

THE BREEDING OF AUDUBON'S SHEARWATER
(*PUFFINUS LHERMINIERI*) IN THE GALAPAGOS¹

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FROM February 1963 to April 1964, in the course of studies on the behavior and breeding seasons of Galapagos sea-birds, my wife and I made fortnightly visits to South Plaza Island, an islet just off the east coast of Santa Cruz Island. Most time was devoted to the Fork-tailed Gull (*Creagrus furcatus*), but a considerable number of nests of Audubon's Shearwater (*Puffinus lherminieri*) were also found and regularly checked, and the adult and nestling shearwaters were banded when they were accessible. I am grateful to my wife for much help in the field, and to the Charles Darwin Foundation for the Galapagos and UNESCO for making the work possible.

As regards breeding periodicity, the most interesting result of these visits was the discovery that both the Fork-tailed Gull and Audubon's Shearwater have non-annual cycles, though this is not obvious in either species because breeding is continuous. The present paper deals with our observations on Audubon's Shearwater; the data on the Fork-tailed Gull will be dealt with more fully in a separate publication.

In the Galapagos, Audubon's Shearwater (belonging to an endemic subspecies, *P. l. subalaris*) is a resident and abundant species. It is very much a coastal bird, being uncommon far from land. When sailing among the islands, one frequently passes groups of them feeding on shoals of small fishes. The birds are in constant circulation, flying upwind, landing in the water among the shoal, ducking the head and front part of the body under water as they lunge at their prey, or submerging completely, then fluttering on a few yards to alight again, and so on until they reach the windward edge of the shoal, whereupon they fly round and come up again on their prey from downwind. These feeding groups are often accompanied by Noddies (*Anous stolidus*), which flutter among them and dip down to take the same prey. According to Loomis (1918), who gives a good account of the Galapagos subspecies (quoted by Murphy, 1936), crustaceans are also taken, and at times the birds dive for as long as a minute.

Audubon's Shearwater has previously been reported as breeding in the Galapagos in several different months. Loomis (1918) concluded that some breeding went on throughout the year, as also did Lack (1950), and this was confirmed by L  v  que (1964). In general nesting behavior the Galapagos birds do not appear to differ much from their close relatives in the genus. A single egg constitutes the clutch.

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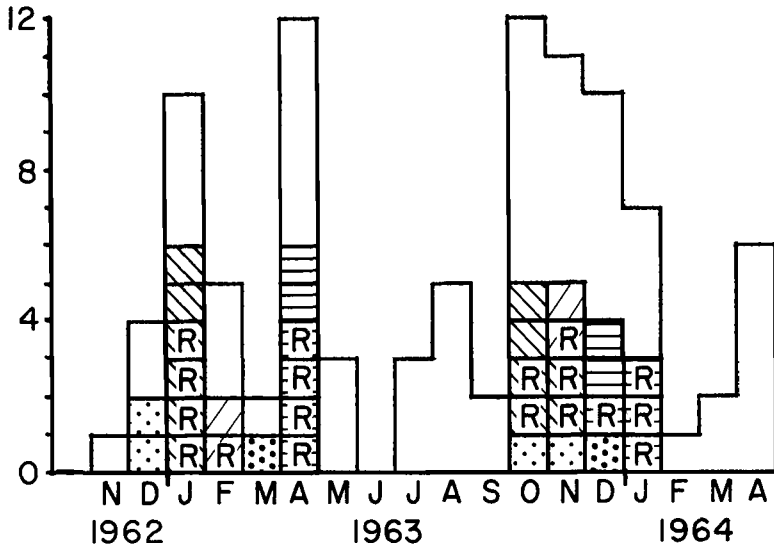


Figure 1. Breeding periodicity of Audubon's Shearwater at South Plaza Island, November, 1962, to April, 1964. The complete histogram shows the months in which the egg was laid in all nests recorded. Nests which were first used in December 1962–April 1963 and then re-used are shaded distinctively for each month: those marked R are nests in which it was proved by banding that one or both of the original pair took part in the second nesting.

On South Plaza Island most of the nests are in holes, recesses, or short tunnels in the broken lava cliff-face, from a few feet above high tide level to the cliff-top (about 60 feet). There are some nests among the boulders at the foot of the cliffs, and a few were found in holes a few feet back from the top of the cliffs. Many of the nests are inaccessible.

The South Plaza shearwaters are preyed upon throughout the year by the Galapagos owl, *Asio flammeus galapagoensis*. During our visits single owls visited the island at dusk from the neighboring North Plaza Island 200 yards away: previously, we heard, a pair had nested on South Plaza Island itself. In the course of 15 months, the wings of over 100 freshly killed shearwaters were collected, as well as smaller numbers of *Oceanodroma castro*, the only other breeding tubenose. In view of this heavy predation by owls, it is of interest that Audubon's Shearwater is strongly diurnal in the Galapagos, though clearly not exclusively so as the owl does not hunt by day.

THE BREEDING SEASON

Figure 1 shows the monthly distribution of 96 nests started from November, 1962, to April, 1964. The numbers recorded from November, 1962, to January, 1963, are relatively too low, as our visits did not begin until Febru-

TABLE 1
INTERVALS BETWEEN LAYING DATES AT 30 NEST SITES

	<i>Interval in Months</i>							<i>Total</i>
	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>10</i>	<i>11</i>	<i>12</i>	
After successful nesting	—	1	3	11	3	2	—	20
After unsuccessful nesting attempt	1	2	2	3	—	1	1	10
Total	1	3	5	14	3	3	1	30

ary, so that of the nests begun earlier we could record only those that had survived until February. In addition, since new holes continued to be discovered throughout the course of the work, the numbers recorded early in the period are somewhat too low relative to the numbers recorded at the end of the period. These sources of bias do not, however, invalidate the conclusion that breeding does indeed continue throughout the year (the gap in June, 1963, being clearly due to chance), but that there were, in this 18-month period, major "peaks" and "troughs" of egg laying.

There was no apparent connection between the amount of breeding and the state of the weather, which was fairly typical of the average. From February to May the weather was calm, hot, and sunny. June marked the transition to the "garua" season, characterized by much stronger winds and more overcast skies and a reduction in sea temperature. December became hot again, and generally hot weather, with weak winds, continued until the study ended. Rainfall in the low-lying Plaza Islands is extremely slight and can hardly be of importance. The peaks and troughs of egg laying may have had some connection with changes in the availability of food, but we have no data on this.

The most striking aspect of the breeding periodicity is, as already mentioned, that it is non-annual: individual birds have a cycle of around 9 months. There were 20 nest sites which were re-used after a previous successful nesting. The intervals between the two laying dates ranged from 7 to 11 months, with a pronounced peak at 9 months (Table 1). In 9 out of these 20 cases banding showed that at least one member of the original pair was involved in the second nesting, and there was no case of a ringed adult, which had bred successfully, re-nesting after any different interval. These results are also shown graphically in Figure 1, from which it can be seen that the pronounced peak of breeding from October, 1963, to January, 1964, was due in large part to the re-nesting of birds which had bred successfully in the less well pronounced peak of January to April, 1963.

There were 10 nest sites in which an unsuccessful nesting attempt was followed some time later by another nesting. In 8 of these 10 cases the intervals between the two laying dates were from 6 to 9 months; the other two were longer, 11 and 12 months (Table 1). In one case, banding showed that the same individual was involved in the two nestings (interval, 8 months). There was no evidence for renesting after any shorter intervals.

There were, however, two cases where the intervals between the laying dates of successive eggs in the same hole were unusually short, but they were exceptions which prove the rule. In the first case, with a two-month interval between eggs (the first egg having disappeared), it was proved by banding that a different pair had taken over the nest hole. In the second case the nest hole was used four times, with unusually short intervals between all the layings. The dates were, however, exactly those that would have been expected if two pairs were alternating at this site. Unfortunately, this could not be proved, as the hole was too deep for the birds to be banded.

The incubation and fledging periods are long, about 50–53 and 70–80 days respectively (see next section). Nevertheless, the average interval between successive layings appears to be little different whether the first nesting attempt fails or whether it is successful. Hence the internal process leading to regression of the gonads (and presumably also the molt) must be initiated very early in the nesting cycle and then proceed unaffected by the subsequent fate of the nesting attempt. Indeed, since eggs that were lost were never found to be replaced, it is probable that the onset of regression of the gonads is determined at the time of laying of the egg. However, other factors must also be involved in determining the date of the next breeding attempt, since the intervals between laying dates are quite variable, ranging from 6 to 12 months, and moreover seem to be more variable when following unsuccessful than when following successful nestings (Table 1).

External, and perhaps also social, factors probably play a part. Otherwise it would be very difficult to account for the markedly uneven distribution of nests throughout the year; instead, whatever the original pattern, after a certain length of time a more or less even distribution of nests throughout the year would surely result. Figure 1 shows that 17 successful nestings, distributed somewhat unevenly in the five months from December, 1962, to April, 1963, were followed by a more compact group of 17 renestings in the four months from October, 1963, to January, 1964. This suggests that, although the second peak was, as mentioned above, in part a simple consequence of the fact that there had been a high level of breeding some 9 months earlier, it was accentuated by some other factor.

For a few weeks before the main peaks of egg laying, we noted a marked

increase in a kind of aerial display. Groups of adults would spend much time whirling round near the cliff face, flying up to it as if to enter their nests and then wheeling away, calling excitedly the whole time. This behavior was not given detailed study, but it seems possible that it may lead to some degree of synchronization between pairs that are about to breed and so contribute to the uneven distribution of nests throughout the year.

INCUBATION AND FLEDGING PERIODS

Since our visits were fortnightly, and on each visit we stayed for only one to three days, it was not possible to obtain very precise figures for the length of the incubation and fledging periods. At a few nests, however, where the hatching date was obtained fairly exactly, the limits of error were reduced sufficiently for the figures to be of some value.

The incubation periods so obtained were: 48 ± 7 , 49 ± 7 , 56 ± 7 , and 56 ± 8 . These are all consistent with a period of 48–55 days, with the average falling probably between 50 and 53 days, which agrees with the 51-day incubation period of *P. l. lherminieri* in Bermuda (Wingate in Palmer, 1962). The very similar Little Shearwater (*P. assimilis*) has an incubation period of 52–53 days (Glauert, 1946), the larger Manx Shearwater (*P. puffinus*) an average period of 51 days (Lockley, 1942), and the Mutton-bird (*P. tenuirostris*) a period of 52–55 days (Serventy, 1958).

The young bird becomes more mobile in the last week or two before it leaves the nest, and in some deep holes, or holes with ramifications, the young tend to retreat out of sight and it is sometimes difficult to be certain whether or not a young bird is present around the time when it is nearly ready to leave. For this reason it is possible that one or two of the recorded fledging periods may be too short. The following twelve periods were recorded:

68 ± 7	71 ± 7	76 ± 7
69 ± 7	73 ± 7	83 ± 7
70 ± 6	75 ± 10	83 ± 8
70 ± 6	76 ± 7	88 ± 8

Clearly the period must be variable, with a minimum range of from 75 to 80 days; probably the great majority fall between 70 and 80 days. Thus it appears to be a little longer than that of *P. l. lherminieri* in Bermuda (about 72 days), *P. assimilis* (70 days), and *P. puffinus* (average, 72 days).

In several cases, one or both adults were found in the hole on the last visit before the young bird left the nest, whereas adults were very seldom found in the nest with half-grown young. And occasionally one or both adults were found in the hole on the visit after the young bird had departed. Hence it seems that the adults' tendency to spend time in the nest

hole at the end of the nesting cycle is to some extent independent of the presence of their offspring.

NESTING SUCCESS

Of 53 nests that could be analyzed for success (those found with eggs, or before the egg was laid, excluding those in which the egg was laid after December, 1963), 31, or 59 per cent, were successful. The causes of failure could not be properly ascertained; in some nests the egg was deserted, in others the egg or nestling disappeared, and in three nests the nestling was found dead.

Marine iguanas (*Amblyrhynchus cristatus*), which scramble all over the cliffs of the Plaza Islands and shelter in the crevices, may have caused some losses: they were sometimes found lurking in nest holes that had been occupied by shearwaters on the previous visit. Other nests must be lost when one of the breeding adults is taken by an owl.

In addition to the losses of known nests, six dead chicks were found lying at the foot of the cliffs, two with their heads bitten off, and two more chicks were found, still alive, crouching at the foot of the cliffs. It may well have been that one of the parents of these chicks had been taken by an owl, and that hunger had driven them to leave the nest. The two that were decapitated had probably been found by an owl after they had fallen to the foot of the cliff.

DISCUSSION

Whenever a bird population is found to breed more or less evenly throughout the year, there is a *prima facie* case for suspecting that the individuals' breeding cycles may be non-annual. For if seasonal variation in the environmental factors that affect breeding success is so slight, or unpredictable, that selection has produced no restricted breeding season, there is no reason why individuals should not revert to an internally controlled cycle. Since Audubon's Shearwater in the Galapagos was already known to breed in all months, it is thus not surprising to find that its cycle is less than annual.

It should be stressed that the reason for the non-annual cycle must be connected with the lack of any effective "ultimate" factors (those factors in the external environment that affect breeding success). There is no lack of "proximate" factors which could serve to time the onset of breeding. Most Galapagos seabirds have normal annual breeding seasons, and in some, such as the albatross, *Diomedea irrorata*, and the petrel, *Pterodroma phaeopygia*, the starting date apparently shows little variation from year to year.

For the present, however, it is quite unclear why Audubon's Shearwater, and also the Fork-tailed Gull, whose food and feeding habits are quite different, should differ in this way from most other Galapagos seabirds. The answer will come only from an intensive investigation of seasonal changes in the marine environment of the Galapagos, the study of which has only just begun.

SUMMARY

Regular checks were made on the nests of *Puffinus lherminieri* on South Plaza Island, Galapagos, from February, 1963, to April, 1964.

Breeding occurs throughout the year, but individual birds were found to have a cycle averaging about 9 months. The average length of the intervals between successive nesting attempts did not appear to be affected by success or failure of the first attempt, but intervals following a failure were more variable.

There was in addition some degree of synchronization between pairs, of unknown cause, leading to peaks and troughs of breeding in different months.

Knowledge of seasonal changes in the marine environment of the Galapagos is insufficient to show why *P. lherminieri*, in contrast to most other Galapagos seabirds, should be emancipated from a fixed breeding season.

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