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### Age of First Breeding in Common Murres

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An accurate assessment of the age of first breeding is an essential prerequisite for the formulation of population models. Relevant quantitative data, however, are difficult to collect in species having long periods of delayed maturity. We report on the ages of first-recorded breeding of Common Murres (*Uria aalge*) obtained from long-term studies at two Scottish colonies: the Isle of May, Firth of Forth (56°11'N, 2°33'W) in the North Sea; and Canna, Inner Hebrides (57°03'N,

6°35'W) on the Atlantic coast. On the former island, data reported here were collected from 1981 through 1992, a period during which numbers declined slightly. On Canna, the population more than doubled between 1974 and 1983, but then declined slightly before stabilizing from 1987 through 1992.

*Methods.*—On the Isle of May, murre breeding ledges are accessible, and chicks have been banded in small numbers for over 30 years. Banding has been

TABLE 1. Common Murres of known age and breeding status on the Isle of May, 1991 and 1992.

	Age (years)				
	4	5	6	7	8
<b>1991</b>					
Number seen <sup>a</sup>	21	55	18	19	7
Definitely breeding <sup>b</sup> (%)	0	18	55	42	43
Definitely had never bred (%)	95	75	44	37	14
<b>1992</b>					
Number seen <sup>a</sup>	68	16	35	14	15
Definitely breeding <sup>b</sup> (%)	1	13	51	71	80
Definitely had never bred (%)	99	75	34	14	13

<sup>a</sup> Breeding status of a few individuals was not determined.

<sup>b</sup> Includes a few individuals that bred in a previous year.

carried out in a regular and systematic manner since 1981, with chicks being marked with numbered hard-metal bands (which display the number upright on both sides of the leg) and most with an additional plain or individually numbered year-specific color band. With practice the numbered bands can be read with a telescope at ranges up to 60 m. However, the birds are relatively tame and, normally, can be approached much more closely. Careful searches for banded birds were made daily during each breeding season 1981–1992. The breeding status of each banded bird located was recorded. In 1991 and 1992, almost daily checks were made of the sites held by most known-aged birds (regardless of whether or not the birds had previously bred there) and where non-breeders gathered. Thus, we have details of the birds of each age seen at the colony each season, including their breeding status. A few birds could not be so classified. Some murres were sexed based on mating behavior.

On Canna, breeding areas were only visited once each year 1974–1992. During these visits chicks were banded and attempts were made to catch banded birds that were incubating or brooding.

The age of a bird is given here as the number of calendar years after banding (e.g. a chick hatched in 1982 and found breeding in 1986 is described as being four years old). The term cohort is applied to all chicks banded in a given year. We equate the first record of breeding as the first instance of breeding, although some birds could have bred undetected one or more years before.

**Results.**—We found 42 known-age individuals breeding on the Isle of May. Their ages at first recorded breeding were three years (1 bird), four years (1), five years (15), six years (16), seven years (3), eight years (4) and nine years (2). The median age and modal age were both six years. The records included females breeding at five years (five birds) and six years (two), and males at five years (one) and six (four). The difference between the sexes was not significant (Fisher exact test,  $P = 0.24$ ). In 1991 and 1992, over

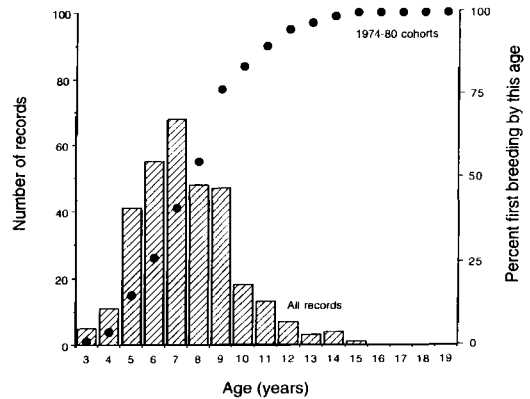


Fig. 1. Ages of first-recorded breeding of 321 known-aged Common Murres (histogram, left axis), and accumulated percentage of 152 individuals from 1974–1980 cohorts found breeding by any age (filled circles, right axis) on Canna.

one-half the six-year-olds seen at the colony bred, or had bred in a previous season, and about one-third definitely did not breed (Table 1). Three (14%) of 22 eight-year-olds were not breeding and, as far as we knew, had never bred.

Both median and modal ages of first breeding of the 321 known-aged individuals on Canna were seven years. The range was 3 to 15 years (Fig. 1). Considering just the 1974–1980 cohorts, most surviving members of which have now probably recruited to the population, the median age of recorded breeding was eight years and the mode nine. There was no evidence that the modal age of first breeding changed systematically during the study. It was: 7 years in the cohort from 1977 ( $n = 31$  individuals), 1978 (26), 1982 (43), 1983 (37) and 1984 (36); 9 in 1975 (21), 1976 (22), and 1980 (33); and 10 in 1981 (15). For the 1974 cohort (13), modal age was either six or eight years. The 1979 cohort produced only four breeding records.

**Discussion.**—Results from both study colonies indicate a considerable range in the age of first breeding of Common Murres. Thus, while some birds were sexually mature and bred when they were three years old, others did not breed until at least nine years. The median age of first breeding appeared to be one or two years earlier on the Isle of May than on Canna, but this may have been an artifact due to differences in methodology. The most obvious potential bias in our estimates concerns the degree to which we failed to detect an individual on the first occasion that it bred. Such errors undoubtedly occurred since many murres breeding for the first time frequently lose their egg soon after laying (de Forest 1993, pers. obs.). This effect could have contributed to the higher age of first breeding recorded on Canna, where our observation schedule was minimal. Both these estimates are higher than those normally used in population

models for the species (e.g. five years; Birkhead and Hudson 1977, Hatchwell and Birkhead 1991).

The best method of obtaining an accurate estimate of the age of first breeding for a species is to follow a series of cohorts until all surviving members have bred. In the Common Murre such a study would require a minimum of 15 to 20 seasons of intensive fieldwork. Even then, there will be problems of interpretation if there are marked differences in the survival of different cohorts. The postfledging survival of chicks reared on the Isle of May does vary from year to year, but resightings of breeding birds spanned seven cohorts, some of which had high survival rates, whereas others had low survivorship (Harris et al. 1992, unpubl. data) Any bias, therefore, should have been reduced. The Canna results should be less affected. Ideally, observations should be made both in the colony where the chicks were banded and elsewhere to determine whether ages of first breeding differ between birds returning to the natal colony and those which emigrate. This is rarely possible.

On the Isle of May we minimized the bias caused by birds losing eggs soon after laying by determining whether or not particular individuals bred by daily observations, but this introduced another bias in that it was undoubtedly easier to see a nonbreeder at the edge of the colony than a brooding or incubating bird in the center. Breeding birds, therefore, may have been underrepresented in our samples. Some non-breeding birds were subsequently never seen again. A proportion of these may have died, but some presumably moved to other colonies or out of sight. For instance, of the 1986 cohort, 72 individuals were recorded in 1990, 55 in 1991, and 35 in 1992, figures that suggest annual survival rates of 76% between 1990 and 1991, and 64% between 1991 and 1992. The survivals of breeding adults over these two periods were 92% and 95%, respectively (unpubl. data). Immatures could well have a greater overwinter mor-

talinity than do adults, but we interpret such large differences as being due to some birds residing, and probably breeding, in areas where we could not observe them. We see no method of reducing these biases.

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