

COLONY ATTENDANCE PATTERNS AND RECRUITMENT IN IMMATURE COMMON MURRES (*URIA AALGE*)

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ABSTRACT.—The behavior of immature Common Murres (*Uria aalge*) two to seven years of age was studied at a colony in southeastern Scotland during two breeding seasons. Immatures tended to arrive progressively earlier in the season as they aged, and were seen at the colony more frequently. Timing of final departure from the colony did not vary between cohorts. Within a day, five-year-old birds spent longer at the colony in the early part of the breeding season compared to later. Immature Common Murres seen at the colony in previous breeding seasons arrived earlier, were seen more often, and were more likely to attempt to breed than birds of the same age that had not been seen before. Overall, recruits invested almost triple the amount of time in colony attendance in the prelaying period than nonrecruits of the same age. Among birds of the same age seen in both 1990 and 1991, those arriving earlier and seen more often in 1990 were more likely to attempt to breed in 1991. The great majority of birds attending "clubs" on intertidal rocks were two- or three-year-olds. Some two- and three-year-olds, and almost all older immatures, were found on ledges above the breeding area of the colony. Three-year-olds that showed a shift in the course of a season between attending at sea rocks and attending on or above the colony almost all shifted from sea rocks to on or above the colony. Older immatures visited fewer breeding subcolonies within a season compared to younger birds. However, most immatures attending areas/ledges on or above breeding ledges were sedentary, visiting only one subcolony. We recorded 69% of immatures in 1990 and 64% in 1991 primarily attending their natal subcolony. Also, 57% of birds breeding for the first time recruited to their natal subcolonies. These frequencies were greatly in excess of those expected if birds were dispersing randomly. Age did not affect the likelihood of attending the natal subcolony, but in one cohort immatures seen in previous season(s) were significantly more likely to attend their natal subcolony than birds not seen previously. Received 5 August 1994, accepted 27 January 1995.

THE LONG PERIOD of colony visiting prior to recruitment in most seabirds has provided a natural system in which the development of behavior can be studied in detail (for review, see Danchin et al. 1991). A number of studies have shown that, as seabirds age and/or gain experience, more time is spent at the colony both in terms of the length of the season and/or the number of visits (e.g. Razorbill, *Alca torda* [Lloyd and Perrins 1977]; Atlantic Puffin, *Fratercula arctica* [Harris 1983]; Pigeon Guillemot, *Cephus columba* [Nelson 1987]; Wandering Albatross, *Diomedea exulans* [Pickering 1989]; Black-legged Kittiwake, *Rissa tridactyla* [Porter 1988]; and Thick-billed Murre, *Uria lomvia* [Noble 1990]). Also, many seabirds return not only to the natal colony, but to the precise area where they were

reared (e.g. Manx Shearwater, *Puffinus puffinus* [Harris 1966, Perrins et al. 1973]; Herring Gulls, *Larus argentatus* [Chabrzyk and Coulson 1976]; Shags, *Phalacrocorax aristotelis* [Aebischer 1985]; and Atlantic Puffins [Harris 1983]).

A population of individually identifiable Common Murres on the Isle of May in southeastern Scotland provided an opportunity to investigate the development and nature of colony attendance in detail. We examine the frequency, timing, and location of visits of Common Murres to the colony in relation to age and to previous experience at the colony, from first return to the first breeding attempt.

METHODS

Study site and study population.—Our study was conducted on the Isle of May (56°11'N, 2°33'W) in the mouth of the Firth of Forth, southeastern Scotland. The island is described in detail in Eggeling (1974). About 12,000 pairs of Common Murres breed on the

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island (Harris 1990), mainly on cliffs on the northwestern side. Immature Common Murres usually attended the periphery of breeding ledges, top ledges above the breeding colony, and "clubs" (sensu Birkhead and Hudson 1977) on intertidal rocks at the base of the colony. Birds first visited the colony from the age of two years (i.e. after their second winter of life); the median age of first breeding was six years (Harris et al. 1994).

Systematic banding of chicks with metal bands and cohort color bands began in 1983 and continued to the end of the study. The number banded each year varied between 184 and 581; survival rates to older than one year differed widely between cohorts (Harris et al. 1992). Most bands displayed the number upright on both sides of the leg and could be read easily with 10× binoculars or a 15–45× telescope at ranges up to 60 m in good light. On the Isle of May it was normally possible to approach birds much more closely (within 10–20 m). From 1988, some of the color bands were engraved with unique one- to three-digit numbers. Comparisons of sighting frequency suggested that marking of birds with color bands, or engraved color bands, did not significantly increase frequency of detection compared to metal-band-only individuals, although it did make identification more rapid (Halley 1992).

Data collection.—The presence of individual immatures at the colony was monitored each season from 1985 onwards, but the location and frequency of attendance were not noted. Intensive fieldwork to collect data for this paper was carried out 30 April through 20 July in 1990, and 13 April through 22 July in 1991. However, a few individuals of the 1984 and 1985 cohorts were recorded as early as late March in both 1990 and 1991.

Among adults, laying was from 19 April to 24 May in 1991, with the bulk 1–10 May. Most hatched in the first half of June and chicks "fledged" (i.e. departed to sea) in late June/early July (range 19 June–14 August). In 1992, laying was slightly earlier—15 April to 15 June (bulk 25 April–5 May). Most hatched in late May/early June and fledging was from 1 June–25 July (bulk 25–29 June).

Searches for banded immatures were made daily. Date, time (GMT), subcolony, and location were noted for each bird each time it was seen. Murres are sexually monomorphic; however, immature birds occasionally exhibit sexual activity. The sex of birds seen copulating was recorded. We assumed that reverse mountings did not occur.

The colony was partitioned into 16 subcolonies based on geographic features so that we could analyze location. Ideally, all sections of the colony would have been covered evenly, but for reasons of topography (Walsh et al. 1995) and time this was not practical. However, the sampling technique is appropriate for investigating relative differences between cohorts. Coverage of the colony was divisible into four categories:

(1) Focal subcolonies. These were a continuous area of 600 m of cliff, containing about 3,200 breeding pairs (26% of the island total) and 10 subcolonies. Most of the chicks banded and almost all of the adult and nonbreeding birds banded came from these subcolonies. Fieldwork was carried out on a regular and systematic schedule. Two complete searches of cliffs and intertidal rocks were made each day, commencing at 0600 and 1700, respectively. Each check took two to three hours to complete. Once each week in 1991 the above schedule was replaced with repeated searches commencing at 0600, 0900, 1200, 1500, and 1800.

(2) Nonsystematically covered. These were three outlying broken-rock subcolonies containing 700 pairs (5% of total). They were visited most days but the timing of visits varied. Chicks were banded at all of these subcolonies.

(3) Irregularly covered. This category applied to two sections of high cliffs (forming two subcolonies) comprising the center and north of the main Common Murre colony. These were large, containing 8,000 pairs (66% of total). Chicks were not banded. Vantage points from which to view the subcolonies were fairly distant and angles of view were difficult. Searches of these cliffs were made about twice weekly.

(4) Not covered. A single subcolony of 200 pairs (2% of total) at the southern tip of the island, which was inaccessible without causing excessive disturbance to breeding birds. The subcolony was visited once or twice each year to band chicks, but there were no opportunities to search for visiting immatures.

Data analysis.—All known-age birds seen in 1990–1991 not previously recorded breeding were terminated immatures. Birds breeding for the first time were termed recruits. Recruits were excluded from analyses of immature behavior for the season they recruited and later. Some immatures were sexed by observations of real or attempted copulations. Immatures and recruits were defined as experienced if they had been recorded on the Isle of May in previous field seasons, and as inexperienced if they had not. The number of experienced birds in the 1986 cohort was large enough in 1991 to further subdivide experienced immatures into birds seen previously in the 1990 season, and those seen both in 1989 and 1990.

Arrival date was defined as the first date on which an individual was observed; departure date was defined as the last date on which an individual was observed, where the bird has been observed more than three times in that season. Attendance period was the number of days between these figures; attendance frequency was the number of days on which an individual was recorded.

An index of the relative amount of time spent attending the colony within a day (i.e. visit length) was calculated from the number of times birds were recorded during repeated counts of the focal subcolonies in 1991 (see above). Multiplying average visit length by the number of days on which the bird was

seen in the prelaying period (prior to 30 April, before which no pairs containing recruits laid) provided an index of the total time invested in colony attendance for each bird (i.e. attending focal area) at that time. Attendance generally was too infrequent among individuals later in the season to allow index values to be calculated.

Subcolony philopatry is the tendency of immature birds to attend the colony, or for recruits to breed at their natal subcolonies more than would be expected if they chose their location within the colony at random. Individuals were defined as attached to a subcolony if the majority (>50%) of visits to breeding areas of the colony (i.e. excluding intertidal rocks) were to that subcolony. Birds attached to their natal subcolony were defined as philopatric. A few birds could not be classified as primarily attending one subcolony; these were by definition nonphilopatric.

A major problem with assessing levels of subcolony philopatry is that subcolonies may vary in attractiveness to immatures due to the availability of a wide top ledge above the breeders, or some other physical or social factor. To allow for this possibility, the observed frequencies of philopatric birds can be compared with the expected frequencies if birds selected subcolonies without respect to natality. This expected frequency (E) was calculated as:

$$E = (n_{\text{attached}} \cdot n_{\text{natal}}) / n_{\text{total}} \quad (1)$$

where n_{attached} is the number of birds attached to the subcolony, n_{natal} is the number of birds natal to the subcolony seen, and n_{total} is the total number of birds.

For example, in 1991 we observed 134 immatures of known age and origin. Of these, 32 were attached to a subcolony known as colony B. Forty-two subcolony-attending immatures hatched at colony B were seen that year. The expected frequency of philopatric birds would be 10 (i.e. $E = [32 \cdot 42] / 134$). In fact, 26 of the 42 immatures reared at colony B were attached to their natal subcolony. We compared the expected frequency of attachment to natal subcolonies to the actual frequency using chi-square tests.

Birds banded at the subcolony that was not covered (category 4, above) were excluded from analyses of subcolony philopatry, since philopatric individuals could not be observed. Birds seen only on intertidal rocks (where birds could not breed) also were excluded.

RESULTS

Arrival dates.—The mean date of arrival became progressively earlier with age up to age 5 in 1990, and age 4 in 1991: two-year-olds arrived around mid-June (corresponding to early nestling period for most breeding Common Murres); three-year-olds in early June (late incubation/early chick rearing); four-year-olds in

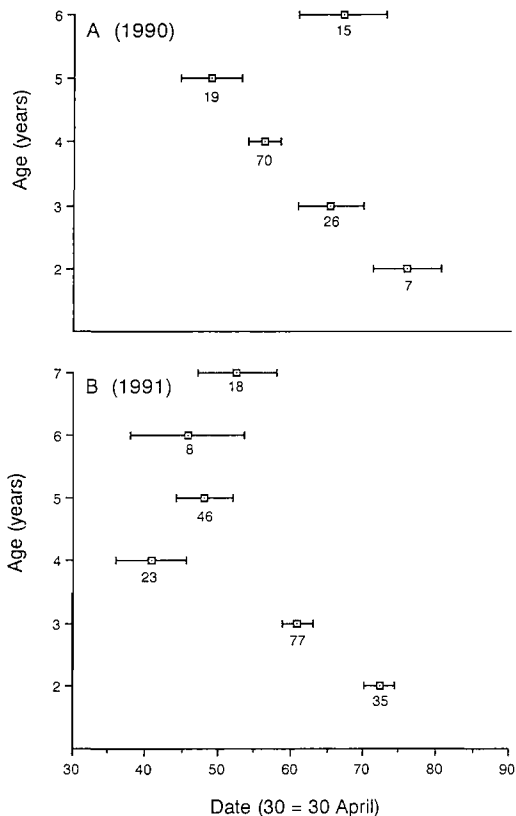


Fig. 1. Mean dates (whiskers indicate \pm SE) of first observations of individually identifiable immature Common Murres in (A) 1990 and (B) 1991 in relation to age. Difference between cohorts was highly significant in both years (Kruskal-Wallis tests; 1990, $H = 16$, $df = 4$, $P = 0.003$; 1991, $H = 30$, $df = 5$, $P < 0.001$). Multiple comparison testing indicated significant pairwise differences between three- and five-year-old cohorts ($P < 0.05$) in 1990. Comparisons between two- and four-, and two- and five-year-old cohorts approached significance ($P < 0.1$). In 1991, multiple comparison testing indicated significant pairwise differences between two-year-olds and all other cohorts, and three- and four-year-old cohorts ($P < 0.05$). Number of birds indicated.

late May 1990 or early to mid-May in 1991 (incubation and laying periods respectively); five-year-olds in mid-May (incubation). Six-year-olds arrived later than five-year-olds, in early June of 1990, but both six- and seven-year-olds arrived at about the same time as five-year-olds in 1991 (Fig. 1). There was a significant effect of age on arrival date in both years. Pairwise comparisons indicated that in 1990 the three-year-old cohort arrived significantly later than

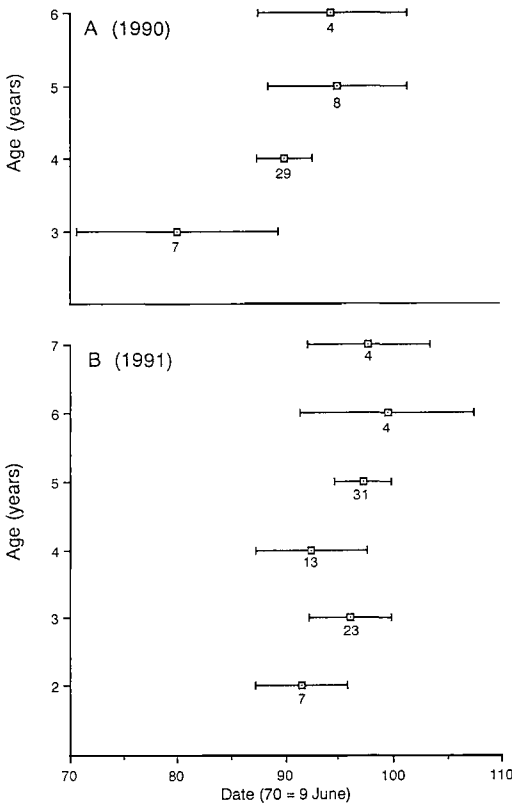


Fig. 2. Mean date (whiskers indicate \pm SE) of last observation of individually identifiable immature Common Murres in (A) 1990 and (B) 1991 in relation to age, based on individuals seen on four or more occasions. Differences between cohorts were not significant (Kruskal-Wallis tests; 1990, $H = 1.12$, $df = 4$, $P = 0.77$; 1991, $H = 4.9$, $df = 5$, $P = 0.43$). In 1990, all two-year-olds were seen fewer than four times. Number of birds indicated.

five-year-olds, and the differences between two- and five-year-olds and two- and four-year-olds approached significance. In 1991, the two-year-old cohort arrived significantly later than all other cohorts, and the three-year-old cohort significantly later than four-year-olds.

Departure dates.—Departure dates varied little with age, centering around the end of June and early July (Fig. 2). There were no significant differences between cohorts in either year. None of the birds in the two-year-old cohort in 1991 were seen more than three times, so no figure could be given for the cohort.

Attendance frequency.—The number of days on which a bird was recorded (Fig. 3) and the attendance period were highly significantly

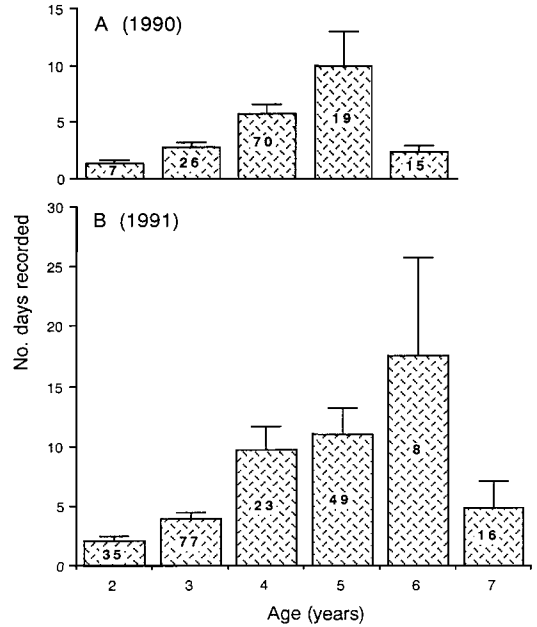


Fig. 3. Average number of days (whiskers indicate SE) on which individual Common Murres were recorded in relation to age in (A) 1990 and (B) 1991. Difference between cohorts was significant (Kruskal-Wallis tests; 1990, $H = 12.2$, $df = 4$, $P = 0.016$; 1991, $H = 23$, $df = 5$, $P < 0.001$). Multiple-comparison tests were not significant ($P > 0.05$) in 1990. In 1991, significant pairwise differences occurred between two- and four-, and two- and five-year-old cohorts ($P < 0.05$), and comparison between two- and three-year-old cohorts approached significance ($P < 0.1$). Number of birds indicated.

correlated in both years (1990, $r = 0.74$, $n = 46$, $P < 0.01$; 1991, $r = 0.62$, $n = 78$, $P < 0.01$). There was a strong effect of age on the number of days individuals were recorded in both years, with a trend in both years for the number of observations to increase with age until birds were about five years old. However, the number of observations of birds of the 1983 cohort, six years old in 1990 and seven in 1991, were at a level similar to three-year-olds in both years. Pairwise comparisons indicated that the two-year-olds were seen on significantly fewer days than both four- and five-year-olds in 1991, and the comparison between two- and three-year-olds approached significance.

Sex differences.—Sample sizes were adequate to test for sex differences in colony attendance only among four-year-olds in 1990. There were no significant differences in arrival date (Mann-

TABLE 1. Mean arrival date (\pm SD) of immature Common Murres in relation to experience. Experienced birds were those recorded at colony in one or more previous breeding seasons. Very experienced birds (data for 1991 only) were those recorded in two or more previous breeding seasons. Sample sizes in parentheses.

Age	Very experienced	Experienced	Inexperienced	P
1990				
4	—	15 May \pm 16 days (24)	31 May \pm 7 days (54)	<0.001 ^a
5	—	12 May \pm 19 days (8)	23 May \pm 17 days (11)	0.070 ^a
6	—	6 June \pm 22 days (10)	6 June \pm 28 days (5)	0.760 ^a
1991				
3	—	19 May \pm 20 days (5)	1 June \pm 19 days (72)	0.190 ^a
4	—	4 May \pm 20 days (14)	25 May \pm 23 days (9)	0.025 ^a
5	3 May \pm 20 days (9)	15 May \pm 30 days (18)	11 June \pm 24 days (15)	0.003 ^b

^a Mann-Whitney test.

^b Kruskal-Wallis one-way ANOVA. Multiple comparisons indicated significant pairwise differences ($P < 0.05$) between birds not seen previously and both other categories.

Whitney test, $W = 35$, $n_F = 5$, $n_M = 6$, $P = 0.40$) or number of days recorded ($W = 21$, $n_F = 5$, $n_M = 6$, $P = 0.65$).

Experience effects.—With the exception of six-year-olds in 1990, experienced immatures arrived earlier at the colony than inexperienced immatures of the same age by 10 to 30 days (Table 1). The overall effect was significant for all cohorts that were testable, except for six-year-olds in 1990 and three-year-olds in 1991. However, as with age, experience had little effect on departure date and there were no significant differences between experienced and inexperienced immatures of any age (Mann-Whitney tests, $P > 0.05$).

Experienced birds also were recorded on more days than inexperienced birds of the same age, the difference in the average number of records varied from 2 to 10 depending on the cohort (Table 2). The effect was significant for four-

year-olds in 1990 and five-year-olds in 1991 and the results for three- and four-year-olds in 1991 approached significance.

Visit length.—In general, five-year-old birds spent more time attending the colony (on days when they visited at all) than three- or four-year-old birds in the early part of the season, but there was little difference later (Fig. 4; for sample sizes, see Table 3). The apparent decline in the amount of time spent at the colony within a day among five-year-olds might have been due to changes in effort by individual birds, or to birds arriving later in the year having shorter average visit lengths, thus lowering the cohort mean. To remove this source of ambiguity, where birds were seen on at least one occasion both in the early part of the season (prior to 10 June) and later (on or after 10 June), the mean visit length was taken for each period and compared in a Wilcoxon matched-pairs test. The

TABLE 2. Number of days immature Common Murres recorded at colony (\pm SD) in relation to experience. Experienced birds were those recorded at colony in one or more previous breeding seasons. Very experienced birds (data for 1991 only) were those recorded in two or more previous breeding seasons. Sample sizes in parentheses.

Age	Very experienced	Experienced	Inexperienced	P
1990				
4	—	10.5 \pm 10.6 (22)	3.6 \pm 3.9 (47)	<0.001 ^a
5	—	15.7 \pm 5.7 (9)	4.9 \pm 7.1 (9)	0.220 ^a
6	—	2.9 \pm 3.0 (10)	1.2 \pm 0.4 (5)	0.350 ^a
1991				
3	—	8.3 \pm 5.3 (4)	3.7 \pm 4.2 (73)	0.090 ^a
4	—	12.6 \pm 11.1 (14)	5.2 \pm 5.7 (9)	0.080 ^a
5	20.7 \pm 19.4 (12)	12.3 \pm 15.4 (21)	1.8 \pm 1.6 (14)	0.001 ^b

^a Mann-Whitney test.

^b Kruskal-Wallis one-way analysis of variance. Multiple comparisons indicated a significant pairwise difference ($P < 0.05$) between very experienced birds and birds not seen previously. Difference between experienced and inexperienced birds approached significance ($P < 0.1$).

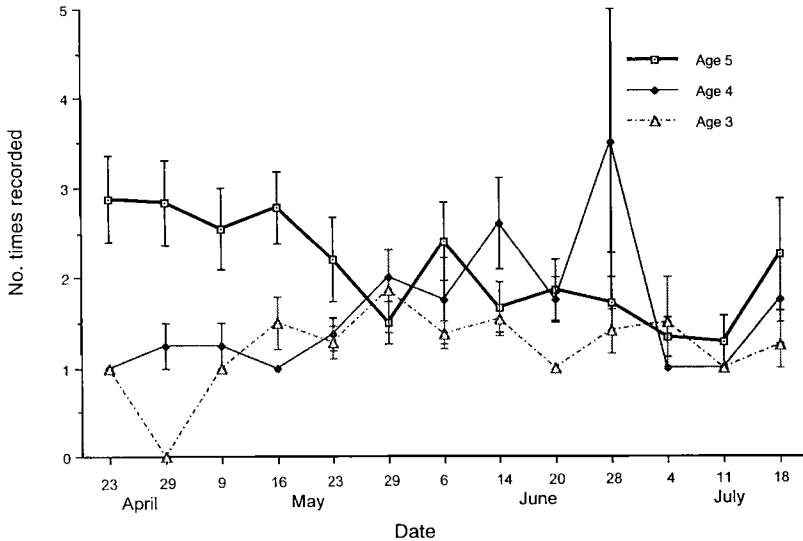


Fig. 4. Mean number (whiskers indicate \pm SE) of records within a day of individually identifiable immature Common Murres during systematic all-day searches of focal area of colony in 1991 (see Table 3 for sample sizes). Difference between cohorts in mean number of records on 29 April (between four- and five-year-olds; no three-year-olds seen) approached significance (Mann-Whitney test, $W = 42$, $n_{\text{four-year-olds}} = 6$, $n_{\text{five-year-olds}} = 4$, $P = 0.07$). Significant effects were found between cohorts on 9 May (Kruskal-Wallis, $H = 5.98$, $df = 2$, $P < 0.05$), 16 May (Kruskal-Wallis, $H = 7.7$, $df = 2$, $P = 0.02$), and 20 June (Kruskal-Wallis $H = 7.34$, $df = 2$, $P = 0.03$). There were significant pairwise differences between four- and five-year-olds on 16 May (multiple-comparisons test, $P < 0.05$); all other pairwise comparisons not significant, $P > 0.05$).

result indicated that time spent visiting within a day was shorter later in the season ($n = 13$, $T = 7$, $P = 0.04$). No such effect was apparent in three- and four-year-olds (three-year-olds, $n = 9$, $T = 10$, $P = 1.0$; four-year-olds, $n = 10$, $T = 6.5$, $P = 0.17$).

Recruitment.—Birds that recruited in 1991 ar-

TABLE 3. Numbers of individually identifiable known-age immatures attending focal subcolonies during systematic all-day watches (see Fig. 4).

Date	Age		
	3	4	5
23 April	1	8	2
29 April	0	4	6
9 May	3	4	11
16 May	4	3	9
23 May	7	8	10
29 May	7	3	12
6 June	11	4	10
14 June	19	5	12
20 June	8	4	7
28 June	5	2	7
4 July	2	5	6
11 July	3	4	7
18 July	4	4	4

rived at the colony earlier than did individuals of the same age that did not breed (nonrecruits, $\bar{x} = 20$ May \pm 3.4 days; recruits, $\bar{x} = 18$ April \pm 1.2 days; Mann-Whitney test, $W = 3401$, $n_{\text{nonrecruits}} = 71$, $n_{\text{recruits}} = 14$, $P < 0.001$). Furthermore, birds that recruited in 1991 arrived earlier the previous (1990) season than birds that did not subsequently recruit (nonrecruits, $\bar{x} = 29$ May \pm 4.3 days; recruits, $\bar{x} = 14$ May \pm 3.8 days; $W = 183.5$, $n_{\text{nonrecruits}} = 24$, $n_{\text{recruits}} = 13$, $P < 0.05$). The 1991 recruits also were seen on more days in 1990 than same-age birds that did not recruit in 1991 (nonrecruits, $\bar{x} = 5.8 \pm 2.0$; recruits, $\bar{x} = 12.25 \pm 3.2$; $W = 302.5$, $n_{\text{nonrecruits}} = 24$, $n_{\text{recruits}} = 12$, $P < 0.007$).

Among five- and six-year-olds, the age groups in which recruitment occurred in 1991, overall effort in the prelaying period (prior to April 30, before which no recruits laid) was significantly related to subsequent recruitment. Future recruits invested nearly three times as much time at the colony than nonrecruits (index values: recruits, $\bar{x} = 26.2 \pm 7.0$, $n = 7$; nonrecruits, $\bar{x} = 9.1 \pm 2.7$, $n = 12$). This difference was significant (Mann-Whitney test, $W = 94$, $n_{\text{recruits}} = 7$, $n_{\text{nonrecruits}} = 12$, $P < 0.05$).

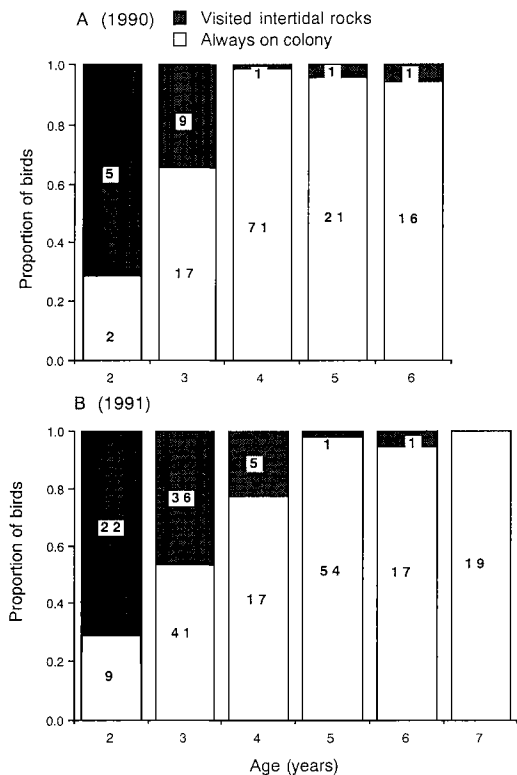


Fig. 5. Proportions of immature Common Murres that visited intertidal rocks in (A) 1990 and (B) 1991 seasons based on sightings of individually identifiable birds. Difference in 1990 between two- and three-year-old, and older birds is significant (Fisher exact test, $P < 0.01$); the difference between age classes in 1991 is highly significant ($X^2 = 70.6$, $df = 5$, $P < 0.001$). Number of birds indicated.

Sea rock and colony attendance.—Most birds native to the Isle of May that visited sites on intertidal rocks (“clubs,” sensu Birkhead and Hudson 1977) were two or three years old (Fig. 5). One adult, which had bred unsuccessfully in 1991, was seen once on sea rocks. All six Isle of May native birds more than four years old seen on sea rocks were at sites below their natal subcolony. Age differences in the type of site visited were highly significant in both 1990 and 1991 (Fig. 5).

In the course of the 1990 breeding season, five three-year-olds changed from attending sea rocks to attending sites in or above the colony; none changed in the opposite direction. This effect approached significance (binomial test, $P = 0.064$). In 1991, 12 three-year-olds moved from sea rocks to on or above the colony, and 1 from

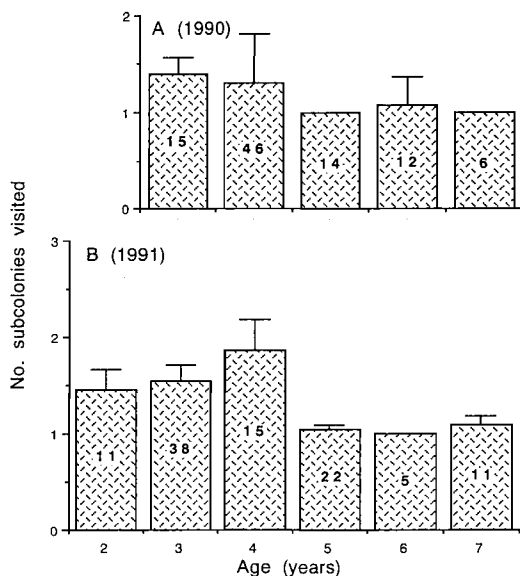


Fig. 6. Mean number (whiskers indicate SE) of subcolonies visited by individually identifiable immature Common Murres in (A) 1990 and (B) 1991. Older birds recorded at significantly fewer subcolonies in year compared to younger birds (Jonckheere trend tests; 1990, $z = 2.8$, $P < 0.003$; 1991, $z = 2.6$, $P < 0.005$). Number of birds indicated. All five- and seven-year-olds in 1990, and all six-year-olds in 1991 attended only one subcolony. Thus, there is no error term for these categories.

colony to sea rocks, a highly significant bias (binomial test, $P = 0.004$).

Movement between subcolonies and subcolony philopatry.—Immatures attending sites in the colony were mainly sedentary, rarely being recorded at more than one or two subcolonies. Nevertheless, the number of subcolonies visited varied significantly with age in both years (Fig. 6). More subcolonies were visited by younger birds. There were no differences in the number of subcolonies visited by experienced and inexperienced birds of any age (Mann-Whitney tests, $P > 0.05$). Of the 51 individuals seen in both years that were nonbreeders in both years, 47 (92%) remained attached to the same subcolony. Three of the remaining four birds moved less than 50 m.

There was little variation with age in levels of philopatry to the natal subcolony; all statistical comparisons were not significant ($P > 0.05$). From the limited evidence available (most birds were of unknown sex), philopatry did not vary between the sexes—69% (9/13) of males and

TABLE 4. Subcolony philopatry among immatures. Attachment to natal subcolonies was highly significantly in excess of theoretical figure if birds dispersed without a natal subcolony preference (1990, $X^2 = 57.2$, $df = 1$, $P < 0.001$; 1991, $X^2 = 70.3$, $df = 1$, $P < 0.001$).

Subcolony	Number of			Theoretical frequency of philopatric birds at subcolony ^b
	Philopatric birds attached to subcolony	Non-philopatric birds natal to subcolony	Birds attached to subcolony ^a	
1990				
Low light	1	0	1	0.0
Hide	0	1	0	0.0
Stack	1	1	6	0.1
Colony 4	6	7	8	1.1
South Face	12	9	14	1.9
Colony B	24	6	28	8.8
South Horn	5	1	6	0.1
Mill Door	5	3	5	0.4
Rona	13	2	15	2.3
Total	67	30	83 ^c	14.7
1991				
Low light	3	1	4	0.1
Stack	2	0	7	0.1
Colony 4	5	6	6	0.5
South Face	10	10	11	1.6
Colony B	26	16	32	10.0
Chatterstones	2	2	9	0.3
South Horn	8	3	13	1.1
Mill Door	10	3	10	1.0
Rona	20	7	23	4.6
Total	86	48	115 ^c	19.3

^a Whether natal to subcolony or another subcolony.

^b If birds showed no preference for natal subcolony.

^c Fourteen birds (1990) and 19 birds (1991) not attached to any subcolony, to subcolonies where no birds natal to that subcolony were seen, or to areas of colony where chicks were not banded.

73% (8/11) of females were philopatric (Fisher exact test, $P = 0.34$). All ages and sexes were combined in subsequent analyses.

Most immatures returning to the Isle of May selected their natal subcolony as their visiting site. In 1990, 69% (67/97) of all colony-attending immatures (i.e. excluding those seen on sea rocks) were philopatric and, in 1991, 64% (86/134) were philopatric (Table 4). Comparisons between actual natal subcolony attachment frequencies and those expected if birds were selecting subcolonies without a natal subcolony preference indicated highly significant philopatry in both years. Subcolony philopatry was significantly more common among experienced

TABLE 5. Subcolony philopatry among recruits. Recruitment to natal subcolony was highly significantly in excess of theoretical figure if birds selected recruitment sites without a natal-subcolony preference ($X^2 = 8.4$, $df = 1$, $P < 0.005$).

Subcolony	Number of birds			Theoretical frequency of philopatric recruitment ^b
	Natal to subcolony recruiting there	Natal to subcolony recruiting elsewhere	Recruiting into subcolony ^a	
Colony 4	2	1	2	0.3
South Face	0	4	0	0.0
Colony B	3	3	4	1.1
South Horn	0	1	0	0.0
Mill Door	4	0	4	0.8
Rona	3	0	4	0.6
Total	12	9	14 ^c	2.8

^a Whether natal to subcolony or another subcolony.

^b If birds showed no preference for natal subcolony.

^c Seven birds recruited into subcolonies from which no native birds recruited at any subcolony, or to areas of colony where chicks were not banded.

four-year-olds (19/21; 90%) compared to inexperienced birds (15/25; 60%) in 1990 ($X^2 = 5.5$, 1 df , $P < 0.05$); however, comparisons in all other age classes and in 1991 were not significant.

The preference for the natal subcolony during immaturity was followed through into recruitment. Of birds known to have recruited in 1990 or 1991, 57% did so at their natal subcolony (Table 5). This level was highly significantly greater than the expected level if birds selected breeding sites without a natal subcolony preference.

DISCUSSION

Not only do birds spend more time in colony attendance as they approach recruitment age, but those attending the colony more often both in the year of recruitment and in the previous year are more likely to begin breeding than same-aged birds investing less in colony attendance. A partial exception to this pattern is found among birds of the 1984 cohort, six years old in 1990 and seven in 1991, which behaved in many respects like younger birds. The reasons for this are unclear, but it may be that most birds of that age class had already recruited (locating banded birds in the dense masses of breeders was very difficult), and the remaining nonbreeders were poorer-quality individuals.

The observed pattern of immature colony attendance appears to be widespread in other seabirds (see Introduction). In Common Murres, Birkhead and Hudson (1977) and Hudson (1979) also concluded that younger birds arrive at the colony later, based on the earliest sightings of birds of known age. There has been little previous work on the effect of experience on immature attendance patterns and recruitment in seabirds. Pickering (1989) found a direct effect of experience on attendance in immature Wandering Albatrosses such that, as experience increased (independent of age), return to the colony became earlier and birds spent more days ashore. Porter (1988) found that all Black-legged Kittiwakes recruiting to the colony being studied in northeastern England had been recorded there in at least one previous breeding season, and Cadiou et al. (1994) found that older immature kittiwakes were more likely to "squat" on other pairs' chicks, or unused nests, as compared to younger immatures. In addition, Noble (1990) suggested that arrival date might be related to experience in the Thick-billed Murre.

Therefore, much of the variation between cohorts may reflect experience (which will usually be correlated with age) rather than age per se. Alternatively, greater levels of experience (i.e. first attendance at an earlier age), enhanced attendance levels, and earlier recruitment may all be secondary reflections of the underlying quality of individual birds. Variations in individual quality affect many aspects of the recruitment process in Black-legged Kittiwakes (Wooler and Coulson 1977, Porter 1988, 1990). The proximate underlying factor may be foraging efficiency, which improves with age in many seabird species (for review, see Burger 1988); more efficient foragers should be capable of investing more time in behaviors preparatory to recruitment, such as colony attendance.

Data on attendance levels within a day suggests that five-year-olds generally spent longer at the colony than younger age groups early in the season, but not later. Visit lengths of younger birds did not vary significantly as the season progressed. The period of longer visiting coincided with the adult prelaying and laying period. Breeding opportunities were still available; it seems likely, therefore, that five-year-olds were assessing or pursuing opportunities to recruit into the breeding population (and possibly also, if male, to gain extra-pair copulations). Many birds of this cohort (excluded

from the analysis) recruited; no younger bird did so in 1991 (Halley 1992). Later, with no prospect of recruitment until next season, attendance for such extended periods would no longer be so advantageous.

Suggestions as to the function of attendance at sites on intertidal rocks by younger immatures can only be speculative; clearly, there is no proximate relationship with recruitment. Probably, it serves as an initial arena for practicing social and sexual behaviors without the risk of attack by aggressive breeding individuals. Attendance at sea rocks also would allow birds to gain experience in the location and value of local fishing grounds. Hudson (1979) suggested that sea-rock areas functioned at least partly as arenas for pairing, since birds engaged in sexual activity there more often than in subcolonies. However, on the Isle of May there was no evidence that pairs formed on sea rocks were other than temporary.

Birds usually visit only a few subcolonies, visit fewer as they age, and concentrate attendance at the same subcolony between years, which suggests that there is some advantage gained by concentrating visits rather than dispersing them across the whole colony. Obvious potential advantages include defending a potential breeding site, building up a pair bond, and gaining information on a local area of the breeding colony in order to monitor opportunities for recruitment. Site defense is unlikely, since none of the birds recruiting in 1991 did so at the exact place that they attended in 1990. Pairing is difficult to assess, since no two marked birds were paired together, however, pairing appeared to be temporary and unstable in most immatures prior to recruitment. Monitoring for breeding opportunities is likewise difficult to assess. Immatures typically seemed to take great interest in nearby breeding ledges (Halley 1992). Different sites vary widely in quality at some colonies (related mainly to site density; Birkhead 1977), and breeding for the first time with an experienced mate enhances reproductive success in several seabirds (Nelson 1966, Davis 1976, Ollason and Dunnet 1978, Hunt 1980). Presumably, there would be an advantage for individuals to be able to recognize and exploit the good-quality-site/mate-acquisition opportunities that arise.

The subcolony chosen for attendance by immatures is usually the one in which they were reared, and this tendency varies little with age

or experience. Note that this applies only to those birds that returned to the Isle of May. The level of emigration to other colonies, and whether this varies between subcolonies, is unknown. However, substantial numbers of immatures from other British and Irish colonies were detected visiting the Isle of May, and Isle of May birds were found visiting other colonies (Halley and Harris 1993). It is surprising that no differences between sexes in subcolony philopatry were detected, although birds may be able to recognize kin as in other species (Bateson 1983), and/or one sex may have a higher tendency to emigrate outright (females in most seabirds studied; for review, see Greenwood 1980). Both mechanisms would serve to reduce inbreeding risk.

Natal philopatry is common in vertebrates (Greenwood 1980). In seabirds, philopatry to subareas within a colony also appears to be common (see Introduction). Although previous studies did not adjust for the "attractiveness" of different areas, this is unlikely to have significantly affected results. In the genus *Uria*, Gaston and Nettleship (1981) inferred subcolony philopatry in Thick-billed Murres by observing that types of egg marking (a heritable trait) were clumped.

Subcolony philopatry in Common Murres and other seabirds is particularly interesting because of its bearing on the functional mechanisms of natal philopatry in general. Standard explanations often include: inheritance of the parental territory and its resources (Bekoff 1987); adaptation to a microhabitat (e.g. Part 1991); and dangers of predation or starvation during dispersal (e.g. Murray 1967, Waser 1985). None of these are credible as explanations of Common Murre subcolony philopatry since the subcolony has no resources except the physical site itself, and banding recoveries indicate that birds disperse very widely outside the breeding season (Halley 1992). By elimination, social factors would appear the only likely function (unless birds are imprinting on a natal area as a means of recognizing the colony as a whole, with subcolony philopatry occurring as an accidental byproduct). Common Murres sometimes brood one another's offspring and failed/nonbreeding birds may attack potential nest predators (Birkhead 1977), although whether these behaviors are confined to kin is unknown. Breeding adults engage in mass defense by bill pointing against avian nest predators (Birkhead 1978).

While all birds gain at an individual level from this behavior, additional fitness would accrue to a bird if neighbor's offspring were related to it as well.

In conclusion, the development of colony-attendance behavior in immature Common Murres suggests that progressively more effort is invested in activities at the colony as birds age, and that within an age group individuals vary consistently in their effort. Birds expending greater effort in colony attendance over an extended period are more likely to recruit than same-aged birds expending less effort (up to three times as much effort in the prelaying period of the recruitment year). Whether this effort is a function of different resource-allocation decisions, and/or of the different underlying quality of individuals, is unclear. Birds are highly attracted to the small area of the colony from which they fledged, both for colony attendance as immatures and subsequent recruitment; the function of this attachment is unclear but seems likely to be related to social, kin-selective factors rather than any intrinsic value of the area itself. Future research could profitably attempt to separate individual fitness and resource allocation, and investigate the function of subcolony philopatry in the behavioral ecology of Common Murres.

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LITERATURE CITED

- AEBISCHER, N. J. 1985. Aspects of the biology of the Shag *Phalacrocorax aristotelis*. Ph.D. thesis, Univ. Durham, Durham, England.
- BATESON, P. P. G. 1983. Mate choice. Cambridge Univ. Press, Cambridge.
- BEKOFF, M. 1987. Group living, natal philopatry, and Lindström's lottery: It's all in the family. *Trends Ecol. & Evol.* 2:115-116.
- BIRKHEAD, T. R. 1977. The effect of habitat and den-

- sity on breeding success in the Common Guillemot *Uria aalge*. *J. Anim. Ecol.* 46:751-764.
- BIRKHEAD, T. R. 1978. Behavioural adaptations to high density nesting in the Guillemot *Uria aalge*. *Anim. Behav.* 26:321-331.
- BIRKHEAD, T. R., AND P. J. HUDSON. 1977. Population parameters for the Common Guillemot *Uria aalge*. *Ornis Scand.* 8:145-154.
- BURGER, J. 1988. Effects of age on foraging in birds. Pages 1127-1139 in *Acta XIX Congressus Internationalis Ornithologici* (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Science, Ottawa.
- CADIOU, B., J.-Y. MONNAT, AND E. DANCHIN. 1994. Prospecting in the Kittiwake, *Rissa tridactyla*: Different behaviour patterns and the role of squatting in recruitment. *Anim. Behav.* 47:847-856.
- CHABRZYK, G., AND J. C. COULSON. 1976. Survival and recruitment in the Herring Gull *Larus argentatus*. *J. Anim. Ecol.* 45:187-204.
- DANCHIN, E., B. CADIOU, J.-Y. MONNAT, AND R. R. ESTRELLA. 1991. Recruitment in long-lived birds: Conceptual framework and behavioral mechanisms. Pages 1641-1656 in *Acta XX Congressus Internationalis Ornithologici* (B. D. Bell, Ed.). Christchurch, New Zealand. 1990. New Zealand Ornithol. Congr. Trust Board, Wellington.
- DAVIS, J. W. F. 1976. Breeding success and experience in the Arctic Skua *Stercorarius parasiticus*. *J. Anim. Ecol.* 51:327-341.
- EGGELING, W. J. 1974. The Isle of May. Oliver and Boyd, Edinburgh.
- GASTON, A. J., AND D. N. NETTLESHIP. 1981. The Thick-billed Murres of Prince Leopold Island—A study of the breeding ecology of a colonial High Arctic bird. *Can. Wildl. Serv. Monogr. Ser.* 6.
- GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* 28:1140-1162.
- HALLEY, D. J. 1992. Behavior, ecology and recruitment of immature Guillemots *Uria aalge*. Ph.D. thesis, Univ. St. Andrews, St. Andrews, Scotland.
- HALLEY, D. J., AND M. P. HARRIS. 1993. Intercolony movement and behavior of immature Guillemots *Uria aalge*. *Ibis* 135:264-270.
- HARRIS, M. P. 1966. Age of return to the colony, age of breeding, and adult survival of Manx Shearwaters. *Bird Study* 13:84-94.
- HARRIS, M. P. 1983. Biology and survival of the immature Puffin *Fratercula arctica*. *Ibis* 125:56-73.
- HARRIS, M. P. 1990. Population changes in British Common Murres and Atlantic Puffins, 1969-1988. Pages 52-61 in *Studies of high latitude seabirds. 2. Conservation biology of Thick-billed Murres in the northwest Atlantic*. (E. J. Gaston, and R. D. Elliot, Eds.). *Can. Wildl. Serv. Occas. Pap.* 69.
- HARRIS, M. P., D. J. HALLEY, AND R. W. SWANN. 1994. Age of first breeding in Common Murres. *Auk* 111:207-209.
- HARRIS, M. P., D. J. HALLEY, AND S. WANLESS. 1992. The post-fledging survival of young Guillemots *Uria aalge* in relation to hatching date and growth. *Ibis* 134:335-339.
- HUDSON, P. J. 1979. The behaviour and survival of auks. D.Phil. thesis, Univ. Oxford, Oxford, England.
- HUNT, G. L. 1980. Mate selection and mating systems in birds. Pages 113-168 in *Behavior of marine animals, vol. 4*. (J. Burger, B. L. Olla, and H. E. Winn, Eds.). Plenum Press, New York.
- LLOYD, P. J., AND C. M. PERRINS. 1977. Survival and age of first breeding in the Razorbill *Alca torda*. *Bird-Banding* 48:239-252.
- MURRAY, B. G., JR. 1967. Dispersal in vertebrates. *Ecology* 48:975-978.
- NELSON, J. B. 1966. The breeding biology of the Gannet *Sula bassana* on the Bass Rock, Scotland. *Ibis* 108:584-596.
- NELSON, D. A. 1987. Factors influencing colony attendance by Pigeon Guillemots on Southeast Farallon Island, California. *Condor* 89:340-348.
- NOBLE, D. 1990. Factors affecting recruitment of Thick-billed Murres on Coats' Island, N.W.T. M.Sc. thesis, Queen's University, Kingston, Ontario.
- OLLASON, J. C., AND G. M. DUNNET. 1978. Age, experience, and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis*, in Orkney. *J. Anim. Ecol.* 47:961.
- PART, T. 1991. Philopatry pays: A comparison between Collared Flycatcher sisters. *Am. Nat.* 138:790-796.
- PERRINS, C. M., M. P. HARRIS, AND C. K. BRITTON. 1973. Survival of Manx Shearwaters *Puffinus puffinus*. *Ibis* 115:535-548.
- PICKERING, S. P. C. 1989. Attendance patterns and behavior in relation to experience and pair-bond formation in the Wandering Albatross *Diomedea exulans* at South Georgia. *Ibis* 131:183-195.
- PORTER, J. M. 1988. Prerequisites for recruitment in Kittiwakes *Rissa tridactyla*. *Ibis* 130:204-215.
- PORTER, J. M. 1990. Patterns of recruitment to the breeding group in the Kittiwake *Rissa tridactyla*. *Anim. Behav.* 40:350-360.
- WALSH, P. M., D. J. HALLEY, M. P. HARRIS, A. DEL NEVO, I. M. W. SIM, AND M. L. TASKER. 1995. Seabird monitoring handbook for Britain and Ireland. JNCC/RSPB/ITE/Seabird Group, Peterborough.
- WASER, P. M. 1985. Does competition drive dispersal? *Ecology* 66:1170-1175.
- WOOLLER, R. D., AND J. C. COULSON. 1977. Factors affecting the age of first breeding of the Kittiwake *Rissa tridactyla*. *Ibis* 119:339-349.