Age of first breeding in Puffin, *Fratercula arctica* (L.)

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Data from the Westmann Islands (Iceland) were used to investigate the age of first breeding in Puffin. Most of the data are from ringing recoveries, with supplementary information from dissections using two criteria: bursa of Fabricius and convolution of oviduct. No 1-, 2-, or 3-year old Puffins were found in burrows, and only two 4-year olds. Very few, if any, 4-year old Puffins are thought to breed Most Westmann Islands Puffins start to breed when 5 or 6 years of age. Males may start to breed before females. The age of first breeding in relation to the state of the population is discussed.

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Long-lived seabirds pose a particular problem when it comes to assessing the age at which breeding starts. Birds of same sex from the same colony and raised in the same year may start to breed at different ages (Lack 1966, Ashmole 1971). There may also be a difference between the sexes in the age at which breeding commences. Coulson (1966) found that most female Kittiwakes, *Rissa tridactyla*, started to breed for the first time when 3 or 4 years old, but most males when 4 or 5 years of age. Conversely, in the Herring Gull, *Larus argentatus*, Drost et al. (1961) found that males commenced earlier than females. Males started when 3–5 years old, but females first bred when 5 years old.

In addition, there may be variations between different colonies of the same species. These variations may be in connection with density or status of the colonies, i. e. whether they are stable, declining, or increasing (Ashmole 1963, Lack 1966). This also means that for any given colony, the age at which birds start to breed may change with time. Information for this is still largely non-existent in birds, although well documented, for example, in the Southern Elephant Seal, *Mirounga leonina* (Carrick et al. 1962). Brooke (1973) found that the age at which Manx Shearwater, *Puffinus puffinus*, first bred had apparently increased over a period of 10–15 years in the Skokholm population (Wales). Furthermore, in Grey Herons, *Ardea cinerea*, which normally breed at the age of two or older, breeding by yearlings may be the chief mechanism by which spectacular population increases take place after heavy mortality during hard winters (Milstein et al. 1970).

The age at which Puffins start to breed has hitherto not been accurately known. Salomonsen (1944) realized that Puffins, in common with many seabirds, had deferred maturity and did not start to breed until they were several years old. Lockley (1953) suggested that Puffins might breed at the age of three and that most bred when four years old. Dickinson (1958) stated that Puffins paired at four, but he considered production of young unlikely. Although this may be the case, Dickinson did

not present any evidence to support his statement.

In the present study, ringing data as well as dissection data on Puffins of known age, collected in Iceland, have been used to add information on the age of first breeding in the species.

MATERIALS AND METHODS

Ringing

Ringing data used in the present study resulted from a massive ringing effort in the Westmann Islands (approx. 63°26′ N, 20°16′ W) off the south coast of Iceland, mainly by Mr. Oskar J. Sigurdsson. The ringing was carried out within the Icelandic Bird Ringing Scheme under the auspices of the Natural History Museum, Reykjavik.

Between 1953 and 1974 (inclusive), a total of 32,121 Puffins were ringed in the Westmann Islands, producing 4,554 recoveries (up to 15th February 1975). Recovery is here taken to mean handling of a Puffin on at least one occasion, dead or alive (or ring only), after ringing. Controls (retraps) are included here. A further 204 recoveries were discarded, 176 of the rings being illegible and details being insufficient for the remaining 28 recoveries.

During the first years of ringing, aluminium rings were used, but since 1959, ringing has mainly been carried out using stainless steel rings. The latter type of rings has proved extremely durable for Puffins and not a single bird has had to be re-ringed on a later recovery, in contrast to those wearing aluminium rings.

From the above total of 4,554, 3,527 were steel-ring recoveries. The present paper is based on 3,494 (99.1%) of these steel-ring recoveries, which were of birds recovered in Iceland during the breeding season (May–September). The remaining 0.9% are of birds recovered abroad, mainly outside the breeding season. These birds were omitted to avoid having to choose arbitrarily a dividing line between consecutive years. Since all the recoveries used here were made during the breeding season, a bird recovered anytime during its 5th summer after ringing (not counting the one in which it was ringed), was regarded as being at least 5 years old.

At the time of ringing, 3 age categories of Puffins were recognized: chick, full-grown, and adult.

Chick: Most of these were ringed when in burrows, although a certain number were ringed during fledging.

Full-grown: These were mostly taken in pole-nets and were at least 1 year old (see section on pole-netting later).

Adult: Birds which were full-grown but taken in burrow, irrespective of whether the burrow was inspected for egg or chick. It is possible that some of these birds were non-breeders, but in the present study all birds caught in burrows were considered breeding birds. A small proportion of Puffins are known to spend time in burrows without breeding (R. E. Ashcroft pers. comm.). In these cases the birds involved would not be distinguished from actual breeders. Another group of non-breeders, frequenting the centre of the colony, can be recognized. These are birds which may spend much of their time inspecting burrows but do not become attached to any one in particular. These visitors could in theory be classed as breeders (= adults) on the criterion given above. However, they are assumed to spend considerably less time in burrow than its rightful occupants and are therefore much less likely to be caught.

Dissections

Dissection data on 91 Puffins ringed as chicks and collected for museum specimens 2–8 years later, between 3rd July and 18th August, were analyzed. The majority of these birds was collected in 1970. The birds were dissected by Dr. F. Gudmundsson to establish sex, reproductive condition (as far as time allowed), and presence (or absence) of bursa of Fabricius.

In the present study, two criteria were used to determine whether birds of known age had reached breeding condition. These were presence (or absence) of bursa Fabricius and oviduct convolutions.

Gower (1939) seems to have been the first to propose that presence of a bursa indicated immaturity in birds. This lymphoid organ is thought to be important in the production of antibodies in juvenile birds (Payne 1971). Involution and later disappearance of the bursa starts just before or at the onset of maturity (Riddle 1928, Hochbaum 1942,

Kirkpatrick 1944, Al-Hussaini & Amer 1959). While the presence or absence of a bursa is thought to be a sure method for ageing birds in species which normally breed at the age of one (e.g. *Lagopus mutus:* F. Gudmundsson pers. comm., *Passer domesticus:* Klima 1957), the situation seems more complicated in birds, like the Puffin, which have deferred maturity (see Elder 1946, Johnston 1956). In these birds it has not yet been demonstrated that known breeders have no bursa while non-breeders of same age have a bursa. For this reason, it is unwise to place too much reliance in absolute terms on this ageing technique in birds with deferred maturity. Condition of bursa is, however, useful as a supplement to other data.

Convolutions of oviduct were used to indicate whether females had laid eggs or not. In birds which have not laid eggs, the oviduct is more or less straight and usually relatively narrow. During the breeding season, the oviduct enlarges enormously and becomes heavily convoluted (Romanoff & Romanoff 1963). The egg rotates when passing down the oviduct (Romanoff & Romanoff loc. cit.) and this rotation presumably produces the spiralling of the oviduct seen in birds which have laid eggs. This condition normally remains thereafter although the degree of convolution and spiralling can be somewhat variable (see Ticehurst 1925). The oviduct may be only slightly convoluted in some birds. In these cases, the females involved have probably never laid eggs. As with the bursa, one has to interpret the data on oviduct convolution with some caution. There is little information in the literature on the reliability of oviduct convolution technique for determining laying in birds, despite the fact that oviduct condition is often recorded as a part of routine museum work.

Pole-netting

Pole-netting is the traditional method in Iceland of catching Puffins for human consumption, as in the Faeroes (see Williamson 1948). The Pole-net (the 'fleygastong' of the Faeroese) was introduced to Iceland in 1875 from the Faeroes (Johnsen 1946).

To be able to evaluate the results set forth in the present paper, it is necessary to outline and consider the pole-netting method, how it works, and its effects on the Puffin population.

Puffin-catchers sit at edges of cliffs where there is good 'flight' of Puffins. Good flights occur at points where circling Puffins come close to the cliff edge, within reach of the catchers. It is important to note that pole-netting does not produce a random sample of the population present at the colony, but samples mainly immature but full-grown birds which spend much of their time circling around the outskirts of the colony (Johnsen 1928, Lockley 1953). Breeding birds, which are engaged in feeding young during the Puffin-catching season (July–August), generally fly straight out to sea on leaving the burrow (Jonsson 1896) and straight back when returning, but disturbance, e. g. from catchers, may cause breeders to circle along the cliffs when returning with food. There is a tradition among Westmann Islands Puffin-catchers not to take birds carrying food, thus unequal sampling is enhanced. Moreover, breeders are said to be more difficult to catch since they are warier than immatures (Johnsen 1928).

Of the ringing total of 32,121 Puffins, 15,079 (46.9%) were caught with pole-nets for ringing purposes and these birds constituted the 'full-grown' category. Moreover, the majority of the recoveries was produced by Puffin-catchers with pole-nets, particularly recoveries of those birds which had been ringed as chicks or full-growns.

RESULTS

Ringing

As mentioned in the preceding section, immature non-breeders characteristically spend much time circling along cliff-edges at the outskirts of the colony. Thus pole-netting as a sampling method differentially samples the colony birds. This is clearly seen if we compare the proportions of different age classes of Puffins taken by Puffin-catchers. Of 1306 Puffins ringed as chicks and later recovered, 1225 (94.0%) were taken by catchers. Similarly, of 1330 Puffins ringed as full-growns and later recovered, 1270 (95.5%) were taken by catchers. In a striking contrast, out of 858 Puffins ringed as adults and later recovered, only 62 (7.2%) were taken by Puffin-catchers.

Table I. Age of Puffins ringed as chicks and subsequently recovered in burrows at the place of ringing in Westmann Islands (Iceland)

Age	Total numbers recovered at place of ringing*	Number recovered in burrows (%)
1	1	0 (0)
2	259	0 (0)
3	386	0 (0)
4	197	2 (1)
5	49	9 (18)
6	28	13 (46)
7	16	8 (50)
8	17	12 (71)
9	16	11 (69)
10	9	7 (78)
11	3	3 (100)
12	5	3 (60)
13	2	2 (100)

*Since no birds were recovered in burrows at other colonies than that of ringing, the total includes only birds later recovered at the place of ringing.

Since most of the recoveries of Puffins ringed as chicks were produced by Puffin-catchers, the age distribution of these birds gives a clue to the age of first breeding, bearing in mind that few breeders are caught by pole-netting. Only the relevant part of the total number of recoveries is given here. There is an unusually abrupt fall in numbers recovered at age 3 (n = 511) to age 4 (n = 246) to age 5 (n = 62), after which numbers decrease at a constant rate up to age 13. The actual fall in numbers is a little smaller than shown by these figures since the figures have not been recalculated to take into account the probabilities of getting 3, 4, and 5 years of age relative to the numbers ringed. The maximum age Puffins ringed as chicks could have reached was 15 years, but no 14 or 15 year old birds were recovered. Although some of this abrupt fall in numbers between age 3 and 5 is due to mortality, most of it probably represents a general change in behaviour of 4- and 5-year old Puffins, which at these ages start to spend more time in the central part of the colony, inspecting burrows and possibly breeding. Consequently, the time spent on circle-flights along cliffs is greatly reduced, and these (plus older) birds are therefore less likely to be caught by Puffin-catchers.

A total of 70 Puffins ringed as chicks were later recovered in burrows, and most of them were presumably breeding. Table I shows the age of Puffins ringed as chicks, later recovered in burrows at the place of ringing. We need not concern ourselves with yearlings since these do not normally come to the breeding colony (Petersen in prep.). It is particularly interesting that no 2- or 3-year old Puffins were recovered in burrows, yet these cohorts formed 66.5% of all Puffins ringed as chicks and later recovered. Thus, the youngest Puffins recovered in burrows were 4 years old (n = 2). One of these birds was recovered (on 22nd June) with an unringed Puffin, presumably its mate, but no egg or chick was found in the burrow. This bird was either occupying the burrow without breeding or had failed in its breeding attempt. On the other hand, many of the older Puffins must certainly have bred at least twice before being recovered.

Of the 70 Puffins ringed as chicks and later recovered in burrows, 14 were refound in burrows containing chicks. The rest may or may not have had chicks in the burrows. Of those 14, five were aged 5, three aged 6 and six aged 8 or older. No 4-year old Puffins were recorded with chicks. In view of this and the few birds aged four recovered in burrows, breeding by 4-year olds is probably rare in Westmann Islands Puffins. R. E. Ashcroft (pers. comm.) found on Skomer Island (Wales) that out of twenty 4-year old Puffins seen prospecting for burrows in 1974, only 2 managed to occupy a burrow over any length of time. Neither of these 2 Puffins bred although 1974 might have been an abnormally poor year for breeding. However, Ashcroft observed one 4-year old Puffin in another study plot carrying food, presumably to a chick. The other 4-year old Puffins which did not obtain burrows, were ousted by Puffins already occupying the burrows entered by the visitors. Moreover, Ashcroft did not record 3-year old Puffins attempting to occupy burrows. Thus, the Skomer Island situation seems similar to that found in the Westmann Islands.

In Table I, we see that progressively more and more birds were recovered in burrows as age increased. It can be expected that once breeding age was attained, numbers recovered in burrows would at once have approached 100% (making allowances for some non-

Table II. Index (length x breadth) of the size of bursa of Fabricius in Puffins of known age from Westmann Islands (Iceland)

Age	n	Range (mm^2)	$\bar{x}$ (mm^2)	SD*
2	5	66.5 - 178.5	101.3	44.2
3	15	31.2 - 117.9	47.6	21.4
4	24	13.4 - 56.8	40.1	9.4
5	3	14.4 - 35.7	24.0	10.8
6	1	- -	(39.6)	-

*SD = Standard deviation

Table III. Presence (+) or absence (-) of bursa of Fabricius and condition of oviduct in Puffins of known age from Westmann Islands (Iceland)

Age	Sex	n	Bursa					Oviduct				
			+	%	-	%	?	Convo-luted	%	Straight	%	?
3	♀♀	14	9	100	0	0	5	(1)*	9	10	91	3
	♂♂	8	8	100	0	0	0	-	-	-	-	-
4	♀♀	18	16	100	0	0	2	(2)*	11	16	89	0
	♂♂	12	12	100	0	0	0	-	-	-	-	-
5	♀♀	3	2	100	0	0	1	(1)*	33	2	67	0
	♂♂	3	1	33	2	67	0	-	-	-	-	-
6,7,8	♀♀	5	1	25	3	75	1	4	100	0	0	1
	♂♂	3	0	0	3	100	0	-	-	-	-	-

*Only slightly convoluted. See text for further explanation.

breeding in every cohort). Since this was not the case, the most likely explanation is that this steady, but somewhat erratic increase, may represent ever-increasing reproductive success of birds in their first few years of breeding. To explain this further, most breeders have chicks in their burrows during the Puffin-catching season. Breeders which have failed in their breeding attempts might have deserted their burrows by this time to join the non-breeding birds circling along cliffs at the periphery of the colony. If reproductive performance increased with age, relatively fewer and fewer birds would be recovered by Puffin-catchers with increasing age after first breeding. This is indeed what was found. Richdale (1957) found in the Yellow-eyed Penguin, *Megadyptes antipodes*, that in the first years of breeding, females showed an increased hatching success with increasing age. Furthermore, Carrick & Ingham (1967) found that no 5-year old Royal Penguins, *Eudyptes chrysolophus schlegeli*, managed to fledge a chick, while reproductive performance of 6–10 year olds was less than that for older adults. If these findings also apply to Puffins, one would infer from Table I that maximum reproductive output was not reached until the birds are 10–11 years old.

Dissections

Data obtained from dissections are summarized in Tables II and III. Measurements of the bursa (Table II) showed that 2-year old Puffins had much larger bursa than 3- and 4-year old birds. The difference between 3- and 4-year old birds was not significant ($t = 1.52$, d. f. $= 37$, $P > 0.1$), whereas the difference between 2- and 3-year olds was ($t = 3.70$, d. f. $= 18$, $P < 0.01$).

All 3- and 4-year old Puffins examined ($n = 52$) possessed a bursa (Table III). In the case of 3-year old females ($n = 11$), one had a slightly convoluted oviduct while the rest had straight oviduct, indicating that most had not bred. Furthermore, in 16 out of 18 females aged 4, the oviduct was straight, while slightly convoluted in the other two. This perhaps indicates that they had laid, but this is by no means proven as pointed out in the Materials and Methods section. Therefore most, if not all, 4-year old females had not bred. It is more difficult to say anything about 3- and 4-year old males since the presence of a bursa cannot be taken to indicate that Puffins have not bred.

Of three 5-year old females examined, 2 had straight oviduct indicating that they had not bred, and one female had a slightly convoluted oviduct. It does not necessarily mean that this last female had laid an egg. As for 5-year old males, two out of 3 examined had no bursa so they may have been sexually mature. The third 5-year male had a bursa. The data on 5-years old Puffins could indicate that males reached maturity on average earlier than females. However, much more material is needed for a final assessment.

All 6-, 7-, and 8-year old Puffins had had breeding experience since all the females possessed heavily convoluted oviducts, and all the Puffins of these ages (except one female) had no bursa.

Involution of the bursa takes several years (3–4) to reach completion. What exactly governs the rate of involution is unknown.

CONCLUSIONS AND DISCUSSION

The present study has shown that Westmann Islands Puffins do not breed in their first two years of life. No 3-year old Puffins were found to have bred, not even prospecting for burrows. An unknown proportion of 4-year old Puffins frequent the centre of the colony, prospecting for burrows. Some of these Puffins may establish themselves as burrow owners but apparently very few breed. Many more 5-year old Puffins occupy burrows and breed. All 6-year old Puffins have probably bred at least once. Although 6-year old Puffins breed, it is suggested that maximum reproductive output is not reached until the birds are 10–11 years of age. There is some indication that sexual difference in age of first breeding occurs, males starting earlier than females.

Although this information now exists on age of first breeding in Westmann Islands Puffins, the different proportions of any given cohort starting at different ages are not known. Such information would be crucial for proper understanding of the population dynamics of the species. This kind of information is still scanty in seabirds in general, as it is very difficult to obtain.

Information on age of first breeding now exists for a number of seabird species (see Lack 1968, Ashmole 1971). Such information on wild birds has, however, usually been based on relatively few ringed birds. For the family Alcidae to which Puffins belong, information is largely lacking. C. S. Lloyd (pers. comm.), using colour-ringed birds, found that on Skokholm Island (Wales) in a sample of 20, 7 Razorbills, *Alca torda*, bred for the first time at the age of four (35%), 12 (60%) at the age of five, and 1 (5%) at six. Published data on other North Atlantic alcid species are mostly inconclusive. However, information exists on the small North Pacific alcid, Cassin's Auklet, *Ptychoramphus aleuticus*. Manuwal (1972) found 3 out of 10 two-year old birds breeding, but over 80% in this species did not breed until at least 3 years of age.

Even where information on age of first breeding exists for birds of a given colony, the same situation (pattern of first breeding of a given cohort) may not apply to other colonies of same species. The variation in age of first breeding, which can be both sex-related and can vary between individuals of same sex, usually extends over 2–3 years (table II in Ashmole 1971). Lack (1968, p. 298) mentioned that some of these variations in age of first breeding were probably hereditary while others were correlated with local conditions. The latter may govern the status of different colonies such that age structure will be quite different depending on whether the colonies in question are expanding, stable, or decreasing (see Odum 1971, pp. 175–179). Consequently the age structure of any given colony may show variations from time to time which in turn may effect the age at which birds start to breed in that colony. Brooke (1973) pointed out that for Manx Shearwaters on Skokholm Island (Wales) the age of first breeding had apparently increased over a period of only 10–15 years. He attributed this change to the colony having increased in the past so that competition with experienced breeders for burrows had led to the exclusion of young inexperienced birds. The expansion of the colony had apparently slowed down or ceased altogether by the end of the 10–15 year period in question. As a second example of differences in age structure between colonies of the same species, Coulson & White (1960) in England found that newly established colonies of Kittiwakes had much higher proportions of young birds than long-established ones.

The information that exists on Westmann Islands Puffins seems to suggest that the population is stable. After a drastic decline between 1850 and 1870 due to undue persecution, the population recovered (Jonsson 1896), and appears to have remained relatively stable since then. Approximately 100,000 Puffins are now taken in the islands every year for human consumption (O. J. Sigurdsson, pers. comm.). There are yearly fluctuations, of course, depending on weather, catching effort etc. As only 7.2% of the catch are breeding birds (as indicated by ringing results) and the Westmann Islands Puffin population is several million strong, there is little danger of overexploitation using present-day methods for catching. The age of first breeding for Puffins in the Westmann Islands should therefore be indicative for a long-established, stable population.

For seabirds in general, we do not know what factors induce birds to breed upon return to the colony. We do know, however, that many seabird populations have non-breeding segments which may include birds fully capable of breeding. The presence of mature non-breeders (so-called 'floaters') seems to have been shown convincingly in one alcid species only. Manuwal (1972, 1974) gave evidence for Cassin's Auklet that a proportion of the sexually mature birds did not breed. On removal of known breeders, Manuwal found that their burrows were rapidly taken over by floaters which laid eggs very soon after start of occupancy of the burrows. Most of the floaters (80%) did not have any previous breeding experience.

A population of floaters may well be present in seabird species other than Cassin's Auklet (including Puffin) which have large non-breeding populations. Presumably, this would mainly hold true for stable and declining populations where potential breeders (floaters) are being excluded from breeding although fully capable. In newly expanding colonies, all (or most) floaters would be expected to breed. This would lead to a general lowering of the age of first breeding for those colonies as a whole, compared to stable colonies. The same effect would probably be produced if stable colonies are too heavily exploited by breeding birds.

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