FALL COLONY ATTENDANCE AND BREEDING SUCCESS IN THE COMMON MURRE[1]

M. P. HARRIS AND S. WANLESS

Institute of Terrestrial Ecology, Hill of Brathens, Banchory, Kincardineshire AB3 4BY, United Kingdom

Abstract. The visits of Common Murres (*Uria aalge*) to breeding sites were documented in each October 1982–1987. Individually-marked birds almost invariably returned to their own breeding sites. There was no evidence that immatures, or adults from other colonies, visited the colony. The most frequently occupied sites were those which had been successful the previous season. The numbers of visits to sites increased with increasing numbers of neighbors and were higher for sites in the center of the cliff than for sites at the top and bottom. Blocking sites for 4 months did not prevent birds breeding the next season. Fall colony visiting could be explained by (a) competition for the best sites, or (b) birds returning to maintain the pair bond.

Key words: Common Murre; Uria aalge; competition for breeding sites; breeding success; density; position in colony; pair bond.

INTRODUCTION

In many species of seabirds, individuals spend a relatively small proportion of the year at their breeding sites. This may be because conditions during many months are unsuitable, e.g., high latitude colonies may be icebound, or because adults migrate outside the breeding season. However, in a few species such as Northern Fulmar (*Fulmarus glacialis*) and Shag (*Phalacrocorax aristotelis*), birds may be present at colonies for much of the year (Macdonald 1980, pers. observ.). The Common Murre (*Uria aalge*) has a variable pattern of colony attendance; birds from the most northern populations do not return to the colonies until March or April whereas at the southern edge of the species' range in both the east Atlantic and the east Pacific some individuals start to visit the colonies in the fall (Belopol'skii 1961; Taylor and Reid 1981; Ainley and Boekelheide, in press). In many colonies murres return when they are still in basic plumage and undergo the molt into alternate (or breeding) plumage while visiting the colonies (Thomas 1984; Harris and Wanless, in press).

Counts of birds at colonies in the fall and winter have sometimes exceeded the estimated breeding population which has given rise to the suggestion that birds from different areas may join local birds at colonies during fine weather (Bourne 1981, Taylor and Reid 1981). Presum-

ably there is some advantage accruing to the individuals visiting colonies in the fall and winter. Salomonsen (1955) suggested that winter attendance by Northern Fulmars was a response to competition for nest sites. This explanation has also been suggested for the Common Murre (Greenwood 1972, Birkhead 1978) but up until now no data have been collected to test this hypothesis.

Murres can be seen at the colony of about 12,000 pairs on the Isle of May, Firth of Forth, Scotland in all months of the year except September. This paper reports on early fall attendance at this colony and documents the relationship between the frequency of visits to breeding sites in early fall and the breeding success of the pairs occupying them, and their breeding density and position in the colony.

METHODS

The study area was a 20-m long section of the 20-m high near-vertical cliffs. Although murres bred on adjacent cliffs the area was discrete, being bounded on one side by a gully and on the other by a protruding promontory of rock. The area was photographed in detail in 1981, and in 1982 the positions of all the 207 sites held by breeding and nonbreeding pairs were numbered on large black-and-white prints. The very few sites colonized in later years were excluded from the study. Each site was checked visually from a permanent blind about 24 m away from the colony two to five times a day during the breeding seasons of 1982–1987 to determine which pairs bred and

TABLE 1.   Percentages of 207 sites which were visited each mid-October and the number (and percentage of available sites of each category) visited in relation to the breeding success the previous season. The mean number of days each site was visited is also shown.

Year	Occupied at least once No. (%)	Not occupied (0) No. (%)	No egg (1) No. (%)	Failed to hatch (2) No. (%)	Young died (3) No. (%)	Young fledged (4) No. (%)	$\chi^{2\,b}$	Days visited $\bar{x}$	H^c
				Breeding success				Days visited	
1982	192 (93)	0[a]	9 (69)	29 (83)	8 (89)	146 (97)	17***[d]	4.6	26***
1983	116 (56)	3 (50)	3 (51)	18 (60)	9 (75)	83 (56)	4.1	1.6	4.0
1984	180 (87)	8 (89)	3 (27)	23 (77)	24 (92)	122 (93)	23***	5.0	19***
1985	156 (75)	1 (20)	7 (64)	9 (64)	6 (75)	133 (79)	7*	2.8	13*
1986	184 (89)	2 (25)	6 (60)	26 (90)	7 (87)	143 (94)	40***	5.9	31***
1987	131 (63)	3 (33)	1 (20)	12 (46)	3 (50)	112 (69)	14**	1.2	14**

[a] No observation because sites not occupied in 1981 were excluded.
[b] χ^2 after grouping breeding success into 'no breeding' (0 + 1), 'failed breeding' (2 + 3) and fledged (4) except for 1982 where columns 1–3 were pooled (df = 1).
[c] Kruskal-Wallis H with 4 df.
[d] *, **, *** = $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively.

their nesting success (details in Harris and Wanless 1988). The status of each site in each season was scored as 0 (unoccupied that season; no records possible in 1982 as the sample of sites considered here were all bred at in this the first year of the study), 1 (pair present but no egg seen), 2 (egg failed to hatch), 3 (chick lost), or 4 (chick reared). Categories 0 and 1, and 2 and 3 were combined to give 'No breeding' and 'Failed breeding,' respectively. An overall measure of each site's breeding success (0–6) was calculated by summing the number of successful breeding attempts (category 4) over the 6-year period. Each site was also given a density score, ranging 0–14, which was the maximum number of other pairs of murres which bred within three bird lengths of the site in any season. As a measure of position within the colony, the distance of each site below the cliff top was measured. In this paper we do not attempt to separate the effects of bird and site quality on either fall visiting or breeding success.

Data on fall attendance were collected on 10 consecutive mornings either 14–23 October or 15–24 October each year 1982–1987 from the same blind used in the breeding checks. Observations were made from before dawn (when the first birds arrived) until most birds had left the cliffs (usually 1–3 hr later). Birds did not visit the cliffs later in the day. During each observation period we recorded which sites were occupied, the maximum number of individuals present, and the incidence of fights and matings. These data were used to calculate the number of days each site was visited (by either one or two birds) during each 10-day period; these annual totals

were then summed to give an overall total for the 6 years of the study i.e., each site could have a theoretical score from zero (none visited) to 60 (visited every day of every year). The proportion of sites visited and the mean number of days a site was occupied varied between years (Table 1). However, the factor(s) responsible for these annual differences will be reported elsewhere, here we consider only the relationship between breeding success, density and spatial position on the cliff, and fall occupancy.

In 1983 and 1985 observations were made between 5–28 October and 14 October–2 November, respectively. We used these extended data sets to look for temporal differences in the proportions of sites, of different breeding success, density or position, which were visited, by grouping the data into 4-day periods and comparing the distributions using χ^2-tests.

An estimate of the proportion of sites visited and the number of visits to each site during midwinter was obtained from observations made between 23 December 1982–1 January 1983, using the same methods as in the fall.

Additional data on the birds' behavior on the cliffs were obtained by systematically scanning through the study area (after most birds had come ashore) and recording what each bird was doing at that moment on each morning 11–23 October 1982. Casual observations were also made of any birds not on the cliffs and these were supplemented by 11 days of records from a Common Murre carrying a radio tag in 1986 (full details of radio tracking methods are given in Wanless et al. 1988).

Information about the identity of birds present

on the sites in the study area came either from 87 color-banded murres or from birds previously banded as chicks with year-specific color bands. Additional, but less systematic, observations were also made on a further 250 color-banded murres elsewhere in the colony.

The effect of depriving murres of breeding sites during the winter was assessed by putting 20- × 20- × 20-cm pyramids of concrete or wood on 21 individual sites on a nearby cliff on 27 October 1983 and removing them on 28 February 1984. All 21 sites had been occupied during the 1983 season. The timing of laying and success of breeding at these sites was followed in 1983 and 1984.

Mean values (and 95% confidence intervals) of the numbers of visits are shown in the figures but most statistical analyses on these data were undertaken using nonparametric tests—Spearman's coefficient of rank correlation (r_s), Kruskal-Wallis (H) one-way analysis of variance by ranks, and Mann-Whitney U-tests in MINITAB.

RESULTS

Murres were first recorded ashore between 1 and 6 October each fall from 1982 to 1986 (Isle of May Bird Observatory records); no observations were made in early October 1987. All 207 sites in the study area were occupied at least once during the six October periods and the median total of visits was 32. The colony attendance of murres at this time was extremely variable. In some years birds were present on most mornings whereas in others the colony was deserted for several days at a stretch. Thus the proportion of sites occupied at least once in any mid-October period varied from 56% (1983) to 93% (1982), while the mean number of days a site was visited varied from 1.2 days in 1987 to 5.9 days in 1986 (Table 1).

IDENTITY OF OCTOBER BIRDS

Of 1,182 sightings of color-banded murres, 1,161 (98.2%) were at the sites which they had bred at or occupied previously. Additional but less systematic observations on a further 250 color-banded individuals elsewhere in the colony confirmed that sites were almost invariably occupied by their owners. The commonest reason for a murre being elsewhere in the colony was the presence of a roosting Shag on its breeding ledge. Prospecting murres which did not have a site (including individuals color-banded as chicks in previous years and which visited the colony during the summer) were never recorded.

BREEDING SUCCESS

Although there were annual differences in the overall proportions of sites occupied, within each year there were consistent differences in occupancy associated with breeding success the previous season. Thus, in each mid-October period the proportion of sites which were visited at least once was higher at sites where breeding had been successful, lower at sites where breeding had not occurred, and intermediate at sites where a breeding attempt had been made but had been unsuccessful (Table 1).

Similarly the number of days that a site was visited was generally higher at successful sites, lower at those where breeding had not occurred, and intermediate at unsuccessful sites. The differences were significant in each year of the study except 1983, when relatively few sites were visited (Table 1). Examples of the trend in a year when the mean number of days a site was visited was high (1986) and low (1987), and statistical details, are presented in Figure 1. The most successful sites, i.e., those from which a young fledged each season, were, on average, visited six times as often as the least successful sites during the 6 years of the study (Fig. 2). There was no evidence that these differences were due to consistent differences in the date birds from successful and unsuccessful sites returned to the colony (1983: $\chi^2 = 8.9$, df = 5, ns; 1985: $\chi^2 = 1.1$, df = 4, ns).

All categories of sites were visited slightly more often during the 10 days in December compared to the comparable October period (Fig. 3). However, the differences associated with breeding success earlier in 1982 were maintained so that successful sites were visited more frequently than unsuccessful sites which in turn were occupied more than those which were not bred at ($H = 9.82$, df = 3, $P < 0.05$). The proportion of sites visited at least once was the same as the previous October (93%). Eleven sites not occupied in October were visited in December and this was balanced by 10 sites which were visited in October but were not occupied in December. Of the four sites which were not visited in either period, three had been occupied but not bred at, and one had held an egg which did not hatch. Thus by the end of December at least 203 (98%) of sites had been visited at least once. 1982 had the highest percentage October occupancy rate of any year
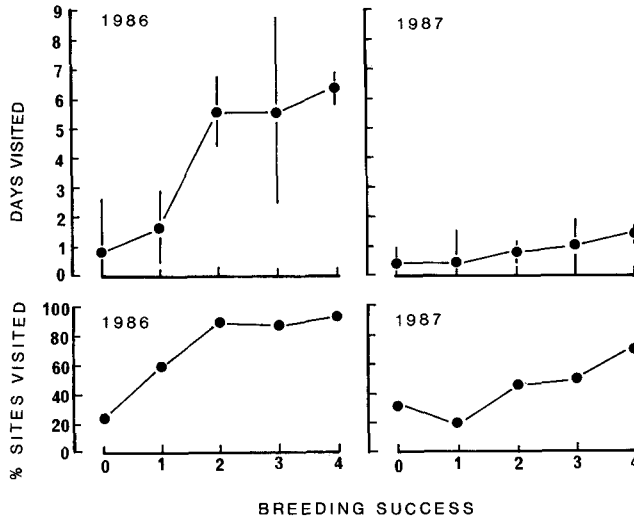
FIGURE 1.   The proportion of sites visited in mid-October 1986 and 1987 in relation to whether the site had been unoccupied (0), occupied but no egg laid (1), egg lost (2), chick lost (3), or chick fledged (4) in the previous breeding season. The mean and 95% confidence intervals are shown. Sample sizes and statistical analyses are given in Table 1.

(Table 1); it would be interesting to look at December occupancy in a year with a lower proportion of sites visited in October.

In the above analyses we examined the effect of breeding success on fall attendance. However, we could also have looked at the effect of fall attendance on breeding success the following season. Breeding success at a site in one year is
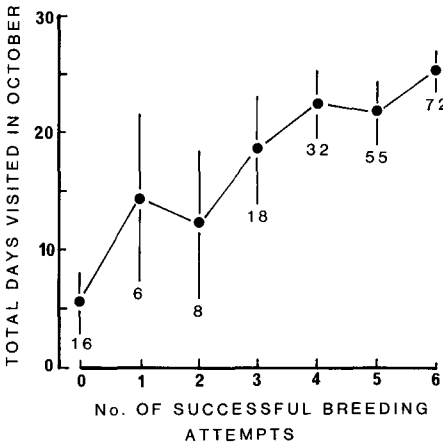

FIGURE 2.   The total number of visits in mid-October in relation to the number of successful breeding attempts at the same sites, 1982–1987. The mean and 95% confidence intervals and the sample sizes are shown.

closely related to success in other years. Thus, many more sites produce no young or many young than expected (Table 2). A similar result has been noted elsewhere (Birkhead and Nettleship 1987). Sites with a relatively high number of fall visits had, on average, a high chance of fledging a chick the following season and vice versa. For instance, sites which fledged a chick in 1987 had been visited significantly more often (median = 8 times, $n = 161$) in the mid-October period in 1986 than had been sites where no chick was produced (median = 4, $n = 46$; Mann-Whitney $z = 17, P < 0.0001$).

SITE DENSITY

The number of visits to sites increased significantly with site density ($r_s = 0.71, P < 0.01$) with an abrupt increase between densities of three to four and five to seven neighbors within three bird lengths (Fig. 4). Although breeding success (in terms of the total number of chicks produced during the study) also increased slightly with density, the differences were small and not significant ($H = 10.3$, df = 14, ns). There was no evidence that the variation in the number of visits to sites of different density was due to consistent differences in the dates these sites were first occupied (1983: $\chi^2 = 35$, df = 40, ns; 1985: $\chi^2 = 40$, df = 60, ns).
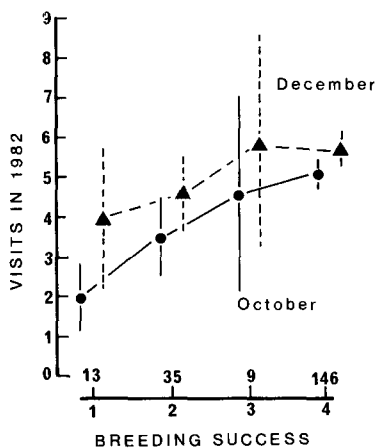
FIGURE 3. The mean number of visits (with 95% confidence intervals) to sites which had been occupied (1), lost an egg (2), or chick (3), or fledged a young (4) on 10 days in mid-October (circles) and late December (triangles) 1982. Sample sizes are also shown.
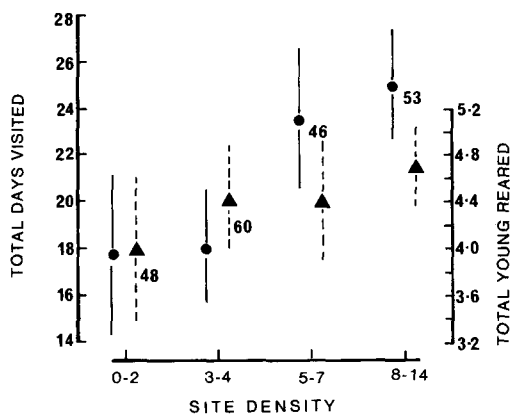

FIGURE 4. The total number of days sites were visited in the observation period in mid-October (left axis, circles) and the total number of young reared at them (right axis, triangles) in relation to site density. Mean values, 95% confidence intervals and sample sizes are shown.

POSITION IN THE COLONY

The total number of visits to sites varied with the distance from the cliff top ($H = 43.5$, df = 15, $P < 0.001$); sites at the very top of the cliff (0–2 m) and very bottom (14–16 m) were visited significantly less often than those in the main central part (Fig. 5; Mann-Whitney $z = 2.4$ and 25.0, $P < 0.01$ and $P < 0.001$, respectively). Within the 3-to 13-m category, height had little effect on the number of visits. In contrast, the total breeding output of a site was not influenced by the distance below the cliff top. There were no significant differences in the proportions of sites at different distances from the top of the cliff which were visited during October 1983 and 1985 ($\chi^2 = 41$, df = 30, ns; $\chi^2 = 41$, df = 36, ns, respectively).

BLOCKED SITES

All 21 sites which were blocked during the 1983–1984 winter were used during the 1984 breeding season. Thirty-three of the adults which bred on them in 1983 were color-banded, 14 of these were seen in October 1983 and all but two bred at the same sites in 1984. Of these two, one was reported dead away from the colony during the winter, the other failed to breed after being displaced by another male. In 1983 the 21 sites fledged 19 young, in 1984 all were successful. On average, the laying date at these sites in 1984 was 3.3 days (SE = 1.5) earlier than in 1983. Forty-

nine adjacent sites were also used in both seasons, the mean laying date in 1984 was 0.4 days (SE = 1.4) earlier than in 1983 which was not significantly different from the experimental sites ($t = 1.56$, ns).

BEHAVIOR

The arrival of birds at the colony each day was fairly synchronized. A few arrived just prior to dawn but the majority flew in 30–40 min after first light and individuals rarely arrived more than 2 hr after dawn. During the main arrival period large numbers of birds circled in front of the cliffs in much the same way as Atlantic Puffins, *Fratercula arctica*, fly in wheels over their breeding colonies. Visual observations suggested

TABLE 2. Breeding success of 207 Common Murre sites, 1982–1987.

Number of chicks produced in the period	No. of sites	Expected[a]	χ^2 [b]
0	16	1	225.0
1	6	11	2.3
2	8	25	11.6
3	18	36	9.0
4	32	40	8.0
5	55	35	11.0
6	72	59	2.9

[a] Expected values were calculated from the Poisson distribution assuming that breeding success in each year was independent.
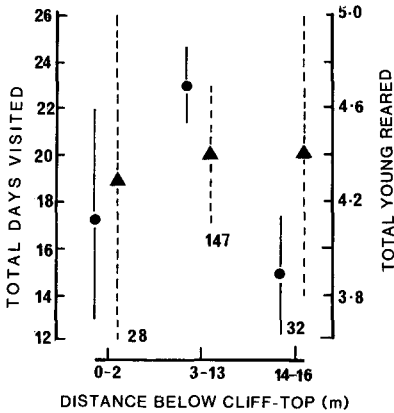[b] Total $\chi^2 = 270$, df = 5, $P < 0.001$.

FIGURE 5. The total numbers of days sites were visited in the observation period in mid-October (left axis, circles) and the total number of young reared at them (right axis, triangles) in relation to the distance the site was below the cliff top. Mean values, 95% confidence intervals and sample sizes are shown.
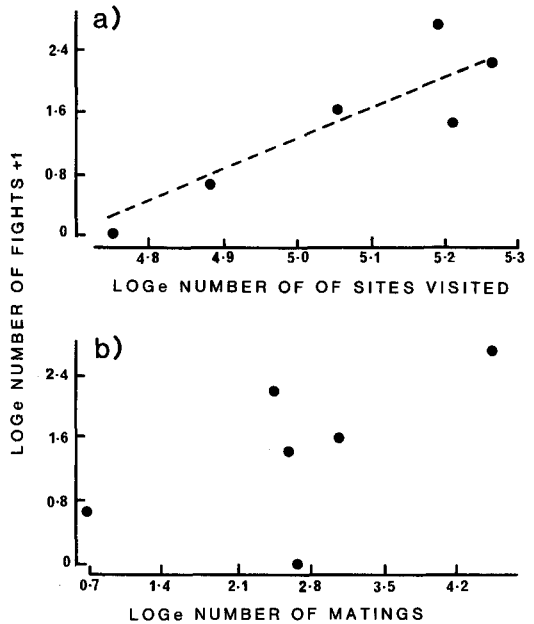

FIGURE 6. The relationship between (a) the number of fights observed and the number of sites visited during 10 days in each October 1982–1987 ($r = 0.89$, df $= 4$, $P < 0.02$), and (b) the number of fights and the number of matings ($r = 0.62$, df $= 4$, ns). All data are log transformed.

that some of these circling birds subsequently landed on the cliff while others went down onto the sea from whence they also apparently flew onto their sites. These observations were confirmed by information obtained during tracking sessions of a Common Murre carrying a radio tag which showed that it flew in from the open sea and went directly to the ledge (five times), flew in and circled in front of the cliff before landing either on the ledge (twice) or on the sea and later came to the ledge (twice), went directly to the sea and later to the ledge (once) or flew in front of the cliff and then departed without landing (once).

The distribution of birds on the cliffs was the same as during the breeding season, except that areas occupied by nonbreeders were deserted. Of 3,893 spot checks of birds on the study area in October 1982, 2,641 (67.9%) showed birds standing or sitting at their site, in 777 (20.0%) birds were preening themselves while on their site, in 245 (6.3%) they were preening their mate or neighbor, and in the remaining 230 (5.9%) murres were involved in miscellaneous activities such as walking, bowing, copulating, or looking at their feet. The high incidence of preening was associated with the majority of birds molting out of winter plumage (Harris and Wanless, in press). Only 12 birds (0.3%) showed any aggression; two were fighting with each other, five were jabbing at neighbors, and five were jabbing at Shags which were occupying the murres' sites. Fights were

very rare and only 31 were recorded in about 120 hr of observation over the six mid-October periods. However, in Octobers when many sites were visited, there were many more fights (Fig. 6). The numbers of fights were positively correlated with matings but the relationship was not statistically significant (Fig. 6). All the matings observed were apparently between members of established pairs and we saw no evidence of extra-pair copulations which are characteristic of the prelaying period (Birkhead et al. 1985).

DISCUSSION

More than half the breeding sites were visited by murres in each mid-October period. The most frequently visited sites were those where birds bred successfully and which were at a high density or in the main part of the breeding area. Color-banded individuals were almost invariably seen at the sites where they had bred the previous season and we have no evidence that immatures, or adults from other parts of the colony, visited the study area during the fall. Taylor and Reid (1981) reported counts of murres on the Isle of May in October 1977 which were ap-

parently three to four times greater than the estimated number of breeding pairs. Consequently, they wondered whether or not the colony might be visited by murres from other colonies. Bourne (1981) saw thousands of murres at another east Scottish colony on Christmas afternoon. These were mainly in a compact group in the center of the colony, rather than dispersed around the ledges as in summer, and he also questioned whether they were all local birds or perhaps included visitors from elsewhere. Our individually identifiable murres were never seen more than a few meters from their breeding sites. It is all but impossible to show that birds do not make casual visits to other colonies outside the breeding season but it seems most unlikely. The number of murres on the Isle of May in the late 1970s is now thought to be much higher than originally recorded (Harris and Galbraith 1983) and thus there is less discrepancy between the summer and fall counts. Bourne's observations describe well the situation on the Isle of May in October with birds concentrated in the central part of the colony whilst the fringe ledges are mostly deserted.

Regular fall occupancy of a site was linked with high breeding success. This could be explained in two ways. First, there could be competition for the best sites, thus murres occupy sites to prevent other birds taking them. This view is supported by the progressive advance in the date of fall return by murres at both the Isle of May and Fair Isle as both populations increased (Taylor and Reid 1981, Harris and Galbraith 1983). In contrast to the findings of Greenwood (1972) and Birkhead (1978) who recorded relatively high levels of aggression in the fall and winter respectively, fights and lower intensity threat displays were rarely seen in Common Murres on the Isle of May. However, in years when high numbers of sites were visited there were many more fights. Our experimental blocking of sites showed that birds did not need to occupy their sites for 4 months in the winter in order to breed successfully. The displaced birds could, however, have spent the winter just watching their sites from nearby ledges. Furthermore, other pairs would also have been prevented from taking the blocked sites. A better experiment would have been to have removed the adults and to have left the sites available for other birds to claim and to have released the original owners later. However, captivity would probably have caused the

birds to lose condition and thus it would be difficult to separate the effects of captivity and site occupation. Fall attendance as a response to competition for nest sites was also considered to be a likely explanation for the Northern Fulmar's return to land in October and November (Salomonsen 1955), but Macdonald (1980) could find no relationship between either the date of return or the frequency of visits and breeding success the previous season. Few data are available on changes in colony attendance by other North Sea seabirds but Black-legged Kittiwakes (*Rissa tridactyla*) returned progressively earlier to one colony in east England each year between 1963 and 1978 (after which the trend was reversed) (Coulson and Thomas 1985). In Britain, Northern Gannets (*Sula bassanus*) spend about 9 months of each year at the colonies and many Shags return nightly to roost at their nest sites (Nelson 1965, pers. observ.). The importance of nest sites for good breeding success and/or competition for nest sites has been shown in all of these species (Coulson 1968, Nelson 1978, Potts et al. 1980).

A second possible explanation is that the birds return to the site in order to maintain or reinforce the pair bond. In many avian species, e.g., the Black-legged Kittiwake, individuals which maintain a stable pair bond have a higher breeding success than individuals which divorce and form new pairs (Coulson and Thomas 1983). In some species there is a resurgence of display and mating at the end of the breeding season which may help to keep a pair together (Nelson 1978). The Common Murre has a rather unusual breeding strategy in that a successful female is left alone at the end of the breeding season while the male takes the chick to sea; she then sometimes associates with other males but these liaisons do not appear to be maintained the next breeding season, at least if the original mate is alive (Wanless and Harris 1986). Therefore, in the Common Murre there is no chance for display until after the birds have completed the postbreeding molt. The return to the colony in fall would thus allow the pair to maintain contact during the winter. In the Black-legged Kittiwake late returning birds have an increased chance of losing their mates (Coulson and Thomas 1983). The same could occur in the Common Murre.

ACKNOWLEDGMENTS

Greenwood, A. T. Sigfusson, and M. D. Mountford improved the manuscript with their criticisms. The Nature Conservancy Council allowed us to work on the Isle of May National Nature Reserve and during part of the summer fieldwork SW was employed as their summer warden. Part of the study was commissioned by the Nature Conservancy Council as part of their program of research into nature conservation.

LITERATURE CITED

AINLEY, D. G., AND R. J. BOEKELHEIDE [EDS.]. In press. The Farallon Islands seabird community: ecology, structure and dynamics in an upwelling system. Stanford Univ. Press, Palo Alto.

BELOPOL'SKII, L. O. 1961. Ecology of sea colony birds of the Barents Sea. Israel Program for Scientific Translations, Jerusalem.

BIRKHEAD, T. R. 1978. Behavioural adaptations to high density nesting in the Common Guillemot Uria aalge. Anim. Behav. 26:321–331.

BIRKHEAD, T. R., S. D. JOHNSON, AND D. N. NETTLESHIP. 1985. Extra-pair matings and mate guarding in the Common Murre Uria aalge. Anim. Behav. 33:608–619.

BIRKHEAD, T. R., AND D. N. NETTLESHIP. 1987. Ecological relationships between Common Murres, Uria aalge, and Thick-billed Murres, Uria lomvia, at the Gannet Islands, Labrador. II Breeding success and site characteristics. Can. J. Zool. 65:1630–1637.

BOURNE, W.R.P. 1981. Winter colony attendance by auks and the danger of oil pollution. Scott. Birds 11:254–257.

COULSON, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of the colony. Nature 217:478–479.

COULSON, J. C., AND C. S. THOMAS. 1983. Mate choice in the Kittiwake Gull, p. 361–376. In P. Bateson [ed.], Mate choice. Cambridge Univ. Press, Cambridge.

COULSON, J. C., AND C. S. THOMAS. 1985. Changes in the biology of the kittiwake Rissa tridactyla: a 31-year study of a breeding colony. J. Anim. Ecol. 54:9–26.

GREENWOOD, J.J.D. 1972. The attendance of Guillemots and Razorbills at a Scottish colony. Proc. XV Int. Ornithol. Congr., (1970):648.

HARRIS, M. P., AND H. GALBRAITH. 1983. Seabird populations of the Isle of May. Scott. Birds 12:174–180.

HARRIS, M. P., AND S. WANLESS. 1988. The breeding biology of Guillemots Uria aalge on the Isle of May over a six year period. Ibis 130:172–192.

HARRIS, M. P., AND S. WANLESS. In press. Moult and autumn colony attendance by auks. Br. Birds.

MACDONALD, M. A. 1980. The winter attendance of Fulmars at land in NE Scotland. Ornis. Scand. 11:23–39.

NELSON, J. B. 1978. The Sulidae. Oxford Univ. Press, Oxford.

POTTS, G. R., J. C. COULSON, AND I. R. DEANS. 1980. Population dynamics and breeding success of the Shag, Phalacrocorax aristotelis, on the Farne Islands, Northumberland. J. Anim. Ecol. 49:465–484.

SALOMONSEN, F. 1955. The food production in the sea and the annual cycle of Faroese marine birds. Oikos 6:92–100.

TAYLOR, K., AND J. B. REID. 1981. Earlier colony attendance by Guillemots and Razorbills. Scott. Birds 11:173–179.

THOMAS, A. 1984. Observations sur la mue prenuptiale des Guillemots de Troil (Uria aalge) de la Reserve du Cap Sizun (Finistere). Travaux des Reserves S.E.P.N.B. (France) 2:54–61.

WANLESS, S., AND M. P. HARRIS. 1986. Time spent at the colony by male and female Guillemots Uria aalge and Razorbills Alca torda. Bird Study 33:168–176.

WANLESS, S., J. A. MORRIS, AND M. P. HARRIS. 1988. Diving behaviour of guillemots Uria aalge, puffin Frantercula arctica and razorbill Alca torda as shown by radio-telemetry. J. Zool. Lond. 216:73–81.