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BRITISH BIRDS

THE BREEDING OF THE STORM PETREL

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INTRODUCTION

THE Storm Petrel (*Hydrobates pelagicus*) is a breeding bird of the eastern shores of the North Atlantic and the western basin of the Mediterranean. Nearly all the known colonies are on small islands, and probably more than half are in western Britain. The winter range is imperfectly known, but some elements enter the south Atlantic, and numbers have been seen well south of the Cape of Good Hope (Van Oordt and Kruijt, 1953).

This is one of the smallest of the world's sea-birds, averaging about 15 cm. (6 in.) in length, and about 28 grammes (1 oz.) in weight.

R. M. Lockley (1932) was responsible for most of the breeding information given in *The Handbook of British Birds* (vol. IV, p. 27). In a study made at Skokholm, Pembrokeshire, in 1931-32, he obtained six incubation- and six fledging-periods from a total of about twenty nests. His paper gives a general account of the bird's habits during the six months in which it comes to land.

The present paper summarizes some of the results of three seasons' work on this species in 1954-56. I have tried to fill in some of the details, and to add to Lockley's results, using nest-holes in the same stone-faced banks as those he watched twenty-five years ago. Two serious difficulties have had to be contended with: the petrel's exclusively nocturnal activity on land, and a high degree of intolerance of disturbance on the part of many individuals. Moreover, it was not until the summer of 1955 that

I learned of a reliable and simple method of sexing the birds, by cloacal examination after the egg was laid. This technique, pioneered by D. L. Serventy in Australia, was successfully employed on my birds in 1956. Fortunately, most of the 1954 and 1955 breeders returned, and were sexed, in this year.

METHODS OF INVESTIGATION

Thirty-three occupied burrows near the Observatory buildings at Skokholm were selected in the spring of 1954, and provided with observation-shafts leading into the nest-chamber. The same holes were used in 1955, when only twenty-four were reoccupied, and in 1956 when twenty-two were reoccupied. The number of breeding pairs was twenty in 1954, nineteen in 1955, and eighteen in 1956. All birds found in the burrows were ringed, a total of eighty "adults" in 1954, seventy-three (including thirty-eight recaptures) in 1955, and fifty-five (forty-three recaptures) in 1956.

In 1954 the burrows and their occupants were examined daily at about noon and midnight* from 18th May until the egg was laid, or until 16th July in the case of non-breeding holes. Regular night-visits were then discontinued, and were not made in 1955 or 1956, since the disturbance involved seemed out of proportion to the information gained. Day-examination in 1955 and 1956 began before the return of the first birds in April. An additional check on activity in the pre-egg stage and at the non-breeding holes was kept by placing light lattices of bracken-stems in the entrances and the scrapes.

At four burrows in 1954, automatic recorders of a type devised by Dr. John Gibb were used to give more detailed information of the time of visits by the birds throughout the breeding-season. These gave some interesting results, though the clocks which were part of the mechanism were frequently stopped by the entry of vast numbers of earwigs (*Forficula*).

In 1954 and 1955 the bird found on the new-laid egg was marked with red cellulose paint on the head and rump, and a daily check on the share of the sexes in incubation was maintained at those nests where a clear view of the sitting bird could be had. The rest were opened on most days to confirm that incubation was continuing. The lattice checks were continued at the entrances to several burrows during incubation. From the thirty-seventh day, the sitting bird was raised gently with a stick so that the egg could be seen. If it was seen to be chipping, visits might be made twice or three times each day until the hatch.

The chick was weighed at twenty-four hours old, then every forty-eight hours until the first interval in brooding by the parents. For the rest of the fledging-period, in 1954 and 1955, it was weighed twice daily, in the morning and evening. In 1956 only evening weighings were made, apart from a series of special mid-night and morning weighings designed to find the actual rate of

*All times G.M.T.

loss. The beam-balance used weighed accurately to one tenth of a gramme. As a protection against the weather, it was suspended inside a wooden box. Chicks accustomed to the procedure sat quietly on the pan without any covering.

Many observations made away from the study-burrows, and also some references in the Skokholm Bird Observatory records for earlier years, have been made use of in this account.

ATTAINMENT OF MATURITY

The age at which a Storm Petrel may breed is still not accurately known. *The Handbook* (vol. IV, p. 29) says that birds completing moult in May, June and July are probably a year old, and Mayaud (1950) found that one such bird had undeveloped breeding-organs. It is not known if the birds return to the colony in their first summer. Roberts (1940) concluded that some Wilson's Petrels (*Oceanites oceanicus*) spend a non-breeding year at sea, but his evidence was not positive. Some of the larger petrels spend several years away from the colony; Manx Shearwaters (*Procellaria puffinus*) do not normally return until they are three years old, and may not breed until they are five or older. Gross (1947) reports the recovery at a colony of five Leach's Petrels (*Oceanodroma leucorhoa*) ringed as nestlings. Two were one year old, but were not known to be breeding; a three-year-old bird was breeding.

The ringing of young Storm Petrels has not so far thrown much light on this problem: Very few young were ringed at Skokholm before 1954, and only one of these has been recaptured. This bird was two years old. Twenty-seven were ringed at Skokholm in 1954, and sixty-nine in 1955, but none of these has been recaptured, though one 1955 chick was found dead at Bude, Cornwall, only seventy miles from Skokholm, in August 1956. These birds, with forty young ringed in 1956, may provide some recaptures in our trammel-nets in the future.

The limited amount of evidence obtained so far, suggests that once an immature bird has returned, it normally spends no more than one season in the colony as a pre-breeder. Thus of seven birds which occupied burrows throughout the 1954 season without breeding, and which returned to these holes in 1955, all bred in the second year. Five definite non-breeders of 1955 were recaptured in 1956; four bred, and one disappeared early in the season. I have not encountered a case of a bird spending two entire seasons in ownership of a burrow without nesting in the second; but it is possible that immatures may not adopt a regular burrow in their first season in the colony.

THE INEFFECTIVE BIRDS

Before embarking on the account of breeding activities, I must mention the large body of birds which have no breeding responsibilities for all or most of the season. This body consists

of the pre-breeders (immatures, perhaps nearly all of one age-group), the other non-breeders (the very small number of mature birds which do not breed), and the failed breeders (birds which have lost or deserted their egg or chick). Most of these birds possess, or quickly acquire, burrows of their own, but many pay casual visits during the season to birds in other holes.

Of the eighty "adults" ringed in my burrows in 1954, only thirty-eight (48%) were known to be breeding. In 1955 the proportion was thirty-eight out of seventy-three (52%), and in 1956 thirty-six out of fifty-five (65%). The 1955 and 1956 figures will be biased in favour of the established breeders, since no new burrows were opened in these years.

It is not possible to infer from these figures that all the remainder of the birds I caught belonged to the "ineffective" category. I have found, in a few instances, that established breeders may visit strange burrows and even spend twenty-four hours there, during the pre-egg stage. However, such behaviour seems rather uncommon, so that on the basis of the first (1954) sample, the ineffectives may number nearly half the total catch in one season, before any allowance has been made for the return of breeders failing in the study-burrows.

The failed breeders undoubtedly provide a large contingent in this army of unemployed. Birds which have lost their eggs may return for up to ten weeks afterwards, and those which have lost small chicks for up to four weeks. Many do not finally desert the island until after the middle of August, the time of departure for most non-breeders also. In the cases of desertion, one bird of the pair usually fails to return in the rest of the season, but the other continues to visit the nest.

Some idea of the proportion of failures may be gained from the results of an examination of over a hundred and twenty burrows carrying Storm Petrel scent, made in September 1955. Evidence of breeding was found in eighty-two of these holes: fifty-nine held chicks, twenty-three had cold or broken eggs. Three other eggs known earlier in the season had disappeared without trace, and some other holes may have also lost all trace of nesting. The proportion of failures was therefore in excess of 25%, in a summer quite free from adverse weather. A short series of thirty-nine nests carrying evidence of breeding was examined in the very wet and windy summer of 1956. This yielded only twenty-four live chicks, so that the minimum of 38% had failed. The study-burrows are not included in these figures: four out of nineteen failed in 1955, and nine out of eighteen in 1956.

THE BURROW

At Skokholm, where the community at midsummer may exceed fifteen hundred birds, a wide variety of sites is occupied. Of these, perhaps half are in natural crevices—among boulders above high-

water mark, under slabs of Old Red Sandstone broken from the cliffs and outcrops, or in fissures of the solid rock. The remainder are either in the hedge-banks of the old fields, with a few in dry-stone walls, or in burrows of rabbits (*Oryctolagus cuniculus*), shearwaters, and Puffins (*Fratercula arctica*) in more open country. Exceptionally, nests have been found in woodpiles, under wooden huts, and the like.

At the more complex holes several pairs of breeding petrels may share the same entrance, but the nests are usually in different branches of the system. In rabbit, shearwater or Puffin holes, where these are still in use by the original owners, the Storm Petrels excavate a small side-tunnel, or use one which has partially collapsed and can no longer be entered by the larger animals. The entrance to my Burrow No. 22 was shared in 1954 by a pair of shearwaters and several rabbits. The hazards faced by the small petrels in such burrows are considerable. Battered corpses were found in 1955 in both shearwater and Puffin holes. There have also been cases of Puffin (Burrow 10, 1954) and shearwater (Burrow 11a, 1955) entering and destroying nests in my study-burrows. For the most part, however, the entrances are too small to allow the entry of the larger birds. Some of my burrows have entrances barely two inches in diameter.

Many of the burrows must obviously, from their small size, have been excavated by the birds themselves, and birds with earth-encrusted bills and feet have been found on several occasions. Burrow 26 was a mere hollow, where a stone had fallen from a wall, when I first found a bird present on the night of 7th June 1954. Two nights later two birds were there, both engaged in digging. Their actions continued for a few seconds after the beam of my torch shone upon them—a downward scraping motion with the bill, the loosened earth thrown backward with the feet. The hole was a foot deeper on the following day.

The nest-scape, at burrows I have examined, has been from four inches to eight feet (average about $2\frac{1}{2}$ feet) from the entrance, and may be considerably further in some cases. The birds apparently prefer to have a low ceiling over the nest, and often, where my observation shaft appeared directly over the original scrape, they have made a new scrape in a niche at the side of the tunnel, though every effort is made to ensure that the cover is lightproof. Most nests are in complete darkness, but I have found a few so exposed that the sun may shine on to the sitting bird for part of each day.

The nest itself is usually just a shallow depression about three inches in diameter in dry earth or fragments of stone. A few short pieces of bracken and other dry vegetation are very occasionally present, and the stems I used as lattices were often incorporated. Many nests acquire contour-feathers from the sitting birds in late July and August, when a body-moult is taking place. I have never proved that the birds deliberately carry material to the nest, but

David Wilson has shown me a photograph of a very substantial nest, taken at Roaninish, Donegal. This had almost certainly been built by the birds. A. Gordon (1920) found that a rough nest was often made in shallow holes where material was at hand. Roberts (*loc. cit.*) has shown that Wilson's Petrel will construct a substantial nest, and Ainslie and Atkinson (1937) showed the same for Leach's Petrel.

OWNERSHIP OF THE BURROW

In the Skokholm files there are several pre-war records of Storm Petrels returning to the same burrow in successive seasons, but no long-term study of this propensity has been made.

Recaptures of breeders in my burrows serve to demonstrate the attachment of individual birds to particular holes. Thirty-seven 1954 breeders were potentially available for recapture in 1955, if none died in the winter. Sixteen had bred successfully, and fourteen of these returned in 1955, all to the same holes. Twenty-one had failed in 1954; twelve of these returned, ten to the same holes. There were again thirty-seven breeders of 1955 potentially available in 1956. Twenty-nine had been successful, and of these twenty-eight returned in 1956, all to the same holes (the twenty-ninth may have returned, but its burrow was visited only for a few nights in 1956, and it was not caught). Eight birds were failed breeders in 1955, and six of these came back, to the same burrows, in 1956. To summarize, forty-two out of forty-five successful breeders, and eighteen out of twenty-nine failed breeders, were recaptured in the following year, and only two, both failed birds, had changed their burrows.

Most of the failed breeders which did not return in the subsequent year were individuals which had deserted their egg, and never came back to the original burrow, even in the same season.

The forty-two ineffective birds of 1954 provided only eleven recaptures in 1955, seven of which were in the same burrows; and of the thirty-five ineffectives of 1955, only nine were recaptured in 1956, all in the same holes. Twelve of these twenty recaptures had been regular occupants of eggless burrows in the previous year; ten of these were in their original holes.

These figures suggest a very strong sense of ownership on the part of successful breeders. Probably the factor of human disturbance is reflected in the lower level of returns in the failed breeders. Unfortunately my records do not allow me to divide the ineffectives into clear-cut groups of non-breeders and failed breeders, but there seems to be a fairly strong attachment in the non-breeders which have settled down to regular occupation of one hole, and little or no attraction to one hole on the part of wandering failed breeders and casuals.

Mutual ownership of a burrow, coupled with an early return by established breeders (discussed later), would tend to bring the same

birds together as mates in successive years. The burrow is likely to be the prime bond between the pair, for the difficulties of maintaining contact away from its vicinity would seem too considerable to be overcome. Pairs known to me have been permanently dissolved when one bird has forsaken the burrow in the pre-egg stage; such birds have bred elsewhere with new mates. The "pull" of the burrow is not always broken when one bird deserts in the egg stage, for several deserters have turned up again in the original holes in the next year. There was an interesting case in 1954 of both birds of an established pair deserting their burrow in the pre-egg stage, both being found subsequently in new burrows with new mates.

On one occasion in May 1955 I found two birds together in Burrow 12, which had been mates in Burrow 2 in 1954. They were reunited only on one day, and this could have been merely a chance encounter, for the new burrow was very near the old.

The Pre-egg Stage

ARRIVAL

In most years the first Storm Petrels return to Skokholm in the last week of April. To judge from the 1955 and 1956 figures, which the Observatory records for earlier years seem to support, numbers are fairly low until the middle of May, the bulk of the population returning in the second half of that month. Most of the birds I have found to be non-breeders arrived towards the end of May and in early June. The number of strange visitors to the burrows also increased sharply about this time. The population then remains at its highest level until late July or early August; it is only during this period that trammel-netting for ringing purposes is really profitable.

The earliest arrivals appear to be experienced breeders. Twelve birds were caught by day before 15th May 1955, and all these had bred in 1954. All the fifteen burrows visited by that date were breeding burrows in the previous year. In 1956 thirty-one birds were caught by day before 15th May, twenty-four of which were known to have bred in 1955. No bird known to be a non-breeder in one year has been caught earlier than 15th May in the next, its first breeding-season.

THE DURATION OF THE PRE-EGG STAGE

The figures given in Table I are derived only from nests where the pre-egg stage was not lengthened or complicated, to my knowledge, by visits from strange birds.

TABLE I—DURATION OF PRE-EGG STAGE OF THE STORM PETREL
(*Hydrobates pelagicus*)

Burrow No.	Year	1st visit (evening)	Egg laid (early)	Duration of stage (days)	Status of pair comp'd. previous year
8	1954	23 May	1 July	38	—
1	1955	7 May	19 June	42	Same
4		8 May	16 June	39	Same
5		24 April	4 July	71	♂ same, ♀ new
6		27 April	26 June	60	♂ same, ♀ prob. same
8		29 May	29 June	31	Same
9		27 April	12 June	46	Same
11A		3 May	15 June	43	Same
12B		28 April	20 June	53	♀ same, ♂ prob. same
14		28 April	18 June	51	♂ same, ♀ prob. same
19		23 May	27 June	34	Non-breeders 1954
33		9 May	23 June	45	Same
2	1956	3 May	2 July	58	♀ same, ♂ new
6		8 May	21 June	53	Same
11A		1 May	18 June	47	♂ same, ♀ new
11B		4 May	25 June	51	Same
12B		6 May	27 June	51	Same
14		5 May	8 June	33	Same
15		7 May	25 June	48	Same
17A		3 May	25 June	52	Same
17B		6 May	11 June	37	Same
19		6 May	20 June	44	Same
20		30 April	28 June	58	Same
24		30 April	15 June	45	Same
28		16 May	24 June	39	Same
33		8 May	25 June	47	Same

Average duration of the pre-egg stage: 46.8 ± 9.1 days.

In general I have no means of accounting for the considerable variation in the length of the pre-egg stage, but probably much depends on the physiological condition of the individual birds. It is, however, possible to hazard an explanation for some of the longer periods. It will be noticed that the longest period (71 days) was at a nest where an established breeder had to find a new mate. In this instance over a month passed before he succeeded in doing so. There were also three other nests, which I have not included in the table, where the unusually long pre-egg stage can be accounted for. These were Burrows 2 and 24 in 1955, and Burrow 9 in 1956, which had pre-egg stages of 68, 65 and 67 days respectively. In all these nests one bird of the established pair deserted in June, and the remaining birds had to find new mates. They quickly did so, but about thirty days then elapsed before the eggs were laid, on 30th July, 16th July, and 7th July. Such rematings must be responsible for some of the very late eggs and chicks recorded from time to time in Storm Petrel colonies.

FREQUENCY OF VISITS

Lockley found that in the pre-egg stage his birds spent "roughly

one day in every three at the nest", and added "my observations tend to prove that they do not necessarily return on the next evening, and that, if they do, they may not stay over the following day. More often, they do not appear to visit the nest for perhaps two or three nights". In writing this he was striving after a generalization, and I can appreciate his difficulties, for the frequency of night-visits and of day-occupation varies greatly, and no two of my nests have had an exactly similar pattern.

In Table II, I have summarized the records of day-occupation at twenty-eight nests where the pair remained intact in the pre-egg period. It ignores any day-occupation of these nests by strangers.

TABLE II—DAY-OCCUPATION IN THE PRE-EGG PERIOD OF THE STORM PETREL
(*Hydrobates pelagicus*)

Burrow No.	Year	♂ alone	Both birds	♀ alone	Total days occupation	Duration of pre-egg period (days)
4	1955	0	1	0	1	39
6		2	6	0	8	60
8		0	3	0	3	31
9		2	3	1	6	46
11A		0	2	0	2	43
11B		2	2	0	4	>27
12B		1	5	0	6	53
14		1	4	3	8	51
17A		1	2	1	4	>39
17B		2	1	0	3	>23
19		6	3	1	10	34
20		0	4	1	5	>34
28		5	5	0	10	>27
33		6	3	1	10	45
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2	1956	0	4	2	6	58
6		3	4	0	7	53
11B		0	5	1	6	51
12B		0	6	0	6	51
14		1	2	1	4	33
15		0	4	2	6	48
17A		1	4	1	6	52
17B		0	3	2	5	37
17C		0	2	3	5	>52
19		4	5	1	10	44
20		0	4	2	6	58
24		1	3	1	5	45
28		8	4	2	14	39
33		5	5	1	11	47
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Totals		51	99	27	177	

It will be seen that the number of occasions when the birds remained in the nest by day bears no close relationship to the length of the pre-egg stage. One interesting fact that emerges is the tendency for males to remain by day more often than females. L. E. Richdale (personal communication) suggested that this might be due to a stronger and more protracted urge to mate, and hence a greater attachment to the mating chamber, on the part of the male. This state of affairs is common to a wide variety of animals.

Day-occupation had a haphazard distribution throughout the

pre-egg stage, except in the last week when it was uncommon to find a bird in the nest by day. There have been only eleven instances of day-occupation in the week before laying, at fifty nests observed, and only three cases of occupation on the day before laying (in two of these three the occupant was known to be male). The full explanation of this almost complete cessation of day-occupation remains to be found, but it makes available the maximum amount of feeding-time just before the long spells of the incubation begin. It may suggest that the time of actual mating has passed.

Intervals between the days of occupation have varied greatly in length, but a few nests have shown some regularity over short periods, usually with a three-day cycle. Birds have occasionally remained in the nest for two successive days; of twenty-six instances recorded, such birds have been accompanied by their mates on the first day three times, on the second day nineteen times, and on both days twice. In one other case a "visitor" was present on the second day, and only once was the bird alone on both days. In addition, there has been one case of a bird remaining for three days, accompanied by its mate on the second and third. Apparently the usual incentive for a prolonged stay is the arrival of a fresh bird on the second night.

Night-visits, lasting only three or four hours at most, are very much more frequent than day-occupation. The twenty-eight burrows listed in Table II had 439 night-visits quite apart from the 177 occasions when birds remained during the day. Again there is no constant interval between visits; my burrows have been visited for up to twenty-three successive nights, though visiting for more than about ten successive nights is rare. There have also been gaps of up to seven nights between visits; the longer gaps were all early in the pre-egg period.

It is possible that some of the night-visits recorded were made by "visitors" alone, but I believe that it is unusual for strangers to enter unless one of the owners is present, and calling. I have no reliable figures to show how often the visits of the pair coincide, but my 1954 experience of night-visits suggested that the birds are together on more than half of the nights when visits are made.

Many of my nest-records suggest a tendency for visits to become more frequent as the pre-egg period progresses. In an attempt to express this, I reduced the visits at twenty "uncomplicated" nests to "visit-units", in which each unit represents one night of activity at the nest, day-occupation counting two units, and two successive days of occupation counting three units. The average attendance figures at these twenty nests were: first week of the period 4.1 units, second week 4.2; third week before laying 4.6, second week before laying 4.7, last week before laying 5.2; and attendances in any intervening weeks average about the 4.5 level.

SONG AND COURTSHIP

The song of the Storm Petrel is described in *The Handbook* as

“a not loud but penetrating sound consisting of a harsh, uneven purring ‘urr-r-r-r-r’ long sustained . . . ending abruptly with ‘chikka’, almost a hiccough”. I have no quarrel with this description, though Charles Oldham’s statement that the hiccough sounded “like a fairy being sick” evokes for me something much nearer the actual noise. I have not attempted to beat Oldham’s record of an unbroken run of churring with 983 “chikkas”, though I have no doubt that this could be done, for the sound will issue from the burrow for literally hours at a stretch. I have rarely heard a complete burst of song from a bird on the wing, and I doubt if one could prove *The Handbook* assertion that it is used, even “exceptionally”, “as call by flying bird to sitting mate”.

The song may be heard at any time from late April to early September, but the peak is in late May and June, before the eggs are laid. Incubating birds do not sing much, and there is no song after the chicks hatch, so that birds singing in late summer are almost all ineffectives. I believe that the most sustained singers are birds alone in the nest, and I seldom heard song from a burrow which proved to have two birds, when I was making night-examinations in 1954. It is not uncommon to hear a bird singing during the day, particularly in the afternoon and early evening, and this often seems to be a response to noise or movement outside the burrow.

The song appears to serve a dual function of announcing ownership and attracting the notice of other birds. This attraction seems a powerful one, and strange birds, even established breeders from other nests, may often be found at the entrance of a burrow where a bird is singing, if one visits a colony after dark.

The burrow is apparently not defended against intruders in the pre-egg stage, but I have never found a stranger in the scrape after the egg was laid, and only rarely when two birds were already present in an eggless hole. The less sustained nature of the singing, or its complete absence, in such circumstances, may account for this. It is possible that Storm Petrels behave promiscuously at times, though I have no proof of it. Fidelity to one mate could be explained by the fact that intruders rarely return twice to the same hole, whereas the pair meet frequently in their burrow.

In late May, June and early July there takes place a “display-flight” which can often be watched by moonlight or twilight. (Storm Petrels are not at all inhibited by moonlight, rather the reverse; and the earliest birds arrive while there is still some daylight, about ninety minutes after sunset, the latest leaving less than an hour before sunrise). This flight may take place at any hour of the night, and occurs in a fairly limited area above the burrow, where it probably begins and usually ends. One bird closely pursues the other, often within six inches of its tail, and the flight is more rapid and direct than the normal fluttering, erratic action. The course followed is often roughly circular, more

often extremely irregular. At times the birds part, together forming a figure of eight, and resume the chase when they meet again in the centre. A loud call which I write as "terr-chick" is given at intervals, and becomes louder and more frequent as the excitement mounts, particularly if a third bird joins in, as sometimes happens. Snatches of the purring song are given, and several variations of the "terr-chick" call, with the syllables transposed or the first one omitted. There is also a very rapid "wick-wick-wick" which I have heard very rarely.

Occasionally birds can be heard to collide in the air, though I have never actually seen this happen. Williamson (1948) saw collisions between Leach's Petrels in the Faeroes, and regarded them as part of the bird's behaviour pattern, a prelude to entry into the burrow. His birds fell to the ground after colliding, and apparently disappeared into holes.

Roberts has suggested that the white rump (of Wilson's Petrel) may act as a releaser of the aerial chases. Certainly it is designed to elicit a visual response of some kind, and there are many analogies with other birds and mammals, in which white rump-markings displayed by a retreating animal bring pursuit reactions into play.

COPULATION

I have not distinguished any sound from the burrow which might be particularly associated with copulation, though light scufflings and squeakings may be heard when two birds are in occupation. Ainslie and Atkinson (*loc. cit.*) heard a distinctive sound from Leach's Petrels, which they suggested was uttered only during the act of mating, and apparently only once in a season.

It is not impossible that copulation may sometimes occur outside the hole. At Skokholm on 10th June 1955 Geoffrey Stansfield saw two birds hovering close to the ground, one directly above the other. They remained almost motionless for several seconds in the beam of his torch, before flying off into the darkness. It seems not unlikely that he had interrupted an attempted mating.

The Egg Stage

There is no record of a Storm Petrel laying a clutch of more than one egg at Skokholm; indeed, I have not so far traced any well-authenticated record of a clutch of two, though most reference-books imply that this may occur. The egg is pure white, often with a few red-brown speckles at the large end, and weighs about 5 grammes (not .387 as stated in *The Handbook*—a figure which, however, applies to the blown shell alone).

The period of time during which the eggs are laid is protracted. The earliest egg-date for Skokholm is 28th May (several years), and the latest about 20th August (a chick which hatched about 28th September 1956). Most of the eggs are produced in the second half of June and the first few days of July. The graph

in Fig. 1 is derived from the data for fifty-seven eggs laid in my burrows in 1954-56, and shows the percentage of eggs laid by the end of each five-day period through the laying-season.

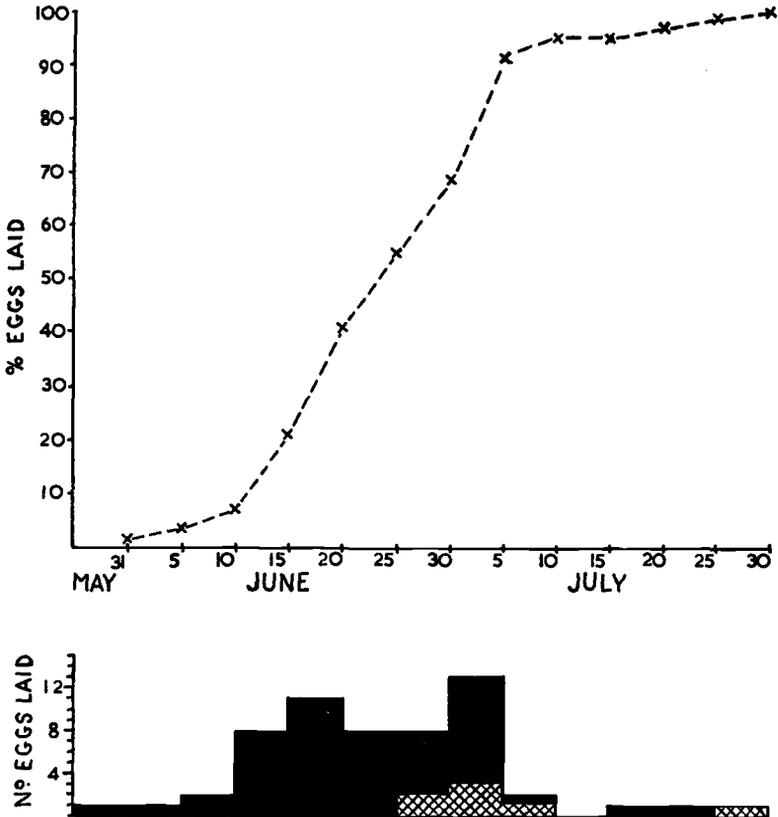


FIG. 1.—THE EGG-LAYING SEASON OF THE STORM PETREL (*Hydrobates pelagicus*). The graph at the top (Fig. 1a) shows the percentage of the season's total of eggs laid by the end of each five-day period, while the histogram below it (Fig. 1b) shows the actual number of eggs laid in each period.

The histogram (Fig. 1b) is derived from the same data, but shows the actual number of eggs laid in each five-day period. The double peak is present when the three years are plotted independently, but is obscured slightly in Fig. 1b, because the 1956 peaks were a day or two later than those of 1954 and 1955. My nest-records for 1955 and 1956 indicate that the bulk of layings in the first peak were by experienced breeders, whilst many of those in the second peak were by newly-formed pairs, or birds which had not previously bred. The cross-hatched sections of the histogram represent eggs which were laid by pairs including at least one non-breeder of the previous year.

Three of the very late eggs have already been referred to in the discussion of the pre-egg stage, and explained by the prolongation of that stage due to rematings. Another (22nd July 1954) was a replacement laid twenty days after the loss of the first egg in Burrow 15a. The laying of replacements is evidently rare in the petrels, though Gross (1935) records one instance in Leach's Petrel, and there is another record for the present species (S. Gordon, 1931). Very late (November) chicks have been found by several writers, and late layings are not rare, but the proportions due to remating and to replacement cannot yet be assessed.

In 1954 and 1955 I found that all the eggs had been laid between midnight and noon, and knew that in four nests they must have been laid during the hours of darkness, for these were left unincubated on the first day. It was not until the cloacal examinations of 1956 that I discovered that the male usually (33 out of 39 records) takes the first incubation shift, which means that the female must return, lay the egg, and depart, all within the space of four hours or less. This seems to imply that she has some physical control over the actual time of laying. She may not always succeed in reaching the burrow, for on several occasions in the 1954-56 seasons I have noticed fresh eggs in open sites to which they could not have rolled or been pushed by the bird. There were usually suitable holes near-by.

THE INCUBATION PERIOD

Table III condenses information about thirty-six nests where the eggs were successfully hatched. The incubation period is given, to the nearest twelve hours. The days on which the egg was not incubated are listed, where known, in the last column; the words "probably continuous" mean that the nest was not examined on all days, but that I have no reason to think there was any interruption in the incubation.

TABLE III—INCUBATION PERIODS OF THE STORM PETREL (*Hydrobates pelagicus*)

Burrow No.	Year	Egg laid	Egg hatched	Incubation period (days)	Remarks on incubation
I	1954	14 June	24 July	40	—
I	1955	19 June	28 July	39	Probably continuous
4	1954	18 June	29 July	41	Not incub. 1st day
5	1954	1 July	11 Aug.	41	—
5	1955	4 July	13 Aug.	40	Probably continuous
6	1955	26 June	5 Aug.	40	—
6	1956	21 June	31 July	40	Probably continuous
8	1955	29 June	7 Aug.	39	Probably continuous
9	1954	9 June	21 July	42	Not incub. 3rd, 29th, 40th day
9	1955	12 June	23 July	41.5	Not incub. 1st day
9	1956	7 July	17 Aug.	41	Not incub. 25th, 30th day
11A	1954	21 June	31 July	40	Continuous
11A	1956	18 June	29 July	41	Not incub. 2nd day
11B	1955	3 July	15 Aug.	38	Continuous
11B	1956	25 June	4 Aug.	40	Not incub. 37th day

Year	Egg laid	Egg hatched	Incubation period (days)	Remarks on incubation
1954	2 July	11 Aug.	40	Probably continuous
1955	20 June	29 July	39	Not incub. 6th day
1956	27 June	6 Aug.	40	Probably continuous
1954	30 May	8 July	39	Probably continuous
1955	18 June	27 July	39.5	Probably continuous
1956	25 June	6 Aug.	42	Not incub. 2nd day, ? later
1954	3 July	15 Aug.	43.5	Not incub. 3rd, 4th day
1955	1 July	9 Aug.	39	Continuous
1956	25 June	14 Aug.	50	Not incub. 7th, 33rd, 35th-39th, 43rd, 44th, 48th, 49th day
1955	26 June	7 Aug.	42.5	
1956	11 June	24 July	43	Not incub. 2nd, 3rd, 4th day
1955	27 June	7 Aug.	41.5	Not incub. 12th day
1955	26 June	5 Aug.	40	Probably continuous
1956	28 June	9 Aug.	42	Not incub. 4th, 35th day
1955	16 July	24 Aug.	39	
1956	15 June	26 July	41	Not incub. 6th day
1954	4 July	13 Aug.	40	Continuous
1955	20 June	29 July	40	Continuous
1956	24 June	2 Aug.	39	Probably continuous
1955	23 June	1 Aug.	39	Continuous
1956	25 June	4 Aug.	40	Probably continuous

Average incubation period: 40.6 ± 2 days.

ockley's six incubation-periods ranged from 38 to 40 days, with average of 39.5. He considered that 38 days was "probably rest the true period" since a nest with this incubation-period had less disturbance than the other five. Two of his forty-hatchings were of eggs which had been left unincubated on day early in the period.

ooking through my records, it is apparent that an egg continuously incubated may take up to forty days to hatch, perhaps htly longer, whereas another may hatch in 39 days despite one of non-incubation. As might be expected, most of the eggs ng over 40 days to hatch are known to have undergone chilling. ggs in my burrows have hatched successfully after two rrow 16, 1954) and three (Burrow 17B, 1956) successive days chilling early in the period, and after up to three widely arated days. Much more remarkable is the case of Burrow (1956) where the egg was chilled for eleven days in all, uding spells of five, two and two days late in the period, and hed after 50 days. Matthews (1954) has discussed resistance hilling by the embryo Manx Shearwater and its value. Well- eloped eggs hatched after up to seven days chilling in the row, and were viable after thirteen days in the laboratory. :thews suggests that resistance to chilling would be more "use- ' to the smaller petrels, particularly in times of erratic food- ply, since they cannot undertake the lengthy incubation-shifts hich the shearwater is capable.

he immediate cause of gaps in the incubation is the failure of

the off-duty bird to return when the sitting bird is ready to depart, and this may not always be related to problems of food-supply. Non-incubation on the first day, which has occurred at four of my fifty-seven nests, is a special case, for here it cannot be hunger that compels the female to leave again on the same night that she has returned to lay the egg, and the likelihood of the male's returning on that night can be no greater than it was in the week preceding laying. At the burrow with exceptionally long chilling-periods, one of the pair was lost in a big gale at the end of July 1956, and never returned; the other bird hatched the egg alone. Several birds from other eggs were prevented from returning at the right time by this same gale, with the result that there were gaps of one or two days in the incubation. Some other gaps, and particularly on the second day after laying, are likely to have been caused by my interference.

SHARE OF THE SEXES IN INCUBATION

Table IV shows the share taken by each bird in the hatching of eight successful eggs, and the number and length of the individual shifts.

TABLE IV—SHARE OF THE STORM PETREL (*Hydrobates pelagicus*) SEXES IN INCUBATION

Burrow No.	Days incub.		No. of shifts				
	♂	♀	1	2	3	4	5 days
9 (1954)	18	21	2	5	9		
9 (1955)	18	23	1	4	8	2	
11 (1954)	20	20	2	4	7	1	1
17A (1955)	17	22	2	6	7	1	
19 (1955)	22	19	4	9	5	1	
28 (1954)	19	21	1	3	8	1	1
28 (1955)	24	16	3	5	5	3	
33 (1955)	20	19	2	8	7		
Totals	158	161	17	44	56	9	2

A larger sample than that given in the table would certainly be desirable, but it seems very probable that the sexes take an equal share of the work. Three-day shifts were the most common, and some nests had a fairly strict three-day cycle of change-overs for a part of the incubation-period.

An interesting feature at all these nests was a change-over during the time the egg was chipping, even though at several nests the previous shift had only lasted for one day.

NIGHT ACTIVITY AT THE NEST

In 1954 the lattices and recorders maintained at the entrances of several nests showed that the nests were being visited, during incubation, far more frequently than change-overs were taking

place, and more attention was paid to this activity in 1955. Whereas change-overs occurred on 38% of the nights available (35-44%, eight nests), visits were made on 70% of the nights (63-83%, five nests), or almost twice as frequently.

I think that these visitors would usually be the unoccupied birds of the pairs; change-overs at irregular intervals, and the rarity of non-incubation spells of more than 24 hours, support this view. I have already suggested that incubating birds do not sing much, and that silent burrows are unattractive to outsiders. (There was nothing to make me suspect that the incubating birds were leaving for short outings—the lattices were pushed inwards.)

It would have been interesting to have had a series of weights of incubating birds, to find how much weight the birds lose during the shifts, and whether they are ever fed by their mates; but after bitter experience in 1954 I have had to avoid this extra disturbance. I did, however, obtain two short series of weights from a particularly stolid pair. The female was weighed during a two-day shift, and fell steadily from 32 to 29.5 grammes in the 48 hours; and in a three-day shift the male fell from 33.5 to 29.

INFERTILE EGGS

There have been four eggs in the study burrows which have been incubated continuously, or with only a one-day gap, for longer than the normal incubation-period, but failed to hatch. One of these was incubated until the 55th day, and again on the 58th and 62nd days; another for 52 days and then broken; another for 50 days, and the fourth for 46 days. None of these had any sign of an embryo. Several other eggs may either have been infertile or excessively chilled, for although they were abandoned not long before the expected time of the hatch, they had no developed embryo when examined. The only one of these which was incubated for over forty days had been chilled for two periods of 48 hours, and one of 72 hours in the second half of the period, and probably this had killed the embryo.

THE HATCH

Chipping of the egg became visible from 72 to 24 hours before the chick emerged, and a low peeping note might be given by the chick from the time a small hole was made. Incubating birds at this time showed more marked signs of anxiety, when disturbed, than at any other time in the incubation-period, and would peck fiercely at the slim stick with which I raised them to see the egg.

(To be concluded)