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THE FLEDGING OF COMMON AND THICK-BILLED MURRES ON MIDDLETON ISLAND, ALASKA

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Three species of alcids, Common and Thick-billed murres (*Uria aalge* and *U. lomvia*) and the Razorbill (*Alca torda*), have post-hatching developmental patterns intermediate to precocial and semi-precocial modes (Sealy 1973). The young leave their cliff nest sites at about one quarter of adult weight and complete their growth at sea. At departure, an event here loosely referred to as "fledging," neither primary nor secondary flight feathers are grown, but well-developed wing coverts enable limited, descending flight.

The adaptive significance of this pattern may be that leading the young to distant feeding areas is more efficient than lengthy foraging flights by adults once the chicks' energetic requirements exceed some critical level (Sealy 1973, Birkhead 1977). The risk to predation is probably greater in exposed nest sites than at sea, contributing further to the selective advantage of early fledging (Cody 1971, Birkhead 1977). Given these constraints, however, larger chicks would be expected to better survive the rigors of fledging, increased activity at sea, and the vagaries of weather.

Hedgren (1981) analyzed 278 recoveries of Common Murres banded as fledglings and found no significant relationship between fledging weight and subsequent survival. This result is paradoxical in view of a strong expectation to the contrary and evidence that such an effect occurs in other species of birds (Perrins 1965, Perrins et al. 1973, O'Conner 1976). Hedgren suggested the nestling period of murres, averaging about 3 weeks, is determined not by a threshold in body size, but by the relatively constant time required to complete feather growth. Birkhead (1977) also emphasized the need for chicks to attain a critical weight : wing-area ratio prior to fledging. Clearly, however, body weight and feather development are not mutually exclusive factors affecting fledgling survival.

Murres breeding on Middleton Island, Alaska use nest sites located so far from the water's edge that direct flights to the sea by the fledglings are impossible. In 1978, I captured nearly 400 fledglings as they made their way overland to the sea. In this paper I analyze mensural data for these birds with a view to testing the above hypotheses regarding optimal fledging condition. My data also document population changes and breeding phenology of murres in a region for which there is little published information.

STUDY AREA AND METHODS

Middleton Island is in the north-central Gulf of Alaska about 115 km from the mainland and 18 km from the edge of the continental shelf

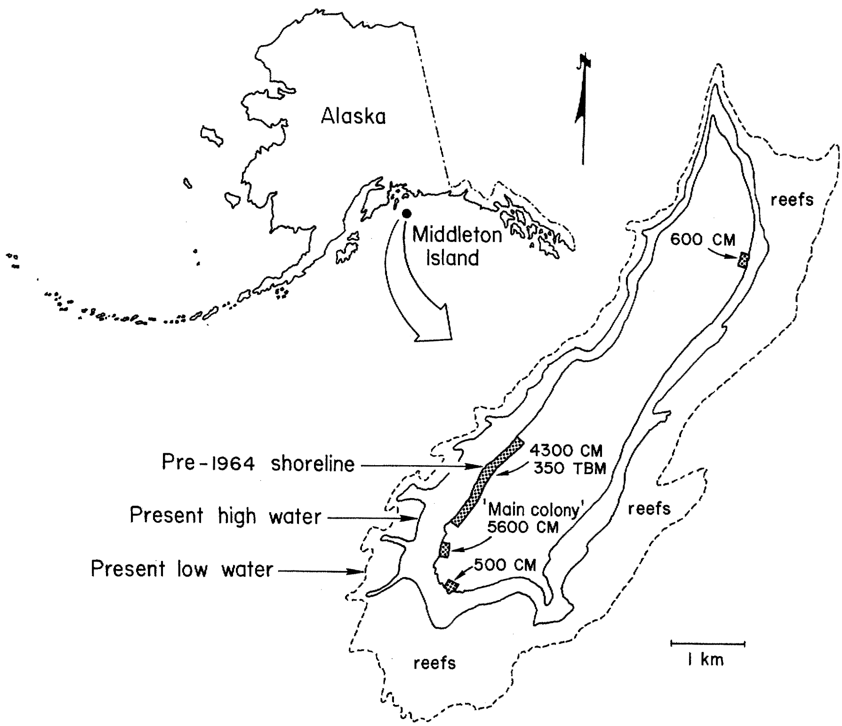

FIGURE 1. Map of Middleton Island showing changes in the shoreline and the distribution of murres in 1978. CM, Common Murres; TBM, Thick-billed Murres.

(Fig. 1). The island is generally flat, and reaches a maximum elevation of about 40 m on its southwest side. The Alaskan earthquake of 1964 raised the island about 4.5 m, exposing large areas of previously submerged land. On the east, south, and southwest the distance between the sea cliffs and the present high water mark averages about 400 m. The intertidal zone extends another 200 to 1200 m seaward.

Most murres nested near the top of a steep cliff surrounding the southern third of the island. Nesting ledges did not exceed about 35 m in height. The largest group of Common Murres, designated the "main colony," nested on a broad ledge only 10–15 m high but 500 m from the high water level. Flats below the cliffs consisted of marshy ground with a scattering of large boulders and numerous shallow ponds of fresh or brackish water.

A census of murres was carried out on 26 July when all birds were counted with a spotting scope from the flats. The proportions of the two species in the population were estimated from the ratio of Common to Thick-billed murres in the population of chicks leaving the cliffs in August.

Chicks frequently did not complete the journey to sea on the same evening they left the cliffs, but spent one or more of the following days accompanied by adults in the ponds. Chicks were captured by hand during daily searches of the ponds between 26 July and 16 August. Wing chord was measured to the nearest mm with a stopped ruler; weight was determined to within 1 g with a 300 g Pesola scale. All chicks were marked with U.S. Fish and Wildlife Service metal leg bands at first capture, which permitted me to separate recaptured chicks from those newly arrived in the ponds each day. Every chick present in the ponds was captured each day, and the measurement of weight was repeated on recaptured chicks.

RESULTS AND DISCUSSION

Census and population change.—A total of 6803 murres was counted in the census. This figure agrees with independent counts by Gould and Zabloudil, and Gould and Nysewander in 1981 and 1982, respectively (P. J. Gould, pers. comm.). Southern et al. (1965) showed that the proportion of murres present on ledges at any time during incubation and brooding is about 60% of the total population (including both breeders and nonbreeding nest-site holders). Extensive counts at the Semidi Islands, Alaska (Hatch, unpubl. data) substantiate this value as a conservative adjustment for nest-site attendance. Thus, the total population on Middleton Island in 1978 was about 11,000 birds (Fig. 1).

Thick-billed Murres occurred only north of the main colony on the west side of the island. Here, they made up about 7.4% of the population, as estimated from the number of Thick-billed Murres among 311 chicks captured in the area during fledging. I assume the two species had similar nesting success. The ratio agrees with my general impression from observations of birds on the ledges. Thick-billed Murres thus made up only 3% of the census total, or about 350 birds.

Rausch (1958) visited Middleton Island in 1956 and found a population of only about 400 murres, mostly Thick-billed Murres. Thus, although the population of Thick-bills has changed little, Common Murres increased greatly between 1956 and 1978. The increase is all the more remarkable in view of physical changes brought about by the 1964 earthquake which might have been expected to discourage murres from nesting on Middleton Island. The change in numbers of murres was paralleled by large increases in the populations of Black-legged Kittiwakes (*Rissa tridactyla*) and Pelagic Cormorants (*Phalacrocorax pelagicus*) (Hatch, unpubl. data).

Timing of fledging.—The distribution of fledging between 26 July and 16 August was approximately normal, except for a conspicuous decline in the number of chicks leaving the cliffs on 31 July and 1 August (Fig. 2). The lull occurred during an unusual spell of foggy weather, although such conditions might have been expected to have the opposite effect. Peak numbers of birds left the cliffs as soon as the fog lifted.

A few chicks probably fledged before daily observations were begun.

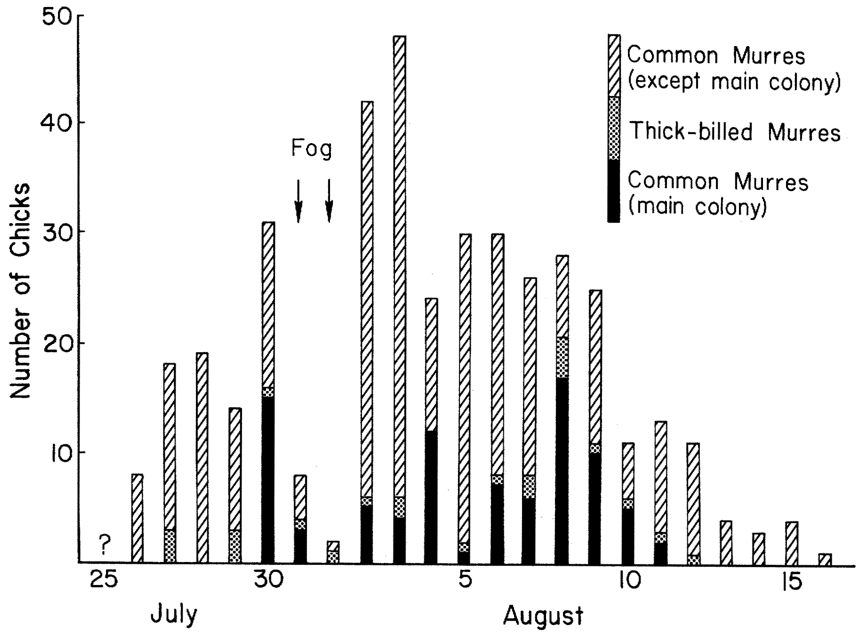

FIGURE 2. Distribution of fledging dates of murres on Middleton Island in 1978.

On 27 May several hundred murres were flushed from ledges and only 3 eggs were present. This date probably marked the commencement of egg-laying. If an incubation period of 33 days and a nestling period of 21 days are assumed (Tuck 1960, Hedgren and Linnman 1979), these young should have fledged about 20 July. Back-calculating the latest fledging dates, I estimate the last eggs were laid about 23 June.

There was no discernible difference between species in breeding phenology. The fledging of Common Murres in the main colony, however, seemed to be more synchronous than elsewhere on the island. There was also evidence that egg-laying may have occurred later within the main colony (see below).

Turnover and survival in ponds.—Lacking information on rates of breeding success or the total production of chicks, I cannot estimate the proportion of fledglings that remained in the ponds long enough to be banded. There is little question, however, that the majority of fledglings of both species reached the sea within hours of leaving the cliff and were thereby excluded from this study.

Thick-billed Murres showed a greater tendency to linger in the ponds than did Common Murres. More than 70% of Thick-billed Murres that remained in the ponds long enough to be banded stayed at least another full day; 23% still remained after 3 days (Fig. 3). By comparison, only 24% of Common Murres were recaptured one or more times.

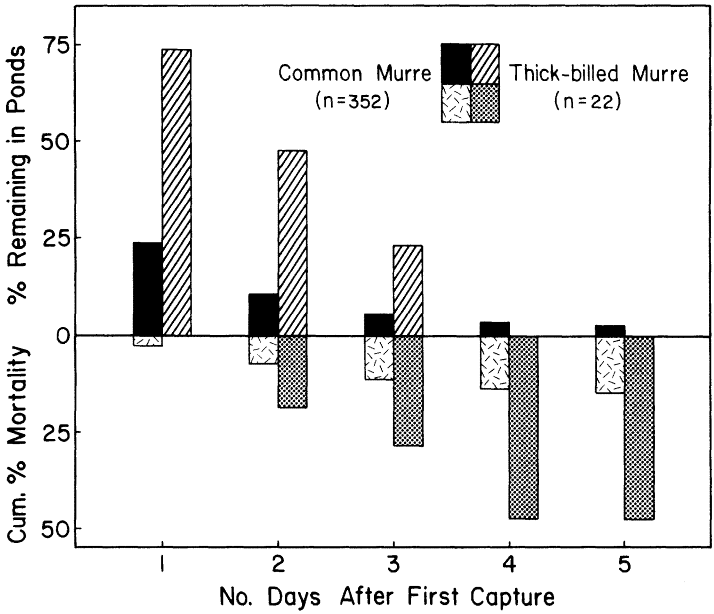

FIGURE 3. Length of residency and mortality of chicks in ponds after fledging.

Most chicks received no food while they stayed in the ponds. They lost weight at a mean rate of 17.7 g/day (samples for both species combined) and faced an increased probability of death each day. Of 374 chicks banded on or before 12 August, 18% were later recovered dead. In contrast, Thick-billed Murres had cumulative mortality of nearly 50% (Fig. 3). These data suggest Thick-billed Murres are behaviorally less capable of dealing with the unusual circumstances that have existed on Middleton Island since the earthquake. Possibly this is a contributing factor in their failure to increase their numbers.

A few chicks were fed while in the ponds and survived a week or more in fresh water, either maintaining weight or showing limited growth. An adult was observed delivering a meal to one such chick. This seemed to be a learned behavioral pattern acquired by only a few adults. At the last visit on 16 August, several chicks that had spent more than a week in one pond were alive and healthy.

Predation by gulls is frequently cited as a major cause of mortality among fledgling murres (Tuck 1960, Greenwood 1964, Williams 1975). Williams (1975) found this risk was substantially increased when access to the sea was hampered by difficult terrain. Some 1400 Glaucous-winged Gulls (*Larus glaucescens*) inhabited Middleton Island in 1978, yet these birds were notably indifferent toward murre chicks under all circumstances observed. Only two murre chick carcasses were encountered that appeared to have been partially eaten by gulls, and these may have

TABLE 1. Measurements of Common and Thick-billed murres at fledging on Middleton Island, Alaska.

Species and area		Weight (g)	Wing (mm)
Common Murre	$\bar{x}$	207.8	74.3
(except main colony)	SD	27.62	8.05
(n = 288)	Range	128–310	54–104
Common Murre	$\bar{x}$	190.7	68.4
(main colony)	SD	19.56	6.86
(n = 86)	Range	141–231	50–91
All Common Murres	$\bar{x}$	203.8	72.9
(n = 374)	SD	26.51	8.17
	Range	128–310	54–104
Thick-billed Murre	$\bar{x}$	200.7	80.5
(n = 23)	SD	35.56	7.84
	Range	125–292	62–101

been scavenged after death from other causes. Observed mortality of murre chicks seemed to result from the depletion of energy reserves and exposure. Chicks were often found in a lethargic and probably hypothermic condition shortly before they died.

To test the possibility that fledging weight affected survival in the ponds, I calculated a regression of initial weight (X) and the number of days survived (Y) for 52 Common Murres that died in the ponds: $Y = -1.89 + .022(X)$. This relationship was highly significant ($P < .001$; $r = .54$). The regression coefficient of 0.022 indicates that chicks survived without food about 1 additional day for each 50 g increment in fledging weight. With a sample of only 9 chicks, the relationship for Thick-billed Murres, although similar, was nonsignificant.

Johnson and West (1975) found that resistance to hypothermia in murres is achieved mainly by a high capacity for metabolic heat production. Consequently, murres have a large daily energy requirement. Although atypical, the situation on Middleton Island simulates what may occur when murres encounter untimely storms and poor foraging conditions soon after fledging. I believe my data demonstrate a real advantage of increased fledging weight which, however, may only rarely be of critical importance.

Fledging condition: means and variability.—Upon leaving the cliffs, 374 Common Murres ranged in weight from 128 to 310 g ($\bar{x}$ = 204 g), while 23 Thick-billed Murres ranged from 125 to 292 g ($\bar{x}$ = 201 g; Table 1). These values are at the low end of the range of means determined at various locations in the North Pacific and North Atlantic Oceans (cf. data summarized by Tuck 1960 and Hedgren and Linnman 1979). Possibly the chicks obtained in the ponds were a relatively undernourished group. I think this is unlikely because all the chicks appeared healthy

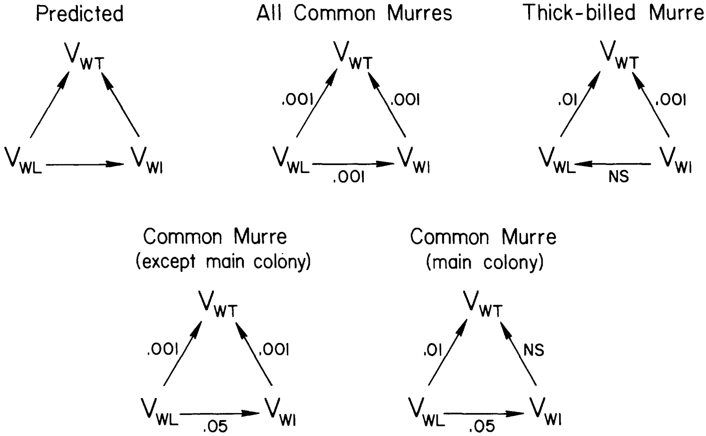

FIGURE 4. Relative variability in size characteristics among murres at fledging. V_{WT}, V_{WI}, and V_{WL} are coefficients of variation for weight, wing-length, and wing-loading, respectively. Arrows point from lower to higher values. Numbers are the probability levels indicated by one-tailed tests. Sample sizes as in Table 1.

and vigorous when they were first captured. Younger chicks, however, may well have been more inclined to stay in the ponds.

The species did not differ significantly in fledging weight, but Thick-billed Murres had longer wings ($P < .001$, two-tailed t-test). Adult Thick-billed Murres studied at Cape Thompson, Alaska averaged significantly lighter and had longer wings than Common Murres (Swartz 1966).

Hedgren (1979, also see Hedgren and Linnman 1979) found a marked seasonal decline in the fledging weight of Common Murres, but this was not observed on Middleton Island. There were no significant differences among chicks fledged during early (26 July–1 August, n = 73), middle (2–8 August, n = 165), or late (9–16 August, n = 51) portions of the season. However, Common Murres from the main colony averaged smaller in both weight and wing length than fledglings captured to the north ($P < .001$ in both instances, t-tests). The smaller chicks either grew more slowly or fledged at an earlier age. If the latter was true it would indicate a premium on fledging during a particular interval, although Hedgren (1981) was unable to show such an effect by an analysis of band recoveries. Possibly the age and breeding experience of adults differed between areas, resulting in later breeding times and/or poor quality parental care. Such spatial variability in breeding performance associated with rapid expansion of the colony was indicated in a study of the Black-legged Kittiwake on Middleton Island (Hatch, unpubl. data).

The initial weights of Common Murres that died in the ponds averaged significantly lower than those that eventually made it to sea (199 vs. 210 g, $P < .005$, one-tailed t-test). This result reinforces my conclusion from the regression of fledging weight and longevity for chicks that died: fledging weight affects chances for survival.

An alternative, or additional, factor that may determine the length of the nestling period in murres is the development of an adequate capability for flight. On this hypothesis I would expect wing length to show less variability at fledging than weight. Moreover, if wing-loading is the prime consideration, the ratio of weight to wing length (an index to wing-loading) should be less variable than either character alone. An appropriate test of these predictions is a comparison of coefficients of variation (Sokal and Braumann 1980). I verified the absence of skewness in the distributions of all three characters first, because significance tests for coefficients of variation are highly sensitive to skewness in the underlying data (Sokal and Braumann, loc. cit.). Predicted and observed results of these analyses are summarized by species and area in Fig. 4. With two minor, nonsignificant exceptions, the expected relationships were confirmed: the nestling period of murres would seem to be under selection pressure with respect to both fledging weight and the timing of feather development.

SUMMARY

A 16-fold increase in the population of murres on Middleton Island occurred in 22 years or fewer. The breeding schedules of Common and Thick-billed murres were similar in 1978, with young of both species leaving the cliffs between about 20 July and 16 August. Chicks frequently spent one or more days in fresh water ponds after fledging. Considerable mortality occurred in this situation, especially among Thick-billed Murres. That fledging weight may affect the survival of newly-fledged chicks was indicated two ways: (1) fledging weight was higher among chicks that made it to sea than in chicks that remained in the ponds and died; (2) the number of days survived by birds of the latter group was positively correlated with their fledging weights. The nestling period seems to be further governed by feather development relative to body weight, since wing length and wing-loading are more constant among fledglings than weight.

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