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## Growth of Nestling Thick-billed Murres (*Uria lomvia*) in Relation to Parental Experience and Hatching Date

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**ABSTRACT.**—In many avian species, reproductive success increases with parental age and experience, and declines seasonally. However, it is difficult to evaluate how parental attributes affect reproduction independently of date effects, because young, inexperienced pairs generally lay later than older, experienced pairs. We examined how parental experience and timing affected nestling growth in the Thick-billed Murre (*Uria lomvia*), an Arctic seabird that lays a single-egg clutch, by taking advantage of a natural contrast made possible by marked within-group synchrony. That is a common feature at murre colonies, and enabled us to monitor the breeding performance of experienced pairs over an extended period that overlapped with breeding by inexperienced pairs late in the season. Whereas growth of offspring raised by experienced parents was unaffected by their hatching date, offspring raised by inexperienced parents grew more slowly than those raised concurrently by experienced parents. Therefore, parental experience influenced nestling growth rates whereas timing did not, a result that accords with previous studies on this species. Absence of direct effects of timing of egg-laying on breeding success of Thick-billed Murres stands in sharp contrast to many other avian species, and seems surprising for an Arctic-nesting species often assumed to be strictly time-constrained in its breeding.

**RÉSUMÉ.**—Dans de nombreuses espèces aviennes, le succès reproducteur augmente avec l'âge et l'expérience des parents, et décline avec la saison. Néanmoins, il est difficile d'évaluer comment les attributs parentaux affectent la reproduction indépendamment des effets de date, puisque les couples jeunes, inexpérimentés pondent généralement plus tard que les couples vieux, expérimentés. Nous avons examiné comment l'expérience parentale et la date d'éclosion affectaient la croissance des oisillons chez la Marmette de Brünnich (*Uria lomvia*), un oiseau marin de l'Arctique qui ne pond qu'un seul œuf, en profitant de l'avantage offert par le contraste naturel qui existe dans la synchronie marquée au sein des

groupes. Cette caractéristique des colonies de Marmettes nous a permis de suivre le déroulement de la nidification de couples expérimentés au cours d'une longue période qui chevauchait la nidification plus tardive de couples inexpérimentés. Alors que la croissance de la progéniture élevée par des parents expérimentés n'était pas affectée par la date d'éclosion, la progéniture élevée par des parents inexpérimentés a grandi plus lentement que ceux élevés simultanément par des parents expérimentés. Par conséquent, l'expérience parentale a influencé les taux de croissance des oisillons contrairement à la date d'éclosion, un résultat qui est en accord avec les précédentes études sur cette espèce. L'absence d'effets directs du moment de la ponte sur le succès reproducteur des Marmettes de Brünnich contraste fortement avec la situation retrouvée pour de nombreuses autres espèces aviennes, et semble surprenante pour une espèce nichant dans l'Arctique souvent considéré comme strictement contrainte par le temps dans sa nidification.

In many avian species, breeding performance of individuals improves as they grow older and gain experience (Curio 1983, Forslund and Part 1995, Martin 1995). Young, inexperienced birds often lay too late to take advantage of the seasonal peak in food availability, therefore a declining food supply could explain why they typically raise few offspring (Winkler and Allen 1996). Alternatively, intrinsic characteristics of young birds rather than their tendency to lay too late might explain their poor success. For example, young birds may be unable to obtain high quality nest sites or territories (Pärt 2001), or they may lack important foraging skills gained with experience and be unable to acquire sufficient food over the course of the breeding season (Nur 1984). In addition, young birds may invest less in their offspring than older birds because, having higher residual reproductive value, they take a more cautious approach to breeding (Pugesek 1981).

As a group, marine birds are characterised by high annual adult survival rates, low annual fecundity, and deferred breeding—demographic features that are generally thought to reflect the variability and unpredictability of marine environments (Lack 1968). Given their life-history strategies and the putative nature of their environments, it is not surprising that breeding success of older, more experienced

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pairs is often found to be higher than that of younger, less experienced pairs in marine birds (e.g. Thomas 1983, Wooller et al. 1990). However, because females that differ in age and breeding experience tend to differ in timing of laying, they generally experience different environmental conditions during the various phases of breeding. Consequently, the extent to which age- or experience-related variation in breeding success is caused by attributes of the birds themselves, or by environmental conditions, often remains unclear.

One approach to this problem is to induce older, more experienced birds to breed late in the season (de Forest and Gaston 1996, Daunt et al. 1999). However, those sorts of manipulative studies have been criticized because they introduce several potential biases (reviewed in Moreno 1998). For example, such experiments generally create disparate conditions for treatment groups; typically, older, more experienced females are forced to produce additional eggs or to incubate for extended periods. As a result, negative results (no difference between age classes breeding at the same time) would be difficult or impossible to interpret. The experiments also may create situations in which breeding by young, inexperienced females and older, experienced females does not overlap temporally; typically, the experienced females are induced to reneest, so that they raise offspring later than inexperienced birds. An ideal setup to address the relative importance of parental attributes and timing in driving seasonal declines in success would be one in which older, experienced females laid over an extended period that overlapped with laying by young, inexperienced females late in the season. However, natural contrasts like that are very rare.

Thick-billed Murres (*Uria lomvia*) are colonial, cliff-nesting seabirds of Arctic waters. They employ a life-history strategy that is typical of marine birds: most young murres recruit at 5–6 years of age, after which they experience annual survival rates of 90% or more, but raise only a single offspring per season (Gaston and Hipfner 2000). The three-way correlations among age and experience, laying date, and breeding success are strong in this species (de Forest and Gaston 1996). Moreover, individual females advance their timing of laying and become increasingly likely to raise offspring to nest departure over their initial attempts at breeding (Hipfner et al. 1997, A. J. Gaston unpubl. data), indicating that the correlations involving age and experience are not simply caused by the progressive disappearance of inferior phenotypes (Curio 1983). Attempts to distinguish parental effects from timing effects on performance in this species usually have involved inducing older or earlier-laying females, or both, to relay by removing their first eggs (de Forest and Gaston 1996, Hipfner 1997). Here, we directly examine the effects of parental age and experience and hatching date on

growth of nestling Thick-billed Murres using a natural contrast made possible by within-group synchrony, a common feature at murre colonies, but one that is not well understood (Gaston et al. 1983, Wanless and Harris 1988). We compare growth of nestling murres raised by two groups of experienced birds, one of which bred about a week later than the other, but at the same time as a group of young birds with no prior experience raising chicks. This approach, based on natural contrasts, was previously employed to show that parental age and experience, rather than laying date, influences egg size in this species (Hipfner et al. 1997).

*Methods.*—The study was conducted at the Thick-billed Murre colony of 30,000 breeding pairs at Coats Island, Nunavut, Canada (62°57'N, 82°00'W), during 1994 and 1995. That colony is situated in the low-Arctic oceanographic zone (Nettleship and Evans 1985). A banding program for Thick-billed Murres has been ongoing there since 1984, as described in Gaston et al. (1994).

We measured timing of hatching using Type I methods of Birkhead and Nettleship (1980). All birds involved in this study bred either on plots Q and S, where timing is normal for this colony, or on plot JB, where laying occurs about one week later. Using those three plots, we were able to monitor activities of experienced pairs over an extended period of time. Following Hipfner et al. (1997), we defined experienced pairs (EXB) as those breeding on plots Q and S in which at least one bird had been banded as a breeder at least three years previously, and in which the second member of the pair was not known to be less experienced than that. Late-breeding experienced pairs (LATE EXB) were experienced birds, as defined above, that bred on plot JB. We defined inexperienced pairs (INEXB) as those breeding on plots Q and S that included at least one bird <7 years of age and not known to have bred previously, and in which the second member of the pair was believed to be similarly inexperienced. In the sample of inexperienced pairs, we also included a few unbanded pairs that bred at sites unoccupied prior to 1994 on a broad ledge around the observation blind at plot S (the Thick-billed Murre colony at Coats Island was expanding rapidly during this study, and birds that occupied new sites tended to be recruits [Gilchrist et al. 1994]; see below for an analysis of that potential bias). The blind protected birds breeding there from predatory Glaucous Gulls (*Larus hyperboreus*), which tend to take disproportionate numbers of eggs and chicks belonging to inexperienced pairs (Gilchrist et al. 1994). Predation, combined with high rates of accidental egg loss, largely explains why very few young Thick-billed Murre pairs manage to raise offspring (de Forest and Gaston 1996).

We measured length and maximum breadth of eggs laid by all study pairs using vernier calipers. As a measure of egg size, we used an index of volume

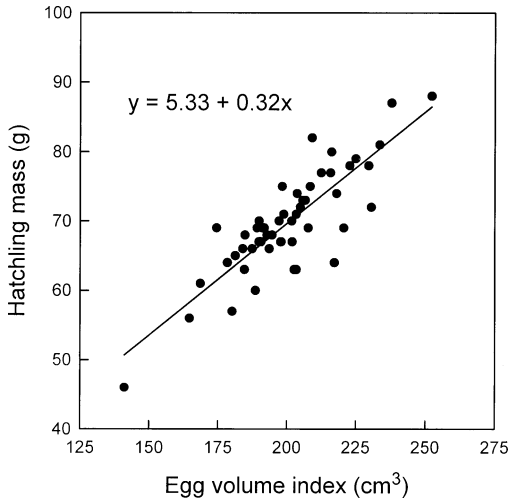


FIG. 1. The relationship between hatching mass and egg volume index in Thick-billed Murres at Coats Island. Egg volume index explained 72% of the variation in hatching mass.

(length  $\times$  breadth<sup>2</sup>) that has a strong linear relationship with fresh egg mass at our study colony ( $r = 0.97$ ; J. M. Hipfner unpubl. data). We measured chick masses once only, at 15 days of age, between 1715 and 1800 EST. Egg size, and therefore hatching mass, varies strongly with female age and experience in Thick-billed Murres (Hipfner et al. 1997). To correct for differences in starting mass, we derived estimates of hatching mass for each chick using the regression line relating hatching mass to volume index based on measurements made at Coats Island in 1994, 1995, and 1998 (Fig. 1). Growth was then defined as the difference between the chick's estimated mass at hatching and its mass at 15 days of age. Previous studies have shown that egg size has no effect on the rate at which nestling Thick-billed Murres gain mass (Hipfner and Gaston 1999, Hipfner et al. 2001).

**Results.**—Hatching dates ( $t_9 = 0.61$ ,  $P = 0.55$ ), egg-volume indices ( $t_9 = 1.02$ ,  $P = 0.34$ ), and nestling

growth to 15 days of age ( $t_9 = 0.07$ ,  $P = 0.94$ ) all were similar between pairs classified as inexperienced (INEXB) on the banded birds of known age and breeding history ( $n = 6$ ), and those classified as inexperienced because they occupied new sites ( $n = 5$ ). That suggests that the birds that bred on the newly occupied ledge were in fact recruits (Gilchrist et al. 1994). In any case, our assumption that those females were recruits produces conservative tests for differences between them and the two groups of experienced breeders.

Within treatment groups, neither egg-volume index nor growth to 15 days of age were systematically related to hatching date. Therefore, data were analysed by two-way ANOVA (rather than ANCOVA), with breeding group (EXB, LATE EXB, and INEXB), year (1994 and 1995), and the year  $\times$  group interaction term as independent variables; and egg-volume index, hatching date, and growth to 15 days of age as separate dependent variables. In none of these two-way ANOVA were the interaction terms statistically significant (all  $F < 0.48$ ,  $df = 2$  and  $42$ , all  $P > 0.25$ ). The only significant year effect was that for hatching date ( $F = 11.77$ ,  $df = 1$  and  $42$ ,  $P = 0.001$ ), which occurred four days earlier on average in 1994 than in 1995 (Table 1). However, that had no subsequent statistically detectable effects. Therefore, we adjusted for differences in hatching dates by measuring those in days from the median hatching date for EXBs in each year. In this analysis, adjusted hatching dates did not differ between years ( $F = 0.00$ ,  $df = 1$  and  $42$ ,  $P = 0.98$ ), and there was little interaction between year and group ( $F = 1.03$ ,  $df = 2$  and  $42$ ,  $P = 0.37$ ). In contrast, egg volume indices, hatching dates, and growth to 15 days all differed significantly among groups (Table 1).

Effects of hatching date and parental age and experience on nestling growth are shown in Figure 2, with data pooled across the two years. Based on Tukey's tests (at the  $P = 0.05$  significance level), breeding group EXB hatched earlier than LATE EXB or INEXB but the latter two groups did not differ in hatching dates. However, growth to 15 days of age was similar in breeding group EXB and LATE EXB,

TABLE 1. Egg size and growth parameters for the three treatment groups (mean  $\pm$  SE). Group effects are from two-way ANOVA.

Parameter	Year	Group			Group effects	
		EXB (n)	LATE EXB (n)	INEXB (n)	F <sup>a</sup>	P
Egg volume index (cm <sup>3</sup> )	1994	197.3 $\pm$ 4.8 (5)	213.3 $\pm$ 2.7 (12)	194.1 $\pm$ 2.9 (6)	5.04	0.011
	1995	209.1 $\pm$ 6.5 (9)	209.8 $\pm$ 3.8 (11)	197.3 $\pm$ 6.6 (5)		
Hatching date (1 June = 1)	1994	52.8 $\pm$ 1.7 (5)	58.4 $\pm$ 0.6 (12)	58.5 $\pm$ 2.2 (6)	9.03	0.001
	1995	57.2 $\pm$ 1.8 (9)	60.4 $\pm$ 0.9 (11)	64.2 $\pm$ 1.5 (5)		
Growth to 15 days (g)	1994	154.6 $\pm$ 15.7 (5)	149.2 $\pm$ 6.4 (12)	130.4 $\pm$ 11.7 (6)	5.78	0.006
	1995	140.8 $\pm$ 7.3 (9)	147.6 $\pm$ 6.2 (11)	113.6 $\pm$ 9.3 (5)		

<sup>a</sup>  $df = 2$  and  $42$ .

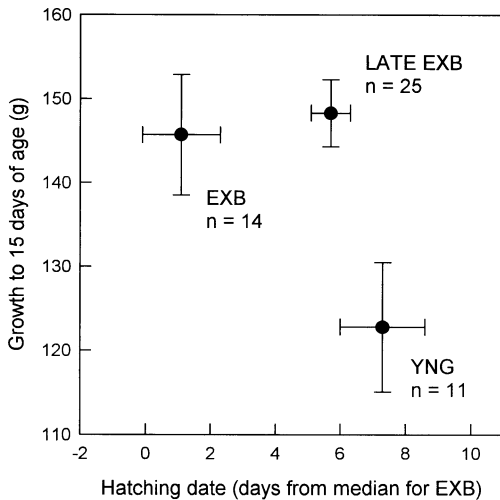


FIG. 2. Growth to 15 days of age in relation to hatching dates for nestlings (means  $\pm$  SE) raised by experienced parents (EXB), naturally late-breeding experienced parents (LATE EXB), and inexperienced parents (INEXB).

but lower for nestlings raised by INEXB parents. In other words, when we controlled for effects of age and experience, timing of chick-rearing had little effect on nestling growth (compare breeding group EXB to LATE EXB). However, when we controlled for timing effects, parental age and experience had strong effects on growth (compare breeding group LATE EXB to INEXB).

**Discussion.**—Our results demonstrate that age and experience affected growth rates of nestling Thick-billed Murres, but that timing of chick-rearing did not. Compared to other measures of breeding performance, growth rate is probably a more sensitive indicator of how much food nestling murres receive, because they show considerable plasticity in growth rates in response to feeding conditions without showing effects on survival (Gaston et al. 1983, Hipfner et al. 2001). Consequently, although we did not measure provisioning rates, our results strongly suggest that young, inexperienced parents brought less food to their nestlings than did experienced parents. Because we only compared birds with no prior experience to birds with at least three years experience, we do not know how many attempts it might take before young birds begin to raise chicks that grow at the normal rate. Moreover, it remains an open question as to whether the young birds were showing reproductive restraint (Pugesek 1981), or whether they were constrained by their physiological state (in some species, young birds may carry smaller endogenous reserves; Alisauskas and Ankney 1987, Weimerskirch 1992), or by their lack of experience (Nur 1984).

Few studies on other species of marine birds have examined relative importance of timing of hatching and parental age and experience on offspring growth. Using multivariate statistics, Nisbet et al. (1998) showed that growth of Roseate Tern (*Sterna dougalli*) chicks was unaffected by parental age when hatching date and egg mass were controlled, a result that differs from ours for Thick-billed Murres. Conversely, as in Thick-billed Murres, experimental manipulations in the Shag (*Phalacrocorax aristotelis*) showed that parental age, but not timing, influenced nestling growth (Daunt et al. 1999). Nestling Wandering Albatrosses (*Diomedea exulans*) raised by inexperienced parents grew more slowly than those raised concurrently by experienced parents, but the effect was short-lived in that species, which has an extremely long nestling period. Nevertheless, there was no systematic relationship between female experience and timing of laying (Lequette and Weimerskirch 1988). In sum, it appears that both timing of hatching and parental age and experience may affect nestling growth in marine birds, but that their relative importance varies among species. Future research might attempt to explain the causes of such interspecific differences.

As in many other species, the biology of Thick-billed Murres is characterized by seasonal declines in egg size, rates of relaying following egg loss, offspring growth rates, and breeding success (Birkhead and Nettleship 1981, Gaston and Nettleship 1981, Gaston et al. 1983). However, experiments have shown that seasonal declines in egg size (Hipfner et al. 1997) and relaying rates (Hipfner et al. 1999) are driven by variation in parental attributes, and not by timing. Moreover, experiments have shown that hatching and nestling success (de Forest and Gaston 1996, Hipfner et al. 1999), nestling growth rates (Hipfner 1997), and survival between nest departure and recruitment age (Hipfner 2001) are similar for offspring that hatch from first and replacement eggs two to three weeks apart but that are raised by parents that lay their first eggs early in the season. For some of those parameters, similar patterns have been reported for Common Murres (*Uria aalge*) breeding at both boreal (Hatchwell 1991) and Arctic (Murphy and Schauer 1994) colonies. Although it may not be surprising that breeding performance improves with age and experience in Thick-billed Murres, it is surprising that timing has so little direct effect, especially given that this is a species that breeds in the Arctic. Seasonal declines in offspring value, driven by the putative seasonal declines in food availability, have been central to theoretical models of breeding by Thick-billed Murres and other Arctic seabirds (Birkhead and Nettleship 1982, Ydenberg 1989). However, the seasonal declines in food availability, which have so strongly shaped the breeding ecology of many birds, seem to be far less important for Thick-billed Murres breeding at low-Arctic colonies.

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