. Nonetheless, their results indicate that there may be direct effects of timing of breeding on the growth of murre chicks at some colonies and in some years.

The timing of breeding effect could have causes other than a reduction in the quality or quantity of food available late in the season (Gaston 1985). Late-hatched chicks may have to expend more of the energy available to them for maintenance as temperatures drop late in the season (Uspenski 1956). In 1994, the experimental birds were raising chicks when the daily mean maximum temperatures were significantly lower (by 3.9°C), and the minimums marginally lower (by 1.1°C), than for the control birds; the corresponding differences were $+0.1$ and -0.6°C in 1995. Also, a reduction in the number of hours of daylight late in the season may affect chick provisioning. The results of day-long feeding watches at Coats Island show that the first feedings of the day tend to occur later, and the last feedings earlier, later in the season (A.J. Gaston unpublished data). Neither colder temperatures nor fewer hours of daylight caused reduced growth in the experimental compared to the control chicks. At colonies in the High Arctic, these effects may be more pronounced than at a Low Arctic colony like Coats Island. The hypothesis that parents of late-hatched chicks invest less in their offspring because late-hatched young are intrinsically less valuable is also not supported (Gaston 1985).

Three observations suggest that the within-season patterns of

food availability differed between years: (i) while 14 d mass was negatively correlated with date of hatching in both years, maximum and departure masses were not in 1995. In that year, departure age was negatively correlated with date, so that late-hatched chicks did not achieve masses similar to early-hatched chicks by remaining longer in the nest; (ii) while the control chicks grew faster in 1994 than 1995 (suggesting that early in the year conditions were better in 1994), the delayed birds grew equally well in the two years (suggesting that late in the year, conditions were similar); and (iii) the 14 d masses of experimental chicks were higher than those of control chicks in 1995, while they were similar in 1994. The simplest explanation for these observations is that, contrary to the expected pattern, feeding conditions improved late in 1995, and this, to some extent, cushioned late-breeding pairs. While the importance of between-year variations in food availability to the breeding success of northern seabirds is well documented (e.g. Murphy et al. 1991), within-year variations have received somewhat less attention. The results presented here, and elsewhere (e.g., Barrett et al. 1987), indicate that variations within years in feeding conditions may also have measurable effects on the growth of nestling alcids.

In studies of Thick-billed Murres breeding at Coats Island, it has been found that parental quality, more than timing of breeding, determines egg size (Hipfner et al. in prep.), reproductive success (deForest and Gaston 1996), and chick growth rates (de Forest and Gaston 1996; this study) and departure masses (this study). High

quality birds breed early, but when forced to breed late, they are as successful as early-laying birds. The breeding biology of the Alcidae is characterized by seasonal trends which reflect declining offspring quality (egg sizes (e.g. Lloyd 1979; Harris 1980; Birkhead and Nettleship 1982), chick growth rates (e.g. Nettleship 1972; Sealy 1981; Gaston et al. 1983), and chick masses at nest departure (e.g. Ydenberg 1989), often decline over the season). Results from Coats Island indicate that the seasonal declines in offspring quality are due mainly to declines in parent quality, and that the putative environmental deteriorations may be of secondary importance. However, exceptions to these trends occur (e.g. masses at nest departure did not decline in 1995), and could be due to within-year variations in food availability.

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Table 1: Inter-year comparisons (Mean $\pm$ S.D.) of growth parameters. P-values are results of t-tests for comparisons between years; * $p < 0.05$, ** $p < 0.01$. For growth 2-14 d, $N = 43$ (1994) and 44 (1995). Hatching dates are days from 1 June = 1.

Year	N	EVI (cm ³)	Date of		Growth	Mass (g) at		Age at			
			hatching	2-14 d		(y)*	14 d**		Maximum**	Departure*	Departure (d)**
1994	57	210.3 ±18.8	55.8 ±4.5	121.2 ±21.2	208.6 ±21.1	232.2 ±23.7	226.0 ±23.7	21.0 ±2.1			
1995	56	207.6 ±18.8	54.9 ±5.0	111.1 ±19.1	189.9 ±19.1	219.6 ±22.8	214.8 ±23.8	22.8 ±2.4			

Table 2: Correlations with hatching date for growth parameters. Slopes are in gd^{-1} or dd^{-1} . For growth 2-14 d, $N = 43$ (1994) and 44 (1995).

Year	N	Statistic	Growth 2-14 d	Mass at		Age at Departure
				14 d	Maximum Departure	
1994	57	r	-0.29	-0.27	-0.30	-0.28
		p	0.07	0.05	0.02	0.04
		Slope	-1.35	-1.24	-1.58	-1.48
1995	56	r	-0.37	-0.29	-0.16	-0.11
		p	0.01	0.03	0.23	0.41
		Slope	-1.39	-1.18	-0.74	-0.54

Table 3: Comparisons (Mean $\pm$ SD) between growth of Control and Experimental chicks. Hatching dates are from June 1 = 1. P-values are results of t-tests or Mann-Whitney U-tests; ** $p < 0.01$.

Parameter	1994			1995		
	Cont (N)	Exp (N)	p	Cont (N)	Exp (N)	p
EVI 1 (cm ³)	212.3 (45) ± 18.2	214.4 (26) ± 16.9		209.1 (49) ± 18.3	213.2 (21) ± 20.3	
EVI 2 (cm ³)		200.4 (26) ± 15.8	** ^a		205.6 (21) ± 16.7	
Hatch date	54.1 (45) ± 2.7	72.5 (45) ± 1.7		53.4 (49) ± 2.2	72.5 (21) ± 1.7	
Growth 2-14 d (g)	124.5 (37) ± 20.1	121.0 (20) ± 21.1		113.1 (39) ± 18.7	121.7 (17) ± 17.6	
Mass 14 d (g)	212.5 (45) ± 19.9	205.0 (26) ± 18.3		191.7 (49) ± 20.8	205.6 (21) ± 16.5	**
Maximum mass (g)	235.6 (45) ± 22.8	226.7 (26) ^b ± 18.6		220.6 (49) ± 22.9	226.8 (18) ± 25.8	
Departure mass (g)	229.3 (45) ± 22.5	228.4 (11) ± 19.9		215.4 (49) ± 23.9	219.9 (18) ± 25.7	
Age (d) at maximum	18.0 (45) ± 2.5	16.7 (11) ± 1.6		19.7 (49) ± 3.3	16.7 (18) ± 1.7	**
Age (d) at departure	21.0 (45) ± 2.1	18.8 (11) ± 1.5	** ^b	23.0 (49) ± 2.2	19.6 (18) ± 1.5	**

^a Comparison with EVI 1 of control group.

^b Probably an underestimate. See text.

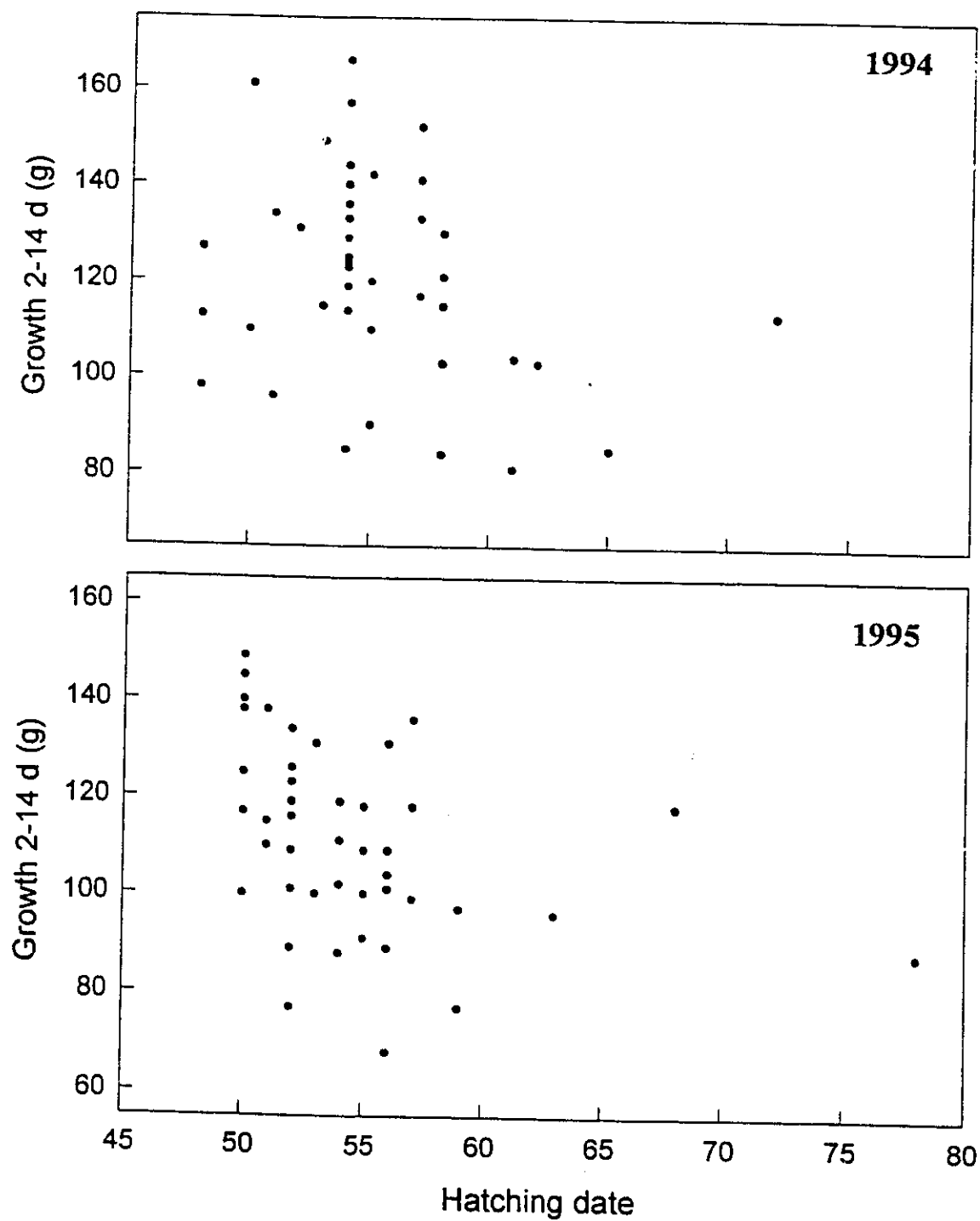


Figure 1: Scatter plot showing the relationship between total chick growth 2-14 d and hatching date in 1994 (top) and 1995 (bottom).

**Chapter 5: Tests of Ydenberg's Model of Alcid Nest Departure
As Applied to an Intermediate Alcid, the Thick-billed Murre**

The Alcidae are unique among bird families in that there are three distinct developmental strategies of the young, from fully precocial (chicks depart the nest at 2-4 d of age), to intermediate (chicks depart at 15-30 d at 12-25% adult size), to semi-precocial (chicks depart with adult proportions after up to 60 d in the nest) (Sealy 1973). The semi-precocial strategy is believed to be the ancestral strategy (Gaston 1992), and the evolutionary forces that might have favoured increased levels of chick precocity have been discussed frequently (Cody 1973; Sealy 1973; Birkhead 1977; Gaston and Nettleship 1981; Murray et al. 1983; Gaston 1985; Ydenberg 1989). Ecological rather than phylogenetic factors are believed to be mainly responsible for the variation (Ydenberg et al. 1995). In the views of different authors, the following might have selected for shortened nestling periods: (i) open nest sites, because chicks are less safe than in burrows, and because one parent must remain at all times with the chick (e.g. Cody 1973; Birkhead 1977); (ii) a patchily distributed or distant food source, because this increases search and travel times during the chick provisioning stage (Cody 1973; Sealy 1973); (iii) large adult body size, because it limits the relative size of egg that can be produced (Birkhead 1977) and limits the size of meals that can be carried back to the chick at the nest, (e.g. Gaston and Nettleship 1981; Gaston 1985); (iv) low chick mortality at sea (Murray et al. 1983); and (v) a

high risk of predation to adult birds during visits to the nesting colony (Gaston 1992).

Ydenberg (1989) and Ydenberg et al (1995) developed a model (hereafter the Ydenberg model) that attempts to explain inter- and intra-specific variation in departure age and mass of alcid chicks, based on the differential growth and mortality costs and benefits of the pre- and post-fledging habitats, i.e. the nest and the sea. Two assumptions are critical to the model: (i) the nest is safe relative to the sea; and (ii) the growth rate at sea exceeds the growth rate in the nest. Consequently, the chick must decide when to leave a low mortality, slow-growth habitat (the nest), for a high mortality, fast-growth habitat (the sea). The chick takes account of (i) its mass, and (ii) the amount of time left in the season. Survival to breeding age is a function of its mass at the onset of winter; larger chicks survive better. The model makes several testable predictions, and has been used to predict the departure behaviour of intermediate (Common Murre *Uria aalge*, Ydenberg 1989) and semi-precocial (Rhinceros Auklet *Cerorhinca monocerata*, Ydenberg et al. 1995) alcids. However, it was less successful in predicting nest departure in the semi-precocial Cassin's Auklet *Ptychoramphus aleuticus* (Moreby 1995). In this chapter, the two main predictions of the model are tested in Thick-billed Murres *Uria lomvia*, using data from colonies in the eastern Canadian Arctic (Birkhead and Nettleship 1981, 1982; Gaston and Nettleship 1981; Gaston et al. 1983; Gaston 1991; A.J. Gaston unpublished data), as well as information presented in previous

chapters of this thesis.

Prediction 1: Fast-growing chicks depart the nest both heavier and younger than slow-growing chicks. Consequently, mass at departure is correlates negatively with age at departure.

The explanation for the negative relationship between departure mass and departure age is as follows: compared to a slow-growing chick, a fast-growing chick approaches a heavier asymptotic mass at a younger age, so its growth rate begins to level off at a younger age. Consequently, it abandons the nest, where its growth rate is too low, for better growth at sea, both heavier and younger than a slow-growing chick. The critical assumption is that at some point, growth in the nest falls below that attainable at sea (Ydenberg et al. 1995).

(i) Inter-colony tests

The growth rates of nestling Thick-billed Murres vary markedly between colonies in the eastern Canadian Arctic (e.g. Gaston et al. 1983). As the model predicts, mass and age at nest departure are negatively correlated when the colony means are plotted together (Figure 3, Ydenberg et al. 1995).

However, a comparison of growth curves between fast- and slow-growth colonies suggests that the mechanism proposed by the model is unlikely to explain the negative correlation. At Digges Island, where chicks grew slowly and departed older, asymptotic masses were lighter, as predicted, but growth began to level off earlier than

at Prince Leopold Island, where chicks grew quickly and departed younger (Figure 21, Gaston et al. 1985). Total growth between 14 d of age and nest departure was greater at fast growth colonies (23.3 ± 11.7 g at Prince Leopold Island (Tables 56 and 57, in Gaston and Nettleship 1981) and 23.8 ± 7.1 g at Coats Island (Gaston 1991, and additional data)) than at slow-growth colonies (9.4 ± 3.7 s.d. g at Digges Island (Table 2, Gaston et al. 1983)). Masses at 14 d averaged 138.0 ± 10.2 g at Digges, 186.7 ± 12.9 g at Prince Leopold, and 206.4 ± 9.8 g at Coats. Therefore, between potential and actual departure age, chicks at fast-growth colonies were both larger and faster-growing than at slow-growth colonies, suggesting that growth in the nest falls below that attainable at sea earlier at a slow-growth colony, yet these chicks remain longer in the nest. This indicates that the negative correlation may have been predicted for the wrong reason.

(ii) Intra-colony tests

Data was collected at four colonies for nine colony-years (Table 1). The predicted negative correlation of mass on age at departure did not occur in any sample. In fact, the relationship was significantly positive in two (Table 1). These correlations were repeated with hatching date partialled out because there is often a negative correlation between age at departure and hatching date in Thick-billed Murres (e.g. Gaston et al. 1983). However, again there were no significant negative correlations, while one of the two significant positive correlations remained significant.

(iii) Inter-year tests

Data was collected in seven years at Coats Island, to test the prediction that in years when chicks grow quickly, they depart young. The correlation between mean departure mass and departure age was negative, but not significantly so ($r = -0.30$, $p = 0.52$), nor was it significant with hatching date controlled in a partial correlation ($r = -0.30$).

Prediction 2: Late-hatched chicks fledge lighter and younger than early-hatched chicks, i.e., both mass and age at nest departure are negatively correlated with hatching date.

The explanation for the negative relationships between mass and age at nest departure and hatching date is as follows: the optimal mass at which to fledge declines with date (the fledging boundary has a negative slope) because of the need for late-hatched chicks to enter the fast growth habitat more quickly than early-hatched chicks. Consequently, late-hatched chicks leave the safety of the nest at lighter mass, and therefore younger age, than those that hatch early. It is assumed that there is no seasonal decline in growth rate.

(i) Intra-year tests

Data was collected at six colonies for thirteen colony-years (Table 1). Significant negative correlations between mass at nest departure and hatching date existed in four of the ten samples for

which this data was available; significant negative correlations of age at departure with hatching date existed in seven of thirteen samples (Table 1). In three samples, negative correlations of mass and age at departure with hatching date occurred together. Hence, there is some support for this prediction of the model. However, departure masses did not decline with hatching date in any of the five samples in which 14 d masses (i.e. growth rates) did not, while in all 4 samples in which departure masses declined, 14 d masses did also (Table 1). This suggests that seasonal declines in mass at nest departure do not occur in the absence of seasonal declines in growth rates, which is contrary to the model. Declines in age at departure with hatching date occurred more frequently, and in the absence of seasonal declines in departure mass. This suggests that the seasonal decline in chick age at nest departure is not a consequence of an adaptive seasonal decline in departure mass, as the model proposes.

(ii) Experimental tests

In 1994 and 1995, the first eggs were removed from samples of early-breeding birds, inducing them to relay, and the growth of the chicks of these experimentally-delayed birds was compared to that of unmanipulated early-breeding birds (see Chapter 4 for details). In both years, chicks of experimentally-delayed breeders departed the nest younger, but at similar mass to chicks of unmanipulated early-breeding birds. This result does not support the model; the delayed chicks did not depart at reduced mass, as predicted by the

model, but did depart young.

(iii) Inter-year tests

Data was collected in seven years at Coats Island. There was no correlation between mean departure mass and mean hatching date ($r = -0.08$, $p = 0.87$). Likewise, there was no correlation between mean departure age and mean hatching date ($r = -0.02$, $p = 0.96$).

Conclusions

The results of these tests of the Ydenberg model suggest that it is inadequate in explaining important features of development and nest departure in Thick-billed Murres. The major discrepancies between the predictions and the observations were: (i) the negative correlation of mass on age at nest departure when colony means were plotted together occurred despite the fact that an assumption of the model necessary to obtain this result was opposite to what was observed. At slow-growth colonies, growth levelled off at younger ages than at fast-growth colonies, yet these slow-growing chicks remained in the nest for a longer time. The simplest explanation is that there are time-dependent developmental processes occurring independently of growth in mass, that cause chicks to remain in the nest, and that these occur more slowly in slow-growing chicks. This will be addressed further below; (ii) within samples from one time and place, the predicted negative correlations between mass and age at nest departure did not occur. In fact, the correlations were significantly positive in two samples. This may result from

the early breeding of high quality birds (see Chapters 2 and 4), coupled with an adaptive seasonal decline in departure age (see below), so that early-hatched chicks grow faster and stay longer than late-hatched chicks; and (iii) while negative correlations between both mass and age at nest departure and hatching date occurred in samples from one colony and year, seasonal declines in departure mass occurred only when growth rates also declined with date (perhaps favouring an explanation based on constraint rather than adaptation), while seasonal declines in age at nest departure occurred more frequently, and occurred independently of declines in departure mass. Furthermore, chicks raised by high quality but late-breeding parents departed the nest younger, but not lighter, which suggests that the optimal fledging mass did not decline with date, while the optimal fledging age did.

One possible alternative explanation for the seasonal decline in mass at departure is that late chicks are offspring of poor quality parents, which are unable to provision their chicks as well as high quality birds which breed early (see Chapter 4). However, the results of Chapter 4 suggest that the seasonal decline in age at nest departure is adaptive. This will be discussed further in the next section.

The following conclusions are drawn from these tests of the Ydenberg model: (i) on large scales, there is a general relationship between fast growth and early nest departure in Thick-billed Murres, but perhaps not for the reason suggested by the model; (ii) at small scales, there is no apparent tendency for

chicks which gain mass quickly to depart heavier and younger; (iii) the seasonal decline in mass at nest departure with hatching date is more likely to be a result of constraint than the adaptive significance given it in the model; and (iv) the seasonal decline in age at departure may have adaptive significance, but perhaps not for the reason proposed in the model. In sum, the model may have shortcomings with respect to important developmental and behavioural considerations of the nest departure decision of Thick-billed Murre chicks. Alternative explanations for some of these observations are discussed below.

Chick development and the nest departure decision

In Chapter 3, I showed that Thick-billed Murre chicks which hatched from large eggs grew their wing feathers more quickly than chicks from small eggs. Chicks with longer wings at 14 d departed to the sea younger than chicks with shorter wings. I argued that there is selection on chicks to reach a threshold wing length, or optimal wing-loading, while at the nest, because mortality at nest departure is high for chicks that fail to reach the sea with their parent on the glide from the nest site. Consequently, chicks with long wings can depart young, and early nest departure may result in increased pre- and post-departure survival (Harris et al. 1992; Hatchwell 1991).

The hypothesis that age at departure is negatively correlated with wing length at 14 d was tested by collecting data from five colonies for a total of twelve colony-years. Significant negative

correlations of age at nest departure on 14 d wing length occurred in 6 samples (Table 2). Conversely, negative correlations of age at departure and 14 d body mass occurred in two samples, and in both of these, the correlations with 14 d wing length were significant (Table 2). This supports the hypothesis that development in terms of wing length is a more important determinant of age at departure than development in terms of body mass for Thick-billed Murre chicks.

This hypothesis might address some weaknesses of the Ydenberg model. Wing length at 14 d is positively correlated with growth rate in body mass (Chapter 3 and Table 2), which might explain why chicks at fast-growth colonies tend to depart younger. In fact, mean age at nest departure is negatively correlated with mean 14 d wing length as a percentage of adult wing length when data from five colonies for a total of 16 colony-years is plotted ($r=-0.57$, $p=0.02$, 15 df). Therefore, this hypothesis explains significant proportions of the variation in age at nest departure both at large (inter-colony) and at small (intra-colony) scales, which the Ydenberg model could not do. Furthermore, in Thick-billed Murres and other alcids, the wing feathers continue to grow after growth in mass has stopped (e.g., Figure 22 in Gaston et al. 1985), so that chicks may remain at the nest longer at slow- than fast-growth colonies because it takes slow-growing chicks more time to reach the threshold wing length, another observation not adequately explained by the model.

The hypothesis that alcid chicks leave the nest upon reaching

a threshold wing length has been proposed previously for Atlantic Puffins *Fratercula arctica* by Barrett and Rikardsen (1992). In this species, the inter-colony variation in departure mass is as marked as in Thick-billed Murres (ca. 45%-80% of adult mass), and the variation in age at departure is even more marked (ca. 36-60 d) (Table 3). However, in all studies the mean wing length at nest departure ranged between ca. 80-85% of adult length, and the wings were still growing when chicks left the nest. These observations are consistent with the hypothesis that chicks remain in the nest until they attain a threshold wing length (Barrett and Rikardsen 1992).

Chick behaviour and the nest departure decision

In the Ydenberg model, the nest is considered safe compared to the sea. Others (e.g., Cody 1973; Sealy 1973; Birkhead 1977; Gaston 1985; Hatchwell 1991) have argued that, in the open-nesting murres, the nest is dangerous, and that this has been one of the important evolutionary forces favouring departure at a young age and in a partly-developed state. The costs and benefits associated with remaining in or departing from the nest may vary on small time scales. In Common Murres *Uria aalge*, Hatchwell (1991) showed that synchrony with neighbours was a key factor influencing the survival of chicks at the nest; the proportion of chicks remaining at the nest which died, likely taken by predators, increased dramatically late in the season. For chicks that hatch late, this would favour departing at a young age, because it would minimize the amount of

time spent at the nest with few neighbours. As well, synchronous fledging has been shown to reduce the proportion of chicks lost to predators during nest departure because predators are "swamped" (Greenwood 1964; Williams 1975; Daan and Tinbergen 1979). This should favour departure at an older age for an early-hatched chick, and at a younger age for a late-hatched chick. Consequently, the seasonal decline in age at nest departure, which has been observed frequently in murres (Gaston and Nettleship 1981; Birkhead and Nettleship 1981; Gaston et al. 1983; Birkhead and Nettleship 1987; Wanless and Harris 1988; Hatchwell 1991) probably is adaptive, as others have argued. For the Ydenberg model, the point to be made is that late-hatched chicks may depart the nest younger because it becomes increasingly dangerous to stay late in the season, as much as for the reason that the time available for growth is becoming limiting. This may be an important behavioural consideration for open-nesting species, and could explain why the seasonal decline in age at nest departure is much more prevalent among open- than burrow-nesting alcids (Table 2, Ydenberg et al. 1995). Because late-hatched chicks are likely to be growing slowly (see Chapter 4) the need to depart young so as to depart synchronously may put them at a substantial disadvantage. It would also tend to work against the hypothesis that better-developed chicks depart younger. Where the declines in 14 d mass and departure age with hatching date were not significant, the negative correlation between age at departure and 14 d wing length was significant in three of four samples.

In conclusion, Ydenberg (1989) and Ydenberg et al. (1995) have

developed a model that generates testable predictions about nest departure in alcids, but the model has weaknesses when applied to the departure decision of Thick-billed Murres, which employ the intermediate strategy. The model may have weaknesses with respect to both developmental and behavioural considerations. In terms of chick development, wing development may be a more important measure than body mass in the departure decision, and the decline in mass at nest departure with hatching date is unlikely to be adaptive, as proposed by the model. In terms of behaviour, the seasonal decline in age at nest departure may be adaptive, but may not result from the time constraint envisaged in the model: the decline may be adaptive because individual chicks adjust the age at which they depart the colony so as to minimize the danger involved in making the transition from nest to sea. While some of the weaknesses of the model in relation to nest departure in the intermediate alcids may equally apply for semi-precocial species, these results do not prejudice the validity of the Ydenberg model when applied to semi-precocial species.

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Table 1: Factors affecting the age and mass of Thick-billed Murre chicks at departure in 13 colony-years at 6 colonies in the eastern Canadian Arctic. In all cases except 14 d mass, the model predicts negative correlations. Correlations are indicated as significantly positive or negative, or not significant (0), at the $p=0.05$ level.

Colony	Year	Mass vs age at departure	Correlations with hatching date		
			14 d mass	Dep mass	Dep age
PLI	1975		0		0
	1976		0		0
	1977		0	0	-ve
Coburg/ Cape Hay	1981		-ve	-ve	-ve
Digges	1980	0	0	0	-ve
	1981	0	0	0	0
	1982	0	-ve	-ve	-ve
Hantzsch	1982	0	-ve	-ve	-ve
Akpatok	1982	0	0	0	-ve
Coats	1992	+ve	-ve	0	0
	1993	0	0	0	0
	1994	0	-ve	-ve	0
	1995	+ve	-ve	0	-ve

Published sources: Table 60, Gaston and Nettleship (1981); Table 1, Gaston et al. (1983); Figure 1, Birkhead and Nettleship (1982).

Table 2: Correlations of 14 d body mass and 14 d wing length on age at nest departure in Thick-billed Murre chicks in 12 colony-years at 5 colonies in the eastern Canadian Arctic. The correlations are indicated as significantly positive or negative, or not significant (0), at the $p=0.05$ level.

Colony	Year	Correlations with age at nest departure	
		14 d body mass	14 d wing length
PLI	1975	0	0
	1976	-ve	-ve
	1977	0	-ve
Digges	1980	0	-ve
	1981	0	-ve
	1982	0	0
Hantzsch	1982	0	0
Akpatok	1982	0	0
Coats	1992	0	0
	1993	-ve	-ve
	1994	0	-ve
	1995	0	0

Published sources: Table 60, Gaston and Nettleship 1981.
 Correlation of 14 d wing on 14 d mass: $r=+0.97$, $p<0.001$, 10 df.

Table 3: Mean masses (g), wing lengths (mm), and ages (d) at nest departure of Atlantic Puffin chicks at different colonies and in different years. Percentages are of adult size.

Colony	Year	Mean departure		
		Mass (%)	Wing length (%)	Age
Rost	1983	301.5 (68)	146.6 (>80)	44.4
	1984	208.2 (47)	?	50.9
	1985	267.5 (60)	146.0 (>80)	ca. 56
Hornoy	1980	342.0 (70)	144.8 (82)	44
Bleiksoy	1982	280.7 (63)	145.2 (84)	56
Rost	1983	330.1 (74)	146.6 (85)	44
Skomer	1973	290.1 (77)	128.5 (82)	36-40
	1974	287.5 (76)	133.5 (85)	36-40
	1975	296.6 (79)	134.3 (85)	36-40
Great Island	1968	261.4 (53)	143.6 (83)	59.7
		247.5 (50)	143.6 (83)	55.5
	1969	261.8 (53)	140.5 (81)	52.3
	1969	248.2 (50)	140.5 (81)	52.2
Funk Island	1969	351.8 (72)	141.5 (82)	?

Sources: Nettleship 1972; Ashcroft 1979; Anker Nilsson 1987; Barrett et al. 1987; Barrett and Rikardsen 1992; .