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Fitness-related Consequences of Relaying in an Arctic Seabird: Survival of Offspring to Recruitment Age

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ABSTRACT.—Seasonal declines in rates of renesting following clutch loss are common features of avian breeding, and are generally thought to reflect underlying seasonal declines in food availability that lower survival prospects for late-season offspring. However, in Thick-billed Murres (*Uria lomvia*), long-lived Arctic seabirds that lays a single-egg clutch, previous research has shown that early laying females will continue to relay until late in the laying period. Moreover, hatching success is similar between first and replacement attempts, as are nestling growth and survival, when parental quality is controlled. I compared survival between departure from the breeding site and recruitment age (4–5 years) for Thick-billed Murres that hatched from first and replacement eggs, but that were raised by parents that laid their first eggs early in the season. Replacement-egg offspring hatched and departed the colony about three weeks later than did first-egg offspring, but despite that, they were no less likely to survive to recruitment age. That result indicates that the potential fitness payoff from a replacement egg is similar to that from a first egg for the more capable members of the population. I suggest that an adequate and predictable late-season food supply ultimately underlies the considerable relaying capacity exhibited by Thick-billed Murres.

Replacement clutches can make important contributions to an individual's lifetime reproductive success, especially in avian species or populations prone to clutch loss (Martin et al. 1989, Keegan and Crawford 1993). However, offspring from replacement clutches tend to experience low rates of survival to recruitment (Martin and Hannon 1987, Verboven and Visser 1998), often because late-fledged young are socially subordinate and fare poorly in competition with those that fledge early (Nilsson and Smith 1988, Spear and Nur 1994). From an evolutionary standpoint, uncertain prospects for late-season offspring, combined with adverse effects of late breed-

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ing on adult survival, might largely explain why the proportion of females that renest shows strong seasonal declines in many species of birds (Feare 1976, Arnold 1993).

Thick-billed Murres (*Uria lomvia*) are highly colonial, cliff-nesting seabirds of Arctic waters. They lay a single-egg clutch, and feed the chick at the breeding site for 15–30 days, at which time the chick departs to sea at up to 30% of adult mass, and covered in a transitional mesoptile plumage (Sealy [1973] called this the "intermediate" developmental strategy; it is unique to the genera *Uria* and *Alca* of the family Alcidae). After leaving the breeding site, young murres are tended at sea by their male parent for a month or more before they reach independence, they return to the natal colony at 2–3 years of age, and all but a very few recruit at ≥4 years of age (Gaston et al. 1994).

As in many other birds, the proportion of Thick-billed Murres that relay after losing their egg declines sharply with date of loss (Gaston and Nettleship 1981, Birkhead and Nettleship 1987). However, in experiments carried out at two low-Arctic colonies, early laying females that had their eggs removed continued to relay until late in the laying period (Hipfner et al. 1999); early laying females are typically older, more experienced members of the population (Hipfner et al. 1997). Empirical studies (Birkhead and Nettleship 1981, Gaston and Nettleship 1981) and theoretical models (Birkhead and Nettleship 1982, Ydenberg 1989) of breeding by Arctic seabirds often assume that late-season offspring are disadvantaged due to a seasonal reduction in food supply. However, in Thick-billed Murres, replacement eggs are as likely to hatch as are first eggs, and offspring from replacement eggs grow as well and are as likely to survive the nestling period as are those from first eggs, if raised by equally capable parents (de Forest and Gaston 1996, Hipfner 1997, Hipfner et al. 1999). In this paper, I compare survival between departure from the breeding site and recruitment age (4–5 years) for Thick-billed Murres from first and replacement eggs that were raised by parents that laid their first eggs early in the season.

Methods.—The study was conducted at the Thick-billed Murre colony of 30,000 pairs at Coats Island, Nunavut, Canada (62°57′N, 82°00′W). Chicks were measured and banded in 1994 and 1995 (Hipfner 1997), and resighted as adults in 1999. A few were first resighted in 1996–1998.

In both years, one control and one experimental plot were selected in each of two areas of the colony prior to the start of laying (areas Z and LF, see Gaston et al. 1994). Those areas were chosen because they are situated close to the top of the colony, and are therefore accessible. I did not enter the control plots until just prior to start of hatching, at which time I mapped and numbered 50 breeding sites at which an egg was present on each of the two plots. All 100 eggs were marked with their site number in permanent ink. Those eggs were subsequently checked at two or occasionally three day intervals. Upon hatching, each chick was marked with a binary code of nail clipping, and banded within one week with a year-specific color band, and a triangular metal band with the number engraved upright on both sides, making it easy to read (Gaston et al. 1994). Hatching date was taken to be the date midway between when an egg was last present at the site and a chick was first present. On all visits, chicks were weighed (±1 g, with a 300 g spring balance), and their wing lengths measured (±1 mm, with the wing held flat and straight along a ruler). Control chicks were considered to be chicks that hatched by 28 July, based on an egg-removal date of 25 June (see below) plus a 33 day incubation period (Hipfner et al. 2001).

To establish experimental groups in the two years, I mapped and numbered 25 breeding sites on each of the two experimental plots, and then measured and removed the 50 eggs. That was done on 25 and 26 June in both years (near median laying date). Polaroid photographs were used to verify that the egg later found at the same site had been laid by the same female, because background color and pattern of markings are repeated on eggs laid by the same female. Experimental plots were rechecked 45 days later, based on periods of 13 days for egg replacement (Hipfner et al. 1999), and 32 days for incubation (Hipfner et al. 2001). At that time, replacement eggs were measured and growth of chicks that hatched from them monitored using the protocol described above for control chicks.

Chicks that survived ≥15 days at the breeding site were considered to have departed the colony (Gaston and Nettleship 1981), and so were used in analysis of postdeparture survival. In 1994, 15 experimental chicks were still at their breeding sites when observations ended in late August (see Hipfner 1997). Because all of those chicks were at least 16 days of age at last check, I assumed that they had departed the colony after I did.

In 1999, when birds from those two cohorts were 4 and 5 years old, watches were carried out at Z and LF from prelaying to early hatching periods to record band numbers. Four and 5 year old Thick-billed Murres are present at the colony throughout the breeding season, irrespective of whether they bred in that year (Noble 1990). Moreover, by that age they tend to be strongly attached to the area where they were raised (U. Steiner and A. J. Gaston unpubl. data); it appears that few birds recruit to other colonies (Gaston et al. 1994, Kampp and Falk 1998). In sum, it seems likely that a large proportion of birds still alive would have been resighted.

Results.—In both 1994 and 1995, masses at departure from the breeding site differed little between control (first-egg) and experimental (replacement-egg) chicks, even though experimental chicks

TABLE 1.   Departure dates (medians) and masses (mean ±1 SD) of control and experimental Thick-billed Murre chicks in 1994 and 1995, and percentages of those birds resighted in 1999.

Parameter	1994 (n)		1995 (n)	
	Control (45)	Experimental (26)	Control (49)	Experimental (18)
Median departure date	13 August	31 August[a]	14 August	1 September
Mean departure mass (g)	229.3 ± 22.5	228.4 ± 19.9[b]	215.4 ± 23.9	219.9 ± 25.7
Percentage resighted	21	27	17	22

[a] A minimum estimate, see text for explanation.

[b] For the 11 chicks that had departed when observations ceased. The 15 chicks that remained averaged 217.1 ± 19.0 g in mass.

hatched almost three weeks later (Table 1; see also Hipfner 1997). Logistic regression showed that probability that one of those young birds was resighted in 1999 differed very little between treatment groups (Wald $\chi^2 = 0.16$, df = 1, P = 0.69) or years (Wald $\chi^2 < 0.01$, df = 1, P = 0.97), with little interaction between those factors (Wald $\chi^2 = 0.03$, df = 1, P = 0.87; see Table 1). Overall, 19% (18/94) of control chicks and 25% (11/44) of experimental chicks were resighted as adults in 1999.

Breeding was confirmed for three of 29 resighted birds: one control bird from each of the 1994 and 1995 cohorts, and one experimental bird from the 1994 cohort (in fact, that latter bird also bred in 1998). Others were clearly holding breeding sites, and it is almost certain that some of them bred (female Thick-billed Murres typically recruit at 5 years of age, males at 6 years; Gaston and Hipfner [2000]). Other breeding attempts could have been missed because young birds tend to lose their eggs soon after laying (de Forest and Gaston 1996), and plots were not observed daily.

Discussion.—Thick-billed Murre chicks that hatched from replacement eggs were as likely to survive between departure from the breeding site and recruitment age (4–5 years) as were chicks from first eggs if raised by parents with similar original laying dates. Previous studies also found that hatching success of first and replacement attempts was similar, as were nestling growth and survival, when parental quality was controlled (de Forest and Gaston 1996, Hipfner 1997, Hipfner et al. 1999). Consequently, the considerable relaying capacity exhibited by early laying females (Hipfner et al. 1999), a capacity that increases with age and experience early in breeding life (de Forest and Gaston 1996), may be largely explained by the fact that the potential fitness payoff from a replacement egg is similar to that from a first egg for more capable members of Thick-billed Murre populations. There could also be indirect fitness benefits involved, if females that relay are more likely to retain their sites or mates for breeding in the future (Hipfner et al. 1999). In species that employ high-survival, low-fecundity life-history strategies (like murres and most other marine birds), individuals are expected to invest cautiously in any single breeding episode, because any offspring they raise in one season contribute little to

their potential lifetime reproductive success (Clutton-Brock 1988). Therefore, regardless of potential fitness benefits, one would expect that fitness costs incurred by Thick-billed Murres through relaying and raising young late in the season would be small. That remains to be tested.

In many other species of birds, offspring from replacement eggs are unlikely to survive to recruitment (Martin and Hannon 1987, Svensson 1997). Late-fledged young may fare poorly in competition for limited and declining food supplies, and that could be an important factor causing them to have low postfledging survival (Spear and Nur 1994). Because neither growth rates nor survival at the breeding site differed between Thick-billed Murres from first and replacement eggs (de Forest and Gaston 1996, Hipfner 1997, Hipfner et al. 1999), it appears that, at the low-Arctic colonies involved, food availability did not decline late in the season to an extent that chicks raised by capable parents were affected. The fact that chicks from first and replacement eggs were equally likely to survive to recruitment age suggests that feeding conditions also remained adequate after departure. Adult–chick pairs disperse widely at sea after they leave the colony (Gaston 1982), so it is unlikely that intraspecific competition would be intense in the immediate postdeparture period, probably the period of highest mortality (Gaston 1998).

Little is known about the lives of young murres between departure from and first return to the colony, and of the role that mortality during the various phases of that period has played in evolution of the intermediate developmental strategy (Ydenberg 1998). The three extant species of Alcidae that employ that strategy (Thick-billed and Common [*Uria aalge*] murres, and Razorbills [*Alca torda*]) probably evolved from a semiprecocial ancestor, in which offspring were raised to independence at the breeding site (Gaston and Jones 1998). After male murres and Razorbills take their small, flightless chicks to sea, they themselves undergo a prebasic molt, becoming flightless. As a result, the speed with which those adult-chick pairs can search for food is limited to the swimming speed of the chick. If the food supply was declining and hard to find during the period after departure from the colony, as has been purported, evolution of

such a strategy would seem most unlikely (Gaston 1992). At sea, the range of suitable diet items also may be increased over that brought to nestlings; adult murres carrying food back to offspring at the breeding site deliver larger items than they themselves feed on (Gaston and Nettleship 1981).

To summarize, I found that survival between departure from the breeding site and recruitment age (4–5 years) was similar for Thick-billed Murres that hatched from first and replacement eggs. Therefore, the considerable relaying capacity exhibited by early laying females may be largely explained by the fact that potential fitness payoff from a replacement egg is similar to that from a first egg for more capable birds. A predictable and adequate food supply during the period of development at sea may ultimately underlie that capacity.

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Protein Requirements of a Specialized Frugivore, Pesquet's Parrot (*Psittrichas fulgidus*)

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ABSTRACT.—For those few bird species that are exclusively frugivorous, the low protein content of fruits is likely a major nutritional constraint. Physiological mechanisms that allow strict frugivory remain enigmatic, but reduced protein requirements may suffice. We investigated protein requirements of Pesquet's Parrot (*Psittrichas fulgidus*), a highly specialized, obligate frugivore. Three isocaloric, fruit-based diets of varying protein content (6.1, 3.3, and 2.6% dry mass crude protein) were used in feeding trials lasting three to five days per diet. A minimum dietary protein requirement of 3.2% dry mass was estimated from balance trials. Endogenous nitrogen losses were 0.05 gN kg$^{-0.75}$ day^{-1} and nitrogen equilibrium occurred at 0.32 gN kg$^{-0.75}$ day^{-1}. Those values are extremely low compared to those of granivorous and omnivorous bird species, but higher than those of nectarivorous species. In terms of nitrogen losses and requirements, Pesquet's Parrot most closely parallels the highly frugivorous Cedar Waxwing (*Bombycilla cedrorum*). Thus, reduced protein requirements appear to play an important physiological role in ability of highly frugivorous birds to subsist on fruit diets.

Although fruits provide a rich source of easily assimilated carbohydrates, they are notoriously low in protein (Morton 1973, White 1974, Berthold 1976, Mattson 1980, Snow 1981, Thomas 1984, Jordano 1992). Furthermore, nonprotein nitrogen (N) in the form of free amino acids and secondary metabolites is common in fruit (Herrera 1982, Cipollini and Levey 1997) and is not discriminated from protein N in traditional Kjeldahl analysis (Izhaki 1993). Thus, true protein content of fruit is likely even lower than most published estimates.

Given the low protein content of fruits, it is not surprising that very few species of birds can subsist on a diet of exclusively fruits (Berthold 1976, Snow 1981, Holthuijzen and Adkisson 1984, Bairlein 1987, Izhaki and Safriel 1989). Although the physiological mechanisms that allow some birds to be strictly frugivorous are not fully understood, proposed mechanisms include high ingestion rates (Sorensen 1984, Bairlein 1987, Izhaki and Safriel 1989, Karasov and Levey 1990, Levey and Grajal 1991, Levey and Duke 1992, Levey and Karasov 1992), short gut retention times (Herrera 1984, Martinez del Rio et al. 1989, Levey and Grajal 1991, Levey and Duke 1992, Levey and Karasov 1994), and low protein requirements (Witmer 1998, Witmer and Van Soest 1998). We investigated protein requirements of an obligate frugivorous bird, Pesquet's Parrot (*Psittrichas fulgidus*). In particular, we examined two related physiological

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