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POPULATION PARAMETERS OF THICK-BILLED MURRES AT COATS ISLAND, NORTHWEST TERRITORIES, CANADA[1]

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Abstract. About 100 adult and 2,000 nestling Thick-billed Murres were banded at Coats Island annually since 1984. Intensive efforts were made in 1990–1993 to estimate the reproductive success of birds of known age and to record the band numbers of as many birds as possible. Adult annual survival, estimated from the numbers of banded birds resighted, was 87% for females and 89% for males. A capture-recapture estimate for the sexes combined gave a mean annual survival of 89%. The youngest age at first breeding was three years, 60% of birds bred at five or younger and nearly 90% at six or younger. Females started to breed about one year earlier than males. Those birds breeding at less than seven years old had a lower apparent survival rate than older breeders. Approximately 50% of chicks that left the colony were resighted again at three years or older. In each year, the mean success of pairs consisting of two experienced breeders, or of one experienced and one unbanded bird was always higher than that of pairs including young birds of relatively less experience. Reproductive success increased with age to at least nine years. The survival of breeding murres from Coats Island, and those from colonies in Greenland, both of which populations are subject to heavy hunting in their wintering area, is generally lower than survival rates of Common Murres populations in Europe and North America, where hunting pressure on breeders is lower. The proportion of birds banded as nestlings that were seen at the colony at three years or older was high compared to Common Murres in Europe. The high survival rate of young birds is apparently sufficient to offset the additional mortality caused by hunting.

Key words: Uria lomvia; *Thick-billed Murres; survival; recruitment; demography; age-specific reproductive success.*

INTRODUCTION

Management and conservation of bird populations requires an understanding of key demographic parameters. The population of Thick-billed Murres (*Uria lomvia*) breeding in the eastern Canadian Arctic is subject to heavy hunting in winter (Wendt and Cooch 1977, Gaston et al. 1983a, Elliot et al. 1991), but little is known of the possible consequences of this hunt at the population level. Nor is there any information on many important demographic parameters for the Canadian population, or for the species as a whole.

Adult and sub-adult survival of Thick-billed Murres was estimated by Kampp (1982, 1991) for birds banded in West Greenland and by Birkhead and Hudson (1977) for birds banded at Cape Hay, Bylot Island. Reproductive success has been estimated for several populations in the north-west Atlantic region: Prince Leopold Island (Gaston and Nettleship 1981), Coburg Island and Cape Hay, Bylot Island (Birkhead and Nettleship 1981), Digges Island (Gaston et al. 1985), and colonies in Upernavik District, West Greenland (Evans and Kampp 1991). Nothing has been published to date on age at first breeding for the species, apart from some preliminary results from the present study (Noble et al. 1991), or on age-specific reproductive success. The only previous estimates of survival to breeding age were based on either questionable assumptions (Birkhead and Hudson 1977, as discussed by Kampp 1991), or data of uneven quality (Kampp 1982, 1991).

Demographic data is available for several populations of the Common Murre (*Uria aalge*)

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breeding in the North Atlantic, especially reproductive success and adult survival (Mead 1974, Hedgren 1980, Harris and Wanless 1988, Hatchwell and Birkhead 1991). A small amount of data on age at first breeding and survival to breeding age for the Common Murre is summarized by Hudson (1985). Additional information has been provided by Hatchwell and Birkhead (1991).

Here we present data from a ten-year banding study of Thick-billed Murres at Coats Island, Northwest Territories, Canada to provide key demographic parameters for the population. Birds from this colony are killed regularly in winter by hunters in Newfoundland, about 2% of first year birds being recovered there each year (G. Donalson, unpubl. manuscript). We compare our results with those for Thick-billed Murres in West Greenland, also subject to hunting in Newfoundland (Kampp 1991) and with Common Murre populations in the eastern Atlantic and discuss the possible role of hunting in the dynamics of this population.

METHODS

STUDY AREA AND BANDS USED

The colony of Thick-billed Murres at Coats Island, Northwest Territories consists of two sub-colonies separated by 1.5 km of unoccupied coast (Gaston et al. 1993). We banded adult and nestling Thick-billed Murres from 1984 through 1989 on an area of cliffs comprising approximately one quarter of the western sub-colony (hereafter "the banding area," Fig. 1). The banding area supported approximately 3,400 breeding pairs in 1990, out of a total of 15,000 pairs on the whole western sub-colony, based on detailed counts from photographs (Gaston et al. 1993). Between 100–278 adults were banded yearly, scattered about the colony, being caught by noosing from above. These birds are referred to as "banded as adults" (BADs). The majority were breeding when caught. About half were banded inside the banding area and of these, from 1986 onwards, 20–44 annually were on breeding sites that were recorded on photographs, where their band numbers could be read from a distance. The breeding status of adults at capture was recorded (presence of an egg or chick). During subsequent observations of breeding success, adults banded as breeders more than three years earlier were taken to exemplify experienced birds and were referred to as "experienced breeders" (EXBs).

Adult birds were banded with three bands: a metal band and a plastic light green band above it on the right leg and a year-code color band on the left leg. In a few cases, where both members of a pair were banded as adults, we reversed the left and right leg arrangements in order to distinguish them from a distance. All chicks were banded with a metal band on the right leg and a year-code color band above it.

Two different types of metal band were used. All birds banded in 1984 and half of the chicks banded in 1985 received a standard U.S. Fish and Wildlife Service band. From 1985 onwards, all adults received a special triangular band manufactured by Lambourne's, U.K. with the number engraved upright on both sides of the band, making it much easier to read than the standard bands (cf. Halley 1992). These bands were also placed on half of the chicks banded in 1985 and all chicks from 1986 onwards. We found that we could read the numbers on the special bands at up to 60 m with a 35 power telescope, although readability varied greatly with light conditions and the angle of the band. Although the special bands were designed so that they could not rotate around the adult tarsus, they could and did rotate on the chicks. For about 50% of chicks that returned to the colony the special band was upside down. We found it no more difficult to read upside-down bands than those right-side up, once we became accustomed to it. The numbers on the standard bands were very difficult to read, even at close range, and some on birds that bred on our study plots were never completely deciphered.

ADULT SURVIVAL

We used resightings of banded murres in successive years to estimate survival (Harris and Wanless 1987, Hatchwell and Birkhead 1991, Sydeman 1992). This method depends on the assumption that murres rarely change their breeding site after they have begun to breed, and that returning breeders are identified on all sites. In our study, several birds moved away from sites attacked by an Arctic fox *Alopex lagopus* in the three previous years. As foxes affect only a small number of sites at the top of the occupied area, we assumed that disturbance by foxes was an exceptional event, not characteristic of most of the colony. Consequently, we omitted those sites from estimates of survival.

After excluding the sites affected by foxes, we

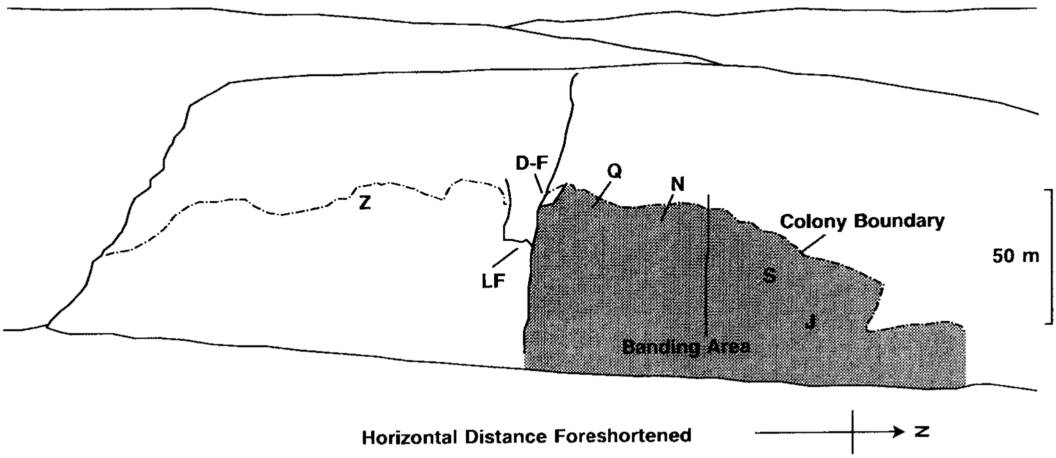

FIGURE 1. Sketch of the west sub-colony at Coats Island, showing the extent of the area within which chicks were banded and the areas where resightings were made.

still recorded some movement among sites (see results). Most involved nearby ledges within the same plot and only one case of a bird breeding on more than one plot was observed during the study. Considering the low rate of movement between sites, we assumed, as others have done for Common Murres (Harris and Wanless 1988, Hatchwell and Birkhead 1991), that movements within the colony by breeding birds were negligible. Hence, the proportion of birds breeding on a given area in one year and absent from it in subsequent years was used as an estimate of adult annual mortality ($1 - s_a$, where s_a = adult survival). We used only data from 1989–1993 to make such estimates, as earlier samples were small (<75) and resightings before 1990 were incomplete.

For each site, we recorded the band combinations of both members of the pair. We took advantage of change-overs and chick-feeding events, when both birds were present and recognizably paired, to check that both members had been recorded. We are confident that practically all birds breeding on our study plots would have been recorded in 1990–1992. For 1993, we have omitted one study plot used in the earlier years, because a shorter observation period made it impossible to obtain data for all sites. For inter-year estimates of mortality we included in our initial sample only birds known to have bred in that year, but for the resighting sample we included all records, whether the birds were breeding or not. A small number of birds reappeared after not having been seen for one or more seasons. We included these birds as having survived, adding them to those recorded for the appropriate years. To take into account the effect of the missing years, survival was also estimated using the capture-recapture program SURGE (Clobert and LeBreton 1985, Clobert et al. 1987).

Birds were sexed, either by their relative positions during copulation, or by recording which bird departed with the chick (normally the male, Harris and Birkhead 1985). Because the timing of brooding shifts differs between the sexes, with males usually being present in the afternoon (Gaston and Nettleship 1981; Gaston, unpubl. data), and because we banded adults mainly in the afternoon, there were more males than females among birds of known sex. Although not all banded birds were sexed, it seems certain that the entire sample contained a preponderance of males.

AGE AT FIRST BREEDING AND SURVIVAL TO BREEDING AGE

Samples of 1,453–2,686 Thick-billed Murre chicks were banded at 4–16 days of age from 1984 to 1991 (Table 1). All of these were banded inside the banding area. We reached the breeding ledges by climbing from above. Banding localities were not recorded in 1984. In 1985–1989 we recorded the banding locality of some chicks, especially those that could be observed from a

TABLE 1. Numbers of birds banded and types of bands used at Coats Island during 1984–1989.

Year	Adults banded	Chicks banded	Dates of chick banding	Type of bands
1984	141	1,453	3–13 Aug.	Old
1985	0	791	3–13 Aug.	Old
	134	828	3–11 Aug.	New
1986	278	2,237	31 Jul.–4 Aug.	New
1987	161	2,250	3–9 Aug.	New
1988	193	2,686	1–6 Aug.	New
1989	100	2,364	3–13 Aug.	New
1990	88	1,351	5–8 Aug.	New
Totals	1,095	13,960		

distance. Areas where chicks were banded that could be easily seen from the cliff top are referred to as "easily visible areas" (EVAs). These comprised only about 10% of the total area viewed in four discrete blocks at D, N, Q and S (Fig. 1). In addition, from 1986–1989, we weighed a sample of 34–48 chicks ("growth chicks") every three days from hatching to more than 16 days old, so that we knew that they had reached the age at which they could have departed successfully (Gaston and Nettleship 1981). All of the growth chicks were in EVAs. Birds banded as chicks returned to the colony at two years or older and on their return were referred to as "known-age" birds (abbreviated as 2Y, 3Y, 4Y, etc.).

From 1988 onwards we carried out intensive reading of band numbers on several different parts of the banding area. In addition, using several observers spread out over the whole colony, we counted simultaneously the number of banded right legs visible on areas within and outside the banding area and recorded the year-code colors seen (see Noble et al. 1991). These observations allowed us to estimate the proportion of known-age birds that settled outside the banding area. By reading band numbers we could also estimate the proportion returning to the area where they had been banded and to other parts of the banding area, for those where the area of banding had been recorded. We read the numbers on very few of the bands seen outside the banding area.

We estimated survival to the age of three years as the number of birds seen at three years or older as a proportion of the number banded, estimated separately for the whole banding sample, for those banded on EVAs, and for the growth chicks. These raw data ($s_{3'}$) were corrected for the proportion that emigrated from the banding area ("e," estimated as 17% for 3Y and 4Y birds by Noble et al. 1991; we omitted from the resighting data any band numbers read outside the banding area), and the proportion that shifted to non-EV areas (r), estimated from the proportion of all birds resighted that were not on the same area where they were banded as chicks, or on closely adjacent areas. This was further corrected to take account of the different chances of resighting birds that settled on growth plots, EV and non-EV areas, by using the ratio ($P = s_{3'gp}/s_{3'else}$, or $P = s_{3'eva}/s_{3'else}$, as appropriate): proportion resighted of those banded on growth plots or EVAs ($s_{3'gp}$, $s_{3'eva}$) to proportion resighted of those banded elsewhere (s_{3else}). Hence the corrected survival from departure to three years was:

$$s_3 = s_{3'}/\{(1 - e) \times [(1 - r) + \frac{r}{P}]\}. \qquad [1]$$

PROPORTION OF BIRDS BREEDING AT A GIVEN AGE

Birds of 2–4 years of age routinely appeared on several different sites in the same year (Noble 1990; G. Donaldson, unpubl. data). Consequently, we could not use the number that bred on a given area as a proportion of all those of that age recorded there as an estimate of the proportion breeding. Also, we could not use extensive scans of the colony to determine the proportion of breeders at a given instant, as breeding status could only be ascertained by watches of fixed study plots throughout the season.

We estimated age at first breeding by two methods: (1) examining changes in the numbers of birds of each cohort breeding at different ages, and (2) comparing the proportion of birds of each age class in a given year that had bred previously. We also compared the distribution of ages at first breeding for the sexes separately.

REPRODUCTIVE SUCCESS

Observations of reproductive success were made at five study plots (D, N, P, Q, and S, Fig. 1) following the protocol described by Birkhead and Nettleship (1980) for "Type I" monitoring of *Uria* spp. This involves mapping all sites on a photograph and making daily observations to record laying, hatching and the departure of the chick. As a few sites may lose an egg before it has been detected, the method tends to overestimate reproductive success by an amount inversely related to the intensity of observation.

We averaged 2–3 hr per plot per day during the period of laying. Consequently only a few percent of eggs laid are likely to have gone undetected (Gaston et al. 1983b). Chicks that reached the age of 14 days before disappearing were considered to have departed successfully unless we observed otherwise. A few that were less than 14 days old when we left at the end of the season were also counted as having departed successfully (<5% in all years). Predation by Glaucous Gulls (*Larus hyperboreus*) removed some chicks between 14 days and the age of departure (median 21, 22, 21 days in 1990, 1991 and 1992, respectively), but probably less than 5% (G. Gilchrist, unpubl. data).

In 1993, observers did not arrive at the colony until mid-way through the incubation period. Consequently the number of pairs laying eggs could not be determined from observations of laying. Instead, we assumed that pairs had laid wherever a site was occupied on more than 90% of days during the period from our arrival to the median date of chick departures (August 15), following the experience of Gaston et al. (1983b).

The study plots were selected primarily for their ease of visibility and hence do not represent a random sample of the colony area. Four of the five plots included ledges that formed the top of the occupied area. Counts of known-age birds on different parts of the banding area suggested that 2Y and 3Y birds tended to concentrate in loafing areas near the cliff top, but that once they began to breed they were more-or-less randomly distributed over the occupied area (G. Donaldson, unpubl. data). Although not randomly selected, the plots did include the full range of aspects and ledge types represented in the colony and we saw no reason why they should be biased with respect to reproductive success. We confined our observations of marked birds to the plots, where we observed the success of all marked pairs, rather than making use of banded pairs elsewhere in the colony. This was done to avoid selecting for sites where birds were especially easy to see. Such sites tend to be in areas where breeding birds are not densely packed and these areas experience lower breeding success than other sites, on average (de Forest 1993).

In 1990 and 1991 eggs were removed from 40 sites on plots D and Q during the first half of the laying period to induce replacement laying (de Forest 1993). These experimental sites were not included in our estimates of reproductive success; nor were any that lost eggs as a result of the disturbance.

To analyse breeding success in relation to age we compared known-age birds with experienced breeders (EXBs). Relatively few pairs consisted of two known-age birds. Where both members of a pair were of known-age, we classified them according to the age of the younger bird. Hence pairs classified as "4Y" might have consisted of a 4Y and an unbanded bird, or a 4Y and a known-age, either the same or older, but not an EXB. Pairs consisting of EXBs and 3–6Ys were treated separately. Pairs consisting of EXBs and 7–8Ys were included with other 7–8Y pairs. In this way we created a hierarchy of probable reproductive experience: 3–5Ys, 6Ys, 7–8Ys, EXB + unbanded, EXB + EXB. The performance of pairs of very mixed experience (4–6Y + EXB) was compared with this series to determine whether success was determined by the less or more experienced partner.

We read the numbers of all bands within range of our watching points along the top of the colony during regular band reading sessions and periodically during other observations. For birds attached to sites on our breeding success plots we made special attempts to read all band numbers and a few birds were captured late in the season, after all eggs had hatched, to verify numbers that had not been read until then. Pre-breeding and breeding birds were sexed on the basis of observed copulations. Birds that mounted other birds were assumed to be males, but those mounted were assumed to be female only if cloacal contact occurred. Repeated observations of the same birds suggested that less than 10% of sexings were incorrect.

All χ^2 values have one degree of freedom and incorporate Yates' correction, unless otherwise specified.

RESULTS

SURVIVAL OF BREEDERS

We observed 17 cases of birds changing their breeding ledge between years: nine BADs in 419 bird-years and eight 4–6Ys in 92 bird-years ($\chi^2 = 8.12$, $P = 0.004$). All six BADs of known sex that changed their ledge were males (χ^2 [based on numbers of bird-years given below] = 1.13, ns). Among 4–6Ys, three were male and four female. Only one male moved between plots and bred, although another male was seen twice in

TABLE 2. Estimates of adult survival rates based on the resighting of a group of banded breeders.

Year sighted	Year resighted	Number sighted	Number resighted	S_a	95% Confidence interval
1989	1990	71	67	0.95	0.87–0.99
1990	1991	136	112	0.82	0.74–0.88
1991	1992	151	135	0.89	0.83–0.94
1992	1993	122	105	0.86	0.79–0.92
All years		480	419	0.87	0.83–0.90

1993 at a different plot from the one at which it had bred earlier in two consecutive years.

Based on resightings, we estimated annual survival rates of BADs at 0.95, 0.82, 0.89 and 0.86. These estimates are not independent, as they involve many of the same birds in successive years. The combined estimate is 0.87 and the mean of the four annual estimates 0.88 (Table 2). For all years combined the survival of birds of known sex was: females 0.87 (83 bird-years), males 0.89 (218 bird-years).

The capture-recapture (SURGE) estimate, assuming constant survival over years and age (time from banding), was 0.89, with 95% confidence interval 0.85–0.92. When we split the first year after banding from subsequent years we obtained estimates of 0.87 and 0.90 respectively. Recapture (resighting) probabilities varied from 0.82–0.95.

Data on the survival of birds banded as chicks was available for those that attempted to breed. For pre-breeders the possibility of their moving between sites was considered too high to be able to use resighting as an estimate of survival. For birds less than seven years old that bred in 1990, 31/39 (0.79) were seen in 1991. Corresponding figures for those breeding in 1991 and seen in 1992 were 42/54 (0.78). The combined survival of 73/93 was significantly lower than the corresponding survival for BADs in the same years (0.88, $n = 279$, $\chi^2 = 4.58$, $P = 0.03$). Only four of 10 birds that bred at three or four years old in 1988 were seen subsequently (Noble et al. 1991).

There was some indication that fewer females survived than males. The combined return rate for females less than seven years old that bred in 1990 or 1991 was 32/44 (0.73), compared to 26/30 males (0.87; $\chi^2 = 1.3$, ns). Some birds that bred at less than seven years returned, but did not breed, the following year. Among males 6/10 birds that bred in one year but not in the next were seen at the colony in the year when they did not breed, whereas this applied to only 2/14 females (Fisher exact $P = 0.03$).

AGE AT FIRST RESIGHTING

We saw 1.5–5.7% of birds banded as chicks in 1985–1991 in the colony in their second year (Table 3). A further 3.7–18.6% were seen at the colony for the first time in their third year and the proportion seen for the first time fell for older age classes. The rather low proportion of the 1986 cohort seen in the third year and of the 1985 and 1987 cohorts in their second year, probably relates to the fact that the reading of band numbers was less intensive in 1987 and 1989 than in other years. Although we saw similar numbers of males and females of known age (91 and 99, respectively), 69% of females were first seen by the age of three, compared to 56% of males ($\chi^2 = 2.72$, $P = 0.1$, Table 3).

PROPORTION OF BIRDS RESIGHTED IN THEIR AREA OF BANDING

For chicks banded in 1985–1988, where the area of banding could be unequivocally identified, we

TABLE 3. Age of first resighting at the colony of birds banded as chicks. Figures in parentheses are proportions (%) of the number banded.

Banding year	Age 2	3	4	5	6	7
1985	12 (1.5)	92 (11.9)	20 (2.6)	20 (2.6)	15 (1.9)	12 (1.6)
1986	72 (3.5)	76 (3.7)	108 (5.2)	58 (2.8)	55 (2.6)	8 (0.4)
1987	48 (2.3)	182 (8.6)	136 (6.4)	111 (5.3)	29 (1.4)	
1988	109 (4.2)	342 (13.3)	195 (7.6)	29 (1.1)		
1989	93 (4.5)	389 (18.6)	71 (3.4)			
1990	77 (5.7)	117 (8.7)				
All males	13	38	30	9	0	1
All females	19	49	21	6	3	1

TABLE 4. Area of banding and resighting for birds banded as chicks in 1985–1988. Areas are arranged in order from south to north along the colony.

Area of resighting	Banding area						
	LF *	D-F *	Q	N *	S *	J	Totals
Z	1	1	1	2	1	0	6
LF	9	9	4	4	3	0	29
D-F	2	38	14	3	2	0	59
Q	3	8	25	11	3	0	50
N	6	4	34	374	77	1	496
S	6	6	9	73	202	4	300
J	0	0	0	10	15	13	38
Totals, area: Same	9	38	25	374	202	13	661
Different	18	28	62	103	101	5	317
Non-contiguous	16	11	48	30	9	1	115

* Indicates areas contiguous to one another. Area Z is not contiguous to any other area.

compared the area of banding and the area of resighting. The areas involved varied in size, in the ease with which bands could be read and in the intensity with which they were observed. We included only birds that were resighted at least twice on the same area and for which 80% or more of records were in the same area. Overall, 67% of birds were seen in the same area where they were banded as chicks. Only 12% of resightings were in areas not adjacent to the area where they were banded (Table 4); we have used this value as our estimate of "r" for use in equation [1], assuming that birds moving more than one area from their banding area would probably have moved outside of EVAs.

SURVIVAL TO AGE THREE

We considered only the survival of chicks banded with special bands. We saw 32–47% ($\bar{x}$ = 40.5%) of chicks banded on growth plots at three years or older. Corresponding proportions for chicks banded on EVAs ranged from 23–45% ($\bar{x}$ = 32.4%), while for other chicks proportions were 16–23% ($\bar{x}$ = 20.8%, Table 5). The proportions resighted did not differ significantly among years for the growth plots, or for the EVAs, but they did for other areas (Table 5). The year with the lowest frequency of resightings was 1986 in all cases.

To compare the completeness of our band number reading on areas of different visibility we examined the proportion recorded at a given age. For this comparison, we used only the sample banded with new bands in 1985–1987, for which we therefore had information until the sixth year. We found that 94% (n = 30) of those banded on the growth plots had been recorded by the age of four, compared to 77% (n = 80) of those on EVAs and 71% (n = 923) of other chicks (χ^2 = 8.38, P = 0.015). These figures suggest that

TABLE 5. Numbers and proportions (%) of chicks banded on areas of different visibility that were seen at three years or older.

Area banded		Banding year					χ^2	df	P
		1985	1986	1987	1988	1989			
Growth plot:	Banded		47	34	48	51			
(GP)	Resighted		15	16	20	21	2.07	3	ns
	% Resighted		32	47	42	41			
EVA:	Banded	53	110	106	51	240			
	Resighted	24	25	34	17	69	9.65	4	0.05
	% Resighted	45	23	32	33	29			
Other areas:	Banded	775	2,080	2,110	2,587	2,087			
(OA)	Resighted	159	335	491	601	437	44.50	4	$<$0.01
	% Resighted	21	16	23	23	21			
Ratio:	GP/OA		2.00	2.04	1.83	1.95			
	EVA/OA	2.14	1.44	1.39	1.43	1.38			

TABLE 6. Numbers of birds of a given age class breeding on breeding study plots in 1990–1993.

Year of banding	Number of breeding at age						
	Three	Four	Five	Six	Seven	Eight	Nine
1984				11	8	19	13
1985			17	22	28	24	
1986		11	23	17	12		
1987	0	8	19	16			
1988	1	13	22				
1989	2	5					
1990	2						
Totals	5	39	81	66	48	43	13
Recorded on breed plots, 1992	165	164	111	60	38	–	
% Breeding, 1992	1.2	7.9	17.1	28.3	74.0		

we had seen most surviving birds from the growth plots by age four, but that many remained unrecorded at that age for the other areas. Hence we have used $s_{3'gp}$ derived from the growth plots as our preferred estimate of $s_{3'}$.

The mean ratio: proportion resighted of those banded on the growth plots/proportion resighted of those banded on neither growth plots nor EVAs (*P* in equation [1]), was 1.95 (range 1.83–2.04). As the use of the growth chicks avoids the need for a correction to take account of loss between banding and departure from the colony, and as the majority appear to have been seen by age four, we have used the mean proportion of growth chicks resighted (0.41) as our preferred estimate of $s_{3'}$. Substituting our values for e, r, P and $s_{3'}$. in equation [1] gives:

$$s_3 = 0.41 \Big/ \left\{\left(1 - 0.17\right) \times \left[0.88 + \frac{0.12}{1.95}\right]\right\} = 0.52.$$

A similar calculation using the mean value for EVAs and incorporating a correction for proportion lost between banding and departure (0.05) gives:

$$s_3 = 0.32 \Big/ \left\{\left(1 - 0.17\right) \times 0.95 \times \left[0.88 + \frac{0.12}{1.95}\right]\right\} = 0.43.$$

PROPORTION BREEDING IN RELATION TO AGE

A few birds bred as 3Ys, although none was recorded doing so in 1990. The numbers of the 1986, 1987 and 1988 cohorts recorded breeding as 5Ys were approximately double the numbers recorded as 4Ys, but the numbers recorded as 6Ys were similar to those recorded at five (Table 6). As a proportion of all band numbers of a given cohort that were read on our breeding study plots in 1992, breeding birds increased from 1.2% (n = 165) at three years to 74.0% (n= 38) at seven years. (We could not use the 1984 cohort in this analysis because special bands were not used in that year.) However, the total number of birds of a given cohort recorded on the breeding plots undoubtedly included some birds still prospecting that would eventually breed elsewhere, or might already have done so. Consequently, per-

TABLE 7. Numbers of birds believed to be breeding for the first time, in relation to age.

Breeding year	Number breeding for the first time						
	Three	Four	Five	Six	Seven	Eight	Nine
1991	1	8	16	14	1		
1992	2	12	9	7	11	0	
1993	2	4	9	6	1	0	0
Totals	5	24	34	27	13	0	0
% That have begun breeding (n = 103)	5	28	61	87	100	100	100

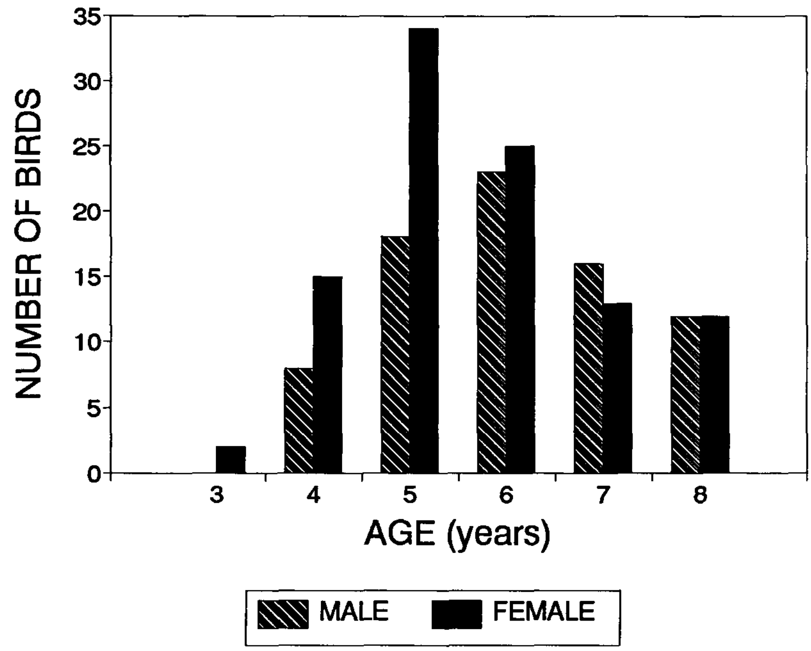

FIGURE 2. Age at first breeding in relation to sex.

centages in Table 6 should be treated as minimum estimates, rather than as unbiased estimates.

All 3Ys and practically all 4Ys that bred were doing so for the first time. Conversely, all birds observed breeding at eight years or older were known to have bred at least once before (Table 7). If the numbers in Table 7 are a representative cross section of the population, then it appears that approximately 60% of birds attempted to breed at five or less and nearly 90% at six or less.

Comparing the age at first breeding for males and females, it appears that 50% of females began to breed by four years, while only 33% of males did so (Fig. 2, median test $\chi^2 = 4.32$, $P = 0.04$). The modal ages at first breeding were four for females and five for males. Among birds breeding at less than five years, 27/40 were female (binomial $P = 0.04$). In 40 pairs where both members were banded, the female was the younger member of the pair in 31 cases (binomial $P = 0.001$). This evidence suggests that females begin breeding, on average, about a year before males.

REPRODUCTIVE SUCCESS

Breeding success in the three years in which observations were continuous throughout the season was 0.51, 0.59 and 0.59 chicks pair^{-1} in 1990–1992 respectively ($n = 415, 361, 466$). The reproductive success of all pairs containing banded birds varied from 0.46 to 0.61 chicks pair^{-1} in 1990–1993 (Table 8). The success of pairs in which both members were experienced breeders was higher in three out of four years than the success of any other combination of birds, varying from 0.78–0.87 chicks pair^{-1} (Table 8). Pairs containing one EXP and one unbanded bird were similar, but more variable, with success from 0.55–0.86. The success of 3–5Y pairs averaged less than a third the success of pairs including an experienced breeder (excluding 3–6Y + EXB combinations) and was significantly lower than the success of 6Ys and 7–8Ys combined. The 6–8Ys, most of which had already bred at least once, were significantly less successful than the EXB + unbanded pairs. Pairs containing one experienced breeder and one bird less than seven years old had success closer to that of 3–5Ys than to that of experienced pairs.

DISCUSSION

Our estimates of adult survival based on combined samples or means of several years (0.86–0.90) fall at the lower end of the range of estimates for *Uria* populations elsewhere (0.87–0.94,

TABLE 8. Reproductive success in relation to age (number of chicks fledged per pair that laid an egg). Sample sizes are given in parentheses.

Age class	Reproductive success 1990	1991	1992	1993	Combined
EXB + EXB	0.87 (16)	0.80 (10)	0.86 (14)	0.78 (9)	0.84 (49)
EXB + Unbanded	0.55 (51)	0.86 (49)	0.66 (73)	0.75 (69)	0.70 (242)
7–8Y		0.61 (13)	0.35 (37)	0.33 (33)	0.39 (83)
6Y	0.40 (15)	0.31 (13)	0.73 (15)	0.27 (14)	0.44 (57)
3–5Y	0.17 (36)	0.34 (32)	0.13 (30)	0.17 (29)	0.20 (127)
EXB + 3–6Y	0.50 (2)	0.0 (3)	0.20 (5)	1.00 (4)	0.43 (14)
All pairs	0.46 (120)	0.61 (120)	0.51 (174)	0.53 (158)	0.53 (572)

Testing samples for all years combined (all χ^2s include Yates' Correction): 3–5Y vs. 6Y; $\chi^2 = 10.4$, $P < 0.005$, 6–8Y vs. EXB + Unbanded; $\chi^2 = 29.9$, $P < 0.001$, EXB + EXB vs. EXB + UNB; $\chi^2 = 3.23$, ns, EXB + EXB vs. EXB + 3–6Y; $\chi^2 = 7.5$, $P < 0.01$.

Hudson 1985). In particular, they are lower than estimates for Common Murres based on the same method (resightings of banded birds at the colony) : 0.94 (North Sea, Harris and Wanless 1988), 0.91 and 0.94 (Irish Sea, Hatchwell and Birkhead 1991) and 0.93 (California, Sydeman 1993, excluding a sub-colony heavily affected by Peregrine Falcon *Falco peregrinus* predation). Three of those estimates exceed the 95% confidence interval given for the SURGE estimate. Although the amount of movement among ledges that we detected (about 2% year^{-1}) suggests that a few birds assumed to be dead may simply have moved to sites out of our view, this reservation may also apply to other studies that used similar methods.

Our survival estimates for breeders are close to those (0.83, 0.87) made by Kampp (1991), based on band recovery analysis, for West Greenland populations of Thick-billed Murres. The latter populations are also subject to hunting in Newfoundland, and in Greenland (Evans and Kampp 1991). There was previously some hunting of North Sea Common Murres in Norway in winter, but this involved mainly first year birds from the British population and probably did not affect birds from the Irish Sea (Hudson 1985, Heubeck et al. 1991). Taken together, the comparisons suggest that the annual survival of breeding adult Thick-billed Murres subject to hunting in winter is lower than that of Common Murres subject to little or no hunting. Whether the survival of Thick-billed Murres would be similar to that of Common Murres for populations not subject to hunting is a matter of conjecture. No estimates of survival exist for Thick-billed Murre populations not subject to hunting.

Our observations on the age of first return of Thick-billed Murres banded as chicks are very similar to those reported for other auks (Hudson 1985, Halley 1992). They suggest that only a small proportion of the 2Ys visit the colony and that some birds may not visit until 4Y or older, although probably some seen for the first time at ages greater than three, had visited in earlier years without being recorded. The preponderance of females among birds visiting the colony as 2Y and 3Ys, together with the observation that females are more likely than males to be the younger member of a pair, suggests that female Thick-billed Murres initiate breeding activities at a younger age than males.

Our best estimate for survival of chicks from departure to age three (0.52) is high compared to other empirical observations of the rate of return of pre-breeding murres (Hudson 1985, Hatchwell and Birkhead 1991). Assessing the accuracy of our estimate is complicated by the fact that "r" and "P" are likely to be underestimated by the method that we employed, because some parts of the banding area could never be examined for bands, hence birds settling on those areas had effectively emigrated. This effect cannot be wholly taken into account by our corrections. Likewise, our estimate of emigration (e) considers only birds moving from the banding area to other parts of the sub-colony. We believe that very few moved to the other sub-colony (only four sightings in four years), but that sub-colony is very hard to observe. The possibility of birds moving to other colonies altogether cannot be evaluated, but presumably such movements must occur to some extent (Harris 1991). Overall, our estimate of s_3 is probably conservative.

The variation among years in the proportion of banded chicks resighted at the colony confirms the finding of Noble et al. (1991) that survival of the 1986 cohort was lower than that of other cohorts. However, inter-year differences observed at Coats Island over five years were much smaller than those observed for Common Murres at the Isle of May, Scotland (Harris et al. 1992).

At present, we know nothing concerning survival at ages between 3Y and the age at which adult survival is attained, except for those birds that bred at 3–6 years, which seemed to have a lower survival than BADs, especially females. However, young breeders seem to be more likely to move sites between years than experienced birds. Consequently, some of the difference in apparent survival rates may be accounted for by birds shifting to sites that we could not observe. There seems little reason to think that annual survival between three years and the age of first breeding would be lower than the annual survival recorded for breeders.

If annual survival from zero to three years was similar, it would have to average 0.80 annually to allow a survival of 0.52 to age three. Mortality is almost certainly higher in the first year than subsequently, because approximately 50% of birds shot in Newfoundland are in their first winter (Elliot 1991) and rates of recovery of Coats Island birds are much higher in the first winter than subsequently (G. Donaldson, unpubl. manuscript). Hence, an annual survival of prebreeders much below that of BADs during the period from the third year onwards seems unlikely. Consequently, the lowered survival of young breeders was either an artifact of movement between sites, or was related to their breeding effort. The fact that some birds failed to breed in the year following their first attempt may have been connected with a relatively high rate of disappearance of their mates. Loss of a mate may make it difficult to find another in time to breed the following year. Unfortunately, not enough pairs consisted of two known-age birds for us to evaluate this possibility.

Our study provides the first data on age-specific reproductive success for the genus *Uria*. Our results suggest that, for Thick-billed Murres at Coats Island, the proportion of birds breeding increases at least up to seven years old. Reproductive success does not reach maximum values before nine years. In addition, the reproductive success of pairs where one member is experienced and the other is not, being closer to that of young birds than that of EXB pairs, suggests that the success of a pair is determined mainly by the age/experience of the younger member. We have insufficient data to evaluate the relative importance of age and experience in determining success (e.g., Pyle et al. 1991), but preliminary results suggest that both contribute (de Forest 1993). The use of low quality breeding sites by young birds may explain part of the difference and will be the subject of a future paper.

Because few BADs change sites, many BADs must remate with young breeders after losing their mate. An adult survival of 0.89 indicates that, while both members of a pair die at only 1% of sites annually, one member dies at 20% of sites. If we assume that all rematings of EXBs are with 4–6Ys (YNG) the breeding success of EXB+unbanded pairs (R_{EXB}) can be estimated:

$$R_{EXB} = 0.8(R_{EXB+EXB}) + 0.2(R_{EXB+YNG}) = 0.76$$

where the values of $R_{EXB+EXB}$ and $R_{EXB+YNG}$ are taken from Table 8. The fact that this estimate for R_{EXB} is similar to the observed value (0.70, Table 8) tends to support the idea that many experienced breeders remate with young birds.

The overall reproductive success of birds on our study plots was lower than recorded at most other Thick-billed Murre colonies in the North Atlantic where similar, non-intrusive, techniques were used (Table 9). Reproductive success at Alaskan seabird colonies over the past two decades has generally been lower than at North Atlantic colonies (Byrd 1989, Byrd et al. 1993), and hence we make no comparisons with the Pacific. The only values lower than those recorded at Coats Island were those obtained by Birkhead and Nettleship (1981) at Cape Hay, Bylot Island and by G. Chapdelaine and P. Brousseau (unpubl. data) at the North colony on Akpatok Island. At Cape Hay exceptional icing conditions, causing regular ice falls on the study plots, was a major factor in lowering reproductive success. At the North colony on Akpatok Island very low chick departure weights suggest that feeding conditions were very poor during the chick-rearing period, perhaps causing reduced survival of chicks to departure age (G. Chapdelaine, pers. comm.). The reason for the poor reproductive success observed at Coats Island is unknown, but is unlikely to be related to feeding conditions, as chick growth rates suggest that food is readily available (Gaston et al. 1983c; Gaston, unpubl. data). Heavy predation pressure from Glaucous Gulls breeding on the colony and

TABLE 9. Reproductive success of Thick-billed Murres at Atlantic colonies where Type I (Birkhead and Nettleship 1980) methods were used.

Colony	Year	*n*	Success	Reference
Prince Leopold Island	1975	358	0.79	Gaston and Nettleship 1981
Prince Leopold Island	1976	359	0.75	Gaston and Nettleship 1981
Prince Leopold Island	1977	351	0.77	Gaston and Nettleship 1981
Coburg Island	1979	632	0.71	Birkhead and Nettleship 1981
Cape Hay, Bylot Island	1979	513	0.48	Birkhead and Nettleship 1981
Digges Island	1980	305	0.64	Gaston et al. 1985
Digges Island	1981	306	0.60	Gaston et al. 1985
Digges Island	1982	318	0.68	Gaston et al. 1985
Akpatok Island:				
South colony	1982	271	0.68	G. Chapedelaine and
North colony	1987	475	0.58	P. Brousseau, unpubl.
Gannet Island	1981	222	0.62	Birkhead and Nettleship 1987
Gannet Island	1982	254	0.66	Birkhead and Nettleship 1987
Gannet Island	1983	219	0.61	Birkhead and Nettleship 1987
Agparsuit, Greenland	1987	550	0.82	Evans and Kampp 1991[1]
Kipako, Greenland	1987	334	0.73	Evans and Kampp 1991[1]
Coats Island	1990	415[2]	0.51	This study
Coats Island	1991	361[2]	0.59	This study
Coats Island	1992	466	0.59	This study

[1] Possibly overestimated, because observations began after the start of incubation.
[2] Omitting some sites that were subject to experimental manipulation and a few sites where breeding success information could not be obtained.

specializing in taking murre eggs and chicks may be a contributory factor (G. Gilchrist, unpubl. data).

In a stable population, adult mortality should equal Bm, where B is the survival of chicks from departure to breeding age and m is the production of young per adult. Hence, B must be equal to $(1 - s_a)/m$. Because the direct calculations based on proportions of birds sighted underestimate survival in a situation where some birds are alive but not seen in a given year, we have used the SURGE estimate (0.89) as our estimate of s_a. Hence:

$$B = 2(1 - 0.89)/0.56 = 0.39$$

where 0.56 is the mean production of young per pair per year. Assuming an average age at first breeding of five years, survival from three to five years as estimated for BADs (0.89), and using our estimate of 0.53 for survival to age three, we calculate B at Coats Island as:

$$B = 0.52 \times 0.89^2 = 0.41$$

The close correspondence between these two estimates suggests that the Coats Island population should be approximately stable. Although it almost doubled between 1972 and 1990, there is no evidence for any change since 1989 (Gaston et al. 1993). Despite their relatively low reproductive success, therefore, the Thick-billed Murres at Coats Island seem capable of sustaining their population through high survival from departure to age at first breeding. Possibly the high departure weights of Coats Island chicks are a factor contributing to their high survival to breeding age.

The combination of relatively low adult survival and relatively high survival during the first three years, compared to Common Murre populations experiencing little hunting, suggests the possibility that density-dependent adjustments in demographic parameters may be involved. Increased mortality through hunting could affect the size of the wintering population, reducing pressure on food supplies, and enhancing juvenile survival. Late autumn "wrecks" of first year Thick-billed Murres were previously a periodic feature of the Great Lakes and the north-eastern United States. However, such influxes have not occurred since 1952 (Gaston 1988). Moreover, the relatively small variation in survival to the third year points to a consistent availability of food during the non-breeding season.

Beginning in the winter of 1993–1994, the Canadian Wildlife Service is applying regulations designed to reduce the kill of murres in Newfoundland by approximately 50%. If the regulations are effective, it should be possible to detect a measurable increase in the survival of prebreeders and breeders at Coats Island. It will be instructive to see whether there is a simultaneous adjustment in other demographic parameters. The next decade may shed light on the role of density dependence in this population.

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