

POSTFLEDGING OCCUPANCY OF BREEDING SITES BY FEMALE COMMON MURRES (*URIA AALGE*)

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ABSTRACT.—Virtually all female Common Murres (*Uria aalge*) continued to visit the colony after their mate had taken the chick to sea. There were significant differences among years, but the average time between a chick fledging and a female last being seen at the colony was 13 days (range 0–36). In over 99% of instances, the female was at her breeding site. On ~5% of days she was joined by another male, and in a few cases (8% of those days) copulation was observed. None of those transient matings persisted into the next season, even when the original male did not return; thus, we found no support for the hypothesis that females might be looking for replacement mates in case they were widowed. The most successful females (in terms of breeding output over several years) tended to have the longest periods of postfledging visiting, apparently because such birds fledged their chicks early in the season, but there was no difference in daily frequency of attendance. We conclude that successful males and females were maximizing time spent occupying the best breeding sites, even to the extent that only one adult took the chick to sea to complete its development. Received 2 February 2002, accepted 14 August 2002.

RESUMEN.—Prácticamente todas las hembras de *Uria aalge* continuaron visitando la colonia luego de que su pareja había llevado al pichón al mar. Aunque existieron diferencias significativas entre años, el tiempo promedio desde el abandono del nido por el pichón hasta la última vez que se observó la hembra en la colonia fue de 13 días (rango 0–36). En más del 99% de los casos la hembra estuvo en el sitio de su nido. En aproximadamente el 5% de los días estuvo acompañada por otro macho, y en otros pocos casos (8% de esos días) se observaron cópulas. Ninguno de estos apareamientos temporales persistió hasta la temporada siguiente, aún cuando el macho original no regresó. Entonces, no encontramos apoyo para la hipótesis de que las hembras podrían estar buscando parejas de reemplazo en caso de que enviudaran. Las hembras más exitosas (en términos de rendimiento reproductivo a lo largo de varios años) tendieron a presentar los períodos de visita post-emplumamiento más largos, aparentemente porque los polluelos de estas aves emplumaron más temprano en la estación, pero no existió diferencia en la frecuencia diaria de visitas al nido. Concluimos que los machos y hembras exitosos estaban maximizando el tiempo invertido ocupando los mejores sitios de anidación, incluso hasta el punto de que sólo uno de los adultos llevó al pichón al mar para completar su desarrollo.

COMPARED TO THE detailed studies on initiation of breeding, remarkably little attention has been paid to the end-of-season behavior and attendance at the breeding site of colonially breeding seabirds. Species accounts in the major handbooks on birds (e.g. Cramp and Simmons 1977, Marchant and Higgins 1990) rarely give more than general statements such as “attends the colony for a week after the young have left” and hint that birds may be at their breeding sites. The Common Murre (*Uria aalge*), Thick-billed Murre (*U. lomvia*), and Razorbill (*Alca torda*) have a rather unusual breeding strategy in that the male alone takes the chick to sea

when it is about three weeks old—only partly grown and flightless—and continues to feed it for one to two months (Varoujean et al. 1979), whereas the female continues to visit the colony for several more weeks (Tuck 1961, Gaston and Nettleship 1981). The same may also be true for the Dovekie (*Alle alle*), though the data are fragmentary (Bradstreet 1982). Thus, in these species, it appears as though the male is investing far more in the rearing of the chick than is the female. What might the advantage be to the female in remaining in the colony? One obvious possibility is that she might be returning to ensure that she retains a proven successful breeding site (Gaston and Nettleship 1981, Harris and Wanless 1986). At the start of a long-term population study of Common Murres, it

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was noted that at the end of the season sites from which a young had apparently fledged successfully were again sometimes occupied by two adults, and copulations sometimes occurred between members of those new pairs. We speculated that a successful female might be looking for a possible replacement mate in case the current mate did not return to the colony the next season. In this article, we describe the end of season behavior of Common Murres and test the hypothesis that females were looking for potential replacement mates.

METHODS

In 14 years between 1983 and 2001, observations were made on Common Murres breeding in four study areas in the main breeding colony on the Isle of May, Firth of Forth, Scotland, several times most days from late June (just after the young started to leave the colony) until late-July (when virtually all birds had departed). The majority of adult Common Murres in those areas were color-banded. Most attention was paid to successful breeders, but in 11 seasons the presence of failed and nonbreeding birds was also recorded. All birds followed were individually identifiable by unique color-bands or plumage characteristics (which were useful only within a season), and most had been sexed by observations of copulations in the prelaying period. In all years, information on the date of the last sightings for every bird was obtained. In nine years, we also assessed the daily frequency of attendance following fledging by multiplying the number of days between fledging and the final sighting of the year by the proportion (always >0.90) of days when observations were made. In most cases, it was noted whether the bird was at its breeding site or elsewhere in the colony. As a result of concurrent studies, we knew whether a bird had bred that year, its breeding success, and, where relevant, the date that the young fledged (defined as the day after the night that a chick aged at least 14 days old disappeared from the site). Where the bird was color-banded, we also knew if it returned the next season and whether it bred; and where its mate was also color-banded, whether or not it kept the same mate. We use the term "divorce" in cases where both members of a pair returned the next year and one at least bred with a new mate. In five years, we recorded whether a successful female was joined by another bird at the site; observations of color-banded birds indicated that a female would not tolerate another female at her site. Therefore, where the visiting bird was not color-banded, we assumed that it was a male. We differentiate between successful breeders, failed breeders, nonbreeders (individuals that had bred in previous seasons but not in the current year), and prebreeders (color-banded birds that had attached

themselves to these small parts of the colony one or more years before but appeared never to have bred). In pairs where both male and female were individually identifiable and both were present in the colony the day after the chick disappeared, we assumed that the chick had not fledged successfully.

Because there were no significant differences between areas in dates that adults were last seen (ANOVA, $F = 1.27$, $df = 3$ and 941 , $P = 0.28$) or in the number of days adults were seen between fledging and last sighting (ANOVA, $F = 1.07$, $df = 3$ and 941 , $P = 0.36$), and neither was there an individual bird effect in the frequency of attendance (later), we pooled observations from the four areas and from all birds. However, to allow for differences in timing of breeding between years, when pooling data across years a standardized last date for each bird was calculated by comparing last observation date with mean fledging date for all chicks leaving that area that year. Tests for individual bird effects were undertaken on individuals where there were four or more annual observations on postfledging attendance. The calculations of average breeding success and laying dates of individuals were based on all breeding records (range 7–20 years) which included all years that observations were made on end-of-season attendance. It was not possible to collect all data on every bird. For instance, in very dense groups of birds we could not determine whether an individual was actually at the site where it had bred or had a mate present; therefore sample sizes vary between analyses. Statistical tests involving proportions were undertaken on arcsine-transformed data.

From other studies we also had annual estimates of the timing of breeding (from first-egg dates), breeding success, feeding frequency of chicks, the time adults spent together after feeding the chick, the proportion of chicks attended by two adults at midday, masses of adults with chicks, and masses of chicks near fledging (see Harris and Wanless 1985, 1988 for details).

RESULTS

Chicks left the colony with the male parent, normally in the evening, and females continued to visit the colony for up to 36 days after that. In only 16 (2%) of 906 successful fledgings the color-banded female was not seen back at the colony after her male and chick had left. In 11 instances where there was no reason to doubt that fledging had been successful, the color-banded male returned to its mate and site 2–13 days later (mean 7 ± 1 [SE]). We assume that those males had lost their chicks at sea subsequent to fledging. Such individuals made up only 1% of 968 records involving 204 males, so we treat them as exceptional and do not consider them further. Daily frequency of attendance between the date

that the chick fledged and the last day the adult was seen varied significantly among the nine years that observations were made (ANOVA, $F = 25.8$, $df = 8$ and 434 , $P < 0.001$), the extreme values being 55% (in 1988) and 88% (in 1986). In 1983, the only year when we attempted to assess the time spent at the site by females, sites were occupied, on average, for ~70% of daylight hours (Harris and Wanless 1986).

Successful females were normally seen at the site where they had reared a chick. Of the 5,573 instances where we recorded locations, in only 21 instances (0.4%) was the female >30 cm from her site. At the very end of the season when very few birds were present at the colony nonbreeders, failed breeders, and prebreeders visited unoccupied sites and sometimes associated with site-holding females. On 90 (4.9%) of 1,847 daily checks, a color-banded female was consorting with a male that was not her mate. In 63 of those cases, the visiting male was color-banded, so we knew that 37 cases (involving eight individuals) involved failed breeders, 23 (three individuals) involved nonbreeders, and in 3 (two individuals) the bird was a prebreeder. In the remaining 27 cases, the bird was unbanded; however, because virtually all breeders and nonbreeders in those areas were banded, it was likely that these were prebreeders. Copulations were recorded in seven of the above cases involving four failed

males, one nonbreeding male, and two probable prebreeders. In none of the 46 instances involving color-banded males did that pairing persist the following year, even though in 13 cases the female's original male was not seen the next year.

The patterns of attendance of successful birds at end of the season were extremely variable (Fig. 1). In most years (e.g. 1999), the proportion of marked birds present declined gradually over a period of weeks; but in a few (e.g. 1994), attendance was cyclic and most birds left over a period of 5–10 days. We have no explanation for those differences between years. The average time between a chick fledging and the female last being seen at the colony was 13.4 ± 0.2 days ($n = 927$, range 0–36 days) after the departure of her mate and chick. However, there were significant annual differences in both the date of last visits and the interval between fledging and departure, with 1992 being the earliest season (mean date 11 July) and 1986 and 1994 the latest (25 July). The years 1983 and 1986 had the longest period of attendance (18 days), and 2001 had the shortest (9 days) (Table 1). The final sightings of successful females were significantly more synchronized (as indicated by the SD) than the distribution of the fledging dates ($n = 14$ years, paired $t = 4.55$, $P < 0.001$).

TABLE 1. Annual measures of colony attendance by female Common Murres after they had successfully reared a chick. ANOVA indicated significant annual differences in both the dates females were last seen ($F = 15.3$, $df = 13$ and 941 , $P < 0.001$) and the intervals between fledging and last sighting ($F = 82.6$, $df = 13$ and 926 , $P < 0.001$).

Year	Date last seen at colony			Days between fledging and date last seen at the colony		
	Number of females	Mean (SE)	Range	Number of females	Mean (SE)	Range
1983	39	21 July (0.5)	13–24 July	39	18.1 (0.9)	4–33
1984	55	13 July (0.5)	2–20 July	49	12.8 (0.7)	0–24
1986	60	25 July (0.6)	11 July–4 August	59	18.2 (0.9)	0–30
1988	81	15 July (0.5)	30 June–22 July	81	12.9 (0.6)	0–24
1992	73	11 July (0.5)	1–19 July	73	11.8 (0.7)	0–27
1993	66	12 July (0.5)	4–19 July	66	11.2 (0.6)	2–21
1994	84	25 July (0.5)	8–30 July	84	17.4 (0.8)	1–28
1995	71	12 July (0.5)	4–18 July	71	10.9 (0.8)	0–25
1996	48	23 July (0.5)	14–26 July	48	14.7 (0.9)	3–28
1997	59	15 July (0.5)	4–19 July	59	13.0 (0.8)	0–26
1998	76	18 July (0.5)	7–27 July	75	11.0 (0.6)	1–25
1999	73	23 July (0.7)	8 July–8 August	72	16.8 (0.9)	0–36
2000	74	18 July (0.8)	2–30 July	71	13.9 (1.0)	0–30
2001	83	14 July (0.4)	2–20 July	80	8.7 (0.6)	0–24

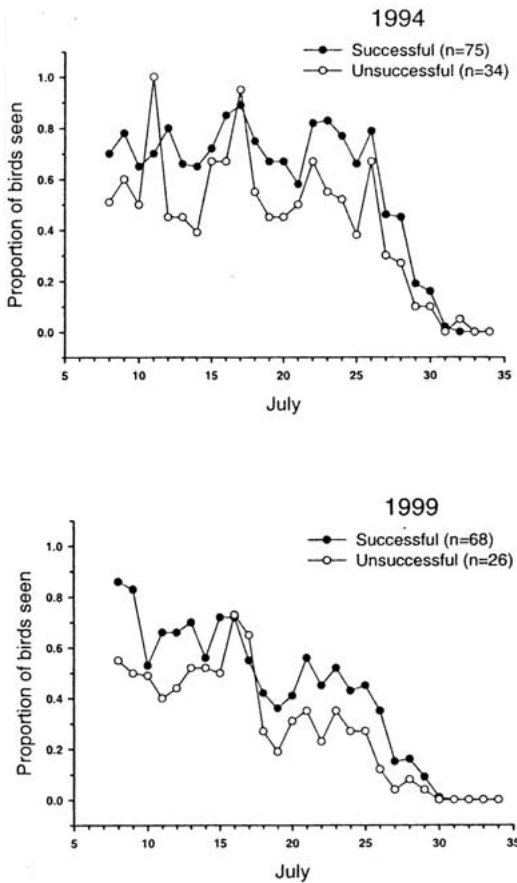


FIG. 1. The frequency of attendance at breeding-sites by color-banded successful and unsuccessful Common Murres in 1994 and 1999. The attendance of successful birds includes only records after the young had left.

For 90 females for which we had observations in at least four years, there were significant among-bird differences in the number of days that birds continued to visit the colony

(ANOVA, $F = 2.21$, $df = 89$ and 547 , $P < 0.001$). This was presumably due to the well-documented consistency in laying date from year to year of individual females (Wanless and Harris 1988, Sydeman 1993). Because breeding success declines with laying date (Wanless and Harris 1988), we anticipated a link between success and the length of postfledging attendance. Such a relationship was evident for 32 females where we had repeated measures of their average breeding success and length of postfledging attendance (linear regression: mean number of days between fledging and female's final sighting = 12.0, mean number of chicks fledged per year = 2.04; $r = 0.69$, $P < 0.001$). For 19 individuals where there were estimates of daily frequency of attendance over several years, there was no significant bird effect (ANOVA, $F = 0.71$, $df = 18$ and 101 , $P = 0.79$) nor a significant relationship between the proportion of days that a bird was seen and its overall breeding success ($r = 0.14$, $P = 0.41$).

There were no significant correlations between average last-visit dates, synchrony of the last dates, or postfledging attendance and any of the parameters of breeding that we measured (Table 2). The frequency of attendance was, however, significantly lower when breeding was late, when members of a pair spent less time together (both during the middle of the day and after the chick was fed), and the adults and chicks were significantly lighter. That indicated that attendance was depressed when food availability was low.

Failed breeders also continued to visit their sites. In 36 instances (1.5% of 2,394 records), we recorded a bird away from its breeding site, a significantly greater frequency than among successful birds (see above; $\chi^2 = 29.9$, $df = 1$,

TABLE 2. Correlation coefficients between annual estimates of postfledging attendance and breeding parameters for Common Murres that had reared a chick. The number of years that data were available for each comparison is given in brackets. Standard deviation is used as the measure of synchrony of the dates of last sighting.

	Date last seen at colony	Days between fledging and last seen at colony	Daily frequency of attendance	Synchrony of dates of last sightings
First egg date	-0.361 (14)	-0.093 (14)	-0.753** (9)	0.004 (15)
Breeding success	0.029 (14)	0.216 (14)	0.519 (9)	-0.260 (15)
Feeds per day	0.125 (14)	0.039 (14)	0.253 (9)	0.191 (15)
Time pair together after a feed	0.110 (10)	0.226 (10)	0.843* (6)	-0.022 (9)
Both adults present at mid-day	0.453 (14)	0.209 (14)	0.960*** (8)	-0.138 (14)
Mass of adult with chick	-0.012 (14)	0.225 (14)	0.636* (9)	-0.240 (14)
Mass of chick near fledging	-0.037 (14)	0.176 (14)	0.691* (9)	-0.146 (14)

Correlations that were significant are indicated * $P < 0.05$, ** $P < 0.02$, *** $P < 0.001$.

$P < 0.001$). Perhaps failed breeders were also prospecting for new sites elsewhere in the colony, but despite regular searches in adjacent areas we found no evidence of that. There was no significant difference in proportion of days that males and females occupied their sites ($t = 1.79$, $df = 214$, $P = 0.08$), but failed females were seen at the colony, on average, 51% of days, significantly less than the 57% recorded for successful females ($t = 7.4$, $df = 214$, $P < 0.001$). The annual mean last-sighting dates for successful and failed breeders were highly correlated ($r = 0.94$, $n = 11$ years, $P < 0.001$). There was a tendency for successful breeders to remain slightly longer (Fig. 1), but in 9 of the 11 years there was no significant differences between the two groups (all t -tests NS). In 2000, failed breeders remained significantly later (mean difference 3.5 days, $t = 2.21$, $df = 44$, $P = 0.03$), whereas in 2001 the reverse was true (mean difference 2.1 days, $t = 2.62$, $df = 86$, $P = 0.01$). There was no significant difference between the standardized last dates for failed males and failed females (mean difference 0.7 days, $t = 0.78$, $df = 191$, $P = 0.44$).

Nonbreeders and prebreeders continued to visit the colony after the peak of fledging until the end of the season, and there was no significant difference in standardized dates of last sightings of successful breeders ($n = 942$; mean = 12.6 ± 0.14), failed breeders ($n = 286$; mean = 12.2 ± 0.38), nonbreeders ($n = 32$; mean = 10.0 ± 1.00), and prebreeders ($n = 83$; mean = 12.1 ± 0.73 ; ANOVA, $F = 2.11$, $df = 3$ and $1,343$, $P = 0.10$). Because nonbreeders and prebreeders were not tied to breeding sites, daily frequency of attendance was not adequately assessed for that category.

In 586 (95%) of 619 instances where both members of successful pair were color-banded and returned to the colony the next spring, the female bred again with the same mate. Following divorce, 21 females bred at the original site with a new mate, 5 bred at a new site with a new mate, and 7 became nonbreeders. There were no significant differences in standardized last dates of females retaining the same mate or divorcing ($t = 0.55$, $df = 34$, $P = 0.58$) or between daily frequency of attendance of 521 nondivorcing and 25 divorcing females (means 0.80 ± 0.01 , 0.77 ± 0.04 , respectively; $t = 0.80$, $df = 27$, $P = 0.44$). There were many fewer data for unsuccessful pairs, but in 72 cases a female retained the same mate and site; there

were 10 cases of divorce, a significantly higher frequency than among successful females ($\chi^2 = 6.3$, $df = 1$, $P = 0.012$). In none of the 43 cases of divorce mentioned above did we record a female consorting with a male other than her mate during the season prior to the divorce. We therefore conclude that mate-change in female Common Murres has little to do with the female's activities at the end of the breeding season.

DISCUSSION

In Common Murres, breeding success depends at least in part on the quality of the breeding site, there is intense competition for breeding sites, and successful birds tend to retain their breeding sites from one year to the next (Birkhead 1978; Harris et al. 1996, 1997). The present study confirmed that successful females continued to visit their breeding site for up to five weeks; found a marked synchronization of colony departure by successful breeders, unsuccessful breeders, nonbreeders, and prebreeders in late July; and evidence that postfledging attendance was significantly depressed in years when feeding conditions appeared to be less good. We have no information on either the ultimate or proximate factors bringing that about, but note a tendency for successful birds to be the last to leave the colony (Fig. 1), which is consistent with the view that they continued to visit until most potential competitors had left.

On the Isle of May, murres return to their breeding sites in October immediately after they have undergone the main molt of the year, during which they are flightless. Birds appear to be reclaiming their sites as quickly as possible because some individuals are still regrowing their primaries when they return (Harris and Wanless 1990a). Breeding adults return before nonbreeders and the most successful sites are occupied more frequently than are less successful ones (Harris and Wanless 1989, 1990b). Thus, it appears as though birds of both sexes are trying to maximize the time that they occupy good breeding sites. In the case of the female, that extends to entrusting the final development of her chick to the male, although it could also be seen as the male entrusting care of a good site to the female. Theoretically, an unsuccessful bird could leave the colony soon after the loss of an egg or a chick, molt, and

return to the colony before successful birds and attempt to occupy a good site. Unsuccessful birds appear not to have adopted that strategy.

Unless there was some advantage in one adult remaining at the colony, both adults might have been expected to take the chick to sea, as occurs in the *Synthliboramphus* murrelets (Gaston and Jones 1998), and to feed and protect it from predation and loss. If only one parent takes the chick to sea, it is reasonable that the division of labor is allocated by sex to prevent confusion as to which parent goes and which stays. In situations where members of a pair take very different roles, it is usual for the behavior to be sex-linked (Partridge and Halliday 1984). It is, however, perhaps unexpected that it is the male that continues to feed the young in Common Murres, Thick-billed Murres, Razorbills, and (probably) Dovekies, because at least in all but the latter species, extrapair matings occur regularly (Hatchwell 1988, Wagner 1992, Gaston and Jones 1998), and Birkhead et al. (2001) found that 7.8% of Common Murre chicks were being reared by cuckolded males. More data on relative costs and benefits of visiting the colony and feeding a chick at sea are needed before we can further elucidate the role of the sexes.

Prolonged attendance of breeding sites after successful breeding appears to be rare (though doubtless under-recorded) among seabirds where many species either have postfledging care (presumably by both sexes) or desert the colony before the chick fledges (references in Schreiber and Burger 2002). Where such attendance has been documented (e.g. Northern Gannet [*Morus bassanus*], Atlantic Puffin [*Fratercula arctica*], and some other auks; Harris 1984, Nelson 2001), site ownership appears to be the primary purpose. The same is probably true for species such as the Herring Gull (*Larus argentatus*), Northern Fulmar (*Fulmarus glacialis*), and Blue Petrel (*Halobaena caerulea*) that attend colonies outside the breeding season (Salomonsen 1955, Coulson and Butterfield 1986, Fugler et al. 1987). During our study, the number of Common Murres breeding on the Isle of May increased by 25%, breeding success (averaging 0.77 young fledged per pair) was high for a species with a single-egg clutch, and adults visited the colony during 10 months of the year. Conditions were obviously very good. It might be instructive to study site attendance where numbers were declining or at a higher

latitude where ice cover results in a much shorter breeding season.

In Thick-billed Murres, males also join successful females at the end of the season and may take over the site the next season if the original male is absent, though it appears unclear whether the end of the season pairings continue (Gaston and Hipfner 2000). Although female Common Murres do form temporary pairs at the end of the season with the occasional copulation occurring, our observations found those to be very infrequent and none of the pairs that we observed continued into the next season. Thus, we found no support for the hypothesis that a female was assessing the potential of future mates and conclude that she was present to retain ownership of a high-quality breeding site.

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