THE BREEDING BIOLOGY OF THE STORM PETREL

Hydrobates pelagicus

By

D. A. Scott

(St. John's College)

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Edward Grey Institute of Field Ornithology

Botanic Garden

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Abstract

The breeding biology of the Storm Petrel Hydrobates pelagicus was studied between July 1966 and September 1969 on Skokholm Island, Pembrokeshire. The Storm Petrel is a small pelagic sea-bird which comes to land only during the breeding season, on Skokholm between late April and the end of October. It is estimated that about 6,200 pairs breed on Skokholm, and that the total community of birds visiting the colony numbers 17,000 - 19,000. The petrels nest in crevices amongst boulders or burrows underground, and visit the colony only by night.

There is a pre-egg stage of about six weeks, during which the birds visit the burrow regularly by night, and occasionally spend days in occupation. The laying season is protracted, although most eggs are laid between mid-June and mid-July. The mean date of laying is subject to slight annual variation. Experienced birds which have previously bred together lay earlier than birds which have changed their mates and birds which are breeding for the first time. Some evidence suggests that a few birds may lay a replacement egg after loss of the first. The incubation period is long (mean 40.8 days), the incubation temperature low (29-32 deg.C.), and the embryo resistant to gaps in incubation of at least 48 hours. Hatching success averaged 62%, the most important single cause of failure being infertility.

The nestling period is long (mean 68 days) and subject to considerable variation according to the rate of feeding (extremes 61 and 86 days). Most of the chicks which weighed less than 4.5 grams at hatching died within the first 48 hours. The chick is usually brooded for the first six or seven days, temperature regulation functioning from about the fifth day.

Average weight curves do not give a true indication of the growth of the chick because of the great variation both in the length of the nestling period, and in the age at which the peak weight is attained. Development of the plumage, and particularly increase in wing-length, were therefore used to record the rate of growth. Three types of chicks were recognized. About half of the chicks under observation showed similar rates of growth, probably corresponding to the optimal rate. The remainder consisted of

"delayed" chicks, in which the onset of feather production had been delayed as a result of a period of poor feeding during the first two or three weeks after hatching, and "retarded" chicks, in which the rate of growth was slower than normal as a result of poor feeding throughout the nestling period. Because of continued feeding by the parents, delayed and retarded chicks may eventually attain weights at fledging similar to those of "normal" chicks. Well-fed chicks lay down large reserves of food, stored mainly in the form of fat, for utilization during periods of starvation. It is concluded that the Storm Petrel has evolved a flexible rate of growth which enables the chicks to attain normal size and weight at fledging under a wide range of feeding conditions.

The chicks are fed by regurgitation, almost entirely on small fish of the macroplankton. The frequency of feeding is very constant from hatching to fledging, chicks being fed on average on 82 per cent of the possible nights. The average size of the feeds increases up to about the twentieth day, and then remains constant at about 8 grams until the age at which the peak weight is attained. The frequency of feeding and size of feeds decline markedly about seven or eight days before fledging, although few chicks are deserted by their parents more than three or four days before departure.

Usually the chick receives a single meal each night, each parent returning with food on alternate nights. The frequency of feeding is greatly reduced during periods of winds of force seven or more (Beaufort scale). The only period of severe food shortage not attributable to gales occurred in early August 1967, when one third of the chicks under observation died of starvation. Neither the frequency of feeding nor size of feeds decline as the season progresses, suggesting that there is no general deterioration in the feeding conditions around the colony until at least the end of October, by which time most chicks have fledged. Inexperienced and newly-formed pairs seemed to be less efficient at raising chicks than experienced pairs which had previously bred together.

Well-fed chicks survive for periods of up to 96 hours without food before the growth of their plumage is affected. The birds then pass into a semi-poikilothermic state, in which the body temperature falls to between 11 and 15 deg.C. below that of healthy chicks. Recovery after a feed is rapid and complete.

Chick mortality after the first 48 hours was low, except during 1967. The average breeding success in the three good seasons 1966, 1968 and 1969, was 0.49 young fledged per pair, as compared with 0.27 in the poor season of 1967. Experienced pairs are more than twice as successful in breeding as newly-formed and inexperienced pairs. The decline in breeding success as the season progresses is due to an increase in the proportion of newly-formed and inexperienced pairs in the later samples.

Between 15 and 30 per cent of the birds with burrows were not breeding. These petrels, mainly birds in their season prior to first breeding, occupy a burrow regularly between late May and early August, and may then wander about the colony for a short period in late summer. In early July, there is a large influx into the population of young birds, here referred to as wandering non-breeders, which do not adopt a burrow, and probably never even alight on the surface. These birds, in their first season on land, comprise up to half of the birds mist-netted at the colony in late summer. It is clear that about half of these non-breeders are visitors from other colonies. There was no indication that the non-breeders perform any social display in the night sky.

Recaptures of 63 petrels ringed as chicks indicate that young birds do not normally return to the colony for the first time until two years of age, and that between a quarter and a third do not return until three. Some birds, however, return to the seas around the colony in their first summer, and it is possible that a very small proportion visit the colony in this year. Most Storm Petrels probably breed for the first time when four or five years of age.

Non-breeders in their first season at the colony show no strong attachment to any part of the island, whereas breeding birds and non-breeders with burrows restrict their aerial activity to that part of the colony in which the burrow is situated.

Non-breeders with burrows develop bare and vascularized brood patches identical to those of incubating adults. The vascularization of non-breeders and breeding birds regresses during periods away from the burrow. About 70 per cent of wandering non-breeders differ from older birds in that they never pass through a completely bare stage in the brood patch cycle, growth of new down commencing before the last traces of old down have been shed.

Wandering non-breeders have significantly shorter wings than adults, indicating that full size is not attained until at least the second moult. Adults and non-breeders prospecting for burrows arrive at the colony at high weights, and show a gradual decline in weight as the season progresses. Wandering non-breeders do not put on fat reserves before visiting the colony, and are on average 1.5 to 2.5 grams lighter than older birds at the same time of year.

Mist-netting on the nearby island of Skomer (which has a breeding population of 500 to 1,000 pairs) has revealed almost complete intermingling of the wandering non-breeders of this island and of Skokholm, but very little movement between the colonies by older birds. Most of the interchange between widely-separated colonies is also thought to be by wandering non-breeders, although there has been one undoubted case of movement by an adult.

Mortality at the breeding grounds is at present due almost entirely to predation by the gull Larus marinus and the owl Asio flammeus. An analysis of the rate of disappearance of marked birds from the population indicates that the mean annual mortality of adults is about 10-11 per cent. Recaptures of birds ringed as chicks indicate a survival from fledging to first return to the colony of about 45-50 per cent, and to the age of first breeding of about 36-44 per cent. Post-fledging survival seems to be little affected by date of fledging, or type of growth achieved during the nestling period, although weight at fledging is of some importance, heavy chicks on average surviving better than light chicks.

A life table constructed for petrels breeding in the study area suggests that the reproductive output of the population is at present insufficient to balance the losses due to mortality of adults. However, the study area is thought to be a suboptimal habitat for petrels, because of heavy predation from gulls and owls, and interference from other hole-nesting species.

Adult Storm Petrels start to moult their body feathers and tail-coverts during the second half of incubation, their tail feathers shortly after hatching, and their primaries usually during the second half of the nestling period. With few exceptions, all moult of the secondaries occurs at sea during the winter. Non-breeders start their moult about three weeks earlier than adults. The timing of the moult of the primaries seems to be determined more by the feeding conditions in late summer than by the timing of breeding.

The 11 primaries are moulted descendently. In some breeding birds, as many as three or four feathers may be replaced in each wing before departure from the colony. As the moult proceeds, the growth rate of individual feathers, and the interval between shedding of successive feathers, increase. It is suggested that the rate of progression of moult slows down in preparation for the autumn migration, and that the rate of moult speeds up again in the winter quarters.

The 13 secondaries are moulted in four groups more or less simultaneously; feathers 1-4 and 5-7, ascendently, and feathers 8-10, and 11-13 (the tertials) in no rigid sequence. In the three seasons for which data are available, between 48 and 66 per cent of adults, and between 30 and 33 per cent of wandering non-breeders, had been unable to complete the moult of the secondaries during the previous winter. A few birds were found completing the growth of one or two feathers after arrival at the colony, but generally the moult was interrupted for the breeding season. Following an incomplete moult, the next cycle commences with the replacement of the oldest feathers first; following a complete moult, the next cycle always follows the basic sequence.

The 12 tail feathers are moulted centrifugally in pairs, except that the outermost pair is usually replaced before the third, the moult being completed in about four months. About 40 per cent of adults replace one or two tail feathers in spring, and may therefore complete the tail moult in autumn in as little as three months.

There is no indication that juvenile Storm Petrels replace their plumage soon after fledging. It is suggested that the first moult occurs about nine months after fledging, and that successive moults are timed so that no feathers are retained for much more than a year.

The Storm Petrel is very unusual in performing a large proportion of

the moult whilst breeding, and then undertaking a lengthy migration to winter quarters in which moult occurs at a very slow rate. The failure of many birds to complete the moult of the remiges before returning to the colony in spring suggests that food is scarce in the winter quarters.

It is concluded that the laying season of the Storm Petrel on Skokholm is so timed that the young are in the nest at the time when food is most abundant. The light nights in mid-summer, and hence increased risk of predation, may be an important factor influencing the timing of breeding at colonies further north. The late breeding of young birds is thought to be due to inexperience in pairing, rather than an inability to obtain sufficient food to produce an egg any earlier. The low reproductive rate of the Storm Petrel is considered to be the maximum which the species can achieve.

Various factors which may limit the numbers of sea-birds are discussed. It is concluded that direct competition for food resulting in density-dependent mortality of young or adults in unlikely to occur in the Storm Petrel, except perhaps under exceptional circumstances during the winter when food is both very scarce and localized, so that petrels must congregate at high densities where food is available. It is suggested that the numbers of Storm Petrels are more likely to be limited by competition for secure nest-sites. Birds unable to obtain secure nest-sites may either be prevented from breeding, or forced to move into suboptimal sites, where their reproductive output is insufficient to balance their losses due to mortality. A model is presented for the limitation of numbers of petrels at a colony in which there is a limited number of secure nest-sites, but an unlimited number of suboptimal sites. Using figures for breeding success and mortality of young and adults based on the results of the present study, it is calculated that at a colony such as Skokholm in which there are 4,300 secure nest-sites, the population will stabilize at about 6,300 pairs, a figure which agrees closely with the present estimate for the population.

Introduction

The Storm Petrel Hydrobates pelagicus is one of the smallest species of Procellariiformes, a diverse and cosmopolitan group of sea-birds which includes the albatrosses Diomedeidae, shearwaters and petrels Procellariidae, storm petrels Hydrobatidae, and diving-petrels Pelecanoididae. H. pelagicus has a relatively restricted range, breeding on small islands off the west coast of Europe from Iceland and Norway south to north-west Spain and Portugal, and in the western basin of the Mediterranean. No good subspecies have been described. The winter range of the species is very imperfectly known, but it is clear that large numbers winter off the coasts of South Africa (van Oordt and Kruijt, 1953). There is also some evidence which suggests that there is a population wintering in the tropical Atlantic off the coast of West Africa. However, many of the records of petrels from this region are of birds seen between September and December, or between March and May, and could therefore refer mainly to passage birds.

The present paper summarizes the results of a study carried out on the breeding biology of the Storm Petrel on the island of Skokholm, which lies about two and a half miles south-west of the western tip of the mainland of Pembrokeshire (Wales). The island was visited for the following periods: 2nd July to 27th October 1966; 15th April to 17th November 1967; 20th April to 18th November 1968; and 24th May to 7th June, 28th June to 12th July, 19th July to 2nd August, and 24th August to 13th September, 1969.

The island of Skokholm is approximately 260 acres in extent, and bounded by cliffs and boulder slopes which range in height from 50 to 150 feet. The coast line is very indented, with a number of small bays and steep-sided gullies, several of which contain boulder beaches and loose scree slopes. The top of the island is relatively flat with a few isolated rocky ridges, the highest of which reaches about 170 feet above sea level. The rock is almost entirely Old Red Sandstone, although there are a few areas of boulder clay.

The vegetation on the top of the island is largely made up of bracken Pteridium aquilinium, heather Calluna vulgaris, and the grasses Festuca spp, Agrostis tenuis, and Holcus lanatus (Goodman and Gillham, 1954). The only mammals present on the island are a few domestic goats, a flourishing population of House Mice Mus domesticus, and a population of Rabbits Oryctolagus cuniculus which in late summer may exceed 10,000 individuals. Skokholm is however best known for its sea-bird colonies, which are amongst the largest in the Irish Sea. Censuses made during the period 1966 - 1969 have shown that the island supports approximately 30,000 - 40,000 pairs of Manx Shearwaters Puffinus puffinus, 5,000 - 7,500 pairs of Storm Petrels, several pairs of Fulmars Fulmarus glacialis, 1,900 pairs of Lesser Black-backed Gulls Larus fuscus, 1,100 pairs of Herring Gulls L. argentatus, 600 - 800 pairs of Razorbills Alca torda, 120 pairs of Guillemots Uria aalge, and 2,000 - 3,000 pairs of Puffins Fratercula arctica (Skokholm Bird Observatory Reports: 1966 - 1969). A few pairs of Great Black-backed Gulls L. marinus are allowed to breed each year, but as this species is a serious predators on shearwaters, petrels, and Puffins, its numbers are controlled by shooting and the destruction of nests. Apart from these gulls, there are no resident birds which regularly prey on Storm Petrels on Skokholm. Short-eared Owls Asio flammeus occasionally visit the island from Skomer or the adjacent mainland to feed on petrels, but the Little Owl Athene noctua, which bred on Skokholm until the mid 1950s, now occurs only as a rare straggler.

For a description of man's activities on Skokholm, see Howells (1968 and 1969). A map of the island, showing the main names used in the text, the localities at which mist-netting was attempted, and the location of the main study area, is given in figure 1.

Prior to the present study, the bulk of our knowledge of the breeding biology of the Storm Petrel was attributable to studies made on Skokholm by Lockley (1932) in 1931 and 1932, and Davis (1957) from 1954 to 1956. Lockley made observations at a small series of nests from laying until fledging, and gave a general account of the petrels' activities on land. Davis carried out a similar study, but on a larger scale. In each year of his study, he made observations at about thirty burrows from their first occupation by adults in spring until the fledging of the chicks and departure of the adults in autumn. Both Davis and Lockley lacked an efficient method of catching petrels in flight, and had therefore to confine their studies to the activity of the birds at the nest.

The aims of the present study were to extend our knowledge of the breeding biology of the Storm Petrel as described by Lockley and Davis, and to investigate some of those aspects of the species' biology which the earlier workers had been unable to study because of lack of suitable techniques. Of particular importance during the present study was the use of mist-nets, with which it was possible to catch large numbers of Storm Petrels of all age classes in flight over the colony.

A valuable feature of the Skokholm population of Storm Petrels was the presence in it of a large number of birds which had been ringed several years previously, and which were therefore known to be of breeding age. Ringing was first carried out on Skokholm in the 1930s, but until mid-summer of 1958, the rings used were of poor quality, and seldom survived in a legible state for more than four or five years. Between 1958 and 1965, 2,300 petrels were ringed with monel rings, which have been shown to survive with negligible wear for at least eleven years. A further 78 birds which had been ringed before mid-summer 1958 with aluminium rings were re-ringed with monel rings. During the four seasons of the present study, 594 of these birds were recaptured, including 102 which had been ringed before 1960, and one which had been ringed in 1950.

Four serious difficulties had to be contended with. Firstly, Storm Petrels are exclusively nocturnal on land, all aerial activity at the colony being confined to the hours of darkness. The feeding grounds of the petrels are some distance from the colony, so that it was not possible to determine the feeding behaviour of the birds, or indeed their movements to and from the island. Secondly, the majority of petrels nest in inaccessible sites in crevices amongst boulders, or in burrows deep underground. Thirdly, it was not possible to age or sex birds on measurements or plumage characters. Some separation of age classes was possible from an examination of brood patches, but it was never possible to say with certainty that any particular bird was breeding. As far as is known, the only method of sexing living Storm Petrels in the hand is by cloacal examination shortly before, or shortly after, laying.

The fourth, and most serious, difficulty encountered during the present study was the sensitivity of the species to interference at the burrow.

It became evident in 1966 that the removal of petrels from the burrow at any time during incubation usually caused the birds to desert. Furthermore, as Davis (1957) discovered, the handling of birds at night during the pre-laying period of occupation of the burrow has a similar effect. Petrels could be handled with relative safety by day during the pre-laying period, but even then, some birds deserted after the first occasion of handling, and few would tolerate regular removal from the burrow. Petrels were at their most tolerant to interference when brooding small chicks. However, although handling at this time never caused desertion, there was some indication that it affected the birds' rate of feeding over the following two or three days, and therefore had a detrimental effect on the growth of the chick.

For the detailed study of the breeding of the petrels, a series of burrows was selected in 1,440 yards of wall around the observatory, in the area in which Lockley and Davis had carried out their studies. (See figure 1). However, since it was clear that this was not the preferred breeding habitat of the Storm Petrel, a further series of burrows was selected in more typical sites on boulder slopes around the cliff-tops. The data on timing of breeding, and overall success of breeding, collected at burrows in these natural sites, were not significantly different from those obtained at burrows in the main study area. It was not possible to carry out a similar study at a series of burrows in the presumed optimal breeding habitats in loose scree slopes and boulder beaches, because of the nature of this terrain, and the inaccessibility of the nests.

Full details of the population census carried out on Skokholm during the present study are given in Appendix VIII. The breeding population was estimated at approximately 6,200 pairs, and not less than 5,000, or more than 7,500. The total population of full-grown birds in late summer probably contains about 17,000 to 19,000 birds.

Methods of Study

The present investigation of the breeding biology of the Storm Petrel followed two main lines; observations of birds in the burrow, and examination of birds mist-netted in flight over the colony at night.

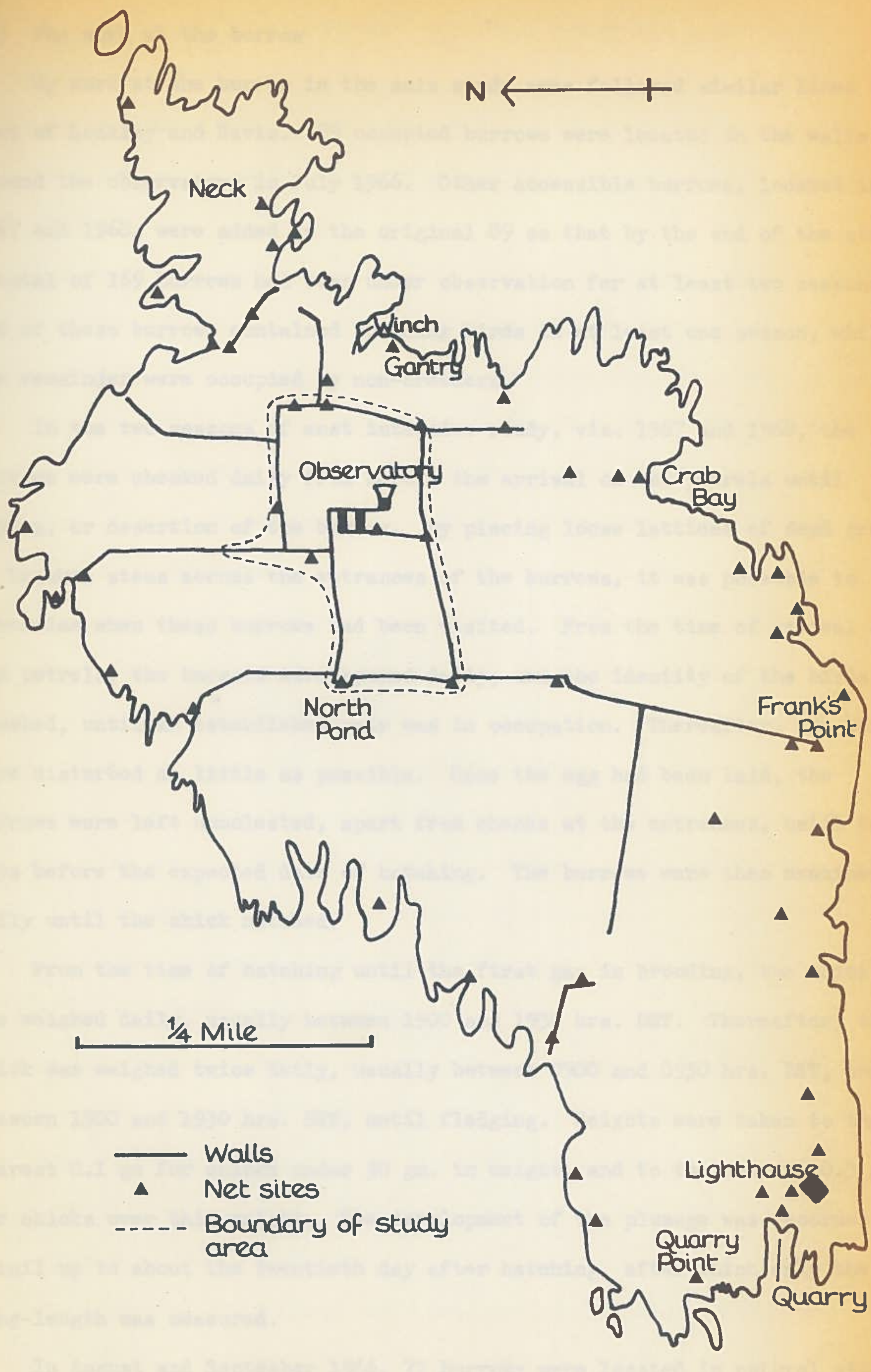


FIG. 1. SKOKHOLM ISLAND

(i) The work at the burrow

My work at the burrow in the main study area followed similar lines to that of Lockley and Davis. 89 occupied burrows were located in the walls around the observatory in July 1966. Other accessible burrows, located in 1967 and 1968, were added to the original 89 so that by the end of the study, a total of 169 burrows had been under observation for at least two seasons. 139 of these burrows contained breeding birds in at least one season, whilst the remainder were occupied by non-breeders.

In the two seasons of most intensive study, viz. 1967 and 1968, the burrows were checked daily from before the arrival of the petrels until laying, or desertion of the burrow. By placing loose lattices of dead grass or bracken stems across the entrances of the burrows, it was possible to determine when these burrows had been visited. From the time of arrival of the petrels, the burrows were opened daily, and the identity of the birds checked, until an established pair was in occupation. Thereafter, the birds were disturbed as little as possible. Once the egg had been laid, the burrows were left unmolested, apart from checks at the entrances, until two days before the expected date of hatching. The burrows were then examined daily until the chick hatched.

From the time of hatching until the first gap in brooding, the chick was weighed daily, usually between 1900 and 1930 hrs. BST. Thereafter, the chick was weighed twice daily, usually between 0900 and 0930 hrs. BST, and between 1900 and 1930 hrs. BST, until fledging. Weights were taken to the nearest 0.1 gm for chicks under 30 gm. in weight, and to the nearest 0.5 gm for chicks over this weight. The development of the plumage was recorded in detail up to about the twentieth day after hatching, after which only the wing-length was measured.

In August and September 1966, 72 burrows were located in natural sites on the cliffs. In 1967 and 1968, these burrows were examined at three day intervals from late May until the egg was laid. From the time of laying, the procedure was identical to that at the burrows in the main study area, except that the chicks were weighed only once daily throughout, usually between 1400 and 1600 hrs. BST.

In 1969, it was not possible to maintain regular checks at the burrows, and the data obtained were sufficient only to determine the approximate date of laying, and success of breeding. In addition, a short series of weights and wing-lengths of chicks were taken in late August and early September to give some indication of the rates of growth achieved during that season.

(ii) Mist-netting

Mist-netting was attempted at least once in all areas which appeared suitable for petrels, and in which it was possible to erect a net. Particular attention was given to the walls in the study area, in an endeavour to capture, and thereby be able to examine, birds of known breeding status throughout the breeding season. Netting in the main study area also provided many useful recaptures of birds which had deserted their burrows as a result of my disturbance.

Mist-netting was attempted on most nights on which the weather was favourable for it. Between 30 and 360 feet of net were erected at the chosen site, and checked every 15 to 45 minutes from dusk until dawn. The birds were either taken back to the observatory or to a sheltered spot some distance from the nets for examination and ringing. In each full examination, the following details were taken: (i) ring number; (ii) locality of capture; (iii) time of capture, usually to nearest 15 minutes; (iv) weight, to nearest 0.1 gm when weighed in observatory, otherwise to nearest gram; (v) wing-length, in millimetres; (vi) condition of brood patch; (vii) condition of plumage with regard to moult, presence of a pale area on the forehead and crown, and presence of albinistic feathers in the normally dark parts of the plumage; (viii) whether or not the bird regurgitated food whilst in the net or during subsequent handling; (ix) presence of ectoparasites; and (x) injuries to the legs or feet.

The number of birds which could be examined in detail in one night was about 80 to 100. However, by dispensing with the examination, and recording details (i) to (iii) only, up to 300 birds could be handled by a single ringer without difficulty. As the catches during much of the season usually varied between 100 and 200 birds, it was customary to start by recording all details, and then to dispense with certain aspects of the examination as the rate of capture increased.

During the present study, mist-netting was carried out at 54 sites (see figure 1) on a total of 208 nights. The monthly totals of nights on which netting was attempted were as follows: April 11; May 33; June 36; July 57; August 39; September 25; October 6 and November 1. The average size of the catches was 87 birds, the largest being 341. In all, 18,147 captures were made, involving 12,213 individuals. The yearly totals of individuals handled were: 1966 1,943; 1967 3,094; 1968 4,907 and 1969 5,518.

To minimize disturbance to breeding birds, netting was not attempted at any one site more frequently than once a fortnight, and in practice, few sites were visited more often than once a month. The scope of the programme of mist-netting was severely restricted by interference from Manx Shearwaters, 30,000 to 40,000 pairs of which breed on the flat top of the island. This species, unlike the Storm Petrel, visits the colony in large numbers only on dark nights. On moonless nights, or nights with thick overcast, netting for Storm Petrels on the top of the island was impossible, because of the damage caused to the nets by the shearwaters. Interference was particularly severe in the petrel colonies in Crab Bay and in the main shearwater colony near the lighthouse. Here, netting for petrels was possible only on nights when there was a clear sky, and a full moon from dusk to dawn. In the study area, where shearwaters were considerably less dense, netting was possible on most nights when there was some moonlight. However, on dark nights, netting activities were confined to colonies of petrels on the cliffs and in the bays, where there were few, if any, shearwaters breeding.

The most important factor influencing the frequency of netting and the choice of net-site was the weather. No mist-netting was attempted in rain, thick mist, or strong winds. Ideally, calm conditions, or a light breeze not exceeding force 2 (Beaufort scale) were required, but netting could be carried out successfully in a wind of force 3 at sites where the nets could be arranged in a line end-on to the direction of the wind. It was possible, when the direction of the wind was between north-west and south (through east), to position the nets in a sheltered bay where netting was feasible in winds of up to force 5. Unfortunately, the prevailing winds on Skokholm are west and south-west, and as there are no suitable sheltered bays on the east end of the island, mist-netting was often impossible, particularly after mid-September.

During 1966, 1967 and most of 1968, the nets were disturbed as little as possible between visits, and it was assumed that the birds caught were a representative selection of the birds in flight over the area. Towards the end of 1968, however, tape-recordings of the churring "song" of petrels were played to attract birds into the nets. It was found that an amplified recording of churring, played under the nets, would increase the catch-size by several fold. This procedure was adopted on most nights in 1969. The major disadvantage of the use of the tape-recording was that the sample of birds caught was no longer representative of the birds in flight over the net-site, since breeding birds were attracted to areas which they would otherwise rarely visit, and non-breeders seemed to be attracted to a greater extent than breeding birds.

(iii) Other lines of study

During the early part of the breeding season in 1967 and 1968, the island was explored at night in an endeavour to locate as many occupied burrows as possible, for eventual estimation of the size of the population. To aid in this, in 1967, counts of birds in flight over the colony were made at 128 sites around the coast, during the period of greatest aerial activity of breeding birds in early June. During the latter part of the breeding season in 1966, the island was explored by day for accessible chicks for ringing. In 1967 and 1968, searches for chicks were undertaken at night during the peak period of fledging in late September and early October. Neither the diurnal searches for chicks in the burrows, nor the nocturnal searches for chicks on the surface, proved very successful, and in the four seasons of study, a total of only 220 chicks were ringed, including those in the burrows in the study area.

Three brief visits were made to the colony of Storm Petrels on the nearby island of Skomer; on 2nd/3rd August 1969, 18th - 24th August 1969, and 6th - 8th June 1970. Work on Skomer was restricted to searches by day for suitable breeding areas, and mist-netting at as many of these sites as possible.

Section I : The Breeding Cycle

Lockley (1932) and Davis (1957) described certain aspects of the breeding cycle and burrowing activities of the Storm Petrel in some detail. The present section is therefore devoted mainly to the findings of the present study which are additional to those of earlier workers. Results which merely confirm the work of Lockley and Davis are summarized in Appendix tables 1 - 7.

(1) The burrow

Storm Petrels breed on Skokholm in a wide variety of sites. Both Lockley and Davis considered that about half of them occupied sites in the walls or in burrows of rabbits, shearwaters and Puffins. A more extensive search during the present study revealed that only about a quarter of the population occupied such sites. (See population census in Appendix II). The remainder were in natural crevices in beaches of raised boulders, or old scree slopes. The largest concentration of breeding petrels on Skokholm was found in a bay, aptly named the Quarry, at the south-west corner of the island. Here approximately 2,000 pairs of petrels were breeding amongst a jumbled heap of boulders less than half a hectare in extent, at the base of one of the highest cliffs on the island. In some of the larger crevices, which extended several yards down amongst the boulders, a few pairs of petrels were found incubating eggs quite openly on the earthen floor. However, the great majority of nest-sites were totally inaccessible to human intrusion, and indeed to anything larger than a petrel.

There was clearly little competition for burrows with other hole-nesting birds and rabbits, since the main petrel colonies were in areas where there were few, if any, rabbits, shearwaters, or Puffins. Only Razor-bills commonly shared similar areas, but they required large crevices which were unsuitable for petrels.

As Davis showed, territorial defence of the breeding site is restricted to defence of the scrape in which the egg is laid. Several pairs of breeding birds or non-breeders may share the same burrow or crevice, occupying scrapes only inches apart, apparently without conflict.

Intraspecific competition for nest-sites in the study area appeared to be rare. Prolonged occupation of a burrow by two pairs occurred on only three occasions at a total of 241 burrows occupied in 1967, 1968 or 1969. In two cases, one of the pairs deserted, and the other assumed undisputed ownership. In the third burrow, one pair laid an egg which was ejected from the burrow soon after laying, presumably by the second pair. The second pair laid an egg nine days later, but this also disappeared soon after laying.

As a result of breeding failure, or excessive human interference, a number of burrows were deserted, and were therefore available for occupation in the following year by birds in search of a burrow. However, in each season of study, a number of burrows which had been deserted in the previous season remained unoccupied, or were visited on only one or two occasions. Of a total of 65 burrows vacated during the study, only 23 (35%) had been reoccupied by breeding pairs or prospective breeders by the end of 1969. In view of the rarity of intraspecific competition for burrows, and the frequency with which suitable burrows were left unoccupied, it is concluded that there was no shortage of nest-sites for petrels in the main study-area. This conclusion does not necessarily apply however in the dense colonies in the scree slopes and boulder beaches, where detailed work at the burrow was not possible.

The nest-sites were clearly chosen for their inaccessibility to the main predators, gulls and owls. The great variety of sites, ranging from burrows extending several yards underground to small and relatively exposed crevices in the cliffs, suggested that the microclimatic conditions in the burrow were unimportant. A short series of measurements taken at two typical burrows in the walls showed that in such sites the temperature inside the nest-chamber was generally 0.5 to 1.0 deg. C warmer than air temperature, and that the diurnal fluctuations in temperature in the nest-chamber were less extreme than outside. In the more exposed sites in crevices amongst rocks, the fluctuations in temperature at the nest-chamber would presumably follow closely those of the outside air, and there can be little doubt that Storm Petrels do not select burrows for their insulation properties. Micro-climatic conditions in the burrow may be of importance only in those species of petrel breeding in an extreme environment at high latitudes (Roberts, 1940).

(2) Activity at the colony

Storm Petrels are present on Skokholm from the last week of April or first week of May until the end of October or early November. The earliest petrels ever recorded on Skokholm were two birds caught on the night of 18th April 1967. The first birds to return in spring are experienced adults, most of which have reoccupied their burrows by 20th May. Birds breeding for the first time and non-breeders prospecting for burrows arrive somewhat later, usually during the second half of May.

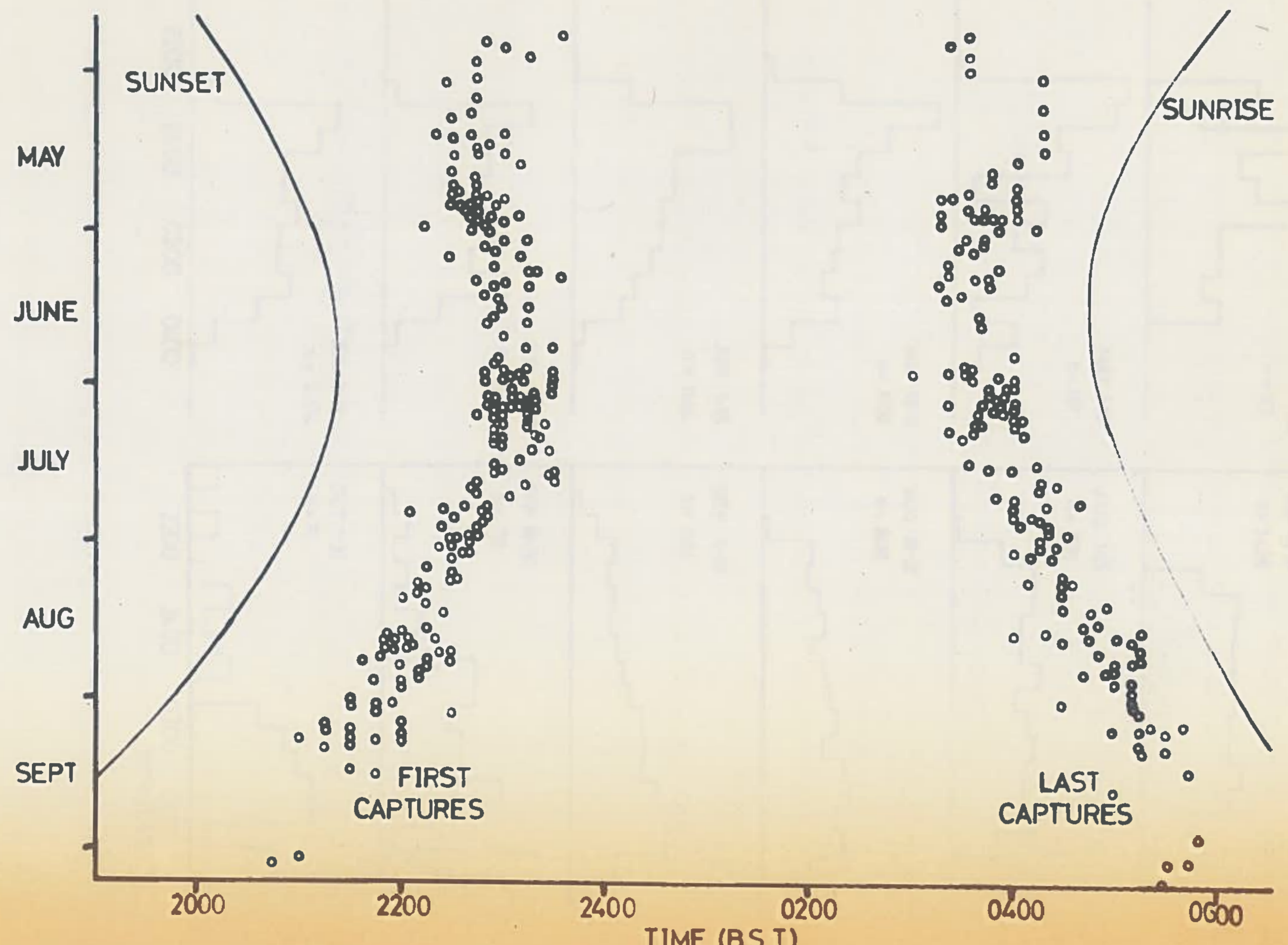
Departure is a more gradual process. Failed breeders and non-breeders which have spent a season in a burrow may leave the colony in late July or August, whereas late breeders may still be feeding chicks in early November. In the late breeding season of 1967, three of the sixty-one chicks under observation were fed regularly up to 12th November, and the last chick fledged on 17th. In general, all those petrels not engaged in rearing chicks have left the colony before the middle of September. Breeding birds depart at about the time that their chicks fledge, usually in the last week of September or first two weeks of October.

All aerial activity at the colony occurs during the hours of darkness. Petrels have never been observed offshore in the evenings, and it appears that the birds remain some distance from the island until after the sun has set. Throughout the season, the first arrivals at the colony appear over the island about 90 minutes after sunset, and the last birds to depart do so about 50 minutes before sunrise. The times of arrival and departure, as determined from the times of first and last capture on nights when netting was continuous from sunset until sunrise, are summarized in figure 2. On cloudy or moonless nights, arrival is slightly earlier, and departure later, than on clear or moonlit nights. Furthermore, birds breeding in secure sites in rocks just above high water mark arrive earlier, and depart later, than those breeding in sites on top of the island. Clearly, the precise timing of arrival and departure is not rigidly fixed by some internal clock, but is dependent on light intensity, and the risk of predation.

The intensity of aerial activity at the colony varies according to time of night, and time of year (see figure 3). In late April, the few adults visiting the colony confine their aerial activity to the middle of

Figure 2. Times of arrival and departure of Storm Petrels at Skokholm colony

Each point gives time when first or last bird was caught on a particular night



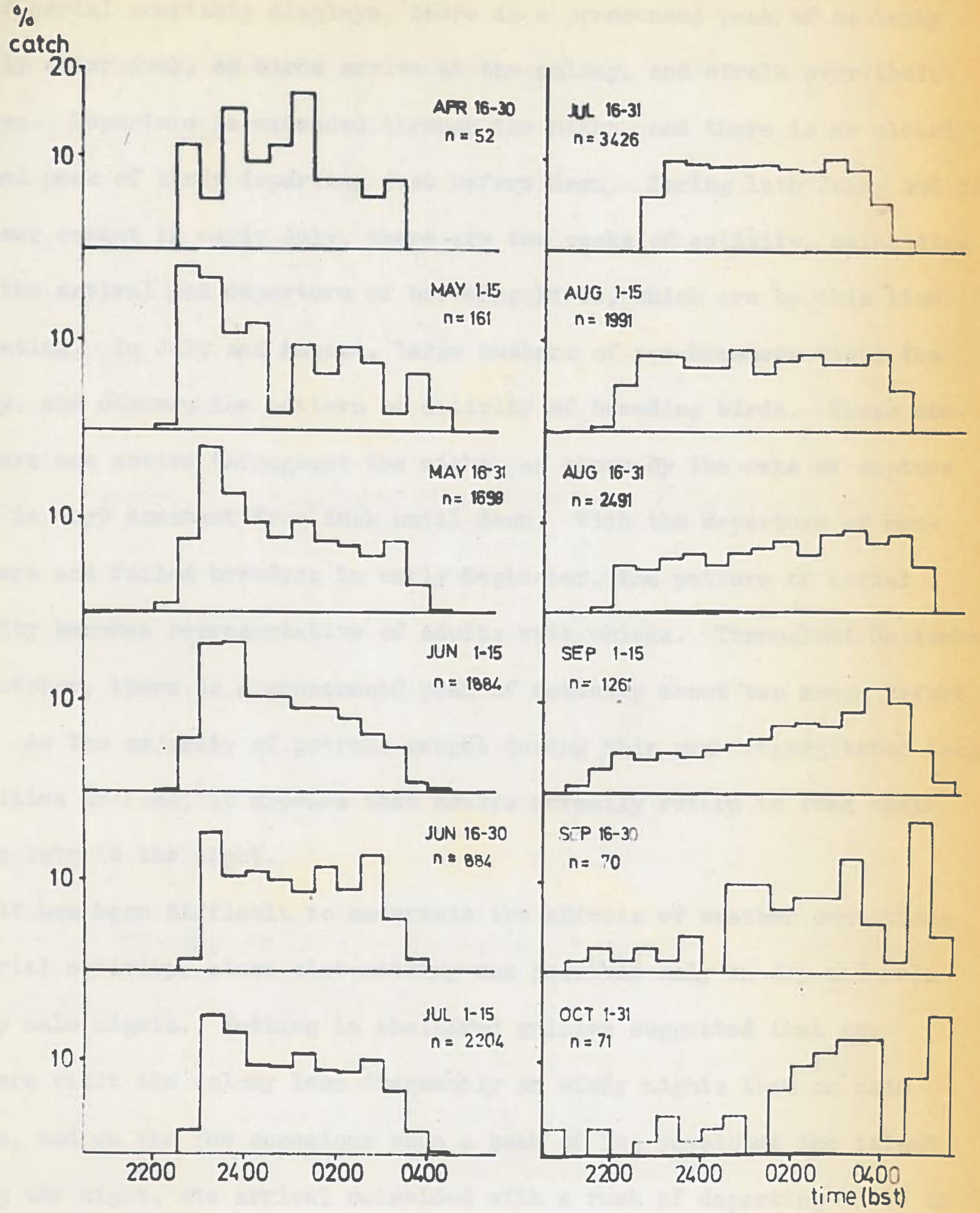


Figure 3. Number of Storm Petrels caught per half-hour throughout night, expressed as proportion of night's catch

the night, and probably never alight on the surface, or enter burrows. Throughout May and early June, at the time of reoccupation of the burrows and of aerial courtship displays, there is a pronounced peak of activity shortly after dusk, as birds arrive at the colony, and circle over their burrows. Departure is extended through the night, and there is no clearly defined peak of birds departing just before dawn. During late June, and to a lesser extent in early July, there are two peaks of activity, coinciding with the arrival and departure of breeding birds, which are by this time incubating. In July and August, large numbers of non-breeders visit the colony, and obscure the pattern of activity of breeding birds. These non-breeders are active throughout the night, as shown by the rate of capture which is very constant from dusk until dawn. With the departure of non-breeders and failed breeders in early September, the pattern of aerial activity becomes representative of adults with chicks. Throughout September and October, there is a pronounced peak of activity about two hours before dawn. As the majority of petrels caught during this peak regurgitated large quantities of food, it appears that adults normally return to feed their chicks late in the night.

It has been difficult to ascertain the effects of weather conditions on aerial activity, since mist-netting was possible only on dry and relatively calm nights. Netting in sheltered gullies suggested that non-breeders visit the colony less frequently on windy nights than on calm nights, and on the few occasions when a bank of fog enveloped the island during the night, its arrival coincided with a rush of departing birds in the nets. From visual observations on light nights, it is apparent that the aerial displays are most frequent on calm, warm nights. Mist-netting was never attempted during rain, and it is therefore not known whether rain affects aerial activity at the colony.

As described in a later section, work at the burrow indicated that breeding birds were prevented from returning to their burrows only on nights of winds of force 7 or more (Beaufort scale). Thick overcast, heavy rain, and thick fog did not affect the petrels' ability to return to the island and locate their burrows.

Many of the Procellariiformes which are nocturnal on land shun light nights, undoubtedly because of increased risk of predation. This is particularly the case in some of the Procellariidae, e.g. Puffinus puffinus (Harris, 1966), but reduced activity on light nights has also been described in three species of Hydrobatidae; Pelagodroma marina (Richdale, 1943); Oceanodroma leucorhoa (Ainslie & Atkinson, 1937) and O. castro (Allan, 1962 and Harris, 1969). The Storm Petrel is somewhat exceptional in that its aerial activity is hardly affected by the phase of the moon. Only on exceptionally light nights of full moon and cloudless skies were the numbers of petrels at the colony below normal. On such nights it was evident that the petrels were present in the vicinity of the island, since partial concealment of the moon by any small cloud was immediately followed by a rush of birds in the nets. On the other hand, catches tended to be smaller than normal on very dark nights. This was most noticeable in the darker gullies and bays, suggesting that non-breeders, at least, were having difficulty in seeing sufficiently well to manoeuvre about the colony. The frequency of visits to the burrow by adults was unaffected by the phase of the moon, once the egg had been laid. However, during the pre-egg stage, when regular visits to the burrow were not essential, visits were less frequent during periods of full moon than at other times.

(3) Site-tenacity and mate-fidelity

As Davis has shown, a Storm Petrel which has bred successfully in a burrow will normally return to that burrow in the following year. Failed breeders usually return to their original burrow when failure is not due to some external cause. Thus birds which have failed as a result of accidentally cracking their egg, infertility of the egg, or the death of the chick within forty-eight hours of hatching show almost as high a rate of return as successful breeders. Birds which have failed as a result of human intrusion, or interference from other petrels, or from rabbits or shearwaters, usually do not return to their burrow in later years. Return is also poor after the death of a chick due to starvation (see table 1). As discussed in section II, non-breeding birds which have occupied a burrow regularly for a season usually return to that burrow in the following season, and breed there. A strong attachment on the part of breeding birds and non-breeders to one particular nest-site appears to be the rule amongst

Table 1. Return of adult Storm Petrels to their burrows of previous years*

Breeding success in previous year	Number possible	Number returned	% returned
Chick fledged	62	54	87
Egg addled, or cracked during incubation	31	20	65
Egg disappeared, or deserted during incubation	33	14	42
Chick died at chipping, or within 48 hours after hatching	24	21	88
Chick died of starvation	11	2	18

* The return of birds marked in 1966 has been omitted because of the high rate of desertion due to my interference in that season.

the Procellariiformes, and occurs widely throught other groups of sea-birds.

Because of the repeated handling of petrels at the burrow during the present study, numerous desertions occurred. Thus each season there were a number of experienced birds which had lost their mates, experienced birds which were prospecting for new burrows, and vacant burrows, in the study area. This resulted in an abnormally large number of changes in mate, and changes in ownership of the burrow (table 2). In all cases in which a pair returned to a burrow in which they had bred in the previous year, and stayed together, the pair bred. When one of the pair deserted early in the season, the other was usually able to obtain a new mate within a few weeks. In slightly more than half such cases, the newly-formed pair bred that year. Breeding occurred more frequently when only one of the original pair returned at the start of the season, and was able to acquire a new mate immediately. On those occasions when a new pair occupied the burrow after the desertion of both of the original pair, breeding occurred rarely. Of the seven pairs which bred in the first season in which they occupied a particular burrow, one was a pair which were known to have bred together in a nearby burrow in the previous year and two pairs included at least one bird which had previously bred elsewhere. The other newcomers were unmarked, and therefore of unknown breeding status. However, it seems likely that some of these were young birds breeding for the first time. As mentioned previously, birds which returned to a burrow after spending a season there as non-breeders usually bred. There were only two cases of non-breeders spending two seasons in a burrow without attempting to breed. In both cases, the bird had remained unmated throughout the first season. Davis suggested that a non-breeding season in a burrow was essential before breeding could occur. However, the evidence suggests that although this commonly occurs, some individuals may breed in their first season in occupation of a burrow.

As far as is known, the only reliable method of sexing living Storm Petrels, and indeed most other species of Procellariiformes, is by cloacal examination shortly before or shortly after egg-laying, a method first described by Serventy (1956). The extreme sensitivity of the Storm Petrel to handling during incubation rendered this technique impracticable for the present study, and few birds were sexed. Davis, however, sexed many of his

Table 2. Breeding and non-breeding in Storm Petrel in relation to previous experience in burrow.

Ownership of burrow	Pair bred	Pair spent season as non-breeders
Breeding pair of previous year returned, and neither bird deserted during pre-egg stage	82	0
One of breeding pair of previous year returned, and obtained new mate at start of season	15	3
Breeding pair of previous year returned, one deserted, and other obtained new mate	14	10
Neither of pair of previous year returned; new pair in occupation	7	16
Non-breeding pair of previous year returned, and neither bird deserted during pre-egg stage	10	0
Single non-breeder, unmated in previous year, returned, and obtained a mate	3	2

birds and thought that attachment to the burrow is strongest in the male. If the establishment of a burrow and the attraction of a mate are the responsibility of the male, it seems likely that those birds requiring a non-breeding season in occupation of a burrow are young males, whereas those birds breeding in their first season of occupation are young females which have become mated to experienced males already in occupation of a suitable site.

Thirty seven of the petrels which deserted their burrows as a result of my intrusions were subsequently rediscovered in other burrows in the study area. Commonly the birds had moved only a few feet to another nest-site in a branch of the same burrow. Seventeen (46%) of the changes involved movement of less than six feet, and 27 (73%) less than 40 yards. A few birds, however, moved much greater distances; six were relocated in a burrow 100 to 250 yards away from the original burrow, and one bird had moved approximately 310 yards. Two cases of change of burrow involving movement to another colony are described elsewhere (see page 88, and Appendix IV).

Twenty-seven of the changes of burrow referred to movement of adults which had bred unsuccessfully in the first burrow. Fifteen were subsequently found breeding at another site, twelve of these in the season following desertion. Only one bird was known to have spent a season as a non-breeder after a change of burrow. Other cases of change of burrow involved casual visitation to a burrow during prospecting. Three petrels which visited a burrow for one day only in the early part of the season were found breeding in another burrow later that year. Of particular interest was one individual which visited a burrow regularly in the early part of the season, and then spent one day in a burrow 15 yards away before returning to the original burrow to breed. This indicates that even established breeding birds may make casual visits to other burrows.

As Davis pointed out, attachment to a burrow will automatically lead to mate-fidelity, especially since experienced birds return to their burrows before the arrival of prospecting non-breeders. Despite my continued interference, 37 pairs bred together for two consecutive years, a further 14 pairs for three years, and two pairs in all four years. Four pairs also remained together during a change of burrow, suggesting that petrels are able to recognize birds with which they have previously bred, and remate with these in preference to strange birds. There was no case of an experienced bird mating with a new bird when its mate of the previous year was in regular occupation of the burrow, all changes of mate following the disappearance of one of the pair.

In conclusion, it appears that in the absence of outside interference, once a pair of petrels have occupied a burrow and bred there, they will normally return to that burrow and breed together in subsequent years. The fidelity of petrels to their burrow is shown strikingly by one individual which Davis found breeding in 1954, and which I found still breeding in the same burrow in 1969. In all species of Procellariiformes hitherto studied in detail, a similar degree of site-tenacity and mate-fidelity have been found, and there can be little doubt that this state of affairs is typical of the group.

(4) <u>The pre-egg stage</u>

Between first arrival at the burrow, and egg-laying, there elapses a period of between 3½ and 12 weeks during which the burrow is visited more or less regularly by night, and is occupied occasionally by day. The nest-scrape is re-organized, the pair bond is established or re-established as the case may be, and copulation occurs. The duration of the period, and the frequency of night visits and occupation by day are exceedingly variable, and as both Lockley and Davis discovered, generalizations are difficult.

(i) <u>The duration of the pre-egg stage</u>

Davis (1957) gave the average duration of the pre-egg stages at 25 burrows in which this was not lengthened or complicated by visits from strange birds as 46.8 days (S.D. $\pm$ 9.1, range 31 - 71). The results of the present study are shown in appendix table 1. The average duration at 26 burrows was 42.7 days (S.D. $\pm$ 9.4, range 24 - 60). The two pre-egg stages of shortest duration occurred in burrows at which first arrival in spring was late, whereas the longer pre-egg periods usually occurred in burrows at which first arrival was unusually early. Experienced birds which returned to the colony earlier than normal did not breed significantly earlier than those experienced birds which returned later. Presumably any advantages in early return to the colony must therefore be related mainly to occupation of the burrow, and establishment of the pair bond, without interference from other petrels. Pre-egg stages of greater duration than 60 days invariably occurred in burrows at which the situation was complicated by one or more changes of mate. At seven burrows in which breeding occurred after a change of mate, there elapsed a period of between 18 and 38 days from formation of the new pair to laying.

(ii) The frequency of visits

From the first occupation of the burrow in spring until laying, one or both members of the pair visit the burrow regularly at night, the frequency of visits reaching a peak during the four weeks prior to laying (appendix table 2). There is however much individual variation; at some burrows, birds were present on ten or more consecutive nights, whereas at other burrows, there were gaps of up to four or five nights between visits. As burrows were not opened at night, the duration of the stay at the burrow, and the frequency with which both of the pair were together could not be determined. Davis, however, thought that the pair were together on more than half of the nights when the burrow was visited.

Occupation of the burrow by day may commence at the same time as night visits, particularly in those burrows to which the pair return late. More usually, however, day-occupation commences between one and three weeks after the first night visit. The pattern of day-occupation at 37 burrows in which the pair remained intact throughout the pre-egg stage is shown in appendix table 3. As both Lockley and Davis discovered, there is much individual variation in the frequency of occupation. In two of the burrows, occupation by day occurred only once, whereas in five burrows, this occurred on ten or more occasions.

At a few burrows, regular patterns of day-occupation were established, with birds present on every second, third, or fourth day. Both members of the pair were together on about half of the occasions. Davis found that when one bird alone occupied the burrow, this was the male on about two-thirds of the occasions, suggesting a stronger and more protracted urge to copulate on the part of the male. Petrels have occasionally remained in the burrow for two consecutive days. Such birds have usually been alone on the first day, and accompanied by their mate on the second. Apparently, the usual incentive for a prolonged stay in the burrow is the arrival of the mate on the second night, as suggested by Davis.

The frequency of day-occupation is at its highest 11 to 20 days before laying, and in 28 of the 37 burrows under observation, both of the pair were together by day at least once during this period (appendix table 4). As Davis found, during the last ten days of the pre-egg stage, there is a marked decline in the frequency of day-occupation. Both birds were never found together less than seven days before laying, and the few individuals which were sexed at this time proved to be males. Presumably, during this desertion period before laying, the females are away at sea collecting food to produce the very large egg. The male also must build up his food reserves during this period in preparation for the first incubation stint. A similar desertion period, or "honeymoon period", has been recorded in several species of Hydrobatidae (Gross, 1935; Roberts, 1940; and Harris, 1969), and has been well documented in a number of other Procellariiformes.

(iii) Pair formation and displays

Because of the sensitivity of Storm Petrels to disturbance, it has not been possible to make any detailed observations on the behaviour of the birds in the burrow. Davis (1957) described in some detail the churring "song", which may be heard issuing from burrows from the last few days of April until early September. The churring of breeding birds is almost entirely restricted to nocturnal visits to the burrow during the pre-egg stage. Once the egg has been laid, there is an almost total cessation of churring, the only sound regularly emitted by incubating birds or birds with chicks being a loud "up-cherk", which may readily be elicited by disturbance near the burrow.

As Davis suggested, the "song" appears to serve the dual function of announcing ownership of the burrow, and attracting the attention of other petrels. The churring does not however appear to have any aggressive function, as is the case in territorial song-birds. Instead, the presence of a churring bird in a burrow attracts other petrels of either sex (How?) to investigate the burrow, regardless of whether or not they are prospecting for a burrow, or have already taken up occupation of a burrow nearby.

The use of an amplified tape-recording of petrel churring has demonstrated the attractive power of the song in a striking way. Recordings played on calm nights in mid- or late summer regularly attracted 15 to 20 petrels to the recorder at one time. The birds flew round in small circles, often hovering momentarily over the machine, and occasionally alighting on the revolving spools. When played at net-sites, a recording of petrel churring increased the catch size by several fold. Recaptures of marked birds from burrows in the study area indicated that adults may be attracted to the recorder from burrows as far as 200 yards away.

Surprisingly, the attraction of the churring was not restricted to prospecting birds during the pre-egg stage, but affected all age classes of birds throughout the season. Breeding birds feeding well-grown chicks, and non-breeders visiting the colony for the first time in late summer, when all churring had ceased, were attracted as readily as prospecting non-breeders in early summer. Presumably, the churring is attractive to prospecting birds because it indicates the presence of a suitable breeding area in which they may be able to settle, but why the churring should lure adults already engaged in breeding away from their duties is not clear.

The aerial courtship displays, which take place in late May, June, or early July, have been described by Davis. Briefly, the pair chase one another in tight circles over the area of the burrow, at intervals uttering a loud "terr-chick", and occasionally giving short bursts of churring. Rarely, the birds may utter a soft "wink ... wink ... wink", reminiscent of the "wink" call of the Chaffinch Fringilla coelebs. The chase usually ends with one or both birds descending to the burrow. Similar aerial chases have been described on Oceanodroma leucorhoa (Williamson, 1948), O. castro and O. tethys (Harris, 1969), and Oceanites oceanicus (Roberts, 1940). Roberts has suggested that the white rump common to all these species, and many other species of Hydrobatidae, may act as a releaser in such aerial displays. A role in the prelude to copulation in the dark confines of the burrow also seems likely.

Davis did not observe copulation, nor did he distinguish any particular sound which might be associated with it. During the present study, copulation was never witnessed in the burrow at night, but on two occasions, birds were interrupted in coitus by day. In both cases, the male was nibbling at the feathers of the female's nape, the birds were silent, and their wings were closed. The wing-shivering, associated with copulation in many groups of birds, might be rare or absent in the Storm Petrel, because of lack of space in the limited confines of the burrow. At one burrow, the egg was laid 36 days later, but at the other, the pair deserted before laying. It seems likely that copulation normally occurs during the period of greatest frequency of day-occupation, i.e. 11 to 20 days before laying. In view of the large size of the egg, a long period between insemination and laying might be expected, to enable the female to obtain the necessary food reserves. This state of affairs seems to be general amongst the Procellariiformes. Prévost (1953) quoted periods of 17 and 21 days between copulation and laying in Fulmarus antarcticus, and Marshall and Serventy (1956) thought that fertilization took place three or more weeks before laying in Puffinus tenuirostris. Harris (1969) witnessed a single mating in Oceanodroma castro in the burrow by day, 33 days before the egg was laid.

(5) The egg stage

(i) The egg

The Storm Petrel lays a single egg, as do all other Procellariiformes for which adequate data are available. The egg, like that of other Hydrobatidae, is white, often with a few red-brown speckles in a ring round the blunt end. To minimize desertions due to handling of incubating adults, only those fresh eggs which were left unincubated for the first day after laying were weighed. The average weight of fifteen such eggs was 7.0 gm. (S. D. $\pm$ 0.5, range 5.9 - 7.8), representing approximately 25 per cent of the adult weight in mid-summer. One female which was kept in captivity during laying weighed 24.1 gm shortly after laying an egg of 7.0 gm, which was therefore equivalent to 29 per cent of her body weight.

A number of eggs were weighed and measured during gaps in incubation, or after desertion by the parents. The weight of the egg decreases steadily throughout incubation at the rate of about 0.04 gm per day, i.e. 1.65 gm between laying and hatching. The weight loss of avian eggs during incubation has been shown to be due to evaporation of water through the shell, and to be directly related to the surface area of the egg (Drent, 1967).

The usual shape of the egg is blunt rhomboidal. However, there is considerable variation, some eggs being almost spherical, whereas others are greatly elongated. The maximum length and width of 94 eggs were measured. The mean length was 2.81 cm (S. D. $\pm$ 0.09, range 2.55 - 3.00) and the mean width was 2.11 cm (S. D. $\pm$ 0.08, range 1.85 - 2.30). The largest eggs measured 2.85 cm x 2.30 cm, and 2.90 cm x 2.25, and the smallest, 2.75 cm x 1.90 cm, and 2.90 cm x 1.85 cm. Volumetrically, the largest egg was approximately 50% larger than the smallest.

Unfortunately, insufficient data on pair status were available to determine whether or not the age and breeding experience of adults had any effect on egg size. Richdale (1957) found that young females of the Yellow-eyed Penguin <u>Megadyptes antipodes</u>, laying for the first time, produced narrower eggs than older birds, and suggested that this might also be true for <u>Puffinus griseus</u> (Richdale, 1963). Serventy (1967) found a similar situation in <u>Puffinus tenuirostris</u>, the width of the egg increasing up to the sixth or seventh breeding season. He showed that the important factor determining egg width was not so much the actual age of the female, but the number of times that she had laid an egg. It is of interest therefore that one of the three smallest eggs of the Storm Petrel found in the present study was laid by a pair known to be breeding for the first time.

Warham (1968), analyzing data from a wide variety of Procellariiformes, found that, on average, the fresh weight of the egg (in grams) was equal to 0.530 x length x width^2 in centimetres. The relationship obtained from fourteen fresh eggs of the Storm Petrel weighed and measured during the present study was of the form: weight = 0.546 x length x width^2 (Figure 4). Using this relationship, it has been possible to calculate the fresh weight of all those eggs for which the measurements of length and width were available. The mean of the calculated fresh weights of 94 eggs was 6.9 gm (S. D. $\pm$ 0.6, range 5.4 - 8.1).

Unfortunately, only twelve eggs which were measured subsequently hatched, so that it was not possible to determine if hatching success was in any way influenced by egg size. However, the contents of all those eggs which were deserted during incubation were examined to discover whether or

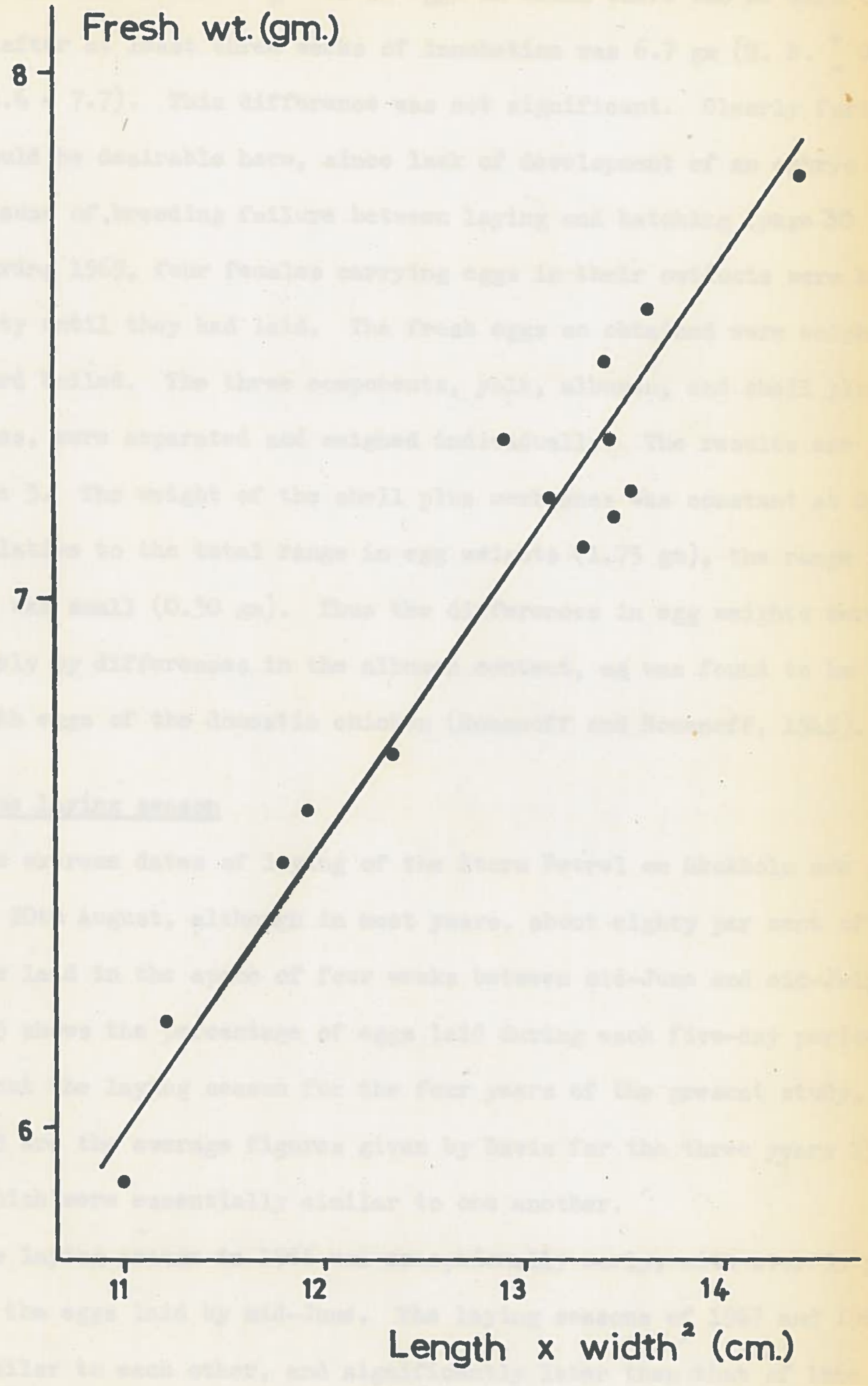


Figure 4. Relationship between fresh weight and length x width[2] of egg of Storm Petrel.

not an embryo had developed. The mean fresh weight of 36 eggs in which an embryo was known to have developed was 6.9 gm (S. D. $\pm$ 0.6, range 5.4 - 8.1), whereas the mean fresh weight of 26 eggs in which there was no sign of an embryo after at least three weeks of incubation was 6.7 gm (S. D. $\pm$ 0.6, range 5.6 - 7.7). This difference was not significant. Clearly further work would be desirable here, since lack of development of an embryo was the major cause of breeding failure between laying and hatching (page 30).

During 1969, four females carrying eggs in their oviducts were kept in captivity until they had laid. The fresh eggs so obtained were weighed, and then hard boiled. The three components, yolk, albumen, and shell plus shell membranes, were separated and weighed individually. The results are given in table 3. The weight of the shell plus membranes was constant at 0.45 gm, and, relative to the total range in egg weights (1.75 gm), the range in yolk weights was small (0.30 gm). Thus the differences in egg weights were made up largely by differences in the albumen content, as was found to be the case with eggs of the domestic chicken (Romanoff and Romanoff, 1949).

(ii) <u>The laying season</u>

The extreme dates of laying of the Storm Petrel on Skokholm are 28th May and 20th August, although in most years, about eighty per cent of the eggs are laid in the space of four weeks between mid-June and mid-July. Figure 5 shows the percentage of eggs laid during each five-day period throughout the laying season for the four years of the present study. Also included are the average figures given by Davis for the three years 1954 - 1956, which were essentially similar to one another.

The laying season in 1966 was exceptionally early, with over 35 per cent of the eggs laid by mid-June. The laying seasons of 1967 and 1968 were very similar to each other, and significantly later than that of 1966 and any of Davis's three years. In 1969, the laying season was more than usually protracted. Although the first eggs were laid early, laying proceeded slowly, so that the mean date of laying was the same as in 1967 and 1968. The details of the laying seasons in the seven years for which data are available are given in appendix table 5.

The pattern of laying within each season has a bimodal distribution with a large peak about fifteen days after the onset of laying, and a

Table 3. Wet weight, in grams, of components of four fresh eggs of Storm Petrel.

Fresh weight	Weight after boiling	Weight of albumen	Weight of yolk	Weight of shell and shell membranes
7.35	7.15	4.25	2.45	0.45
5.90	5.80	3.00	2.35	0.45
7.20	7.10	4.05	2.60	0.45
7.80	7.55	4.45	2.65	0.45

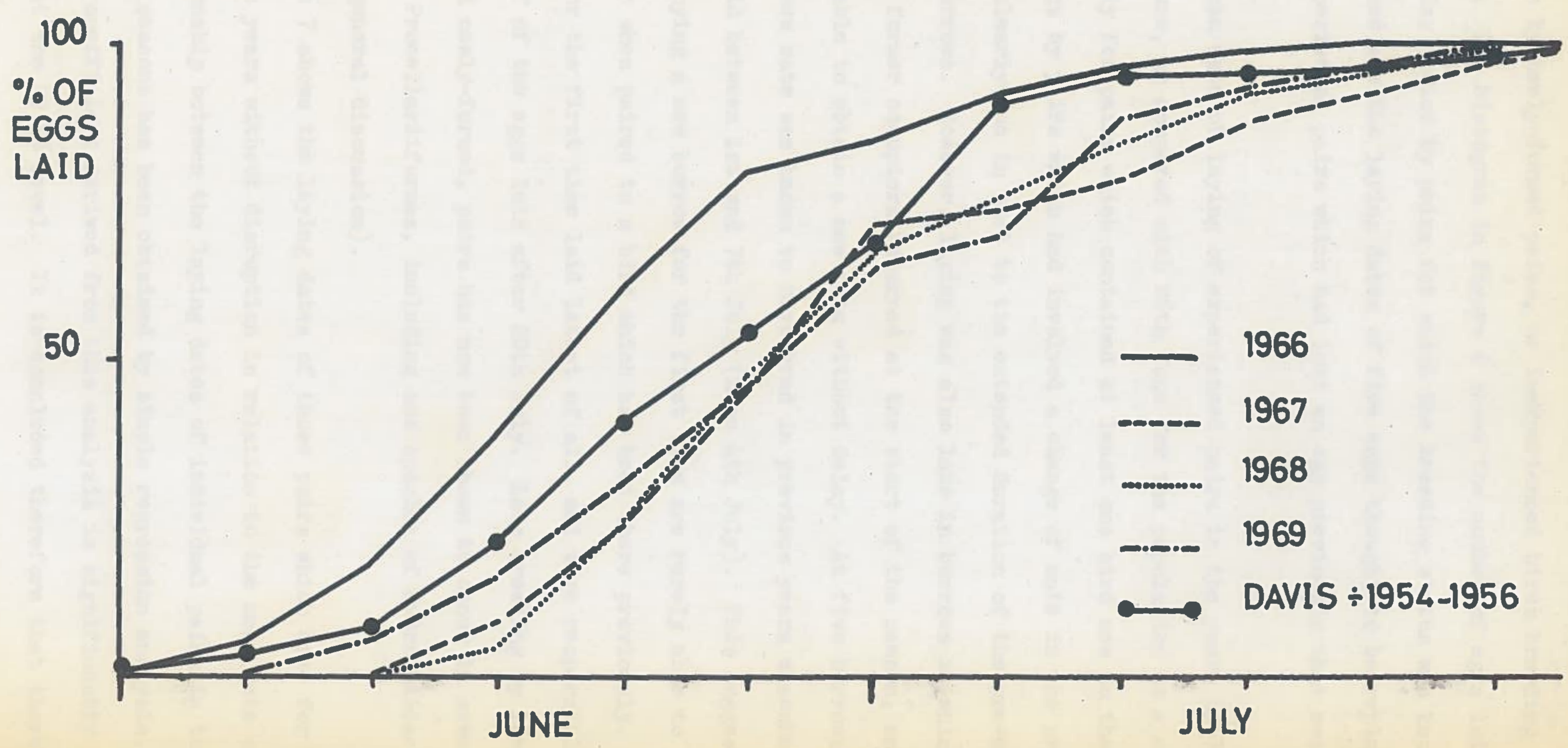


Figure 5. Egg-laying season of Storm Petrel on Skokholm, 1954-1956 (after Davis, 1957), and 1966-1969.

smaller peak about ten days later. Davis found that the majority of layings in the first peak were by experienced breeders, whilst many of those in the second were by newly-formed pairs, or inexperienced birds breeding for the first time. The histogram in figure 6 shows the number of eggs laid in each five-day period by pairs for which the breeding status was known. Also included are the laying dates of five eggs thought to be replacement eggs of experienced pairs which had lost an egg previously that season (see below).

The mean date of laying of experienced pairs in the years 1967 - 1969 was 21st June, as compared with 26th June for the population as a whole, and 8th July for pairs which contained at least one bird new to that burrow. Late layings by pairs which had involved a change of mate in the pre-egg stage was clearly due in part to the extended duration of the pre-egg stage at these burrows. However, laying was also late in burrows in which only one of the former occupiers returned at the start of the season, and was therefore able to obtain a new mate without delay. At five burrows, in which the new mate was known to have bred in previous years elsewhere, the egg was laid between 1st and 7th July (mean 4th July). This suggests that birds occupying a new burrow for the first time are rarely able to breed early, even when paired to a bird which has bred there previously. Pairs breeding for the first time laid latest of all, and were responsible for almost half of the eggs laid after 20th July. Late breeding by inexperienced, and newly-formed, pairs has now been shown to occur in several species of Procellariiformes, including one species of Hydrobatidae (Harris, 1969)(see general discussion).

Figure 7 shows the laying dates of those pairs which bred for two consecutive years without disruption in relation to the mean date of laying. The relationship between the laying dates of individual pairs in the first and second seasons has been obtained by simple regression analysis. The regression coefficient derived from this analysis is significantly different from zero at the 99.9% level. It is concluded therefore that there is a tendency for pairs which lay early in one season to lay early in the next, and for pairs which lay late in one season to lay late in the next. Obviously, the tendency will to a certain extent be obscured, since newly-

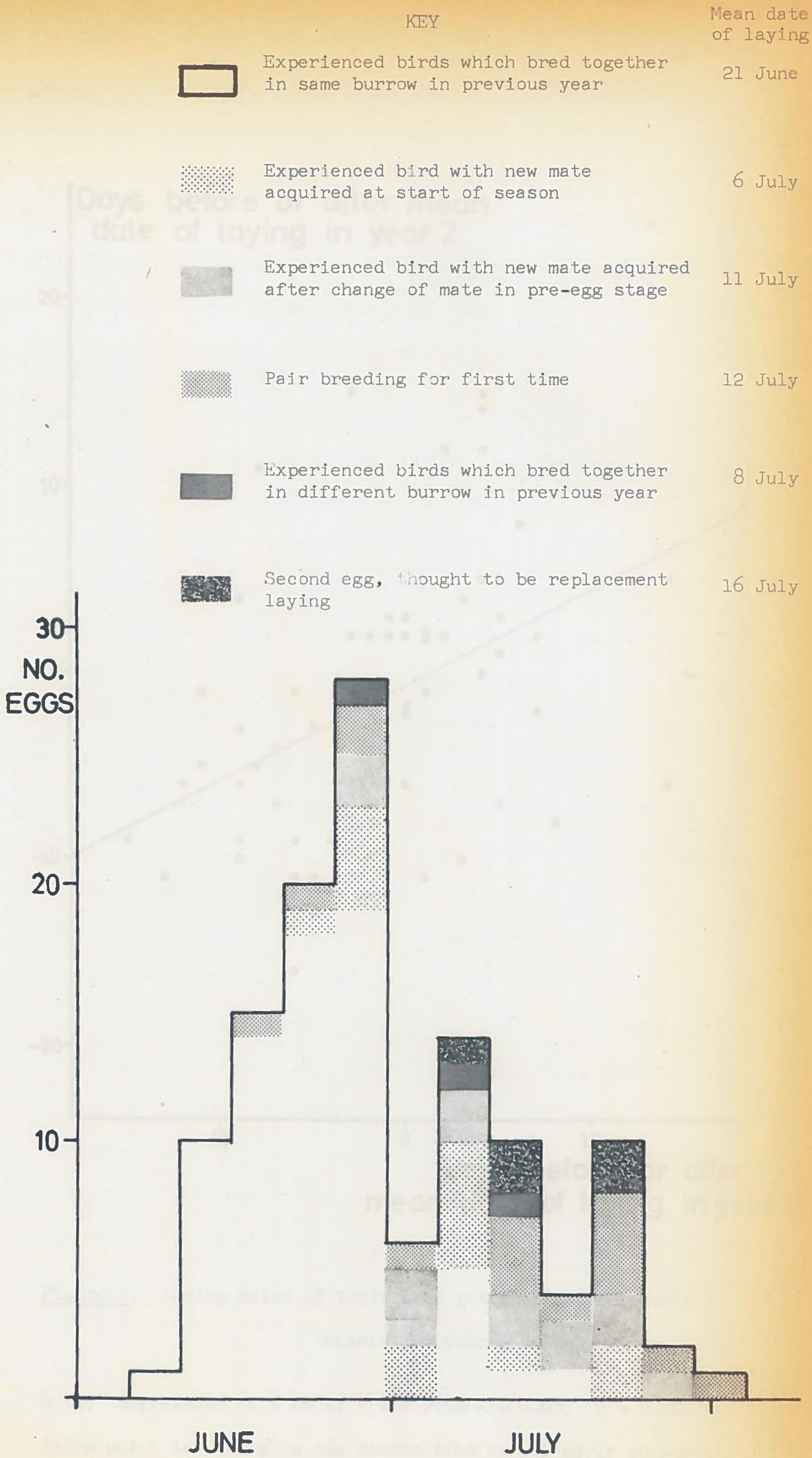


Figure 6. Date of laying of Storm Petrel in relation to previous experience of pair.

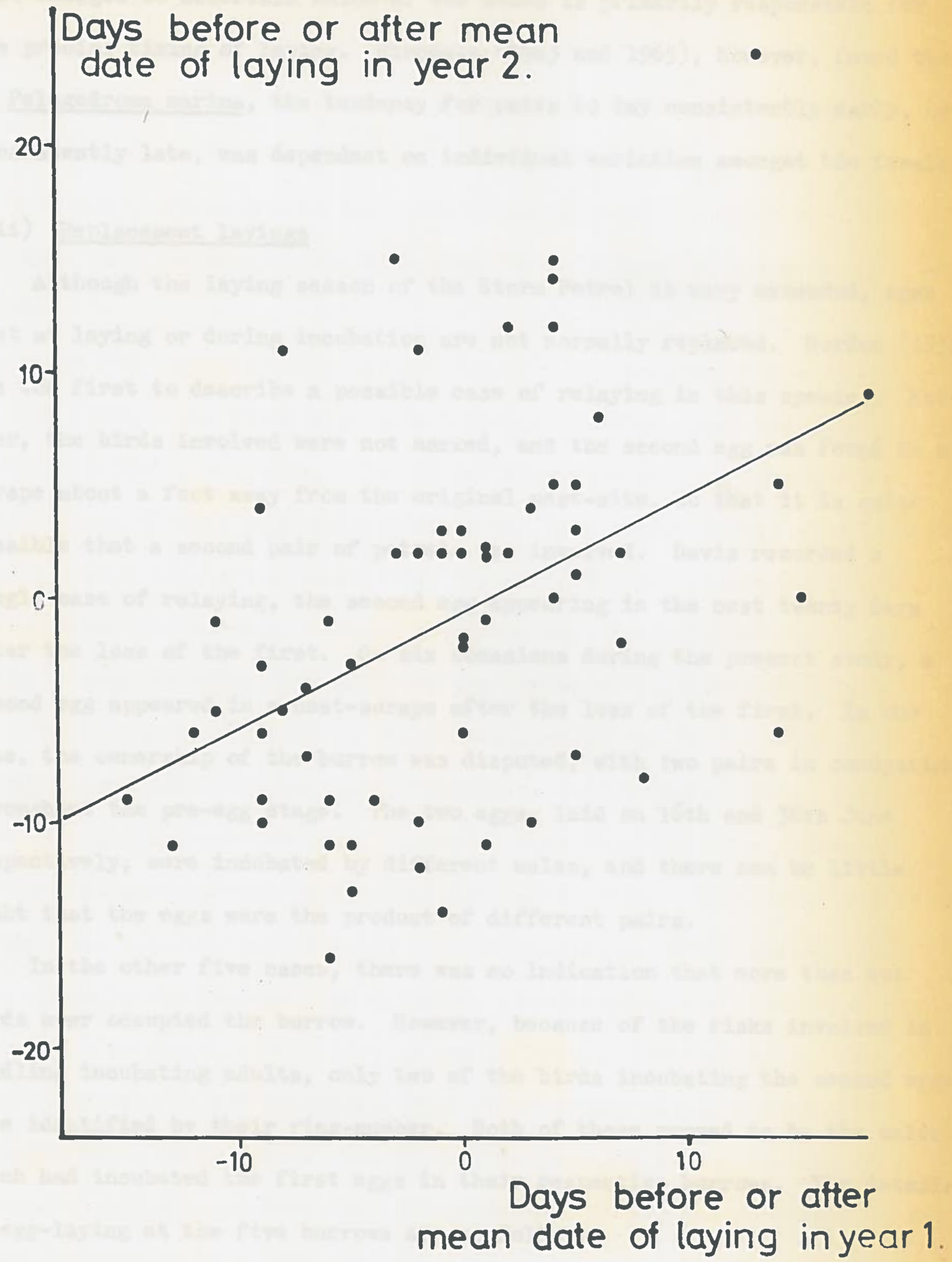


Figure 7. Laying dates of individual pairs of Storm Petrels in consecutive years

Note: Regression of Y on X; $Y = 0.51 X - 0.63$, $p = 0.001$

Pairs which lay early in one season tend to lay early in next, whilst pairs which lay late in one season tend to lay late in next.

formed pairs, or inexperienced pairs, lay later in their first season together than in subsequent years. Insufficient data are available from mate changes to ascertain which of the sexes is primarily responsible for the precise timing of laying. Richdale (1943 and 1965), however, found that in Pelagodroma marina, the tendency for pairs to lay consistently early, or consistently late, was dependent on individual variation amongst the females.

(iii) Replacement layings

Although the laying season of the Storm Petrel is very extended, eggs lost at laying or during incubation are not normally replaced. Gordon (1931) was the first to describe a possible case of relaying in this species. However, the birds involved were not marked, and the second egg was found in a scrape about a foot away from the original nest-site, so that it is quite possible that a second pair of petrels was involved. Davis recorded a single case of relaying, the second egg appearing in the nest twenty days after the loss of the first. On six occasions during the present study, a second egg appeared in a nest-scrape after the loss of the first. In one case, the ownership of the burrow was disputed, with two pairs in occupation throughout the pre-egg stage. The two eggs, laid on 16th and 30th June respectively, were incubated by different males, and there can be little doubt that the eggs were the product of different pairs.

In the other five cases, there was no indication that more than two birds ever occupied the burrow. However, because of the risks involved in handling incubating adults, only two of the birds incubating the second eggs were identified by their ring-number. Both of these proved to be the males which had incubated the first eggs in their respective burrows. The details of egg-laying at the five burrows are as follows:

(i) The first egg was laid on 1st July, and incubated until 9th, but was missing on 10th. The burrow was not then occupied by day until 24th July, when a bird was incubating a fresh egg (15 days after the loss of the first). Incubation continued without a break until 15th August, when this egg was also lost.

(ii) The first egg was laid on 19th June, and the male took the first incubation stint. The egg disappeared shortly after, and the burrow was not visited again by day until 28th June, when the same male, and a female of unknown identity were present. On 15th July, the male was incubating a second egg, which had been laid sometime between 8th and 15th July (19 - 26 days after the loss of the first). This egg also disappeared shortly after laying.

(iii) A male was found incubating a fresh egg on 17th June. Incubation was continuous until 24th June, but on 25th June, the burrow was empty. On 15th July, the same male was again found incubating a fresh egg, which had been laid between 8th and 15th July (14 - 21 days after the loss of the first).

(iv) and (v) The histories of the remaining two burrows were very similar to each other. The first eggs were both laid on 25th June, and lost within twenty-four hours of laying. The second eggs were laid on 10th and 25th July, 15 and 30 days respectively after the loss of the first. One of these eggs was lost soon after laying, but the other hatched successfully. In the latter case, the parents brooding the chick were known to have been the birds in regular occupation prior to the laying of the first egg.

Unfortunately, in none of these five burrows was the evidence for the laying of replacement eggs conclusive, since in all cases, it was possible that two females were involved. However, taken together, the evidence is strongly suggestive that replacement layings do occur. Certainly the period between the loss of the first egg and the appearance of the second would seem adequate for remating and relaying. Furthermore, the resumption of occupation of the burrow by day, by one or both of the pair after the early loss of an egg, is not uncommon. This would surely be an unnecessary expenditure of energy unless the birds involved were re-associating in an attempt to lay a replacement egg. Degeneration of the gonads of one or both sexes immediately after the production of an egg could explain why resumption of day-occupation after loss of the egg is not always followed by the laying of a replacement.

Evidence for the laying of replacements in other species of Procellariiformes is similarly very meagre. Incontrovertible evidence, viz. the capture of a female carrying a fully-formed egg in her oviduct on two separate occasions in one season, has been obtained only for <u>Puffinus puffinus</u> (Perrins, Harris and Britton, in prep.). Amongst the Hydrobatidae, Gross

(1935), Wilbur (1969), and Huntington (in Wilbur, 1969) have documented three probable instances of relaying in Oceanodroma leucorhoa, and Allan (1962) and Harris (1969) have described eight such cases in O. castro. In some of the Procellariidae, however, it appears that replacement layings never occur. Marshall and Serventy (1956), working on Puffinus tenuirostris, found that by the date of laying, the seminiferous tubules of the males were in a state of post-nuptial disintegration. Similarly, Hindwood and Serventy (1941) found that regression of the gonads of Pterodroma leucoptera occurred very rapidly after fertilization. However, as Marshall and Serventy pointed out, the extremely rigid and synchronous breeding season of P. tenuirostris would also preclude the possibility of repeat layings in this species, because of the length of the period between copulation and laying.

To sum up: there is as yet no conclusive evidence that the Storm Petrel, or indeed any of the Hydrobatidae, lay a replacement egg after the loss of the first. However, a considerable body of circumstantial evidence has now been accumulated for three species, including H. pelagicus, suggesting that replacement eggs are occasionally laid. Why this does not occur more frequently is obscure. In all three species, the laying season is very protracted, and there is no obvious reason why it would not be advantageous for those early breeders which lose their eggs soon after laying to replace them.

(iv) Incubation

Davis found that the egg is usually laid during the night, and that the male normally takes over the first incubation stint. Presumably, the energy consumed by the female in the production of the egg demands that she leaves the colony as soon after laying as possible to replenish her food reserves. Occasionally, the nocturnal visits of the male do not coincide with the return of the female to lay an egg, in which case the egg is usually left unincubated for the first day. The time of arrival of the female about to lay an egg is available from the times of capture of 60 females carrying fully-formed eggs in their oviducts. 41 (68%) of these were caught before 0100 hrs BST and only 12 (20%) after 0220 hrs. BST. On the rare occasions when the female was present alone or in company with the male on the first day after laying, she presumably arrived too late to lay the egg and depart again before dawn. This must surely have been the case with a female which was caught carrying an egg at 0345 hrs. BST, only 15 minutes before all aerial activity at the colony ceased. Three females caught twice in the same night, before and after laying, had entered their burrows, laid their eggs, and departed again in the space of 1 hr. 45 mins, 3 hrs. 45 mins., and 4 hrs. 15 mins., respectively. Clearly the females must have some considerable control over the actual time of laying. Of six birds which were kept in captivity until they had laid their eggs, three laid within four hours of capture, and three laid the following night, about 28 hours after capture, indicating that some females are able to retain the egg in the oviduct for at least a day after its production.

The incubation period of the Storm Petrel has been well documented by Lockley (1932), (average of 6, 39.5 days, range 38 - 40), and by Davis (1957), (average of 36, 40.6 $\pm$ 2 days, range 38 - 50). The results of the present study agree closely with these figures; the average incubation period of 33 eggs which hatched was 40.8 days (S. D. $\pm$ 1.4 days, range 39 - 45). Davis showed that for eggs incubated continuously from laying to hatching, the incubation period was between 38 and 40 days. Most of the eggs which were incubated for more than 40 days before hatching were known to have been left unincubated at times. Gaps of one or two days in incubation, resulting from the failure of the off-duty bird to return before the sitting bird was ready to depart, had no effect on hatching succes, but they did lengthen the incubation period by an amount equal to the total period for which the egg was left unincubated. An exceptionally long period of 50 days, recorded by Davis, involved gaps in incubation totalling eleven days, and included one uninterrupted gap of five days.

The ability of eggs to withstand chilling has now been described in several species of Procellariiformes, (notably by Gross, 1935; Matthews, 1954; and Harris, 1969). Matthews suggested that the ability to withstand chilling is concommittant with the long incubation periods of these species, a slower rate of development being less subject to lapses in incubation than a more rapid one. The ability to withstand periods of chilling has obvious survival value to developing Procellariiform embryos because during periods of gales, or food shortage, the off-duty bird may not be able to return before the incubating bird must depart to replenish its food reserves.

A similar resistance to chilling has been described in the Swift Apus apus, which, like the Procellariiformes, is dependent on an erratic food supply, the availability of which is greatly affected by the weather (Lack, 1956).

No attempt was made during the present study to determine the share of the sexes in incubation, or the length of the individual incubation stints. Davis however showed that the sexes take an equal share in incubation, and that the incubation stints are usually of two or three days, but exceptionally of up to five. Davis also found that nocturnal visits to the burrow occurred far more frequently than change-overs on the egg. (The burrow was visited on 70% of possible nights, whereas change-overs occurred on only 38%). During the present study, bracken lattices were maintained at the entrances of 24 burrows throughout incubation to establish the frequency of nocturnal visits. The frequency of visits to some burrows certainly suggested that at times birds were visiting the burrow more often than change-overs were occurring. However, at several burrows, nocturnal visits occurred regularly every second or third night, and probably therefore occurred only when change-overs in incubation took place. Periods when the burrow was not visited at night gave some indication of the frequency of long incubation stints. At the 24 burrows under observation, stints of four days occurred on 17 occasions, stints of five days also on 17 occasions, and stints of six days on 3 occasions.

The significance of the night visits other than those coinciding with change-overs in incubation is not clear. Davis considered that the visits were made by the off-duty bird, since change-overs occurred at irregular intervals, and gaps in incubation of more than one day were rare. Work on other species of Hydrobatidae has revealed differences in the frequency of night visits, and the duration of incubation stints, which suggest that these two might be interrelated. In Oceanites oceanicus (Roberts, 1940), and Oceanodroma leucorhoa in the Eastern Atlantic (Ainslie and Atkinson, 1937), incubation stints are short, usually of two or three days, and off-duty birds visit the burrow regularly between change-overs. However, in Oceanodroma castro (Allan, 1962; Harris, 1969), Pelagodroma marina (Richdale, 1943), and O. leucorhoa in the Western Atlantic (Gross, 1935; Wilbur, 1969), incubation stints are long, usually of four to six days, and the off-duty birds probably never visit the burrow between change-overs.

It seems likely that in the species with long incubation stints, the feeding grounds are at a considerable distance from the colony, in which case it might not be possible for the off-duty birds to return nightly. In the species with short incubation stints, the feeding grounds must be relatively close to the colony. As shown in a later section, during the first week after hatching, and occasionally for short periods later in the nestling stage, individual Storm Petrels return to the colony nightly with food for the chick, indicating that at these times, the petrels are feeding close to the colony. Presumably therefore, almost nightly visits could be undertaken during the incubation period without serious loss of feeding time, and would ensure that the egg was never left unincubated for more than a day or two. Unfortunately, it has not been possible to obtain a series of weights of incubating birds to determine whether or not these are ever fed by their mates.

(v) Incubation temperatures

During July 1969, measurements were taken of the incubation temperature of the Storm Petrel by inserting the end of a thermistor at the interface between the egg and the brood patch of the incubating bird. Steady temperatures in deg. C. at five burrows were 29.2, 29.5, 31.9, 32.0 and 32.0 (mean 30.9). Although a much larger sample would be desirable, these results certainly indicate a much lower incubation temperature in the Storm Petrel than has been found in other types of birds. The temperature at the interface between egg and brood patch of six species of birds from four orders ranged from 38.0 to 39.4 deg. C. (summarized in Drent, 1967).

The cloacal temperatures of five active Storm Petrels, taken immediately after they had been caught in flight at night, averaged 39.2 deg. C. Cloacal temperatures of incubating birds were not taken because of the likelihood of desertion. However, Folk (1949 and 1951) measured the cloacal temperature of fourteen incubating Leach's Petrels Oceanodroma leucorhoa, and found that this was on average 37.2 deg. C.; almost 2.0 deg. C. less than that of active petrels. He suggested that during icubation stints of several days, the incubating petrels go into a semi-torpid condition, which would be compatible with the fasting of the adult, and the long incubation period of this species. The low incubation temperature of the Storm Petrel might similarly be due to a lowered metabolic rate, and hence lowered body temperature in the incubating bird. Clearly, however, further work is needed here.

(vi) Breeding losses during incubation

The fate of 214 eggs which were laid in the burrows in the study area is shown in table 4. Those eggs which were obviously lost as a direct result of my interference have been omitted. However, it is likely that in each year, a few such losses have been attributed to natural causes, so that the estimate for hatching success must be a minimal figure. The presence of a small number of fresh eggs on the surface, where they could not have rolled from a burrow, indicated that females were occasionally unable to return to their burrows before laying. However, these probably account for only a very small proportion of the eggs laid, and have therefore been omitted from the present analysis. The low overall hatching success (62%) obtained during the present study agrees with that obtained by Davis (66%).

As can be seen in table 4, the causes of failure were diverse. The manner in which 18 eggs disappeared from the burrow was unknown, but it seems likely that interference from shearwaters, Puffins, rabbits, and perhaps other Storm Petrels was responsible in some cases. The most important single cause of egg loss, accounting for 49% of all losses, and 19% of all eggs laid, was failure of an embryo to develop. All eggs in which no sign of an embryo could be found after at least three weeks of incubation have been assigned to this category. Death of the embryo at a very early age as a result of excessive chilling may have been responsible in a few cases, but it would seem that the majority of these eggs were infertile. The proportion of eggs which failed to develop an embryo in each of the four seasons of study is shown in table 5. Davis also recorded several similar instances of egg loss constituting about 15% of the eggs laid in his study. Harris (1969) found that only about 6% of the eggs laid by Oceanodroma castro were addled, and Richdale (1943), working on Pelagodroma marina, found only one addled egg in fifty-five.

(6) The chick stage

Like that of other species of Procellariiformes, the nestling period

Table 4. Hatching success of Storm Petrel, and causes of egg loss.

	1966	1967	1968	1969	Total	% of eggs laid
Eggs laid	42	71	51	50	214	-
Hatched	28	39	32	34	133	62
Deserted at laying	0	1	1	0	2	1
Cracked by incubating bird	1	2	2	0	5	2
Deserted during incubation*	3	2	0	0	5	2
Disappeared from burrow	5	6	0	7	18	8
Addled (probably infertile)	5	17	11	7	40	19
Embryo died in incubation	0	2	3	0	5	2
Chick died at chipping	0	2	1	1	4	2
Broken by shearwater or Puffin	0	0	1	1	2	1

* Desertions which were obviously due to my interference have been omitted.

Table 5. Incubation losses of Storm Petrel resulting from infertility, or death of embryo during early stages of development.

Year	Eggs laid*	Eggs in which no embryo developed	%
1966	55	8	15
1967	61	17	28
1968	47	11	23
1969	43	7	16
Total	~~212~~ 206	43	~~20~~ 21

* including only those eggs which hatched, or which were examined for the presence of an embryo after at least three weeks of incubation.

of the Storm Petrel is long. Precise determination of the nestling period is difficult because of the tendency for chicks to wander about the burrow, and occasionally to move to another burrow, in the few days prior to final departure. During the present study, several chicks disappeared from their burrow prematurely, and were located in other burrows close by for up to six days later. Chicks which disappeared from their burrows whilst still at a weight in excess of that of the heaviest chick ever found fledging at night (38.5 gm.) have therefore been ignored. The mean nestling period of 53 chicks for which this was known accurately was 67.9 days (S. D. $\pm$ 5.3, range 61 - 86).

Lockley and Davis obtained average nestling periods of 61 days (sample of 6, range 54 - 68) and 62.8 $\pm$ 3.5 days (sample of 32, range 56 - 73), respectively. The difference between the nestling periods obtained by Lockley and Davis, and those obtained during the present study, may have been due, in part, to the formers' inclusion in their samples of figures obtained from chicks which left their burrows prematurely. This must surely have been the case in the chicks with very short periods of 54 and 56 days. However, as will be shown later, the duration of the nestling period is greatly affected by the feeding conditions during the chick stage, and it is possible that the nestling periods of Lockley and Davis were obtained in seasons which were better for feeding than those of the present study. Certainly, the feeding conditions in the summer of 1967 were unusually poor; 23% of the chicks which hatched subsequently died of starvation, and 70% of the chicks which survived to fledging had poor or retarded rates of growth.

The duration of the nestling period may also be affected by the weather conditions at the time of fledging. Chicks do not normally depart on wet stormy nights, or in thick fog, but remain in the burrow until conditions become more favourable. A period of very bad weather just before the time of peak fledging in 1968 was probably responsible for some of the extended nestling periods in that year.

(i) <u>The first twenty-four hours</u>

Sixty-one chicks which hatched in the burrows were examined within twenty-four hours of hatching. All weights taken at this time are treated as weights at hatching, although it was clear that in a few instances, the chicks had already received a small feed. The mean weight of the 61 chicks was 5.0 gm. (S. D. $\pm$ 0.6, range 3.4 - 6.6). Six chicks were dead when first examined, and nine more died within the next twenty-four hours. A further six dead chicks were located in burrows first examined at the time of peak hatching. The weights of the 21 chicks which died within 48 hours of hatching, and the weights of the 46 surviving chicks are shown in figure 8. The mean weight of those which died (4.2 gm, S. D. $\pm$ 0.5, range 3.1 - 5.1) was significantly less than that of those which survived (5.2 gm, S. D. $\pm$ 0.5, range 4.1 - 6.6).

In only two instances could death of the chick be attributed to parental neglect. At one burrow, the chick hatched at a healthy weight of 5.1 gm, two days after its parents had adopted a newly-hatched chick from a nearby nest-scrape. The former chick was ignored by its parents, and died within 36 hours. At another burrow, the egg was left unattended on the night that it hatched, and the chick died before the return of its parents on the following night. In all other instances of early death, the chick was brooded continuously from hatching until death, and usually for one or two days after this. Interference caused by my intrusions was clearly not responsible for the deaths at twelve burrows, since the chicks were already dead when first found, and there was nothing to suggest that disturbance was responsible at the other burrows. The only likely explanation for the majority of the deaths was that the chicks hatched with insufficient food reserves to enable them to survive until the first feed. A similarly high rate of mortality of chicks at hatching has not been found in any other species of Hydrobatidae and indeed, Davis recorded only one such death in 37 Storm Petrels which hatched in his burrows.

(ii) <u>Brooding of the chick</u>

Davis showed that the chick is normally brooded for the first six or seven days, occasionally until the tenth, and rarely after this. He found that the sexes take an equal share in brooding, and that the shifts are normally of one day. Clearly, at this time of the year, the adults are able to fly out to the feeding grounds, collect sufficient food for themselves and their chick, and return again to the colony, within the space of twenty-four hours. The frequency of brooding at 55 burrows in which the

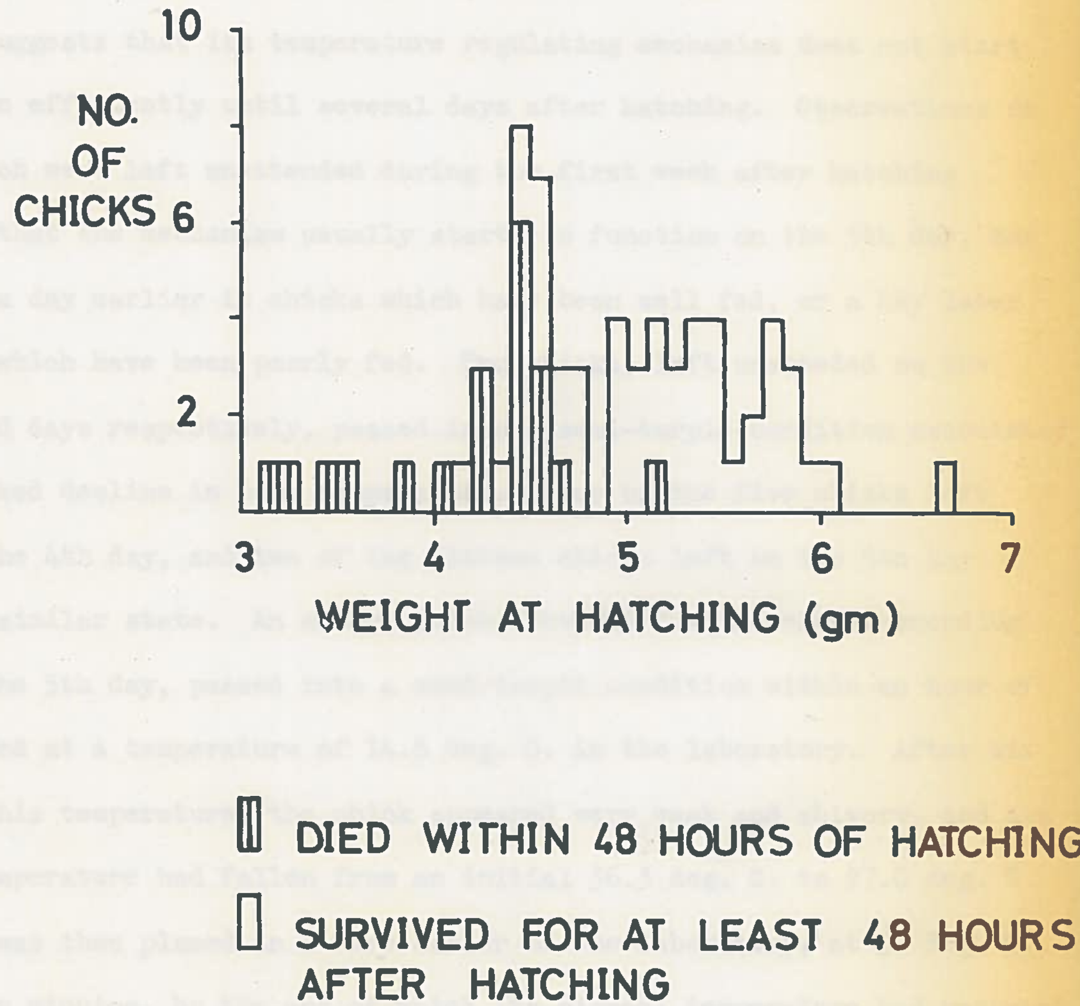


Figure 8. Weights at hatching of 67 chicks of Storm Petrel.

chick survived until at least day 14 is summarized in appendix table 6. The presence of one of the adults with the chick by day after the chick has reached an age of 14 days is very rare. Davis found one bird in attendance on the 16th day, and Lockley recorded one instance of this on the 33rd day. During the present study, adults were found in the burrow by day on the 16th, 17th (twice), 18th (twice), 23rd, and 36th days.

The almost continuous brooding of the chick for six or seven days after hatching suggests that its temperature regulating mechanism does not start to function efficiently until several days after hatching. Observations on chicks which were left unattended during the first week after hatching indicated that the mechanism usually starts to function on the 5th day, but may start a day earlier in chicks which have been well fed, or a day later in chicks which have been poorly fed. Two chicks, left unatteded on the 2nd and 3rd days respectively, passed into a semi-torpid condition associated with a marked decline in body temperature. Four of the five chicks left alone on the 4th day, and two of the sixteen chicks left on the 5th day entered a similar state. An active chick, removed from beneath a brooding adult on the 5th day, passed into a semi-torpid condition within an hour of being placed at a temperature of 14.5 deg. C. in the laboratory. After six hours at this temperature, the chick appeared very weak and shivery, and its cloacal temperature had fallen from an initial 36.3 deg. C. to 27.0 deg. C. The chick was then placed in a warm corner of the laboratory, at 30 deg. C., for fifteen minutes, by the end of which its cloacal temperature had returned to normal. A similar semi-torpid state was found in older chicks only during periods of extreme food shortage (page 52).

Roberts (1940) found that the temperature regulation mechanism of Oceanites oceanicus starts to function about 48 hours after hatching. In this species, the chicks are seldom brooded after the second day. The termination of the brooding phase in other species of Hydrobatidae is probably also related to the development of the temperature regulating mechanism of the chick. The chicks of Pelagodroma marina are brooded for 2 - 4 days (Richdale, 1943), those of Oceanodroma castro for 2 - 3 days (Harris, 1969) or 6 - 7 days (Allan, 1962), and those of O. leucorhoa for 4 - 5 days (Gross, 1935).

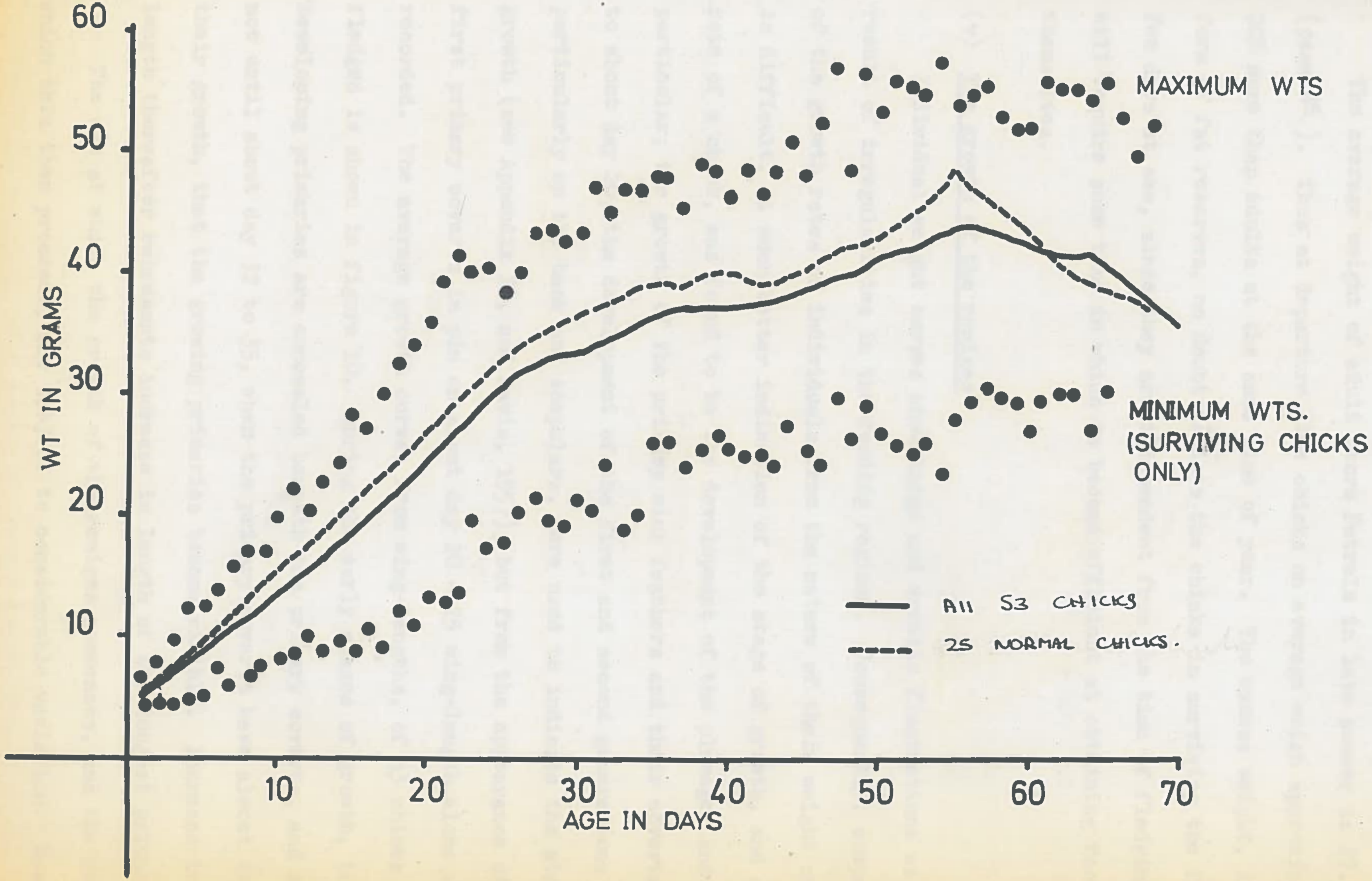
(iii) The growth of the chick

It has become customary, in describing the erratic growth of Procellariiform chicks, to present an average weight curve, obtained by lumping together the data from the entire sample of chicks under observation. Such a weight curve, compiled from the evening weights of 53 chicks weighed throughout the nestling period during the present study, is shown in figure 9. This curve agrees closely with that of Davis, who obtained weights of 32 chicks from hatching to fledging. The curve is of a type recorded for a number of species of Procellariiformes, falling into three stages; an early steep rise in weight (until about day 25 in the Storm Petrel); a more gradual increase until the peak weight is attained (about day 55 in the Storm Petrel); and a decrease in weight prior to fledging.

Because of the great individual variation in duration of the nestling period, and in the age at which the peak weight is attained, an average weight curve, compiled from the weights of all chicks, gives only a poor indication of the true pattern of growth in the Storm Petrel. The average weight curve is particularly misleading with regard to the peak weight, and the abruptness of the pre-fledging decline in weight. The maximum evening weight attained by the 53 chicks under observation averaged 50.3 gm (S. D. $\pm$ 3.3, range 43.5 - 57.5), almost six grams heavier than the peak weight of the average weight curve. The age at which the peak weight was attained varied between 43rd and 76th day, but usually fell in the range 50th to 60th. In three-quarters of the chicks, this occurred between six and twelve days before fledging, the mean for all chicks being 10.4 days. Thus, the pre-fledging decline in weight on average amounted to a drop in weight from 50 gm to 34 gm (see below) in about 10 days, and not a drop from 44 gm to 36 gm in 15 days, as might be supposed from figure 9.

(iv) The weight of the chick at fledging

Determination of the true weight at fledging is subject to the same difficulties as determination of the nestling period, since the young may leave their natal burrow several days before flying. The mean weight of 54 chicks, weighed on their last evening in the burrow, was 34.3 gm (S. D. $\pm$ 3.0, range 24.5 - 38.5). A better indication of the true fledging weight was obtained from the weights of chicks found fledging at night. The



Note: Poorly fed chicks which eventually died of starvation were recorded at much lower weights than the minima shown in the figure.

Figure 9. Average weight-curve of all 53 chicks of Storm Petrel compared with average weight-curve of 25 chicks with "normal" development.

average weight of 51 such chicks was 32.5 gm (S. D. $\pm$ 3.5, range 22.0 - 38.5), which was significantly less than that at which chicks left their burrows, ($t = 2.7$, p = less than 0.01). Chicks caught on the surface at night also had slightly, but not significantly, longer wings than those measured whilst still in the burrow, (average wing-length of chicks on surface, 117.8 $\pm$ 2.4 mm; average wing-length of chicks on last evening in burrow 116.7 $\pm$ 3.3 mm), suggesting that growth of the remiges may not be completed until after departure from the burrow.

The average weight of adult Storm Petrels in late summer is 27.0 gm (page 85). Thus at departure, the chicks on average weigh approximately 20% more than adults at the same time of year. The excess weight, in the form of fat reserves, no doubt assists the chicks in surviving the first few days at sea, since they are independent from the time of fledging and will require some time in which to become efficient at obtaining food for themselves.

(v) <u>The growth of the remiges</u>

Individual weight curves show large and erratic fluctuations as a result of irregularities in the feeding regimen. Consequently, comparison of the growth rates of individuals from the nature of their weight curves is difficult. A much better indication of the stage of growth, and growth rate of a chick, was found to be the development of the plumage, and in particular, the growth of the primary wing feathers and their coverts. Up to about day 20, the development of the first and second generations of down, particularly on the back and scapulars, were used to indicate the stage of growth (see Appendix II, and Davis, 1957), but from the appearance of the first primary coverts in pin on about day 20 - 25 wing-length alone was recorded. The average growth curve, from wing-lengths, of 53 chicks which fledged is shown in figure 10. During the early stages of growth, the developing primaries are concealed beneath the primary coverts, and it is not until about day 32 to 35, when the primary coverts have almost completed their growth, that the growing primaries become visible. Increase in wing-length thereafter represents increase in length of the longest primary.

The age at which the growth of the remiges commences, and the rate at which this then proceeds, are subject to considerable variation. Basically,

1. Average growth-curve of 53 chicks.
2. Average growth-curve of 25 normal chicks.
3. Growth curve of a chick delayed 9 days.
4. Growth curve of a chick retarded 12 days at fledging.
5. Growth curve of an under-nourished chick which died of starvation when 86 days old.

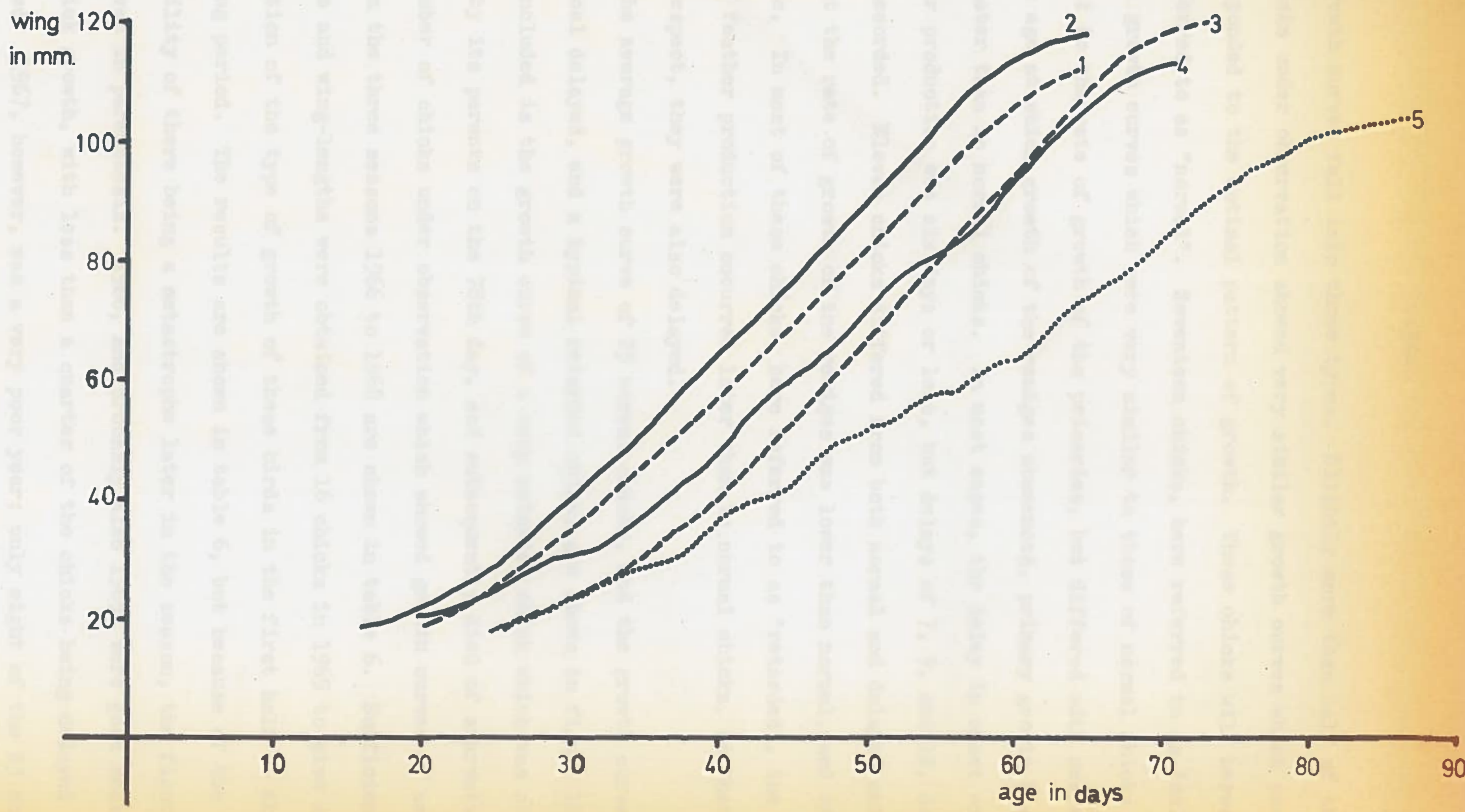


Figure 10. Wing growth of Storm Petrel chicks.

the growth curves fall into three types. Slightly more than half of the 57 chicks under observation showed very similar growth curves which probably corresponded to the optimal pattern of growth. These chicks will hereafter be referred to as "normal". Seventeen chicks, here referred to as "delayed", showed growth curves which were very similar to those of normal chicks with respect to the rate of growth of the primaries, but differed with respect to the age at which growth of the remiges commenced, primary growth beginning later than in normal chicks. In most cases, the delay in onset of feather production was six days or less, but delays of 7, 9, and 12, days were recorded. Eleven chicks differed from both normal and delayed chicks in that the rate of growth of the remiges was lower than normal, and often erratic. In most of these chicks, here referred to as "retarded", the onset of feather production occurred later than in normal chicks, so that in this respect, they were also delayed.

The average growth curve of 25 normal chicks, and the growth curves of a typical delayed, and a typical retarded chick, are shown in figure 10. Also included is the growth curve of a very retarded chick which was abandoned by its parents on the 78th day, and subsequently died of starvation. The number of chicks under observation which showed growth curves of each type in the three seasons 1966 to 1968 are shown in table 6. Sufficient weights and wing-lengths were obtained from 16 chicks in 1969 to give some indication of the type of growth of these birds in the first half of the nestling period. The results are shown in table 6, but because of the possibility of there being a catastrophe later in the season, the figures are given in parenthesis. 1966, and probably also 1969, were good seasons for chick growth, with less than a quarter of the chicks being delayed or retarded. 1967, however, was a very poor year; only eight of the 23 chicks under observation had normal growth curves. The reasons for this will be discussed in detail later (pages 46 & 49). 1968 was a better season, with slightly more than half of the chicks developing normally.

(vi) <u>Weight curves of normal, delayed, and retarded chicks</u>

Of the 29 chicks which showed normal growth curves, 25 were weighed daily. The weight curves of these chicks were essentially similar to each other; all showed an initial steep rise to about day 25, a peak weight

Table 6. Frequency of each type of growth curve in chicks of Storm Petrel in years 1966-1969.

Year	Normal	Delayed	Retarded	% Aberrant
	Number of chicks			
1966	7	0	2	22
1967	8	9	6	65
1968	14	8	3	44
[1969*	12	3	1	25]
Total [excl. 1969]	29	17	11	49

* Figures for 1969 given in parenthesis because study was terminated when most chicks were only half-grown.

between day 52 and day 58, and a rapid decline in weight prior to fledging. The average weight curve of the 25 normal chicks is compared with the average weight curve of all chicks in figure 9. The former curve clearly gives the better indication of the pattern of growth of a Storm Petrel chick, since the nestling periods of the chicks included in the sample were of similar duration.

The average weight curve of normal chicks has been compared with the individual weight curves of delayed and retarded chicks in an endeavour to determine the factors responsible for the different patterns of growth. In figure 11, the normal weight curve is compared with that of three delayed chicks. Obvious in each of these is a period of poor feeding during the first sixteen days after hatching, the weights of the chicks fluctuating well below the normal level. Thereafter, feeding improved, and the weights of the delayed chicks differed little from those of normal chicks, except that the peak weight, and the pre-fledging decline in weight occurred later. The number of days by which the delayed chicks lagged behind normal chicks in their stage of development was closely related to the number of nights when the chick was not fed during the period before the onset of feather production. Once feather production had commenced, the rate of development of delayed chicks did not differ from that of normal chicks. Clearly, a period of poor feeding early in the nestling period does not affect the subsequent rate of growth of the plumage.

In both normal and delayed chicks, periods of poor feeding after day 20 seldom had any affect on the rate of growth of the feathers. A striking example of this ability to continue with the production of feathers during starvation is shown in figure 12a. This chick maintained a normal rate of feather growth throughout a very poor period of feeding from the 33rd to the 42nd day. The chick received only two feeds in nine nights, and as a result suffered a loss in weight of 14 gm., amounting to 33% of its initial weight. 21 of the 46 normal and delayed chicks under observation suffered losses in weight amounting to over 25 per cent of their initial weight within the space of seven days, between the 20th and 55th day. In only one individual was the rate of feather growth in any way retarded. This chick received only two medium-sized feeds and one small feed in the ten nights

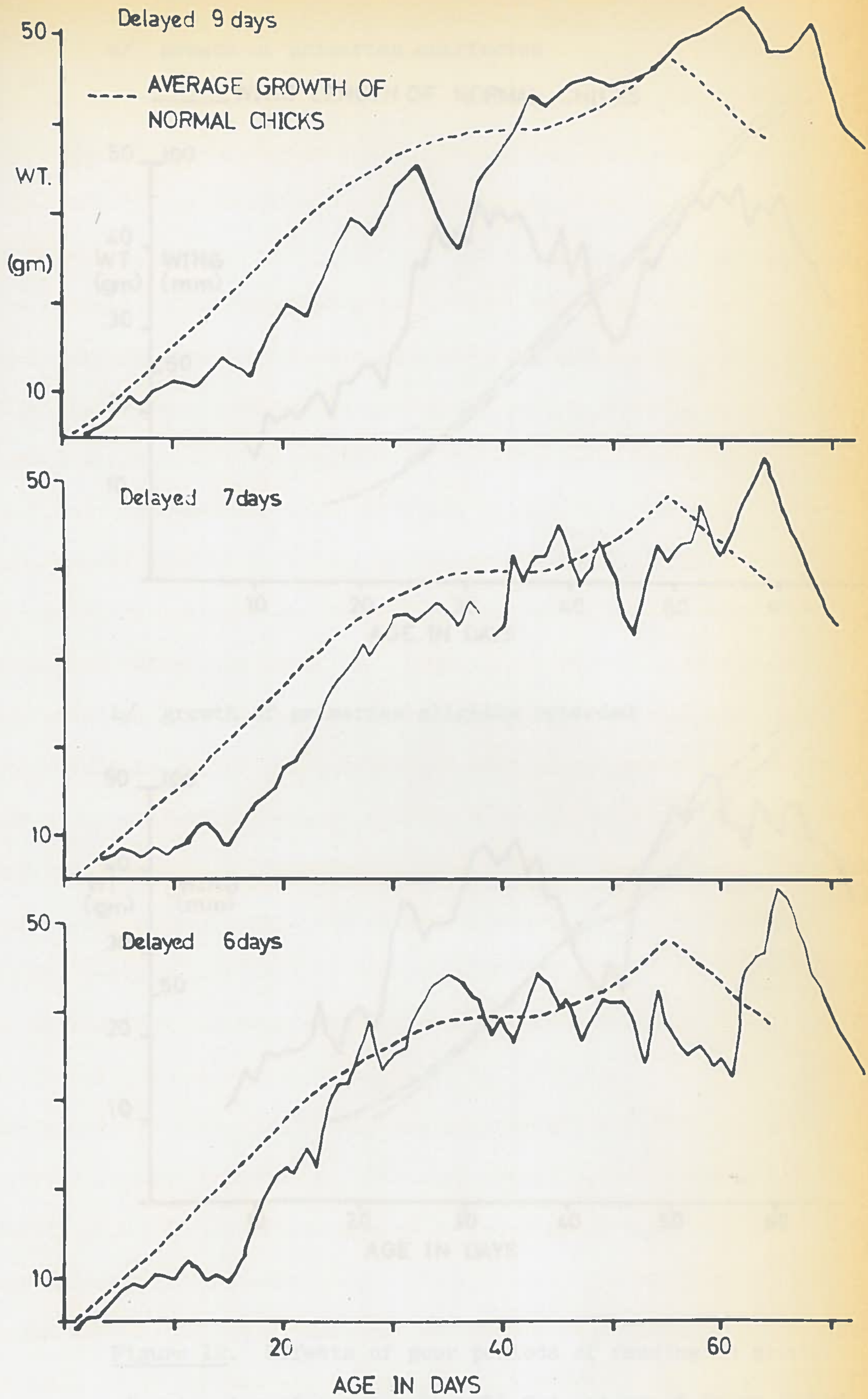


Figure 11. Weight-curves of three delayed chicks of Storm Petrel compared with average weight-curve of 25 "normal" chicks

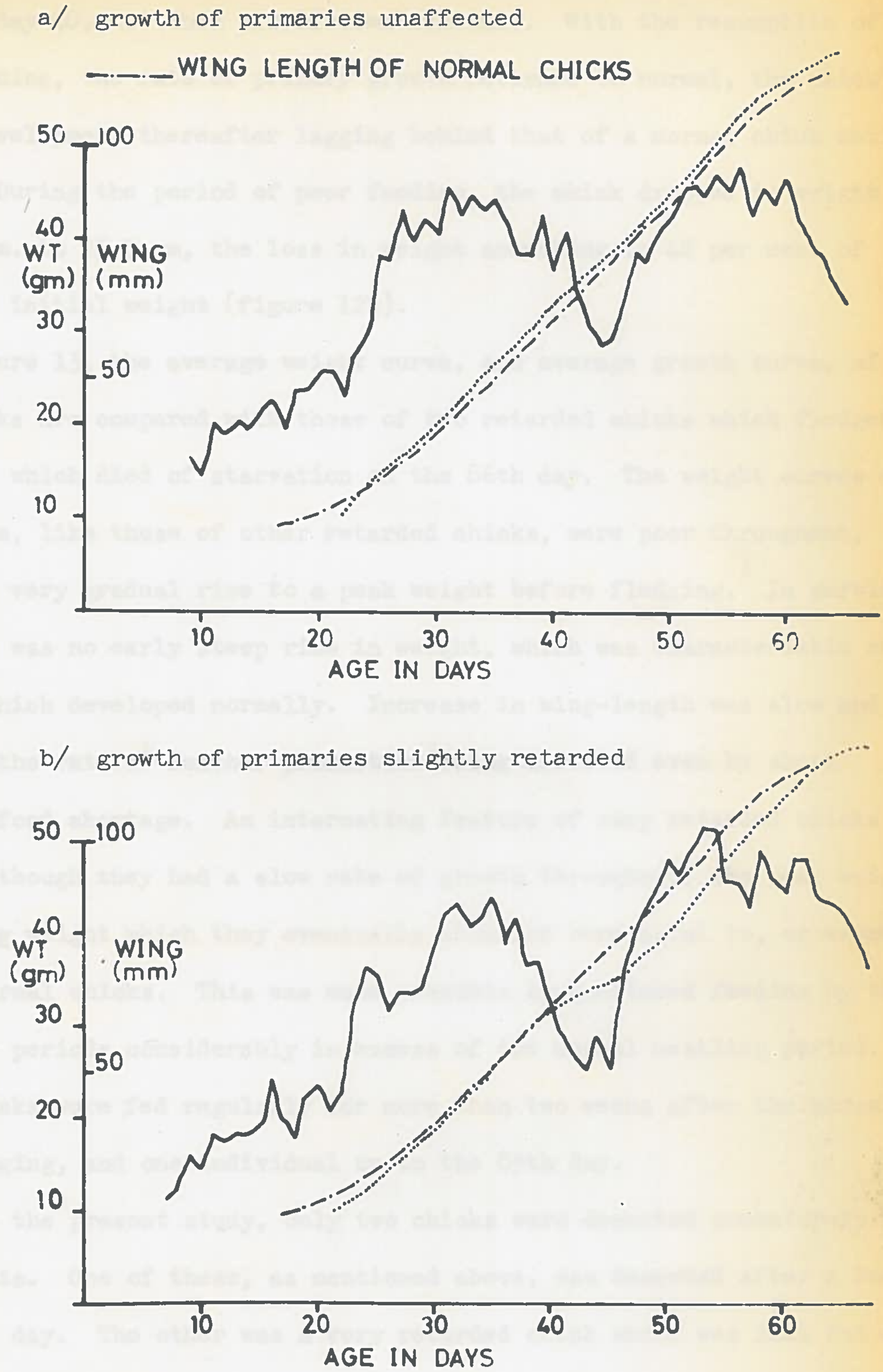


Figure 12. Effects of poor periods of feeding on growth of primaries of previously well fed chicks of Storm Petrel

between the 36th and 45th days. Primary growth was maintained at the normal rate until day 40, but then slowed down somewhat. With the resumption of regular feeding, the rate of primary growth returned to normal, the chick's stage of development thereafter lagging behind that of a normal chick until fledging. During the period of poor feeding, the chick dropped in weight from 44.0 gm. to 25.5 gm, the loss in weight amounting to 42 per cent of the chick's initial weight (figure 12b).

In figure 13, the average weight curve, and average growth curve, of normal chicks are compared with those of two retarded chicks which fledged, and a chick which died of starvation on the 86th day. The weight curves of these chicks, like those of other retarded chicks, were poor throughout, with only a very gradual rise to a peak weight before fledging. In particular, there was no early steep rise in weight, which was characteristic of all birds which developed normally. Increase in wing-length was slow and irregular, the rate of feather production being affected even by short periods of food shortage. An interesting feature of many retarded chicks was that although they had a slow rate of growth throughout, the peak weight and fledging weight which they eventually attained were equal to, or exceeded, those of normal chicks. This was made possible by continued feeding by the parents for periods considerably in excess of the normal nestling period. Several chicks were fed regularly for more than two weeks after the normal age of fledging, and one individual up to the 85th day.

During the present study, only two chicks were deserted prematurely by their parents. One of these, as mentioned above, was deserted after a feed on the 78th day. The other was a very retarded chick which was last fed on the late date of 11th November, when 71 days old. The chick died of starvation eight days later, at a stage in development equivalent to that of a normal chick at 56 days of age. It appears, therefore, that the feeding behaviour of the adults is determined to a large extent by the behaviour of the chick, the parents normally continuing to feed the chick as long as it continues to beg for food.

Table 7 shows the average nestling periods, peak weights, fledging weights, and fledging wing-lengths of normal, delayed, and retarded chicks. The nestling periods of delayed chicks were approximately equal to the

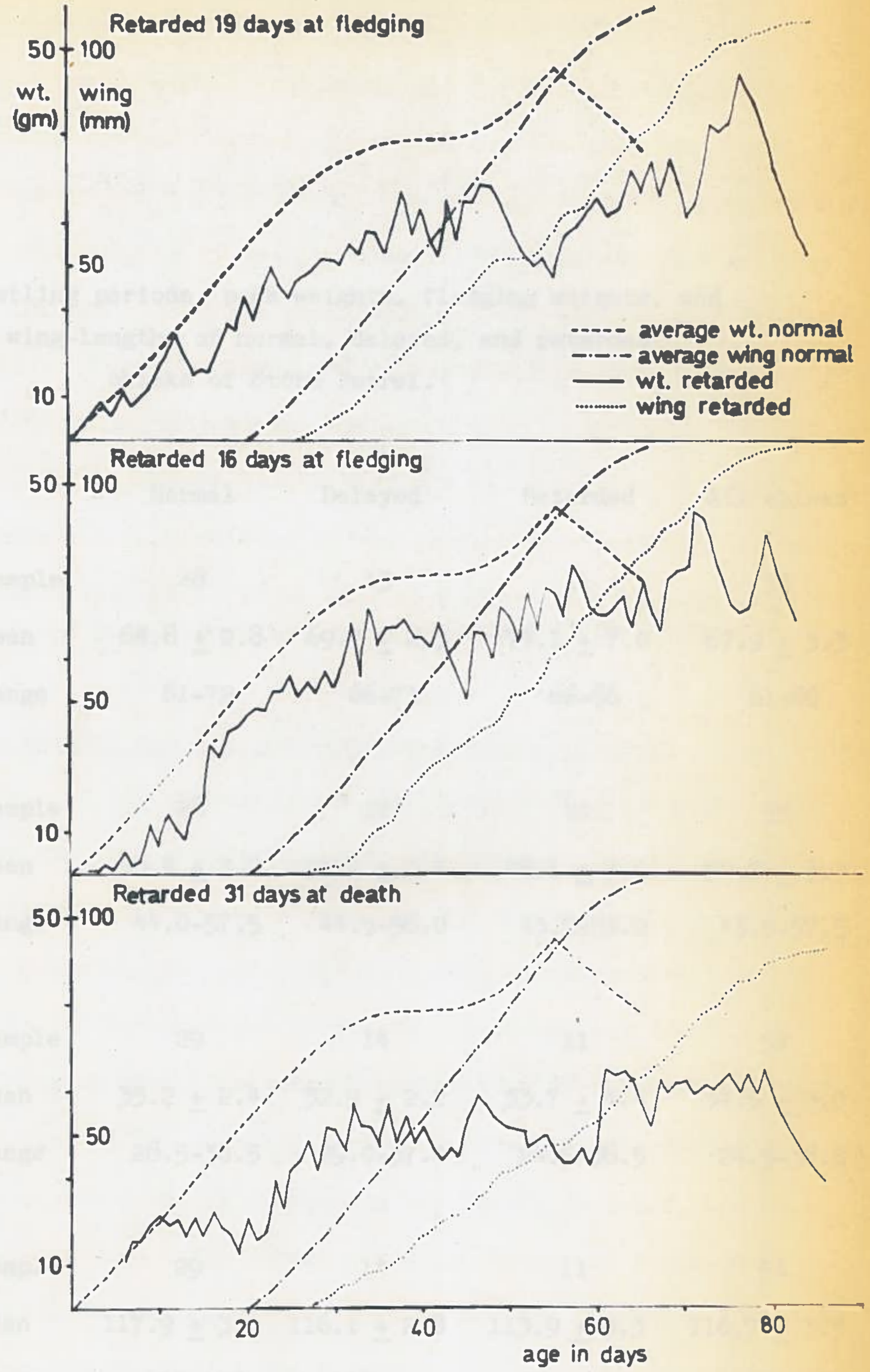


Figure 13. Growth-curves of three retarded chicks of Storm Petrel compared with average growth-curve of 25 "normal" chicks

Table 7. Nestling periods, peak weights, fledging weights, and fledging wing-lengths of normal, delayed, and retarded chicks of Storm Petrel.

		Normal	Delayed	Retarded	All chicks
Nestling period (days)	Sample	28	13	11	53
	Mean	64.8 ± 2.8	69.4 ± 2.3	74.1 ± 7.0	67.9 ± 5.3
	Range	61-72	66-73	66-86	61-86
Peak wt. (gms.)	Sample	28	17	10	55
	Mean	50.4 ± 3.2	51.1 ± 3.4	48.1 ± 3.0	50.3 ± 3.3
	Range	44.0-57.5	44.5-56.0	43.5-53.0	43.5-57.5
Fledging weight (gms.)	Sample	29	14	11	54
	Mean	35.2 ± 2.4	32.9 ± 2.2	33.7 ± 4.4	34.3 ± 3.0
	Range	28.5-38.5	29.0-37.0	24.5-38.5	24.5-38.5
Fledging wing-length (mm.)	Sample	29	14	11	54
	Mean	117.9 ± 3.0	116.1 ± 2.8	113.9 ± 3.3	116.7 ± 3.3
	Range	113-123	112-122	109-119	109-123

average period of normal chicks plus the number of days delay in the onset of feather production, whereas those of retarded chicks were, in some instances, extended by as much as three weeks as a result of a slow rate of growth throughout development. Peak weights and fledging weights were essentially similar for all three types of chicks, the only consistent differences between normal and abnormal chicks being in the wing-lengths at fledging. The wing-lengths of delayed chicks were slightly shorter than those of normal chicks, the difference falling just short of significance at the 0.05 level. The wing-lengths of retarded chicks were on average 4 mm. shorter than those of normal chicks, the difference being highly significant (p = less than 0.001). This suggests that the ultimate size attained by a Storm Petrel chick might be related to the rate of growth during the nestling period, poorly fed chicks being slightly smaller at fledging than well fed chicks.

(vii) The peak weight, and the pre-fledging decline in weight

As the growth of the plumage nears its completion, most chicks show a steep rise in weight to a peak weight much in excess of the normal adult weight. This increase in weight towards the end of the nestling period is typical of many Procellariiformes. Harris (1966) has suggested that the large accumulation of fat reserves serves two complementary functions in allowing the adults to leave the colony earlier than if they had to supply food less regularly but for a longer period of time, and the chicks to have a better chance of surviving if the adults are forced to leave them as a result of a food shortage. The former point is clearly of negligible importance in the Storm Petrel, since there is no true desertion period in this species (see below), and no great urgency for the adults to leave the colony as soon as possible (see below, and page 136). Presumably, therefore, the function of the large accumulation of food reserves is to enable chicks to complete their growth in the absence of parental attention, and to have sufficient food reserves remaining to support them during the first few days of independent life at sea.

Following the peak weight, most chicks show a more or less rapid decline to the fledging weight, interrupted at intervals by small feeds. The chick is seldom deserted for more than four days before fledging, and may occasionally be fed up to the night before its departure. Davis found that visits to the burrow, presumably by the parents, occasionally occurred after the chick had departed. A similar state of affairs has been found in Pelagodroma marina (Richdale, 1943), Oceanites oceanicus (Roberts, 1940), and Oceanodroma castro (Allan, 1962; Harris, 1969). Clearly it is not possible to speak of a true desertion period, as has been described in several species of Procellariidae (e.g. Lockley, 1930; Marshall and Serventy, 1956; Richdale, 1963).

(viii) The growth of the body structures, and the "minimum growth" curve

Large fluctuations in the weight of a petrel chick, resulting from irregularities in feeding, reflect changes in the quantity of the food reserves, and obscure the pattern of growth of the body structures. To obtain a growth curve which is indicative of the true rate of growth of the body structures, it is necessary to determine how much of the total weight is made up of food reserves at any age. No attempt was made to determine the size of the food reserves of a Storm Petrel chick by fat extraction analyses. However, an indirect measure has been obtained by comparing the minimum weights of chicks at which development was unaffected, with the maximum weights at which this was affected (figure 14). There is almost total separation between these two sets of weights. Assuming that retardation of growth occurs only when the food reserves are practically exhausted, the curve separating the two sets of points in figure 14 should represent the rate of growth of the body structures alone. The ability of chicks to survive for one or two days after falling in weight below the level of the minimum growth curve indicates that some other source of energy must be available for maintenance during extended periods of starvation. This is presumably the energy obtained from the breakdown of body proteins. Survival under conditions of extreme food shortage will be discussed in detail in a later section.

The average amount of food reserves available for maintenance and growth in a normal chick can be calculated from the difference between the minimum growth curve and the average weight curve (table 8). Normal chicks hatch with a small amount of food, stored in the form of yolk, to tide them over until the first feed. A rapid accumulation of food reserves

Figure 14.

Note: The minimum weights of chicks showing normal growth-curves are plotted alongside the weights of delayed and retarded chicks at which the rate of development was first affected during periods of starvation. So that it might be possible to compare the weights of normal, delayed, and retarded chicks at a similar stage of development, the weights of delayed and retarded chicks have been plotted against stage of development, as measured by down-growth, or wing-length. The horizontal axis thus becomes the age estimated from the stage of development, and not the number of days from hatching.

Minimum growth-curve

Average weight-curve of normal chicks

Minimum weights at which primary growth was not affected

Maximum weights at which primary growth was affected

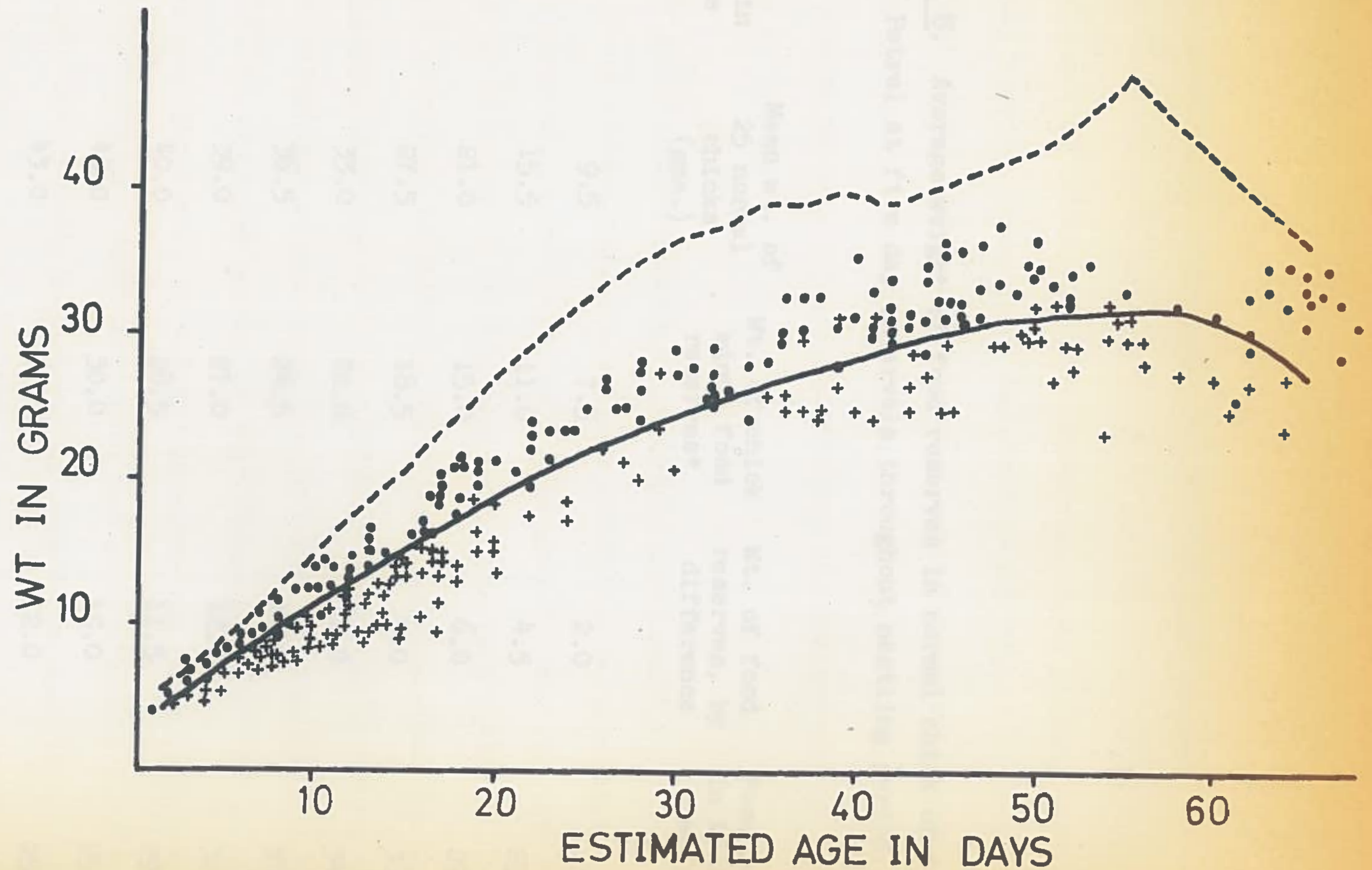


Figure 14. Minimum growth-curve of chicks of Storm Petrel.

Table 8. Average weight of food reserves in normal chick of Storm Petrel at five day intervals throughout nestling period.

Age in days	Mean wt. of 25 normal chicks (gms.)	Wt. of chick minus food reserves*	Wt. of food reserves, by difference	Food reserves in % of body weight
5	9.5	7.5	2.0	21
10	15.5	11.0	4.5	29
15	21.0	15.0	6.0	29
20	27.5	18.5	9.0	33
25	33.0	22.0	11.0	34
30	36.5	24.5	12.0	33
35	39.0	27.0	12.0	31
40	40.0	28.5	11.5	29
45	40.0	30.0	10.0	25
50	43.0	31.0	12.0	28
55	48.0	32.0	16.0	33
60	43.0	31.0	12.0	28
Fledging	32.5	27.0	5.5	17

* The weights of chick minus food reserves have been taken from the minimum growth curve reproduced in figure 14. Points on this curve represent weights of normal chicks at which growth ceases, i.e. weights after exhaustion of food reserves.

is then essential if the chicks are to survive periods of food shortage early in development. For normal chicks, the food reserves reach their maximum, in terms of percentage of body weight, at about day 25, coincident with the onset of feather growth. From then until shortly before fledging, these food reserves, comprising between 25% and 33% of the total body weight, ensure that growth can be maintained at a constant rate, despite marked fluctuations in the rate of food intake. At fledging, the food reserves on average amount to only 5.5 gm., sufficient to maintain the chick for one or two days at the most.

(ix) The weight recession in the minimum growth curve

If it is assumed that the minimum growth curve represents the weight of the body structures alone, the decline in weight after the 54th day cannot be caused by utilization of food reserves. Ricklefs (1968) has discussed the weight recession in nestling birds, and has shown that for the Barn Swallow *Hirundo rustica*, a weight recession amounting to 20.3 per cent of the adult weight can be accounted for entirely by a decrease in water content. From an extensive survey of the literature on growth in birds, he found that the phenomenon of weight recession was restricted primarily to swallows Hirundinidae, swift Apodidae, and several groups of oceanic birds, particularly the Procellariiformes. He considered that in all groups except the Procellariiformes, the magnitude of the weight recession was such that water loss alone probably accounted for it.

Obviously, in the Procellariiformes, the accumulation of food reserves, and subsequent "starvation period", contribute greatly to the peak nestling weight, and magnitude of the weight recession. It might, however, be expected, from Ricklefs' results, that part of the weight recession in Procellariiformes is due to water loss, particularly from the plumage, which, in the long-winged and densely-feathered petrels comprises a relatively high proportion of the body weight. The decline in weight, prior to fledging, in the minimum growth curve of the Storm Petrel, amounts to about 5.0 gm, or approximately 19 per cent of the adult weight. This is well within the range of weight losses found in other groups outside the Procellariiformes. It seems likely, therefore, that a weight recession of the body structures, similar to that of the other groups, occurs in the Storm Petrel, but is completely masked by the loss of weight resulting from utilization of food reserves. Clearly, analyses of the lean dry weight, lipid content, and water content of the Storm Petrel chick are required before this can be confirmed.

(x) The nature and utilization of the food reserves

It is clear, from the literature, that the large accumulations of food reserves in the chicks of many Procellariiformes consist mainly of fat deposits under the skin, and in the body cavity. Roberts (1940) dissected starving chicks of Oceanites oceanicus, and found that the loss in weight was due mainly to the utilization of fat deposits. These deposits undoubtedly provided most, if not all, of the energy for maintenance and growth during periods of food shortage. However, it is clear that fat reserves alone cannot maintain growth during starvation, since the production of body tissues requires a supply of proteins. If growth is to be continued at a constant rate during periods of starvation, then a part of the food reserves must consist of temporary deposits of protein.

Examination of the minimum growth curve of Storm Petrel reveals that the weight of the body tissues of a growing chick increases by about ten grams between day 25 and day 56. Perhaps as much as 5 gm of this is water which is lost again during the weight recession prior to fledging. Therefore the total protein requirements for growth from day 25 to fledging may amount to only about 5 gm, or 0.16 gm per day. Certainly, the protein requirements for feather production are small. The plumage of a fully-feathered chick weighs about 2.3 gm (1.6 gm of contour feathers, and 0.7 gms of flight feathers), and since this is produced in approximately 35 days, the requirements during growth on average amount to only 0.06 gm per day. Thus, for a chick to continue growth throughout a period of starvation of 96 hours (three nights without food), it will require only 0.24 gm of stored protein for feather production, and about 0.40 gm. of stored protein for the growth of the remainder of the body tissues. This represents less than 7 per cent of the average amount of food stored by a normal chick at any time between the ages of 25 and 56 days.

King and Farner (1961) have calculated that the energy requirements for the conversion of proteins to keratins in feather production is approximately 55 k. cals/gm. Using this figure, it has been calculated that the total energy requirements of the Storm Petrel chick for the production of its plumage will be about 132 k. cals., or about 3.8 k. cals./day during the major growth period. According to King and Farner, the metabolizable energy of stored fat is equivalent to 9.5 k. cals./gm. Thus, the breakdown of 0.4 gm of fat per day would provide sufficient energy to maintain growth of the plumage during a period of fasting. Similarly, a small amount of fat will be required to provide the energy for the production of other body tissues. The remainder of the weight loss during starvation is presumably due to the breakdown of fat for the production of energy for maintenance.

(xi) Growth rates in the Hydrobatidae

The results of the present study clearly demonstrate that in the Storm Petrel, the availability of food for the young can affect markedly the growth rate, peak weight, and nestling period. Considerable variation in the duration of the nestling period has also been reported in *Pelagodroma marina* by Richdale (1943), and in *Oceanites oceanicus* by Roberts (1940). The latter author considered this to be due to variations in the availability of food. Individual variation in growth rate within a species has been demonstrated by Harris (1969). He studied two populations of *Oceanodroma castro* breeding in the Galapagos Islands in the hot and cold seasons respectively, and found that chicks reared in the cold season had significantly slower rates of growth, and longer nestling periods (average nestling period 78 days), than chicks reared in the hot season (average nestling period 70 days). Furthermore, both populations had slower rates of growth and longer nestling periods than chicks reared in the Ascension Island group (average nestling period 64 days)(Allan, 1962).

It seems that these species of storm petrel have evolved a flexible rate of growth which can be modified, within very broad limits, to the conditions obtaining at a specific time and specific place. Differences in the growth rates of populations of the same, and perhaps also different, species of storm petrel may therefore not reflect any basic hereditary differences in growth rates, so much as differences in the availability, and perhaps also quality, of the food supply. Probably, with regard to the differences between species, both factors play a part. The chicks of Oceanites oceanicus have a much faster rate of growth and higher peak weight in relation to adult weight than the other species of storm petrel for which these are known. Roberts (1940) has shown that a very rapid accumulation of food reserves early in the nestling period, before the onset of the winter snows, is essential for survival. However, the food supplies in the Antarctic seas, which this species inhabits, are particularly abundant and predictable. Clearly, a rapid rate of growth is both possible and necessary. To what extent the growth rate of O. oceanicus has become specifically adapted to this situation, and to what extent the rapid rate of growth is merely a consequence of the abundant food supply, is not clear.

The advantage of a flexible rate of growth is presumably that it allows chicks to attain normal size and weight at fledging under a wide range of conditions of food availability. This advantage might be outweighed if there was a high premium on completing growth as quickly as possible, a situation which has been shown to exist in several species of Procellariidae (Lack, 1968). Harris (1966) has shown that undernourished chicks of Puffinus puffinus grow their feathers at about the same rate as well nourished chicks, and fledge at approximately the same age. Perrins (1966) found that early fledged chicks on average survive better than late fledged chicks, and concluded that the birds were breeding as early as possible. Lack (1966) therefore concluded that natural selection favours those young shearwaters which leave the colony earlier but undernourished, rather than later but well nourished. However, in the storm petrels, with the possible exception of O. oceanicus, the breeding season is very protracted, and there would seem to be no strong selection pressures favouring an early date of fledging. Furthermore, the meagre evidence available for the Storm Petrel suggests that the date of fledging has little bearing on subsequent post-fledging survival, (see Section III). It seems likely, therefore, that with regard to post-fledging survival, good condition at fledging is of greater importance than an early date of fledging, and hence takes precedence in determining the type of growth to be achieved.

(xii) Food and related topics

(a) The feeding process, and the nature of the food.

Storm Petrels feed their young by regurgitation. The details of the feeding process have not been described, but it is likely that feeding occurs in a similar manner to that described in Oceanodroma castro (Allan, 1962; Harris, 1969). Certainly, towards the end of the nestling period, feeds may be given to chicks in a very short time. In September and October, adults have often been netted on their way in with food only 30 minutes before all aerial activity ceased, and as adults never remain with their chick by day at this time of the year, it can be assumed that the entire feed may be given in less than half an hour.

Adult petrels, except when rearing chicks, rarely regurgitate anything but a strong-smelling, yellowish oil, the function of which is still the subject of some debate. However, breeding birds, when handled, usually regurgitate food which they are carrying for their chick. This is invariably a pre-digested grey pulp mixed with a small amount of the oil. Obvious amongst all regurgitations were the remains of small fish, one to two inches in length, and the 31 food samples collected for microscopic examination were composed almost entirely of these. Of 57 fish which were sufficiently intact to enable some identification to be made, 47 were young stages of the Herring Clupea harengus or the Sprat Clupea sprattus. In addition, nine of the samples contained one or two small crustaceans of the family Hyperidae (Amphipoda), and one sample contained a single crustacean of the suborder Caridea (Decapoda). Clearly small fish of the neritic macroplankton form the staple diet of the Storm Petrel on Skokholm from late July until early October.

(b) The frequency of feeding

It was clear, from the difference between weights on successive days, whether or not a chick had been fed during the intervening night. Even when the feeds were small, resulting in a slight overnight loss in weight, the deviation from the loss in weight expected if no feed had been given was obvious. Twice-daily weighings established that during the brooding stage, in addition to receiving a large feed at night, chicks were commonly given small feeds at intervals throughout the day. The frequency of feeding at 54 burrows under observation in the three seasons 1966 - 1968 is summarized in appendix table 7. From hatching until the 60th day, chicks were fed at a very constant rate, on average on 82 per cent of the available nights.

In the poor season of 1967, when an unusually high proportion of chicks showed delayed or retarded growth curves, the percentage of nights on which the chicks were fed was significantly less than in the other two years (79% cf. 83% and 84%; $\chi^2 = 11.2$, p = less than 0.005). In the three seasons of Davis's study, the feeding frequency agreed closely with those of 1966 and 1968 (chicks fed on 83 per cent of the available nights).

(c) The size of the feeds

From a consideration of the overnight increases in weight of chicks which had been fed, and the rate of loss of weight of these chicks during the day, it has been possible to estimate the actual amount of food given to the chicks during the night. The full calculations are given in Appendix 1. Briefly, it was found that the true size of the feed exceeded the overnight increase in weight by 1.0 to 5.0 gm. for chicks aged 11 - 20 days, 2.0 to 5.5 gm. for chicks aged 21 - 30 days, and 2.5 to 6.0 gm. for older chicks. The difference between feed-size and overnight increase in weight increased slightly with increasing feed-size.

The weight of food received by a chick during a single night varied between 2 and 22 gm., but feeds of more than 15 gm were rare, and at some burrows, this figure was never exceeded. Some of the biggest feeds caused large percentage increases in the weight of the chicks. Davis mentioned a chick of 11 gm. which received a feed of 11 gm., and during the present study, a chick weighing 16 gm. received a feed of about 15 gm. which brought its weight to 28 gm. by the following morning. Feed sizes of as much as 70 per cent of the weight of the previous evening were not uncommon in chicks up to thirty days old, although the average feed-size of chicks up to this age constituted only about 30 per cent of the previous weight. Towards the end of the nestling period, the average feed-size was equivalent to between 15 and 20 per cent of the chick's weight.

The average size of the feeds given to 32 normal and delayed chicks, and 8 retarded chicks is shown in table 9. Feed-sizes are not available for the first five days after hatching, since chicks were weighed only once daily during this period. The size of the feeds given to normal and delayed chicks increased up to day 15, but thereafter remained constant until the peak weight was attained. Retarded chicks, in addition to being fed less

<u>Table 9</u>. Average size of feeds given to 32 normal or delayed chicks, and 8 retarded chicks of Storm Petrel.

Age in days	Normal and delayed chicks: Number of feeds	Normal and delayed chicks: Average size* of feeds(gms.)	Retarded chicks: Number of feeds	Retarded chicks: Average size* of feeds(gms.)
1- 5	-	-	-	-
6-10	43	4.6	12	4.0
11-15	114	6.0	22	5.4
16-20	118	7.7	30	5.8
21-25	123	8.4	33	6.9
26-30	129	8.2	30	6.3
31-35	148	7.9	28	7.4
36-40	128	7.5	30	6.8
41-45	133	7.6	28	6.5
46-50	133	8.4	28	7.1
51-55	140	8.1	25	7.1
56-60	120	7.6	26	6.2
61-65	70	6.5	26	6.7
66-70	14	6.2	17	7.6
71-75	-	-	15	5.6
76-80	-	-	9	6.2

* Size of feeds calculated from overnight increase and rate of loss of weight by day, as described in Appendix I.

frequently than normal chicks, received smaller feeds throughout. Davis's results were essentially similar, except that his average feed-sizes were 1.0 to 1.5 gm. less than those obtained during the present study. This was no doubt due to the inadequacy of his single relationship between feed-size and overnight increase in weight (see Appendix 1).

(d) The last fifteen days in the burrow

As mentioned previously, following the peak weight, most chicks show a marked decline in weight, and eventually fledge at a weight about five grams heavier than that of adults. Table 10 gives the frequency of feeding, and the duration of the "starvation period", at 48 burrows during the 15 days prior to fledging. There is a marked drop in the feeding rate about seven or eight days before fledging, and at four burrows, feeding ceased at this time. However, nearly 60 per cent of the chicks were fed up to three nights before fledging, and 5 chicks (10%) were fed on the night before they left.

Table 11 shows the average size of feeds given to 35 chicks during their last fifteen days in the burrow. As Davis pointed out, the decline in feed-size, commencing about ten days before fledging, must be due, in part, to the reduced number of occasions on which both parents returned on the same night. Many of the feeds were however very small, suggesting either that the parents were bringing less food than previously, or that the chicks were not accepting all the food that they were offered.

(e) The feeding regimen

It was usually possible, from the size of the feeds, to determine whether a chick had received a meal from one, or both, parents. Feeds of more than ten grams were probably the result of visits by both parents. Only one chick ever received a feed in excess of 20 gm, and the highest weight recorded of an adult carrying food was 37 gm, about 10 gm. above the normal weight of an adult in late summer. On the other hand, after day 20, feeds of less than five gm. were rare, so that the number of feeds of less than ten gm. resulting from visits by both parents must have been very small. Consequently, feeds of ten or more grams are here regarded as the result of visits by both parents, and feeds of less than ten grams as the result of a visit by a single parent.

Davis thought that feeding by both parents occurred on nearly half the

Table 10. Frequency of feeding at 48 burrows of Storm Petrel during last 15 days before fledging.

[a] Number of chicks fed

	Nights before fledging														
	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1
Number fed	40	41	34	41	38	41	39	37	37	29	25	26	23	14	5
% fed	83	85	71	85	79	85	81	77	77	60	52	54	48	29	10

[b] Duration of starvation period prior to fledging

	Number of nights without food prior to departure								
	0	1	2	3	4	5	6	7	8
Number of chicks	5	12	11	8	5	3	2	2	0

Table 11. Average size of feeds given to 35 chicks of Storm Petrel during last 15 days before fledging

	Nights before fledging														
	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1
Number of feeds	31	30	25	30	27	32	28	28	27	22	17	15	17	10	3
Average size of feeds (gm.)	9.6	8.3	8.2	9.4	7.9	7.8	7.2	7.7	6.3	6.2	7.5	6.3	4.3	5.2	3.3

nights when the chick was fed. During the present study, 303 (29%) of the 1054 feeds given to chicks between the ages of 21 and 60 days were of ten or more grams. These large feeds usually followed gaps in feeding, and it became clear that, under normal conditions, each parent returned to the colony on every second night. Usually, the visits of the two parents did not coincide, so that the chick received one meal each night. This pattern commenced during the brooding phase, and at a few burrows, was maintained with scarcely a break until fledging. Occasionally, perhaps as a result of bad weather or a temporary shortage of food, one of the parents was a day late in returning to the burrow, so that the visits of both parents coincided. As a result the chick received a large feed on that night, and a new pattern of large feeds alternating with gaps in feeding was set up. This pattern rarely lasted for more than six or eight days, suggesting that the parents generally avoid feeding the chick on the same night. Rarely, both parents fed the chick nightly for short periods, perhaps when there was a rich food supply unusually close to the island. The number of nights on which the chicks were fed by both parents more than compensated for the nights on which the chicks were not fed, so that, on average, the chicks received 1.1 meals per night from hatching until the age at which the peak weight was attained.

(f) The factors affecting frequency of feeding, and size of feeds

The chicks under observation were fed on 2451 occasions out of a possible total of 2996. The duration of the gaps in feeding, totalling 545 nights, is shown in table 12. Single nights were by far the most frequent, constituting 88 per cent of the total. As indicated above, many of the one-night gaps in feeding resulted from a switch to the feeding regimen of double feeds on alternate nights. Other one-night gaps, and some of the longer gaps, resulted from the parent's failure to return to the colony because of bad weather. As Davis has shown, the frequency of feeding is not affected by cloud cover, rain, fog, the phase of the moon, or winds of up to force 6 (Beaufort scale). However, on nights of winds of force seven or more, there was a marked reduction in the feeding frequency (table 13). Nevertheless, even on the worst nights, some petrels managed to get in to feed their chicks. The night of 19th September 1968 was particularly bad

Table 12. Interval between feeds given to chicks of Storm Petrel

Year	Number of feeds given	Number of nights without food since previous feed							
		0	1	2	3	4	5	6	7
1966/1968	1610	1341	240	21	7	0	1	0	0
1967	841	646	168	18	6	1	1	1	0
Total	2451	1987	408	39	13	1	2	1	0

Table 13. Effect of strong winds on frequency of feeding at burrows of Storm Petrel.

Wind force [Beaufort scale]	Wind speed [m.p.h.]	Number of nights	Number of feeds possible	Number of feeds given	% fed
0-6	0-31	265	2657	2265	85
7	32-38	7	115	85	74
8	39-46	14	169	88	52
9-10	47-63	4	55	13	24

with continuous gale-force winds, dense overcast, and torrential rain, and yet three of the twenty-four chicks under observation were fed.

Such extreme conditions seldom persisted for more than one or two nights. The only sustained period of bad weather during the present study occurred in early September 1968, with winds of force 7 - 8 on the nights of 2nd and 3rd, force 8 - 10 on the night of 4th, and force 7 on the night of 5th. Of the seventeen chicks under observation, five were left for two consecutive nights without food, two for three nights, one for four nights, and one, which had not been fed on the night of 1st, for five nights.

Davis considered that strong winds and the associated rough seas affected the parents' ability to collect food. He found that the average of 22 feeds given after a day of gales was 1.8 gm less than the overall average feed-size. The average size of 104 feeds given on nights of rough seas during the present study was 6.6 gm, i.e. 1.1 gm less than the normal feed-size. However, much of this difference was clearly due to the reduced number of occasions on which the chick received two meals in the same night. Only 13 per cent of the feeds given on nights of strong winds were attributable to visits by both parents, compared with 29 per cent of all feeds. Furthermore, the frequency of feeding and size of feeds on nights following periods of gales, when the seas remained rough, were not significantly different from those under normal conditions. It appears therefore that the reduced feeding rate during gales is not due so much to the parents' inability to collect food because of the rough seas, as to the parents' failure to return to the colony because of the strong winds.

Although bad weather locally, and probably also in the feeding areas, was responsible for many of the gaps in feeding, there remained a large number of gaps, some of several days, which could not be attributed to weather conditions. By far the worst period for feeding during the present study occurred in early August 1967. From the night of 9th until the night of 15th, the weather was fine, with little cloud, good visibility, and, for the most part, winds variable, force 2 - 4. However, the eighteen chicks under observation were fed on only 55 per cent of the available nights (on 60 occasions out of a possible total of 109). The size of the feeds was also affected. Of forty feeds of known size, twenty were of less than five grams, and the average (5.6 gm) was 0.7 gm less than the estimated average of chicks of similar ages under normal conditions. It appears therefore that the adults were having difficulty in obtaining sufficient food for their chicks, and as a result, returned less frequently to the colony. Presumably, either food was scarce, or the birds were having to fly further than usual to collect it. As no mist-netting was carried out during this period, it was not possible to determine if the poor feeding conditions had any effect on the weights of the adults.

This period of poor feeding occurred shortly after the period of peak hatching (27th July to 5th August). As shown earlier, chicks are at their most vulnerable, with regard to food shortage, during the first week or ten days after hatching, as they have not, by that time been able to accumulate the large reserves of food necessary for surviving long periods of starvation. Six of the eighteen chicks under observation died of starvation during the week of poor feeding. All were under twelve days old on the 10th August. Four died after two nights without food, one after three, and one after four. Seven other chicks, ranging between 5 and 14 days of age on the 10th August, showed delayed growth curves as a result of the poor feeding. A further chick lost one of its parents on the 12th or 13th August, and was then fed by the remaining parent on alternate nights until 30th August. The chick was unable to build up any food reserves, and died of starvation after two nights without food. Only four chicks survived the poor period without suffering any retardation of growth. One of these, aged four days on 10th August, missed only one night's feed during the period, whilst the others, aged 15, 17, and 18 days respectively, had built up enough food reserves to cope with the shortage. This period of food shortage and a period of very bad weather in early September were clearly responsible for the generally poor rates of growth achieved in 1967.

As shown previously, the frequency of feeding remains very constant from hatching until the age at which the peak weight is attained. Thus it has been possible to lump together the data from chicks of different ages to determine if the frequency of feeding changes as the season progresses (table 14). No significant trends in the frequency of feeding were evident, either in individual years, or in the three seasons taken together. It has

Table 14

Frequency of feeding and average size of feeds given to chicks of Storm Petrel from early August to late October.

Date (5-day period ending)	Nights available	% nights when feed given	No. of feeds of known size	Average size of feed
Aug 1	47	81	2	9.0
Aug 6	107	79	13	10.5
Aug 11	155	81	27	7.6
Aug 16	180	77	51	7.7
Aug 21	202	80	81	8.0
Aug 26	225	91	115	8.0
Aug 31	236	86	132	7.2
Sep 5	243	78	123	7.7
Sep 10	250	85	152	8.4
Sep 15	248	88	154	6.9
Sep 20	227	78	127	7.3
Sep 25	210	83	129	7.8
Sep 30	171	81	96	7.6
Oct 5	148	82	88	7.8
Oct 10	114	82	59	7.5
Oct 15	87	74	35	7.6
Oct 20	62	74	30	8.2
Oct 25	41	85	14	10.9
Oct 30	22	86	9	7.4

also been shown that the size of the feeds remains relatively constant from the age of 15 days until the peak weight is attained. It was therefore possible to determine if the average size of the feeds varies with time of year. As shown in table 14, the average size of the feeds remains relatively constant from early August until mid-October, by which time most chicks have fledged. These results do not suggest that the feeding conditions are any worse for late-hatched chicks than for early-hatched chicks, and it is concluded therefore, that with regard to the average availability of food, the date of hatching is unimportant within the limits encountered in most breeding seasons. Periods of poor feeding, due to shortage of food, or extreme weather conditions, appear to be irregular and unpredictable in their occurrence.

Perhaps the most important single factor affecting the overall rate of feeding is the efficiency of the parents. Davis suggested that some Storm Petrels are more efficient than others at rearing chicks. Two of his pairs bred in the same burrows in consecutive years, and in both years reared retarded chicks. Certainly there is great variation in the frequency with which individual chicks are fed. For example, in 1968, one chick went without food on only four nights before it attained its peak weight, whilst another, which hatched eight days later in a nearby burrow, was not fed on 22 nights, and as a result had a very retarded rate of growth. Both pairs were known to have bred in the same burrows in the previous year. The data were insufficient to determine if some pairs were consistently less efficient than others. However, there was some indication that experienced pairs were more efficient than pairs which included at least one bird breeding for the first time. The previous experience of 26 pairs which successfully raised chicks was known. Only three of the 22 pairs which had occupied the same burrow in the previous year reared retarded chicks, as compared with all four of the pairs which included at least one inexperienced bird. The one pair which included two inexperienced birds bred in a burrow which neither bird had previously occupied. Although the birds maintained a high frequency of feeding - there was no break in feeding up to day 54, and only four one-day gaps before fledging - the feeds were unusually small, and as a consequence, the development of the chick was retarded.

(xiii) <u>The effects of prolonged periods of starvation</u>

As described earlier, the ability of Storm Petrel chicks to maintain an active state and to continue their growth during periods of fasting is dependent on the large reserves of food normally accumulated during the first three weeks after hatching. Individual variation in the length of time that growth can be maintained is clearly related to differences in the amount of stored food. Young, or poorly nourished, chicks may have insufficient food reserves to enable them to continue their growth for more than 48 hours after receiving a feed, whereas well nourished older chicks can withstand periods of as much as 96 hours (three nights without food) without suffering any retardation of growth.

With the exhaustion of the food reserves, growth ceases, and the chick enters a semi-torpid condition associated with violent shivering. The chick's eyes are closed, the wings held stiffly, and the body is cool to the touch. Chicks under ten days of age normally die within twenty-four hours of entering this condition, but older chicks have survived for up to 72 hours, and, with the resumption of feeding, recovered rapidly and completely. Indeed, even during fasting, chicks removed from the burrow and kept in a warm place usually return to their normal level of activity within a few minutes.

96 per cent of the gaps in feeding were of 72 hours (two nights without food) or less, and consequently, few chicks exhausted their food reserves and entered the semi-torpid condition. Four chicks were, however, left for much longer periods without food; one for 120 hours, two for 144 hours, and one for 168 hours. Three of these individuals had previously been well fed, and were able to continue their growth for about 96 hours. Thereafter, they entered the semi-torpid condition, and remained in this state until the next feed. The fourth chick had previously been poorly fed, and was able to continue its growth for only two days before passing into the semi-torpid condition. By the fifth day of its fast, the chick was in very poor condition, but recovered completely on receiving a large feed on the following night.

The chick which survived for 168 hours without food deserves special mention. This bird had been particularly well fed during the few days before the fast, and had attained the high weight of 56.5 gm. by the morning of the 54th day. Then followed an interval of six nights before the next feed was given. During this period, the weight of the chick dropped to 26.5 gm., the loss in weight of 30 gm. being equivalent to 53 per cent of the chick's initial weight. Davis also recorded an instance of a chick surviving for seven days without a feed, between the 46th and the 52nd day.

It was not possible, during the present study, to undertake a complete series of measurements of the cloacal temperatures of chicks from hatching to fledging. However, sufficient temperatures were taken to establish that the cloacal temperature of healthy growing chicks remains very constant from the 4th or 5th day until fledging. The average cloacal temperature of 26 well nourished chicks, ranging in age from 9 to 55 days, was 38.3 deg. C. (S. D. $\pm$ 0.5, range 37.4 - 39.1). the temperatures of four normal chicks, after one night without food, were 37.4, 38.1, 38.1, and 38.5 deg. C. respectively, and therefore not significantly different from chicks which had been fed.

The cloacal temperatures of four retarded chicks were taken on 17 occasions. On ten, these measurements followed a night on which the chicks were fed, and the average temperature of 38.2 deg. C. (S. D. $\pm$ 0.5, range 37.2 - 39.2) was not significantly different from that of normal chicks. On one occasion, the chick had received a very small feed after a period of poor feeding, and its temperature of 36.4 deg. C. was 0.8 degrees lower than that of any other retarded or normal chick which had been fed. The remaining six temperatures were taken after the chicks had been left for one or more nights without food. The details of these chicks, and their cloacal temperatures, are given in table 15.

Five of the chicks were in a semi-torpid condition when examined. Their cloacal temperatures, falling in the range 24.9 to 27.5 deg. C., were some 10 to 13 deg. C lower than those of healthy, active chicks. However, when placed in the laboratory at 21 deg. C., four of the chicks recovered rapidly, their temperatures returning to near normal within fifteen minutes. Chick 36b was in very poor condition when first examined. After fifty minutes at 15.0 deg. C., its temperature had fallen from an initial 27.3 deg. C. to 21.5 deg. C., and the chick appeared almost dead. It recovered somewhat when kept at 21.6 deg. C. for forty minutes, and its temperature rose

Table 15. Cloacal temperatures of retarded chicks of Storm Petrel during periods of starvation

Chick	Age at onset of fast. (days)	Nights without food	Condition when examined	Cloacal temperature (°C)	Cloacal temp. after 15 mins. in lab. at 20°C
7	42	1	semi-torpid	25.9	35.0
7	43	2	active	34.9	37.2
7	46	1	semi-torpid	24.9	35.2
36b	26	2	semi-torpid	27.3	32.8
37a	44	2	semi-torpid	27.5	36.8
37a	45	3	semi-torpid	27.2	37.1

to 32.8 deg. C. After a further period of 95 minutes at 15.0 deg. C., its temperature had fallen to 19.2 deg. C. The chick was once more kept at 21.6 deg. C. for thirty minutes, by the end of which its temperature had risen again to 26.2 deg. C. The bird however remained weak, and died shortly afterwards.

Clearly, as a result of extreme food shortage, these chicks had entered a semi-poikilothermic state, presumably in order to conserve their remaining supplies of energy. The transition from this condition to an active state with normal or near normal temperature is rapidly accomplished with an increase in environmental temperature. However, on several occasions, chicks recovered from their semi-torpid condition at burrow temperatures, as a result of disturbance during weighing. Chick 7 (on day 43) was in a semi-torpid condition, and cool to the touch, when first removed from its burrow, but had recovered almost completely by the time that its temperature was taken, about ten minutes later. Rapid recovery at low temperatures would, of course, be essential, since the arrival of the parents with food often coincides with the coldest part of the night.

The semi-poikilothermic state of starved chicks of the Storm Petrel is similar in many ways to the condition of starving chicks of the Swift *Apus apus*. Koskimies (1948) has shown that during periods of extreme food shortage, Swift chicks enter a poikilothermic state during the sleep period. The body temperature falls to within 2 or 3 deg. C. of the environmental temperature during the night, but returns rapidly to normal at dawn. Recovery in some individuals may be completed in as little as twenty minutes.

An ability to survive for up to five days without food has been described in all species of Hydrobatidae hitherto investigated. (Roberts (1940) recorded one starvation period of 20 days in the subantarctic *Oceanites oceanicus*). However, little work has been done on the physiological condition of the birds during fasting. Davis described a single instance of semi-torpidity in the Storm Petrel, and suggested that survival had been aided by a general slowing of the metabolism. Richdale (1943) recorded several similar instances of semi-torpidity in chicks of *Pelagodroma marina* during periods of food shortage, and Ainslie and Atkinson (1937) found that the body temperatures of poorly fed chicks of *Oceanodroma leucorhoa* were as much as 4.4 deg. C. lower than those of well fed chicks. It seems likely, therefore, that the ability to enter a semi-poikilothermic state during periods of extreme food shortage is widespread amongst this group. However, it is clear that this condition is seldom necessary. Under normal conditions, chicks are able to accumulate sufficient food reserves to enable them to withstand all but the severest periods of food shortage without bringing any special physiological mechanism into operation.

(xiv) Chick mortality

The fate of 133 chicks which hatched during this study is shown in table 16. Chicks which hatched in 1969 have been included, although the study ended when most of these were only about half grown. Any errors in the overall fledging success, resulting from this inclusion, will be small, since the data from the other seasons have shown that very little mortality occurs after the first three weeks. The most important cause of mortality, accounting for 62 per cent of all chick losses, was death of the chick during the first 48 hours after hatching, and before it had received a feed (page 32). Starvation, as a result of a genuine shortage of food, was an important cause of mortality in only one season. In that year (1967), approximately one third of the chicks which hatched before 12th August died of starvation during a period of very poor feeding in the early part of the month (page 50). The only other death from starvation occurred in 1968; the chick died after two nights without food during the first week after hatching. The other losses of chicks were due to a wide variety of causes, each accounting for less than 2 per cent of the chicks which hatched. Interference from other burrowing sea-birds, and rabbits, was not responsible for any of the losses at the burrows under regular observation. However, a single dead chick was found amongst fresh diggings at the entrance of a rabbit burrow in 1967, and it seems likely that the petrels breeding in the midst of dense shearwater colonies must suffer some losses of this nature.

The overall success from hatching to fledging (66%) was substantially less than that obtained by Davis in the three seasons 1954 - 1956. Of the 37 chicks which hatched during his study, only four failed to fledge, giving a success of 89 per cent. Davis recorded only one instance of death immediately after hatching, and found no evidence of food shortage in any of his

Table 16. Fledging success of Storm Petrel, and causes of loss chicks.

	1966	1967	1968	1969	Total	% of chicks which hatched
Chicks hatched	28	39	32	34	133	-
Chicks fledged	21	19	25	23*	88	66
Died within 48 hours of hatching	4	10	5	9	28	21
Died of starvation when more than 48 hrs. old	0	7	1	0	8	6
Died as result of loss of one of parents	0	1	1	0	2	2
Prematurely deserted by parents	0	1	0	0	1	1
Trapped in crevice in burrow	0	0	0	1	1	1
Pecked to death by parents	0	1	0	0	1	1
Attacked by snail *Helix aspersa*	1	0	0	0	1	1
Disappeared without trace	1	0	0	1	2	2
Drowned in rain storm	1	0	0	0	1	1

* Attained age of three or more weeks, and therefore assumed to have survived to fledging

seasons.

7. Breeding success

The breeding success in the four seasons of the present study is summarized in table 17. In the three years 1966, 1968, and 1969, the average hatching success was 66%, and the average fledging success was 74%, giving an overall production of 0.49 fledged young per breeding pair. In the poor season of 1967, the figures were 55%, 49%, and 0.27, respectively. The low success in 1967 was due in part to a high incidence of infertility, but mainly to losses from starvation during the period of food shortage in early August. The overall production obtained by Davis (0.59 fledged young per breeding pair) was slightly higher than in any of the four seasons of the present study, due almost entirely to a very high success from hatching to fledging in all three years of his study (see above).

The figures for the overall breeding success presented in table 17 do not give a true indication of the reproductive output of the community for a variety of reasons. On the one hand, losses incurred at laying, as a result of the female's inability to return to the burrow in time, would have been overlooked. Furthermore, as a result of loss of mate, a small number of experienced birds spend a season as non-breeders, thereby reducing the reproductive potential of the population. On the other hand, although those breeding losses which were clearly caused by my interference have been ignored, it is likely that a few have been incorrectly assigned to natural causes, and included in the samples. Further, because of my repeated intrusions, the burrows were abnormal in that they contained a high proportion of inexperienced and newly-formed pairs, which, as shown below, are less successful than experienced pairs. To some extent, these two sets of biases would counteract each other, but it is considered that in an undisturbed community, breeding success should be slightly higher than the figures in table 17 suggest.

Few reliable data are available for the breeding success of other species of Hydrobatidae. Allan (1962) and Harris (1969), working at two widely separated populations of Oceanodroma castro, found that the overall production was 0.33, and 0.30 young fledged per pair, respectively, and Harris (1969) estimated that in a population of O. tethys in the Galapagos

Table 17. Breeding success in four seasons 1966-1969.

	1966		1967		1968		1969		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%
Eggs laid	42	-	71	-	51	-	50	-	214	-
Eggs hatched	28	67	39	55	32	63	34	68	133	62
Chicks fledged	21	75*	19	49	25	78	(23)	(68)	88	66
Breeding success in young fledged per pair	0.50		0.27		0.49		0.46		0.41	

* Expressed as a percentage of those which hatched.

Islands, not more than 0.23 young were fledged per pair. In these species, the major cause of breeding failure was intraspecific competition for nest-sites.

The influence of date of laying and pair status on breeding success

In table 18, the hatching success, fledging success, and overall production in the seasons 1967 - 1969 are summarized according to the date of laying. The data obtained in 1966 have been omitted, since dates of laying were not known with any accuracy, and could not be calculated for those eggs which failed to hatch. The results show a striking, and highly significant, decline in breeding success as the season progresses. Although the samples are small, it would seem that pairs laying in early June are about three times as successful as pairs laying in late July. The decline in breeding success was entirely due to a progressive increase in the rate of infertility, and mortality within 48 hours of hatching. The proportion of failures due to other causes was not affected significantly by the date of laying (table 19).

The decline in breeding success does not necessarily imply that environmental conditions become less favourable for breeding as the season progresses. Indeed, as shown above (page 51), the data on frequency of feeding and size of feeds suggest that the feeding conditions remain favourable until at least mid-October, by which time most chicks have fledged. Certainly, late hatched chicks may grow at rates comparable to those of early hatched chicks, and fledge at normal weights. Furthermore, there was no indication that the poor success of late breeders is due to an increase in the number of chicks which die of starvation. In fact, the only losses from starvation encountered during the present study affected pairs which had laid in late June. Clearly, some other factor must be at least in part responsible for the decline in breeding success.

As described earlier (page 23), experienced pairs, returning to a burrow in which they have bred previously, on average lay 17 days earlier than pairs which contain at least one bird which is breeding for the first time. In table 20, the breeding success of experienced pairs is compared with that of newly-formed, and inexperienced, pairs. The difference between the two groups is highly significant (χ^2 = 6.9, p = less than 0.01),

Table 18. Breeding success of Storm Petrel in relation to date of laying in three seasons 1967 - 1969

Year		Date of laying Jun 1-15	Jun 16-30	Jul 1-15	Jul 16-31
1967	Eggs laid	3	44	15	9
	% hatched	67	64	33	44
	% fledged*	100	43	60	50
	% success	67	27	20	22
1968	Eggs laid	3	28	14	6
	% hatched	67	68	71	17
	% fledged*	100	84	60	100
	% success	67	57	43	17
1969	Eggs laid	10	21	16	3
	% hatched	90	67	63	33
	% fledged*	89	79	30	100
	% success	80	52	19	33
Total	Eggs laid	16	93	45	18
	% hatched	81	66	56	33
	% fledged*	92	64	48	67
	% success	75	42	27	22

* % of chicks which hatched.

Table 19. Incubation losses of Storm Petrel resulting from infertility, and losses of chicks within 48 hours of hatching, in relation to date of laying.

	Date of laying			
	Jun 1-15	Jun 16-30	Jul 1-15	Jul 16-31
No. of eggs laid	16	93	45	18
No. of chicks hatched	13	61	25	6
% infertile*	7	17	29	56
% dying within 48 hours of hatching**	8	18	40	33
% lost due to other causes during incubation*	12	17	15	11
% lost due to other causes during nestling period**	0	18	12	0

* expressed as percentage of eggs laid.

** expressed as percentage of chicks hatched.

Table 20. Breeding success of Storm Petrel in relation to previous experience of pair.

	Experienced pairs which bred in same burrow in previous year/s			Pair containing at least one bird breeding in that burrow for first time		
	Laid in June	Laid in July	Total	Laid in June	Laid in July	Total
Eggs laid	54	15	69	9	21	30
% hatched	63	73	65	67	52	57
% fledged*	82	64	78	33	36	35
% success	52	47	51	22	19	20
% eggs infertile	17	7	14	11	38	30
% chicks died at hatching*	15	27	18	50	64	59
% eggs/chicks lost due to other causes	22	27	23	33	10	17

* expressed as percentage of chicks which hatched.

experienced pairs being more than twice as successful as newly-formed and inexperienced pairs. The difference in success was entirely due to differences in the rate of infertility, and the freqency of death at hatching. The proportion of failures due to other causes was slightly higher in experienced pairs than in inexperienced pairs, largely as a result of the food shortage in 1967, which affected the young of early, and therefore mainly experienced, breeders.

The difference in success between experienced pairs, and newly-formed and inexperienced pairs, is clearly responsible for some of the decline in breeding success as the season progresses, but does not in itself exclude the possibility that environmental conditions also cause a decline in breeding success. Indeed, it could be postulated that experienced pairs are more successful than inexperienced pairs because they breed earlier. However, as can be seen in table 20, there was no difference in success between experienced pairs which laid in June, and experienced pairs which laid in July, nor between inexperienced pairs which laid in June, and inexperienced pairs which laid in July. It is concluded, therefore, that the decline in breeding success as the season progresses is due entirely to a progressive increase in the proportion of newly-formed and inexperienced pairs in the samples. Environmental conditions would appear to be equally favourable for early breeders and for late breeders.

Why inexperienced, and newly-formed, pairs are so much less successful than experienced pairs is not clear. There was little indication that inattentiveness on the part of inexperienced parents, either during incubation, or at hatching, was responsible for the high rate of failure. Psychological factors, affecting inexperienced females or females with new mates during the courtship period, might perhaps have an adverse effect on the success of fertilization, thereby explaining the low viability of the eggs of these birds. Coulson (1966) has shown that in the Kittiwake *Rissa tridactyla* females breeding for the first time and experienced females which change their mates, lay smaller clutches, and despite this, have a lower breeding success, than experienced birds which have kept the same mate as in the previous year. This suggested to Coulson that the birds in newly-formed pairs are less well adjusted to each other, that they do not stimulate each other to as high a level of reproductive drive, and that they cannot co-ordinate their incubation pattern as well as long-established pairs. However, it is difficult to see how such psychological and physiological factors could account for the poor survival of chicks of newly-formed pairs of Storm Petrels. The amount of food reserves available to the chick at hatching is clearly of some importance, but how this might be influenced by the previous experience of the female is not known. The size of the egg, the relative proportions of its constituents, and the quality of the food utilized in its production, may all be of relevance here. Clearly, much more information is required on the size and composition of the egg in relation to the previous experience of the female, pair status, date of laying, hatching success, and immediate post-hatching survival. In a species as sensitive to disturbance as the Storm Petrel, the collection of an adequate amount of such data is probably an insurmountable task.

Section II : The Community

The community of Storm Petrels on Skokholm consists of several classes of individuals which differ in the frequency and timing of their visits to the island, and in their activity at the colony. In late summer, when the community numbers seventeen to nineteen thousand birds, the following classes of individuals may be recognized:

(i) Experienced breeders engaged in breeding.

(ii) Young birds breeding for the first time. This class probably accounts for about 10 per cent of the breeding birds (see section III).

(iii) Failed breeders lingering on at the colony after the loss of their egg or chick, Because of the poor breeding success, this category may include as many as half of the adults at the colony in July and early August.

(iv) Non-breeders in occupation of a burrow. Most of these are birds in occupation of a burrow prior to first breeding, although there are also a few experienced birds which spend a season as non-breeders after the loss of their mate. Between 15 and 30 per cent of all birds with burrows belong to this class (see below).

(v) Young non-breeders, here referred to as wandering non-breeders, which visit the colony in late summer, show no site attachment, and do not enter burrows. During late July and August, non-breeders of this category comprise about half of the birds mist-netted in flight over the colony. Probably about half of these non-breeders are birds visiting Skokholm from other colonies.

(1) The activity of breeding birds

The activity of breeding birds has been described in section I. Birds usually return to the colony in late April or early May, but do not actually land or enter burrows until mid-May. The birds normally settle to breed in or near to the burrow they have occupied in previous years. Before laying, adults make frequent visits to the burrow at night, and occasionally occupy it by day. Aerial activity is intense, rendering the birds more susceptible to capture in mist-nets than at any other time of the year. Throughout incubation and the nestling period, adults spend little time in flight over the colony, other than that associated with arrival, location of the burrow, and departure. Successful breeders leave the colony in late September or

October. Birds breeding for the first time differ from experienced birds in that they arrive back at the colony and breed about two weeks later, and are much less successful.

Failed breeders, after losing their egg or chick, may return to the burrow by night, and may even resume occupation by day, for a short time. Usually, however, the burrow is deserted immediately, although the birds may continue to make regular visits to the colony at night. Davis recorded failed breeders returning to the colony for up to ten weeks after losing an egg, and up to four weeks after losing a chick. The results of this study suggest that failed breeders seldom linger at the colony for more than four weeks, and usually depart along with the non-breeders in late July or August.

(2) The activity of non-breeders

Davis (1957) considered that once an immature bird has returned, it normally spends no more than one season in the colony as a pre-breeder, but admitted that it was possible that immatures may not adopt a regular burrow in their first season at the colony. He considered that the large body of so-called "ineffectives" consisted of pre-breeders (immatures, perhaps nearly all of one age group), and a very small number of mature birds which do not breed. Davis had no means of catching large numbers of petrels in flight, and was therefore unaware of the large influx in late summer of non-breeders which do not adopt a regular burrow, and probably never alight on the surface.

In the present discussion, non-breeders have been divided into:
(i) Non-breeders in occupation of a burrow; and (ii) wandering non-breeders which do not enter burrows.

(i) Non-breeders in occupation of a burrow

Determination of the proportion of this class of non-breeders in the community presents several difficulties. Non-breeders prospecting for burrows are particularly sensitive to interference. Presumably any interference during the season of prospecting would indicate that the burrow being visited is not safe, and cause the bird to move elsewhere. Because of the necessity of handling for marking purposes, desertions of non-breeders were frequent, and it has therefore not been possible to determine whether or not non-breeders normally visit a number of burrows during the prospecting stage. Davis thought that casual visits by non-breeders to occupied burrows were frequent, and on many occasions during the present study, strange birds appeared in burrows for one day only. Some of these visits may however have been the first of a series which was interrupted by my intrusions. Furthermore, it was often impossible to determine whether pairs occupying a burrow for a brief period in the early part of the season were non-breeders, or mature birds which would have bred but for my interference. Finally, it was discovered that established breeding birds, in occupation of a burrow, may make casual visits to burrows nearby, during the pre-egg stage.

Thus, determination of the ratio of breeding birds to birds which did not breed, in a series of burrows, will give an exaggerated figure for the proportion of genuine non-breeders in the community. Davis thought that between 35 and 52 per cent of the birds visiting his study burrows were not breeding. The results of the present study suggest that the proportion of non-breeders in the population is considerably less than this. In 1966, there was a pronounced bias towards burrows containing breeding birds, since all burrows were located by day in July and August, when most churring had ceased. In a sample of 75 birds, only five were not breeding. During 1967, 1968, and 1969, all known burrows were examined, and regular nightly searches were made for other burrows containing churring birds. Of 125 birds in burrows in 1967, 88 (70%) were known to be breeding, of 105 birds in 1968, 70 (67%) were breeding, and of 102 birds in 1969, 80 (78%) were breeding. It would appear therefore that less than 30 per cent of the petrels occupying burrows are non-breeders, and in view of the sources of error outlined above, the true figure might well amount to much less than this.

Although most authors working on species of Hydrobatidae have commented on the presence of large numbers of non-breeders in burrows, few have attempted to estimate the proportion of these in the population. Allan (1962) working on <u>Oceanodroma castro</u>, found that about 63 per cent of the birds occurring in burrows eventually bred, whilst Harris (1969), working on the same species, found that breeding occurred in about 74 per cent of the burrows occupied in a season. Harris also found that non-breeders commonly visited burrows already occupied by mature birds. Richdale (1943 and 1965), working on Pelagodroma marina, thought that as many as two-thirds of the total population were non-breeders. The majority of these appeared not to have any attachments, visiting a number of burrows including some already occupied by other non-breeders or even breeders. The remainder were tied to a particular burrow which they visited regularly by night, and occupied occasionally by day.

It was seldom possible, during the present study, to determine when a non-breeder made its first nocturnal visit to a burrow. However, daily checks at the burrows indicated the onset and frequency of day-occupation by these birds (table 21). Some burrows were occupied by non-breeders as early as the second half of May, whereas others were not occupied by day until late July. Day-occupation was at its most frequent from late June to the end of July, few birds remaining in the burrows by day after the first week of August. Judging by the low level of churring in early August, it would appear that at most burrows, nocturnal visits were also discontinued at this time. Exceptionally, non-breeders continued to visit the burrow until late August or early September. The last instance of occupation recorded in the study area was on 27th August 1966, but a petrel, almost certainly a non-breeder, was heard churring from a burrow outside the study area on the night of 6th September, 1969. Although some non-breeders continue to visit the colony at night for several weeks after ceasing to occupy the burrow, it appears that the majority leave the island almost immediately.

There is great individual variation amongst non-breeders in the regularity with which they spend days in occupation at the burrow. At a few burrows, non-breeders were present by day on only one occasion, and at most burrows, day-occupation occurred only three or four times during the season. However, at some burrows, particularly those in which a pair were in residence, visits were much more frequent. At two burrows, one or both of the pair were present on ten days between 1st July and 2nd August, and between 15th July and 3rd August, respectively. Checks at the entrances of a small series of burrows occupied by non-breeders indicated that nocturnal visits occurred much more frequently than occupation by day, visits being made on between half and two-thirds of the possible nights.

Table 21. Onset and frequency of occupation of burrows by day in non-breeders of the Storm Petrel.

Date	Number of individuals first recorded in burrows by day	Total number of days spent in occupation
Apr 16-30	0	0
May 1-15	0	0
May 16-31	7	7
Jun 1-15	17	19
Jun 16-30	15	20
Jul 1-15	13	28
Jul 16-31	7	28
Aug 1-15	0	12
Aug 16-31	0	1
Sep 1-15	0	0

The rapid decline in the frequency of courtship flights in late June, before the day-occupation of non-breeders has reached its peak, suggests that this form of display does not occur in non-breeders. These birds probably, however, make up the bulk of the birds found prospecting walls and rock-piles, or churring from the shallower, and obviously less suitable sites, in June and July.

(ii) Wandering non-breeders which do not enter burrows

The number of petrels visiting the colony, as indicated by the size of the mist-netted samples, reaches a peak in late July and early August. Catches decline sharply in early September, and by the end of September, it is clear that only birds still rearing chicks remain at the colony. The great majority of the petrels making up this late summer influx belong to a class of "ineffective" birds completely overlooked by Davis. Intensive netting, and subsequent retrapping, have shown that these birds have no attachments to any particular part of the colony (see below). Furthermore, their arrival in July and early August is not associated with any increase in burrow-occupation or churring, and indeed, very few petrels are found on the surface at this time. It appears therefore that the non-breeders of this category do not enter burrows, and probably never even alight on the surface.

As will be shown in later sections, several criteria are available for the separation of wandering non-breeders from other classes of birds at the colony. Thus it has been possible to calculate the proportion of non-breeders in the samples at different times of the year (Appendix III). At the peak, between late July and late August, between 45 per cent and 55 per cent of the birds mist-netted in flight over the colony belong to this class of petrels.

Large variations in the numbers caught indicate that these non-breeders are not regular in their visits to the colony. Local weather conditions are clearly of some importance, catches being highest on warm, calm, and clear nights. The phase of the moon is relatively unimportant, the numbers of non-breeders being reduced only under exceptionally light, or exceptionally dark, conditions (see page 13). Certain periods of low catches are not however readily explicable in terms of local conditions, and the variation in timing of the greatest activity in the four seasons of the study suggests that other factors are affecting the frequency of visits to the colony. In 1966, wandering non-breeders were present at the colony in numbers from late July to the end of August, with a peak in the middle of that month, whereas in 1967, the only large catches were made in the last few days of July, and on one night at the end of August. In 1967, there were heavy losses of chicks due to starvation in early August, indicating that there was a shortage of food locally. It is therefore possible that non-breeders were either unable to obtain sufficient food to make regular visits to the colony, or feeding too far away. In 1968, the numbers of petrels were high in the second half of July and early August, and again in late August. In 1969, the pattern was essentially similar, except that non-breeders were abundant until early September. It would thus seem likely that the number of non-breeders visiting the island is affected by the availability of food in the area; in times of food shortage, petrels abandon their visits to the colony, and perhaps move to richer feeding areas elsewhere.

The activity of this class of non-breeders was by no means restricted to the areas favoured for breeding, since these birds were most abundant around rocky outcrops on the cliff tops, and along the relatively unindented south coast, many parts of which were unsuitable for breeding petrels. The boulder beaches and scree slopes at the base of the cliffs and in the smaller bays were generally avoided, except on very light nights. Thus comparatively few non-breeders were caught in the Quarry, although this bay contained between a third and a quarter of the breeding pairs on Skokholm. The occurrence of wandering non-breeders in areas where there are few breeding birds, and their lack of site attachment, suggest that these birds are patrolling the cliffs at night.

Similar behaviour can be observed by day in the non-breeding Fulmars _Fulmarus glacialis_ on Skokholm. Fulmars bred on Skokholm for the first time in 1967, but each year since the 1930s, a few birds have occupied ledges as non-breeders. These birds confine the greater part of their aerial activity to the cliff face bearing their prospective nest-sites, and in this respect are comparable to non-breeding Storm Petrels in occupation of a burrow. However, each season, there is a small number of birds which cruise around the island, flying in and out of the bays, over the headlands, and occasionally over the top of the island. They show no attachment to any particular site, and are presumably young birds which have not yet adopted a ledge.

(3) The significance of the aerial activity at the colony

Observations made during the present study do not suggest the presence of any regular type of social display other than the chases of breeding birds in May and June, which are clearly part of the courtship behaviour of established pairs. Other aerial activity at this time of the year appears to be associated with prospecting and location of burrows. In late summer, when the level of aerial activity is at its highest due to the arrival of a large number of wandering non-breeders, the aerial activity of breeding birds seems to be confined to flying straight to and from the burrow, thus minimizing the risk from predation. Observations at mist-nets indicate that the wandering non-breeders behave entirely as individuals; there was no evidence to suggest that birds fly in groups or perform aerial chases. Any true social behaviour in the night sky would seem unlikely, as there is no calling at this time, and the frequency with which petrels fly into mist-net poles one inch in diameter, even on light nights, suggests that their night vision is not exceptionally good. Petrels have been observed deliberately avoiding mist-nets only when these have been clearly visible to human eyes against the night sky.

Nelson (1966) and Harris (1969) have described the flighting behaviour of Oceanodroma tethys at a colony of some 200,000 pairs on Tower Island in the Galapagos Islands. As this species visits the colony by day, these authors were able to describe the flighting behaviour in some detail. During the breeding season, flighting was at its most intense in the pre-egg stage. At this time, Harris observed numerous aerial chases and displays at the entrance to the burrow, which were undoubtedly associated with pair formation and courtship. However, both authors found that large numbers of non-breeders visited the colony outside the breeding season, when the adults were away at sea moulting. The flighting of non-breeders differed from that of breeding birds in that no two individuals were keeping together, as in the courtship displays, and the birds were almost noiseless. Although the non-breeders entered burrows, these were not the same burrows that were subsequently used for breeding. Thus the flighting behaviour of O. tethys would appear to be similar to that of H. pelagicus, except that the large influx of non-breeders occurs outside the breeding season.

J. R. Beck (pers. comm.), working on Oceanites oceanicus, found that the aerial flighting of non-breeders was at its most intense during the pre-egg stage, and that most non-breeders left the colony during the incubation stage. He thought that apart from those non-breeders in occupation of a burrow, there was a large number of non-breeders present which had no attachments to any particular site. Wilbur (1969), working at a colony of Oceanodroma leucorhoa in pine woods, found that one section of the non-breeder community, presumably the youngest age class, flighted in large numbers on the edge of the woods, but did not enter the breeding areas.

Thus in at least four species of Hydrobatidae, there is a large section of the community which returns to the colony for a short period, does not take up permanent occupation of burrows, and shows little site attachment. The obvious suggestion is that these birds are the youngest class of non-breeders which visit the colony for a short time in the year before adopting a regular burrow. The timing of this visit in relation to the breeding cycle varies between species, and is perhaps determined by such factors as availability of food, and risk of predation. An epideictic function for the flightings, as proposed by Wynne-Edwards (1962), would appear to be out of the question, since in three of the species, breeding birds do not take part in the flightings, and in two species, the peak of the flighting occurs during the incubation and chick stages. Thus there is no way in which the non-breeders could get accurate information on the total breeding population.

Presumably, there must be some advantage in spending a non-breeding season at the colony, without adopting a regular burrow, to counteract the waste of energy, loss of feeding time, and risk from predation. Perhaps for a bird highly adapted to the oceanic mode of life, first return to land, and the subsequent adoption of a whole new series of behaviour patterns culminating in breeding, requires much "practice". A season spent visiting the colony under only the most favourable conditions may enable a petrel to gain valuable experience of arrival at, and departure from, the colony; orientation over land; the journey between the feeding grounds and the colony; and the general topography of the breeding area; so that in the following season, the bird will be able to prospect for, and adopt, a burrow; make regular visits to this; and attract a mate; without too great a risk from predation. As discussed later (section III), non-breeders prospecting for burrows probably suffer higher losses from predation than any other age group. The timing of the moult may also be an important factor in determining the activity of non-breeders at the colony (see section IV).

(4) Recaptures of birds of known age

The only way to determine to which age class or classes the categories of birds visiting the colony belong is from recaptures of birds which were ringed as chicks. Between 1947 and 1965, 236 chicks were ringed on Skokholm, but because of the poor quality of the rings used before 1958 and the very limited retrapping effort, only eight were subsequently recaptured back at the colony. 220 chicks were ringed during the present study; 82 in 1966, 59 in 1967, 54 in 1968, and 25 in 1969. Intensive netting in these four years has demonstrated that good rates of recapture can be achieved, and by the end of 1969, a total of 63 birds of known age had been retrapped on Skokholm. A further six birds which were ringed as chicks on Skokholm have been recovered away from the island.

The age in years at which the 63 chicks were first recaptured on Skokholm is shown in table 22a. This suggests that Storm Petrels do not return to the colony, at least in any numbers, until they are two years old. In table 22b, the recaptures during the present study of chicks ringed between 1963 and 1968 are given in detail. Inspection of the dates of all recaptures of birds of known age (figure 15) gives some indication of the duration of the visits of the various age classes. Also shown in figure 15, for comparison, are the dates of recapture of all birds ringed as "adults" prior to 1964, and recaptured between 1967 and 1969. These birds, which were at least five years old when recaptured, are assumed to be breeding adults.

Second year birds appear at the colony in early July (the earliest bird was trapped on the night of 30th June 1969), are present throughout July and August, and depart in early September. Three year old birds arrive earlier, the earliest being a bird caught on the night of 31st May. However,

Table 22. First recaptures of Storm Petrels ringed as chicks on Skokholm.

[a] Age at first recapture of all birds ringed as chicks, 1946-1968

Age in years	Number of individuals recaptured for first time
1	0
2	31
3	23
4	9
5	0

[b] First recaptures, in years 1966-1969, of Storm Petrels ringed as chicks in 1963-1968 (years of most intensive ringing and retrapping)

Year of ringing	Number of chicks ringed	Year of first recapture 1966	1967	1968	1969
1963	20	6	3	0	0
1964	17	2	2	4	0
1965	10	0	2	0	0
1966	82		0	10	14
1967	59			0	12
1968	54				0

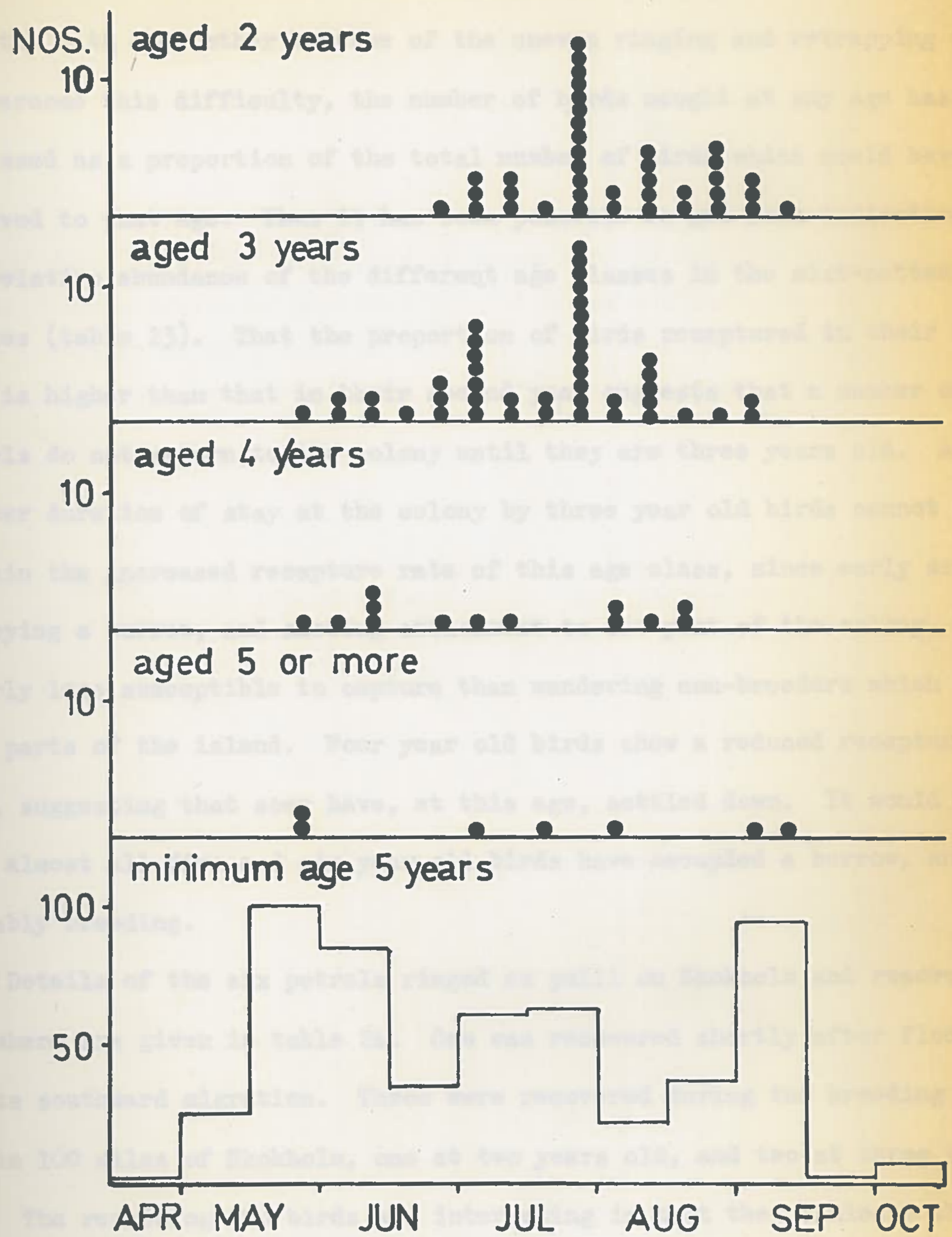


Figure 15. Dates of recapture of Storm Petrels ringed as chicks on Skokholm.

Also shown are dates of recapture of birds known to be at least five years of age, and therefore assumed to be breeding adults.

the largest numbers were again caught in July, and a few birds were still present as late as early September. The dates of recapture of birds caught when four or five years old are generally distributed throughout the season.

The numbers of birds caught at different ages cannot be compared directly with each other because of the uneven ringing and retrapping effort. To overcome this difficulty, the number of birds caught at any age has been expressed as a proportion of the total number of birds which could have survived to that age. Thus it has been possible to get some indication of the relative abundance of the different age classes in the mist-netted samples (table 23). That the proportion of birds recaptured in their third year is higher than that in their second year suggests that a number of petrels do not return to the colony until they are three years old. A greater duration of stay at the colony by three year old birds cannot alone explain the increased recapture rate of this age class, since early arrivals, occupying a burrow, and showing attachment to one part of the colony, are clearly less susceptible to capture than wandering non-breeders which visit many parts of the island. Four year old birds show a reduced recapture rate, suggesting that some have, at this age, settled down. It would appear that almost all five and six year old birds have occupied a burrow, and are probably breeding.

Details of the six petrels ringed as pulli on Skokholm and recovered elsewhere are given in table 24. One was recovered shortly after fledging on its southward migration. Three were recovered during the breeding season within 100 miles of Skokholm, one at two years old, and two at three years old. The remaining two birds are interesting in that they indicate that some young birds return to the vicinity of their breeding grounds during their first summer; one was recovered in Cornwall ten months after fledging, and the other in France, fourteen months after fledging. Whether young birds normally return to the North Atlantic in their first summer, or more usually remain in their winter quarters off West of South Africa cannot be decided until more recovery data become available.

Unfortunately, only five birds ringed as chicks have been recaptured in burrows on Skokholm. One of these, a bird ringed as a chick in 1963, was found incubating an egg on 13th July 1966. The burrow had not previously

Table 23. Number of recaptures of Storm Petrels which were ringed as chicks, expressed as proportion of those available for recapture at that age, to indicate relative abundance of various age classes in mist-netted samples.

Age in years	Number available for recapture	Number recaptured	% recaptured
1	205	0	0
2	168	26	16
3	129	27	21
4	49	7	14
5 & 6	73	3	4

Table 24. Recoveries away from Skokholm of Storm Petrels ringed on Skokholm as chicks.

AA 805	Pull.	14. 9.55	Skokholm
	x	4. 8.56	Widemouth Bay, near Bude, Cornwall. 70 miles SE
AA 1186	Pull.	16. 9.56	Skokholm
	/?/	0.12.56	Off Belle Ille, Morbitian, France. 315 miles SSW
663470	Pull.	11. 9.66	Skokholm
	v	12. 8.69	At lighthouse, Bardsey Island, Caerns. 75 miles NNE
663490	Pull.	14. 9.66	Skokholm
	v	2. 8.69	Skomer Island, Pembs. $2\frac{1}{2}$ miles N
663577	Pull.	17. 9.66	Skokholm
	x	11. 7.68	Kilmore Quay, Co. Wexford, Eire. 65 miles WNW
675184	Pull.	15. 9.67	Skokholm
	x	0.12.68	Lacanau Océan, Gironde, France 500 miles SSW

Key to symbols

v = caught alive and released with ring
x = found dead or dying
/?/= manner of recovery unknown

been disturbed, and it seems likely that this was a genuine instance of a bird breeding at three years old. Although the bird deserted as a result of handling, its mate returned in the following year, and was found, from cloacal examination, to be a male. Breeding at three would be possible either by returning to the colony for the first time when only one year old, or by spending only one non-breeding season at the colony. Evidence presented above indicates that for some birds a season in occupation of a burrow before breeding is not essential. It was argued that such birds would probably be young females which, in their season of prospecting for a burrow and a mate, become mated to an experienced male which has lost its mate of previous years. That the petrel known to be breeding at three was a female would support this.

Two other birds which had been ringed as chicks were found breeding. One of these was found incubating an egg when four years old in a burrow first located on 1st August 1967. Incubation continued until 11th August, but the burrow was then deserted. Subsequent examination of the egg revealed an embryo approximately 15 - 20 days old, indicating a laying date in the second half of July, as typical of birds breeding for the first time (see page 23). The burrow was not reoccupied in later years, but the bird was mist-netted within 30 feet of the burrow on 4th July 1968, and on 7th September 1969, and was presumably breeding close by. The other bird was ringed as a chick in 1961, recaptured in a net in 1963, and found brooding a small chick in 1968, when seven years old. A pair had bred successfully in the same burrow in the previous year (when the burrow was first located), but the adults had not been examined. Thus it is possible that the bird in question had been breeding for several years.

Two petrels which had been ringed as chicks were found in burrows as non-breeders. One bird, ringed in 1963, spent one day in occupation of a burrow in June 1967. This burrow was an artificial burrow which had been fitted with a nest-box in October 1966. There can be no doubt therefore that the bird was visiting this burrow for the first time, and it seems likely that it was still prospecting for a burrow when four years old. The other bird, ringed as a chick in 1966, was mist-netted on 5th August 1968, and again on 31st May 1969. On 2nd June 1969, it was found in occupation of a burrow by day with an unringed bird. The burrow had been examined regularly throughout the three previous seasons, and there can be little doubt that both birds were visiting this burrow for the first time. The three year old bird was again present in the burrow by day on 5th July, this time in company with another unringed bird. Burrow inspections had then to be discontinued until 21st July, so that further occupation would have been missed. It seems unlikely, however, that a pair spending their first day in occupation together on 5th July could go through the necessary courtship, lay an egg, and lose it before 21st July. It is concluded therefore that the bird in question, after spending a season at the colony as a wandering non-breeder in 1968 (when two years old), spent a season in a burrow as a non-breeder in 1969 preparatory to breeding there in 1970 (when four years old).

Very few chicks have been ringed at other colonies in the British Isles, and only one of these has subsequently been recaptured. This bird, ringed at Auskerry (Orkney Islands) in 1964, was found breeding at the same colony in 1968, when four years old.

To sum up, of two birds found in burrows at three years old, one was breeding, and of three birds found in burrows at four years old, two were breeding. A bird found breeding at seven years old had probably bred in previous years.

(5) <u>The site attachment of mist-netted birds</u>

Regular netting at a number of sites revealed that many birds were particularly faithful to one locality, whereas other birds were frequently caught at two or more sites. In the analysis of recapture data, all recaptures have been assigned to one of three categories: a. recaptured at the site where ringed; b. recaptured at a net-site within 200 yards of the site where ringed; c. recaptured at a net-site more than 200 yards from the site where ringed. In table 25, the site of recapture of all birds retrapped on Skokholm is compared with the locality of ringing. (Birds ringed in 1969 have been omitted, as less than one full season's recapture date is available for this group of birds). Of 3,571 petrels ringed and subsequently recaptured on Skokholm, 49% were retrapped where ringed, a further 19% were retrapped within 200 yards, and only 32% had moved more than 200 yards from

Table 25. Locality of recapture of mist-netted Storm Petrels compared with locality of ringing, in relation to date of first capture.

Date of first capture (ie. ringing)	Distance between locality of ringing, and locality of recapture (yards): 0 (same site)	Less than 200 (near)	More than 200 (far)	Total recaptured	% far
Apr 16-30	27	1	0	28	0
May 1-15	60	13	1	74	1
May 16-31	313	78	51	442	12
Jun 1-15	296	102	89	487	18
Jun 16-30	157	66	77	300	26
Jul 1-15	216	115	136	467	29
Jul 16-31	154	74	181	409	44
Aug 1-15	201	118	336	655	51
Aug 16-31	249	75	236	560	42
Sep 1-15	60	19	38	117	33
Sep 16-30	18	3	6	27	22
Oct 1-15	2	2	1	5	[20]
Totals	1753	666	1152	3571	32.3

the place of ringing. Furthermore, the proportion of birds showing long-distance movement varies according to the date of ringing. Site attachment is at its most pronounced in birds ringed at the beginning, and again at the end, of the season, and at its least pronounced in birds ringed during the period of abundance of non-breeders in July and August.

To determine the degree of site attachment in the various categories of birds in the community, the recapture data has been broken down in several ways. In table 26, only those birds which were caught on two or more occasions, two or more years after ringing, are considered. Such birds, when first recaptured, will have spent at least three seasons at the colony, and will therefore be mainly, if not entirely, breeding adults. The locality of all subsequent recaptures has been compared with the locality of this first recapture. Of 906 subsequent recaptures, 73% were obtained at the site of the first recapture, and a further 23% at a site nearby. Less than 5 per cent of the birds considered to be of breeding age when first recaptured were subsequently caught at a locality more than 200 yards away. Clearly, breeding birds are very faithful to their breeding site, and rarely wander to other parts of the island. Slight variations in the degree of site attachment throughout the season can be attributed to changes in the behaviour of the adults. Thus, during the period of aerial displays in late May and early June, the hectic chases may take birds temporarily into nearby net-sites. During late summer, failed breeders, after deserting their burrows, may wander about the colony for two or three weeks before finally leaving the island.

A further indication of the degree of site-attachment of adults comes from an analysis of the locality of capture of birds from the burrows in the study area (table 27). The results of this analysis agree very well with the analysis of the recaptures of old birds; 73% of the recaptures were within 20 yards of the burrow, and only 7% were at a site more than 200 yards away.

As all the burrows were situated some distance from the coast, it seemed likely that some of the apparent wandering of birds with burrows referred to petrels caught on their way between their burrows and the sea. In fact, of the 119 captures of birds more than 20 yards from the burrow,

Table 26. Locality of first capture of Storm Petrels of breeding age compared with locality of subsequent recaptures, in relation to date of first capture.

[First capture refers to first capture two or more years after being ringed as a full-grown bird, i.e. when bird is in at least its third season at colony. Such birds may be assumed to be established in burrows, and to be of breeding age.]

Date of first capture	Recaptured same site	Recaptured near	Recaptured far	Total recaptured	% near	% far
Apr 16-30	2	0	0	2	0	0
May 1-15	26	18	0	44	41	0
May 16-31	171	59	11	241	25	5
Jun 1-15	79	45	8	132	34	6
Jun 16-30	52	11	4	67	16	6
Jul 1-15	79	27	2	108	25	2
Jul 16-31	97	16	9	122	13	7
Aug 1-15	42	11	5	58	19	9
Aug 16-31	11	5	3	19	26	15
Sep 1-15	91	12	1	104	12	1
Sep 16-30	8	1	0	9	11	0
Totals	658	205	43	906	22.6	4.8

Table 27. Locality of capture in mist-nets of Storm Petrels from burrows in study area compared with locality of burrow, in relation to date of capture in nets.

Date of capture in nets	Captured at same site*	Caught near burrow (20-200 yds.)	Caught far from burrow (over 200 yds.)	Total caught
Apr 16-30	1	0	0	1
May 1-15	13	5	0	18
May 16-31	88	30	2	120
Jun 1-15	38	13	6	57
Jun 16-30	19	5	5	29
Jul 1-15	55	12	4	71
Jul 16-31	37	7	5	49
Aug 1-15	38	10	4	52
Aug 16-31	14	2	3	19
Sep 1-15	21	3	2	26
Sep 16-30	3	1	0	4
Oct 1-15	2	0	0	2
Totals	329	88	31	448
Per cent of total	73.4	19.6	6.9	-

* net-site within twenty yards of burrow.

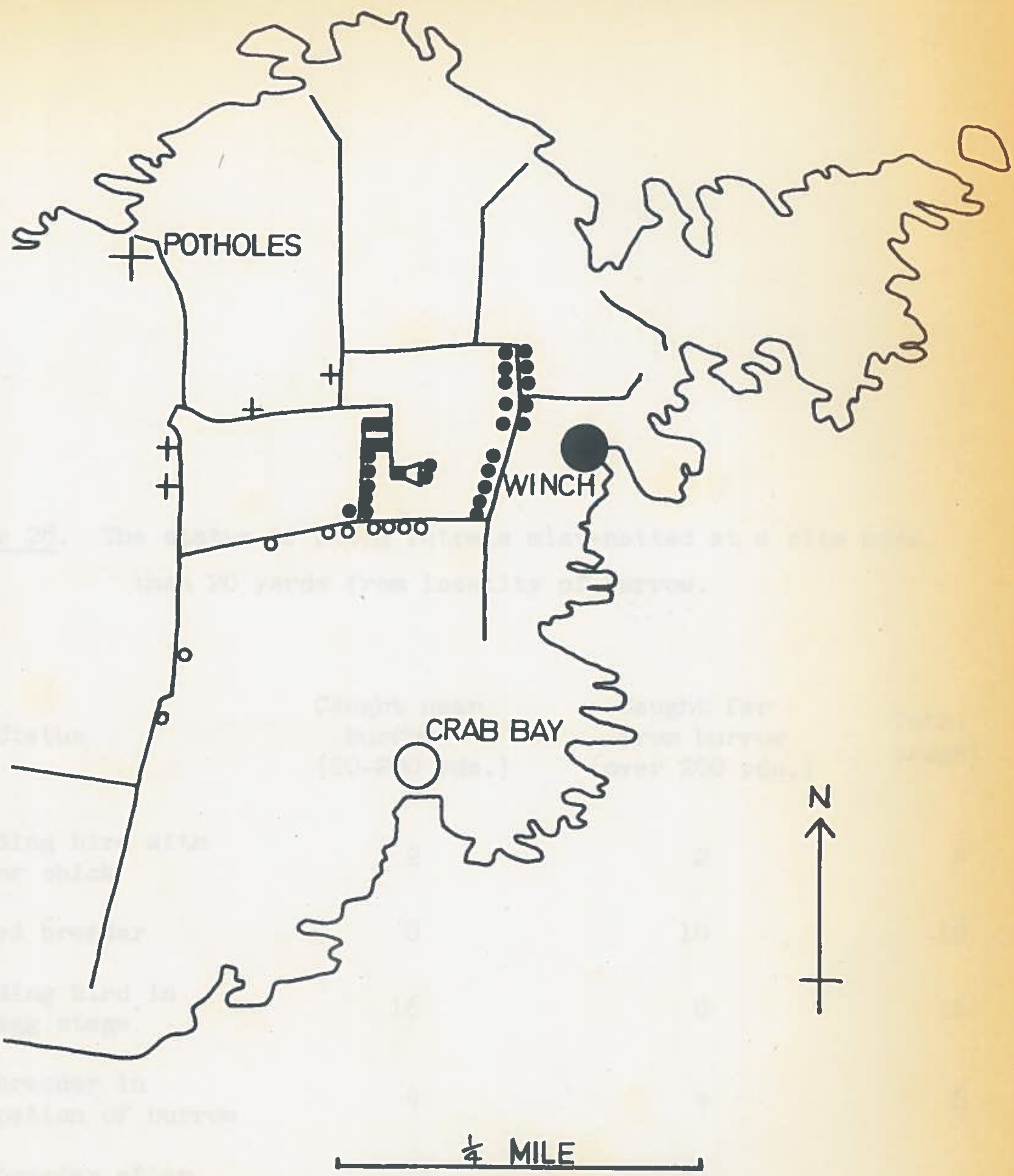
52 were obtained at sites between the burrow locality, and the nearest stretch of coast-line. The burrow localities of those petrels mist-netted at the three bays nearest to the study area at which regular netting was carried out are shown in figure 16. Clearly birds are travelling to and from their burrows by the shortest possible route. The absolute number of recaptures of breeding birds en route between their burrows and the sea was however much lower than might have been expected, presumably because petrels normally fly above the height of the nets (about 8 feet), except in the immediate vicinity of the burrow.

The breeding status of the 67 birds which were caught at a locality which was not obviously on the flight-line between coast and burrow is summarized in table 28. Only twelve of these birds were breeding birds with an egg or a chick, or non-breeders during their period of occupation of a burrow. The remainder were either breeding birds which had not yet laid, failed breeders, or non-breeders which had deserted their burrows after a period in occupation.

From late June until mid-September, catches taken anywhere on the island contain a number of non-breeders which will subsequently be recaptured elsewhere. The distribution of the recaptures of birds ringed at Frank's Point in July and August 1967 and 1968, as shown in figure 17, illustrates this well. Recaptures from other sites show a similarly wide distribution, hence a catch at any site effectively samples the whole of the community of wandering non-breeders on the island at the time.

If, as suggested above, young birds normally spend only one season at the colony as wandering non-breeders, birds ringed as wandering non-breeders should return in late May or June of the year following ringing and, during the early part of the season, show some attachment to one site. The occurrence of wandering non-breeders at the colony in the year after ringing is shown in table 29. As predicted, they return in large numbers in late May, and are most common in the samples taken in early June; by early August they are much scarcer. Hence this class of birds behaves in the same way as the non-breeders in burrows, and presumably therefore shows a similar degree of site attachment.

It is clear that not all wandering non-breeders visit the colony



KEY

○ localities of burrows of birds caught at Crab Bay.

● localities of burrows of birds caught at Winch

+ localities of burrows of birds caught at Potholes.

Figure 16. Localities of burrows of Storm Petrels mist-netted on coast near study area.

Table 28. The status of Storm Petrels mist-netted at a site more than 20 yards from locality of burrow.

Status	Caught near burrow (20-200 yds.)	Caught far from burrow (over 200 yds.)	Total caught
Breeding bird with egg or chick	2	2	4
Failed breeder	8	10	18
Breeding bird in pre-egg stage	16	0	16
Non-breeder in occupation of burrow	4	4	8
Non-breeder after occupation of burrow	6	15	21
Totals	36	31	67

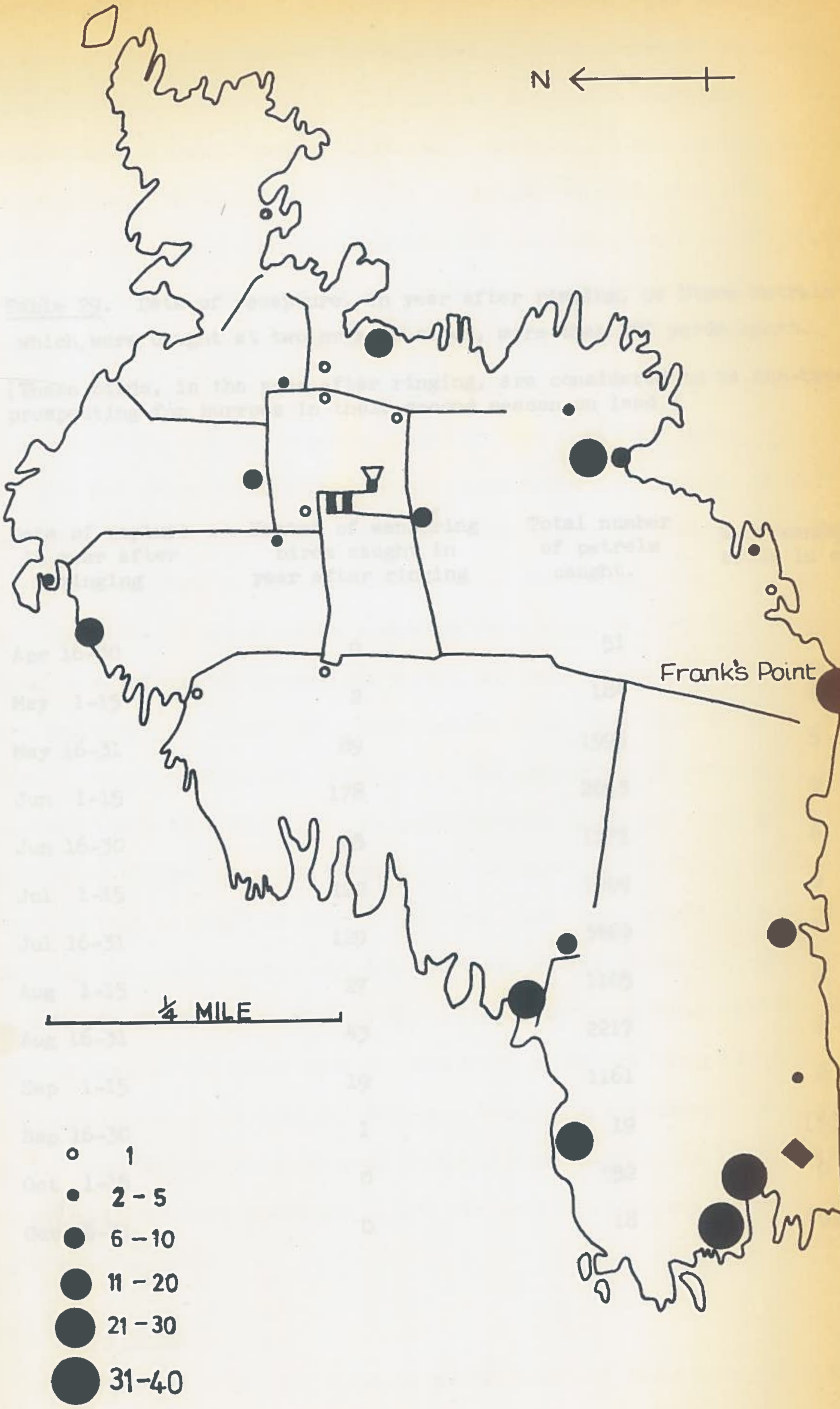


Figure 17. Localities of recapture of Storm Petrels ringed at Frank's Point in July and August, 1968-1969.

Table 29. Date of recapture, in year after ringing, of Storm Petrels which were caught at two or more sites, more than 200 yards apart.

[These birds, in the year after ringing, are considered to be non-breeders prospecting for burrows in their second season on land.]

Date of capture in year after ringing	Number of wandering birds caught in year after ringing	Total number of petrels caught.	% of wandering birds in catches
Apr 16-30	0	51	0
May 1-15	2	184	1
May 16-31	89	1995	5
Jun 1-15	178	2053	9
Jun 16-30	65	1175	6
Jul 1-15	120	1999	6
Jul 16-31	129	3469	4
Aug 1-15	27	1105	2
Aug 16-31	43	2217	2
Sep 1-15	19	1161	2
Sep 16-30	1	19	[5]
Oct 1-15	0	552	0
Oct 16-31	0	18	[0]

regularly for the whole of the period between late June and mid-September. Analysis of the recaptures of non-breeders in their season of wandering indicates that, in addition to fluctuations in numbers determined by weather conditions, and local feeding conditions, there is a constant turnover in the community. By dividing the total recaptured in each week after ringing by the number of week classes available for recapture, (and hence eliminating bias caused by the numbers available for recapture decreasing as time increases) a rough indication of the duration of stay at the colony has been obtained (table 30). A few individuals visit the colony for as much as eleven weeks, but the majority stay for less than four weeks.

The few petrels which were ringed as chicks and recaptured on more than one occasion support the conclusion that wandering behaviour is largely restricted to birds in their first season at the colony, i.e. two, and three year old birds. Long-distance movements were shown by 9 of 11 two year old birds, 6 of eleven three year old birds, and none of seven birds of four or more years of age. When young birds settle down, they tend to do so in the area of their natal burrow (table 31). The proportion of recaptures more than 200 yards from the burrow is significantly lower for birds of four or more years of age, than for birds of two or three (χ^2 = 9.2, p = less 0.005). The fact that 12 (34%) of the two year old birds were caught within 200 yards of the natal burrow, and four of these within 60 feet, suggests that even in the first season back at the colony, the birds show some preference for the area of the natal burrow. One bird, which was ringed as a chick in a burrow in the study area in 1966, was found as a non-breeder in a scrape in the same burrow, only one foot from the natal scrape, in 1969. This was as close as the bird could get, since the original site was occupied in 1969 by a breeding pair.

(6) <u>Brood patches</u>

In 1967 and 1968, the brood patch was examined on as many Storm Petrels as possible in the hope that this might facilitate the determination of the breeding status of mist-netted birds. All age classes of petrels, regardless of breeding status, undergo a complete moult of the brood patch between May and October. Prior to this moult, the brood patch is completely covered with a dense layer of charcoal grey down, 3 - 4 mm in length. This is shed

<u>Table 30</u>. Disappearance of ringed wandering non-breeders from community of Storm Petrels in late summer

Date of recapture, in weeks after ringing	Number recaptured [a]	No. of week classes available for recapture [b]	"Disappearance" [a/b]
1	304	11	27.6
2	201	10	20.1
3	116	9	12.9
4	93	8	11.6
5	62	7	8.9
6	37	6	6.2
7	19	5	3.8
8	11	4	2.8
9	7	3	2.3
10	4	2	2.0
11	1	1	1.0

Table 31. Locality of recapture of Storm Petrels ringed as chicks compared with locality of natal burrow.

Age at which recaptured (in years)	Locality of recapture (yds. from where ringed) Same (0-20)	Near (20-200)	Far (over 200)	Total recaptured	% far
2	4	8	23	35	66
3	4	17	22	43	51
4	1	10	4	15	27
5 or more	0	7	0	7	0

slowly and patchily, eventually exposing a bare, pinkish-grey brood patch, about 6.0 to 6.5 sq. cm. in area. Growth of new down occurs in late summer or autumn. The various stages, and types of brood patch, which were recognized during the present study are listed in table 32. The condition of the brood patch of all petrels examined during the present study is given in detail in appendix table 8, and summarized in figure 18.

(i) <u>The brood patch cycle of breeding birds</u>

Three categories of Storm Petrels taken in mist-netted samples can be assumed to be of breeding age. These are: (a) birds which had been ringed as full-grown birds two or more years previously; (b) birds which regurgitated food during handling; and (c) birds caught before 11th May or after 30th September. The state of the brood patch of birds assumed to be breeders on these grounds is given in detail in appendix table 9, and summarized in figure 18. Almost all such birds start to lose the down on their brood patches shortly after arrival at the colony, and have completely bare brood patches some time before laying. Data from recaptures suggests that loss of down takes between 20 and 35 days. Of 417 birds carrying food for a chick, only 18 (4%) had completely bare brood patches, indicating that growth of new down commences at about the time that the young hatch. The growth of new down is almost entirely synchronous, (passing through stages viii, ix, x, and xii, in table 32) and, as described later, quite distinct from that of many non-breeders. The growth is completed in between 30 and 40 days.

Brood patches were examined on a small number of birds of known breeding status from burrows in the study area. The condition of the brood patch of 67 birds removed from the burrow, and 24 birds mist-netted at night, in relation to the date of laying, is shown in table 33. Loss of down commenced at least five weeks before laying, and was usually completed three weeks before laying. Vascularization was only found in birds removed from burrows, and almost restricted to birds with bare brood patches. In six birds, vascularization had appeared more than thirty days before laying. The sexes apparently lost their down at a similar rate, and commonly both members of a pair were at the same stage. The condition of the brood patches of 149 birds examined between laying and the end of brooding is shown in table

Table 32. Stages in brood patch cycle of Storm Petrel, and types of brood patch recognized during present study.

Stage in cycle		Types of brood patch recognized
I. Loss of down	i.	brood patch completely covered in thick down.
	ii.	first signs of loss of down; small bare patches.
	iii.	approximately half of down lost.
	iv.	only traces of down remaining, mainly in cloacal and xiphisternal regions.
II. Bare	v.	brood patch completely bare; pinkish-grey, or pale pink in colour.
	vi.	brood patch highly vascularized, with obvious system of dilated blood vessels forming complex pattern*.
	vii.	brood patch with one or more greatly distended blood vessels with knotted appearance.*
III. Growth of new down.	viii.	first signs of growth of new down; less than six new down feathers appearing in pin.
	ix.	half of brood patch covered with new down in pin, half bare.
	x.	entire brood patch covered with down in pin.
	xi.	parts of brood patch bare, rest covered with mixture of down in pin, and down in brush stage (restricted to non-breeders).
	xii.	entire brood patch covered with down in brush stage.
	xiii.	brood patch covered with patchy mixture of down in pin, down in brush stage, and new down. (restricted to non-breeders).
	xiv.	brood patch completely covered with new down.
IV Intermediate stage, restricted to non-breeders.	xv.	traces of old down, and new down in pin, together.

*occasionally found in birds with traces of old down (iv), or with some new down in growth (viii) and (ix).

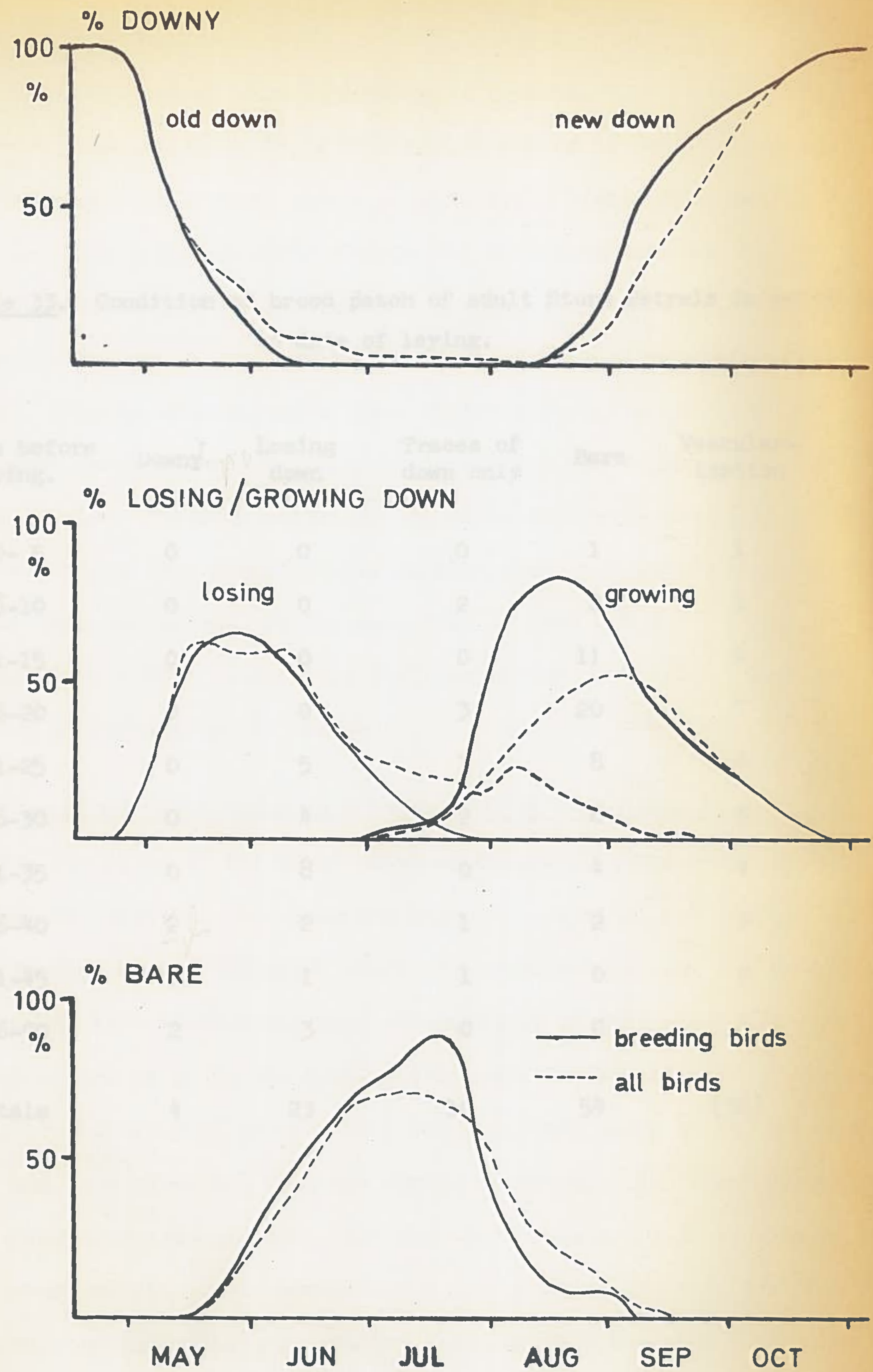


Figure 18. Development of brood patch in Storm Petrels mist-netted at night.

Table 33. Condition of brood patch of adult Storm Petrels in relation to date of laying.

Days before laying.	Downy	Losing down	Traces of down only	Bare	Vascular-ization	Total
0- 5	0	0	0	1	1	1
6-10	0	0	2	2	1	4
11-15	0	0	0	11	6	11
16-20	0	0	3	20	7	23
21-25	0	5	1	8	4	14
26-30	0	4	2	6	5	12
31-35	0	8	0	4	4	12
36-40	2	2	1	2	2	7
41-45	0	1	1	0	0	2
46-50	2	3	0	0	0	5
Totals	4	23	10	54	[30]	91

34. Clearly, loss of down is usually completed before laying, and growth of new down is usually started at the time of hatching, or very shortly after.

The occurrence of vascularization in breeding birds with bare brood patches is summarized in table 35. At all stages in the breeding cycle, birds removed from burrows show a significantly higher frequency of vascularization than breeding birds mist-netted in flight over the colony. Clearly, vascularization is only well developed in breeding birds when they are in the burrow; during off-duty periods, the blood vessels contract rapidly, thereby reducing heat loss. Petrels caught at night with vascularized brood patches are presumably birds leaving the colony after a period in the burrow. The mean weight of 134 birds with some vascularization (26.7 ± 2.6 gm.) was significantly lighter than that of 229 breeding birds with no vascularization, at the same time of year (28.3 ± 2.7 gm.), ($t = 5.6$, p = less than 0.001), suggesting that the former were birds which had spent a period of fasting in the burrow.

(ii) <u>The brood patch cycle of non-breeders in occupation of a burrow</u>

The condition of the brood patch of 63 non-breeders removed from burrows is shown in table 36. Non-breeders lose their down at a slightly later date than breeding birds. However, since all non-breeders examined after the end of June had lost their down, most of the birds of this class must pass through a bare stage in the brood patch cycle similar to that of breeding birds. 7 out of 33 birds with bare brood patches had a little vascularization, and in another 16, this was highly developed. The brood patches of five birds with some old down, and two birds with new down in growth, were also vascularized. Of 19 non-breeders netted at night, only two showed any signs of vascularization, suggesting that, as with breeding birds, the blood vessels contract during periods spent away from the burrow. Few birds known to be non-breeders which had occupied a burrow were found growing new down, and it seems that this normally occurs after the birds have left the colony in late July or August.

(iii) <u>The brood patch cycle of wandering non-breeders</u>

From late June until early September, between 20 per cent and 30 per

Table 34. Condition of brood patch of adult Storm Petrels during incubation and brooding.

Status	Traces of old down	Bare	Traces of new down.	New down in pin	New down at brush stage	Total
Female with egg internal	3 [2]*	42 [37]	0	0	0	45 [39]
Days 1-10 of incubation	0	6 [6]	0	0	0	6 [6]
Days 40 and over of incubation	0	3 [3]	1 [1]	2 [2]	0	6 [6]
Mist-netted in incubation	1 [0]	51 [11]	2 [0]	0	0	54 [11]
Brooding	0	11 [8]	8 [3]	12 [3]	7 [2]	38 [16]

* Figures in brackets refer to number with vascularization.

Table 35. Occurrence of vascularization of brood patch in breeding individuals of Storm Petrel.

Class of birds	Number of birds	Number with vasc. brood patch	% with vasc. brood patch
Birds with bare brood patches removed from burrow during pre-egg stage	47	29	62
Birds with bare brood patches mist-netted during pre-egg stage (mid-May-end of June)	234	32	14
Birds taken off eggs or chicks	20	17	85
Breeding birds from study burrows mist-netted during incubation	51	11	22

During pre-egg stage, and during incubation and brooding, the frequency of vascularization in mist-netted birds is significantly less than in birds removed from burrows.

For birds examined in pre-egg stage: $\chi^2 = 56.9$, p = less than 0.001

For birds examined in incubation and brooding stages:

$\chi^2 = 19.5$, p = less than 0.001

Table 36. Condition of brood patch of non-breeding Storm Petrels in burrows.

Date	Downy	Losing down	Bare	Growing down	New down	Total
May 21-31	3	5 [1]*	1	0	0	9
Jun 1-10	3	12 [1]	12 [6]	0	0	27
Jun 11-20	0	4 [2]	4 [4]	0	0	8
Jun 21-30	0	1 [1]	0	0	0	1
Jul 1-10	0	0	5 [5]	0	0	5
Jul 11-20	0	0	3 [3]	0	0	3
Jul 21-31	0	0	4 [2]	0	0	4
Aug 1-10	0	0	4 [3]	2 [2]	0	6
Totals	6	22	33	2	0	63

* Figures in brackets refer to number with vascularization

cent of the petrels mist-netted in flight over the colony still retain traces of old down on the brood patch. Furthermore, many of these birds start the growth of their new down before the last traces of the old down have been lost (see appendix table 8, and figure 18). Since such a cycle does not occur in birds found in burrows, such birds clearly do not enter burrows, and are probably therefore those in their first season at the colony.

Table 37 summarizes the condition of the brood patches of all those birds caught between 1st July and 20th September which were subsequently recaptured at a site more than 200 yards from the place of ringing. These birds are considered to be mainly wandering non-breeders, although the samples will inevitably include a few failed breeders, and older non-breeders, which, as shown above, may wander about the colony for a short period in late summer. Of 357 birds still losing down, 271 (76%) retained only traces, so it would appear that loss of down in this class of birds normally commences some time before arrival at the colony. A turnover, in the community, of birds all arriving at approximately the same stage in the loss of their down would account for the relatively constant proportion of birds still losing down, in samples taken throughout the period. Only about 30 per cent of these non-breeders would appear to pass through a completely bare stage in the brood patch cycle, the growth of the new down usually commencing during the latter stages of down loss. Of a total of 572 birds examined, only 8 showed any signs of vascularization.

Growth of the new down commences in some wandering non-breeders as early as the beginning of July, but the proportion which have started increases slowly. Furthermore, of 188 birds which had started, only 38 (20%) had more than a few feathers in the pin or brush stage, suggesting that birds normally leave the colony shortly after the onset of growth of new down. The growth of the new down in wandering non-breeders is quite distinct from that of breeding birds in that it is asynchronous, passing through stages viii, ix, xi, and xiii (see table 32). Thus, in some individuals, the brood patch is covered with a patchy mixture of down in pin, down in the brush stage, and new down.

58 birds ringed as wandering non-breeders in 1967 were recaptured in

Table 37. Condition of brood patch of Storm Petrels ringed between 1st July and 20th September, and subsequently recaptured at a site more than 200 yards from the locality of ringing.

[Storm Petrels considered to be non-breeders in their first season at the colony]

Date of capture in 1st season	Condition of brood patch										
	Downy	Losing down	Bare	Old and new down	Growing down	New down	Total	% with some old down	% bare	% with old and new down	% with some new down
Jul 1-10	0	34	12	7	1	0	54	76	22	13	15
Jul 11-20	2	29	23	8	4	0	66	59	35	12	18
Jul 21-31	1	15	11	4	1	0	32	63	34	13	16
Aug 1-10	2	68	51	13	19	0	153	54	33	9	21
Aug 11-20	1	41	16	15	12	0	85	67	19	18	32
Aug 21-31	0	21	7	36	17	2	83	69	8	43	66
Sep 1-10	0	15	7	19	17	0	58	59	12	33	62
Sep 11-20	0	7	1	5	3	1	17	71	6	29	53

1968, and examined for the condition of their brood patch. None had old and new down present on the brood patch simultaneously, and only four of the 31 birds recaptured after 1st July had any traces of old down remaining. Nine birds with new down in growth in August showed sychronous renewal. Thus it appears that during the second year at the colony, young petrels undergo a brood patch cycle resembling that of non-breeders which have occupied a burrow (and breeding birds). This therefore supports yet again the conclusion that immature petrels usually spend only one season at the colony as wandering non-breeders before adopting a burrow.

(iv) The condition of the brood patch of birds of known age

The condition of the brood patches of those birds which were ringed as chicks, and were therefore of known age when examined, is summarized in table 38. The 29 birds caught at two years of age clearly correspond, in the condition of the brood patch, to wandering non-breeders. The 32 birds examined at three years of age included both birds with characteristics of wandering non-breeders, and birds with characteristics of petrels which had occupied burrows. Birds of four or more years of age did not differ, in the condition of their brood patches, from non-breeders in occupation of a burrow, or breeding birds. The brood patches of two birds occupying burrows as non-breeders at three and four years of age respectively, were bare and highly vascularized.

(v) The value of brood patch examinations in determining the status of birds in mist-netted samples

Examination of the brood patch has only limited usefulness in the determination of the breeding status of birds mist-netted at night. No birds can be said with certainty to be breeding, as non-breeders which are in occupation of a burrow develop a bare brood patch which may be as highly vascularized as that of breeding adults. The rapid regression of vascularization at the end of a stint in the burrow results in off-duty breeding birds resembling all other birds with bare brood patches. Thus, the presence of some vascularization may be taken only as indication of ownership of a burrow, whilst absence of vascularization signifies nothing.

The presence of old down after about mid-July, and particularly the

Table 38. Condition of brood patch of Storm Petrels ringed as chicks, and therefore of known age.

[a] Two years after fledging

Date	Downy	Losing down	Bare	Old and new	Growing down	New down	Total
June	0	1	0	0	0	0	1
July	0	11	1	3	1	0	16
August	0	3	2	3	1	0	9
Sept.	0	0	0	2	1	0	3
	0	15	3	8	3	0	

[b] Three years after fledging

Date	Downy	Losing down	Bare	Old and new	Growing down	New down	Total
May	0	1	0	0	0	0	1
June	1	4[2]*	0	0	0	0	5
July	1	8	11[3]	1	0	0	21
August	0	2	0	0	1	0	3
Sept.	0	0	0	1	1	0	2
	2	15	11	2	2	0	

[c] Four or more years after fledging

Date	Downy	Losing down	Bare	Old and new	Growing down	New down	Total
May	0	1	1[1]	0	0	0	2
June	0	3	1	0	0	0	4
July	0	2	0	0	0	0	2
August	0	0	3[1]	0	0	0	3
Sept.	0	0	0	0	0	0	0
	0	6	5	0	0	0	

* Figures in brackets refer to number with vascularization

presence of old and new down simultaneously, indicate that the bird in question is a wandering non-breeder, and almost certainly in its first season back at the colony. The pattern of growth of the new down may also be used to distinguish some birds of this category. However, perhaps as many as 30 per cent of wandering non-breeders pass through a bare phase in the brood patch cycle, during which they are indistinguishable from other classes.

(vi) The brood patch cycle in other species of Hydrobatidae

The only detailed studies to date of the brood patch cycle of a species of storm petrel are those of Allan (1962) and Harris (1969), who worked on Oceanodroma castro. The brood patch cycle of this species is essentially similar to that of H. pelagicus. Both Allan and Harris found that loss of down was completed between 20 and 50 days before laying. The defeathering occurred rapidly; Allan suggested a period of only four days for complete loss of the down, whilst Harris gave a minimum period of 12 days. Vascularization was very pronounced, usually appearing within a week of the completion of defeathering. Neither author commented on any regression of vascularization during off-duty periods. Perhaps for this species, which inhabits warm seas, heat loss from the brood patch is relatively unimportant. Growth of new down usually started about a week after hatching. Harris found that the majority of non-breeders in burrows had bare but unvascularised brood patches, although a few developed vascularized brood patches identical to those of breeding birds. A small sample of birds mist-netted at night included birds with less well developed brood patches, suggesting that some of the birds flighting over the colony were younger than those in burrows.

Wilbur (1969), working on Oceanodroma leucorhoa, considered that one group of petrels was recognizable on the condition of the brood patch. He found that breeding birds, and non-breeders with burrows, had bare brood patches, but that non-breeders without burrows retained some down on the brood patch. He suggested that these latter birds, which comprised up to 56 per cent of the birds caught around the periphery of the colony, were birds in their first season on land. Clearly these birds are directly comparable to the wandering non-breeders in the Skokholm community of Storm

Petrels.

(7) Other evidence relating to the status of birds of known age

Two further sources of evidence have been useful in determining the status of birds of known age which were mist-netted at night, viz. the presence of food reserves in the stomach, and the condition of the ring.

(i) The presence of food reserves in the stomach

Many of the petrels mist-netted at night between late May and the end of the season had greatly distended abdomens, and were obviously carrying large quantities of undigested or partially digested food in the stomach. Such birds, which made up the majority of petrels weighing more than 30 gm. were considered to be either breeding birds or non-breeders coming in to spend a period in the burrow, or breeding birds carrying food for a chick. None of the birds caught when two years of age were obviously carrying extra reserves of food, and their weights were generally low. However, two of the birds caught when three years old were carrying large quantities of food. One of these, caught on 5th June 1969, had a considerable amount of down remaining on the brood patch, and was presumably therefore either a non-breeder or a breeder in the pre-egg stage coming in to spend a period of day-occupation in the burrow. The other bird was particularly interesting in that it had a greatly distended cloaca, and was therefore almost certainly a female which had recently laid an egg. The presence of food reserves in the stomach suggests that the bird was coming in to take over an incubation stint. The bird was netted on 28th July, 1969, and had presumably therefore laid in the secondhalf of that month; a late date which agrees with the finding that birds breeding for the first time lay later than experienced adults (see page 23).

(ii) The condition of the ring

In 1968 and 1969, whilst handling birds which had been ringed as chicks two years previously, it was noticed that the rings of these birds showed a type of wear quite unlike that of the rings put on full-grown birds. The latter rapidly lose their initial gloss, becoming scratched and dull; the edges become blunted; and the inscription blackens, as it collects dirt. The rings of birds recaptured two years after being ringed as chicks, i.e. after almost two complete years at sea, showed no scratching, but an apparently high degree of corrosion. Presumably, as a result of constant immersion in salt water, a thin surface layer of the rings had become corroded and, in the absence of the abrasive action of a hard substrate, had remained to give the rings a very coarse, granular appearance. No dirt had collected in the figures, and owing to the granular nature of the surface, the inscription could often be read only with difficulty. Rings from the same series as used on chicks, when put on adults, showed the normal type of wear, indicating that the rings used on chicks were initially in no way abnormal.

The distinctive nature of the corrosion suggested that two-year old birds had not yet occupied burrows, since the granular surface of the rings would rapidly collect dirt and become scratched. However, of the 18 three-year old birds examined in 1969, seven had scratched and dirty rings, and had clearly been involved in some burrowing activities. (One of these was in fact known to be in occupation of a burrow as a non-breeder; a second, as previously mentioned, was considered, on the presence of a swollen cloaca and distended abdomen, to be a female with an egg; a third was known to be in its second season at the colony and, from its distended abdomen, was also considered to be in occupation of a burrow; and a fourth was known to be in its second season at the colony.) The rings of four birds, caught in June or early July, showed no noticeable signs of scratching. However, at this early date, when some non-breeders are occupying burrows for the first time, pronounced wear would not be expected. The remaining seven birds, all caught between 20th July and 10th September, showed no signs of dirt or scratching on their rings, indicating that these birds had not occupied a burrow regularly during this, their third, year. Four of these birds were caught at two or more widely separated localities, suggesting that they were wandering non-breeders, in their first season at the colony.

(8) <u>A summary of the age of first return to the colony, and age of first breeding in the Storm Petrel, and other Procellariiformes</u>

Using all available sources of evidence, an attempt has been made to assign some status to those Storm Petrels of known age recaptured during the present study. The results are presented in table 39. It is concluded, from these results, and from the various sources of evidence relating to

Table 39. Status, when recaptured, of Storm Petrels ringed as chicks, i.e. birds of known age.

Status	Age in years			
	2	3	4	5 or more
Breeding	0	2	1	3
Non-breeder with burrow	0	1	1	0
Breeder or non-breeder with burrow	0	5	4	1
Non-breeder, with or without burrow	7	5	0	0
Wandering non-breeder	19	9	0	0
Status unknown	0	5	1	1
Totals	26	27	7	5

mist-netted birds, that petrels do not normally return to the colony until two years of age, and that perhaps as many as one quarter to one third of the population do not return until three. Immatures normally spend only one season at the colony as wandering non-breeders, and one season as non-breeders prospecting for, and occupying burrows, prior to first breeding. Hence, birds which return to the colony for the first time two years after fledging will normally breed for the first time when four years of age, whilst those returning at three, will normally breed when five. A few birds, perhaps mainly females, are able to breed in their first season of occupation of a burrow. Thus, by eliminating one of the non-breeding seasons at the colony, breeding may occur at three. Presumably, at the other extreme, a bird returning for the first time at three, and failing to occupy a burrow successfully in its second year at the colony, may not breed until it is at least six years old. The extremes would appear to be rare, and it is concluded that the Storm Petrel normally breeds for the first time at four or five years of age.

The age of first return to the colony, and age of first breeding, of other species of Hydrobatidae are poorly known. The presence, in the community, of two classes of non-breeders corresponding to non-breeders with burrows, and wandering non-breeders, has been demonstrated in Oceanodroma castro (Allan, 1962; Harris, 1969), O. tethys (Harris, 1969), O. leucorhoa (Wilbur, 1969), Oceanites oceanicus (Beck, in press), and Pelagodroma marina (Richdale, 1943 and 1965), but it is not known if these classes represent two distinct age groups, or at what age the birds normally return to the colony for the first time. In the populations of O. castro and O. tethys studied by Allan and Harris, there was considerable intraspecific competition for nest-sites. In both species, failure to obtain a burrow in the first season of prospecting was not uncommon, and resulted in a number of non-breeders spending two seasons as prospectors. Allan therefore concluded that some young birds, although capable of breeding, were being prevented from doing so by the activities of other pairs.

Only in the American studies of O. leucorhoa has the ringing of chicks produced any meaningful recapture data. Gross (1947) reported the recapture of two birds at their natal colony one year after fledging, and three birds, one of which was breeding, three years after. Huntington (in Harris, 1969) found one bird breeding at four, and four birds breeding at five years of age. Wilbur (1969) suggested that young birds may return to the colony in their first year, and breed at three. He thought that there was considerable variation in the age of first breeding which could perhaps be sexual. The limited amount of evidence available therefore suggests that in six species of Hydrobatidae, breeding does not take place until at least three years after fledging.

More precise information on the age of first return and first breeding is available for several other species of Procellariiformes, and has been summarized by Lack (1968). Deferred maturity appears to be the rule, and indeed, storm petrels would appear to be amongst the earliest breeders in the order. Studies of a few species, notably Puffinus tenuirostris (Serventy, 1957 and 1961), and Puffinus puffinus (Harris, 1966a; Perrins, Harris and Britton, in prep.) have revealed a pattern of returns of non-breeders which is very similar to that obtained for H. pelagicus. In the season of first return, birds spend only a short period at the colony in late summer. In the following years, the date of return to the colony gets increasingly earlier, so that by the first or second year of breeding, young birds are returning to the colony at the same time as experienced adults.

(9) Wing-lengths of Storm Petrels

During the present study, 6,681 measurements were taken of the wings of Storm Petrels mist-netted at night. The length measured was the distance from the carpal joint to the tip of the longest primary in the folded wing. Only those measurements taken by myself have been analyzed here, since it was found that different workers, applying different amounts of pressure to the feathers, obtained measurements varying by as much as 6 mm. The overall mean wing-length was 119.7 mm. (S. D. $\pm$ 2.7, range 110 - 129). Very few birds of known sex were measured, and it was not therefore possible to ascertain if there was a size difference between the sexes. However, it is clear, from the standard deviation of the sample, that any difference there might be must be small in relation to the total range, and therefore of little value in individual separation of the sexes.

The mean wing-lengths of samples taken at different times of the year are shown in appendix table 10. The reason for the shortness of the mean wing-length of the birds caught in April (i.e. about 1.5 mm shorter than birds caught in May), is undoubtedly the inclusion, in the April sample, of a few birds still completing the growth of their longest primary. Ten birds (20%) were obviously still growing their outermost primary, and it seems likely that in some of these birds the longest primary was still a few millimetres short of its ultimate length. The proportion of birds completing the moult of their primaries in May was much lower (3.6% in 1967, and 6.3% in 1968), and the effect of these on the mean wing-length of the whole sample would be negligible.

In table 40, the wing-lengths of birds known to be at least four years of age, and therefore assumed to be mainly breeding birds, are compared with the wing-lengths of birds considered, on the condition of their brood patch, or locality of subsequent recapture, to be wandering non-breeders in their first season at the colony. The difference in the mean wing-lengths of the two groups, although only 0.82 mm., is highly significant, and is interpreted as indication that birds in their first season at the colony, i.e. when two or three years old, have not yet attained full size. Assuming that the relationship of body-size to cube of wing-length is valid (see Warham, 1968), the difference of 0.82 mm represents a difference in body-size of approximately 2 per cent. Clearly, the decline in mean wing-length in the whole samples in late summer (see appendix table 10) is caused by the influx of a large number of short-winged non-breeders into the community. With the departure of the non-breeders in September, the mean wing-length of the whole sample becomes representative of that of a sample of breeding birds.

Table 40 also gives the mean wing-length of petrels recaptured at the colony in the year after being ringed as wandering non-breeders. The mean wing-length of this group was not significantly shorter than that of adults, suggesting that most, if not all, birds have attained full size by the time that they occupy a burrow (i.e. at the second moult of the remiges, in birds occupying a burrow when three years old, (see section IV)).

A size difference between adults and first year birds still retaining the first generation of remiges has been reported for a wide variety of

Table 40. Mean wing-lengths of adult and non-breeding Storm Petrels on Skokholm.

Status of birds*	Sample size	Mean wing-length (mm.)	Standard deviation of sample
Adults	1302	120.0	± 2.2
Non-breeders in first season at colony	1010	119.2	± 2.6
Non-breeders in second season at colony	276	119.9	± 2.7

Mean wing-length of non-breeders in first season at colony is significantly shorter than that of adults: $t = 7.9$, $p =$ less than 0.001

Mean wing-length of non-breeders in second season at colony is not significantly shorter than that of adults: $t = 0.87$, $p = 0.20$

* For criteria used in determining status of mist-netted birds, see page 84.

species. However, a significant size difference between adults and birds in their second summer, after at least one complete moult, has not been recorded, although van Balen (1967) found some suggestion of this in the Great Tit Parus major. The significance of the increase in size with increasing age in the Storm Petrel is not clear, although it would seem likely that it is related to an increase in the efficiency at collecting food.

(10) Weights of Storm Petrels

4,997 weights were obtained from Storm Petrels mist-netted at night, and a further 592 weights of mist-netted birds have been extracted from the files of Skokholm Bird Observatory. The overall mean weight was 27.6 gm (S. D. $\pm$ 2.6, range 20 - 37). The mean weights of samples taken during each half-monthly period throughout the season show a gradual decline from about 30 gm in late April, to about 26 gm in early August, and then a slight increase to about 27 gm in October (appendix table 10). The mean weights of breeding birds, non-breeders with burrows, and wandering non-breeders, as identified on the criteria described in previous section, are shown in table 41.

Both breeding birds and non-breeders prospecting for burrows arrive at the colony in Spring at high weights, suggesting that these birds, after completing the spring migration, build up fat reserves before making their first visit to the colony. During the period when most breeding birds are incubating (late June to early August), the samples consist mainly of birds with full stomachs arriving at the colony to take over an incubation stint, and light birds departing after a period of fasting in the burrow. Consequently, the weights of breeding birds at this time show a wide spread (22 - 36 gm.) and a suggestion of bimodality (modes at 26 gm and 30 gm). Breeding birds reach their lowest weights during late summer, when they are feeding chicks, and are in heavy moult (see section IV). At this time, most adults regurgitate some or all of their stomach contents when handled, and the net samples contain relatively few fat birds. Non-breeders with burrows show a decline in weight in the early part of the season similar to that of adults, but are consistently 1.0 to 1.5 grams lighter. The mean weight of wandering non-breeders is constant at 25.3 gm (S. D. $\pm$ 1.8, range 21 - 33) throughout late July, August, and early September. Thus these

Table 41. Weights of adult and non-breeding Storm Petrels on Skokholm, in relation to date.

Date	Adults		Non-breeders in second season at colony		Non-breeders in first season at colony	
	Sample size	Mean weight (gm.)	Sample size	Mean weight (gm.)	Sample size	Mean weight (gm.)
Apr 16-30	6	31.7	0	-	0	-
May 1-15	58	30.0	4	29.3	0	-
May 16-31	217	29.0	32	28.3	0	-
Jun 1-15	146	28.9	70	27.7	0	-
Jun 16-30	29	27.8	18	26.3	0	-
Jul 1-15	143	28.6	24	26.6	96	26.1*
Jul 16-31	57	28.0	31	26.2	103	25.3
Aug 1-15	82	27.9	7	26.3	70	25.3
Aug 16-31	46	28.0	21	27.2	114	25.3
Sep 1-15	84	27.5	1	[30.0]	21	25.3
Sep 16-30	35	26.7	1	[27.0]	0	-
Oct 1-15	13	27.1	0	-	0	-
Oct 16-31	7	26.7	0	-	0	-

* Probably too high because of inadvertent inclusion in the samples of old birds still retaining traces of down on brood patch.

birds are on average 2.0 to 2.5 gm lighter than breeding birds at the same time of year. Clearly, these non-breeders put on little, if any, fat reserves before visiting the colony. Whether non-breeders are lighter than breeding birds because they are unable to obtain sufficient food, or because they do not require large reserves of fat if they are not going to breed, is not clear. There is no indication that birds build up fat reserves in preparation for the autumn migration, whilst still visiting the colony. However, as argued above (page 51), there does not seem to be any shortage of food in the vicinity of the colony until at least mid-October, so it is possible that, after leaving the colony, petrels remain in the North Atlantic to build up fat reserves prior to the migration through the tropics.

Because of the magnitude of the seasonal changes in weight of adults, and the differences in weight between different age classes, the mean weight of a sample of Storm Petrels is of little value unless the date at which the sample was taken, and the status of the birds involved, are known. Davis (1957) gave the mean weight of adult Storm Petrels on Skokholm as 28 gm. His sample of 50 birds included mainly breeding birds removed from burrows in the pre-egg stage. On the other hand, Browne and Browne (1956) gave the mean weight of 28 Storm Petrels from Skokholm as 26.5 gm; presumably this sample contained a number of young birds. Waters (1964) obtained even lower weights of Storm Petrels from St. Kilda (Outer Hebrides). The mean weights of a sample of 27 birds taken in June and early July, and a sample of 35 birds taken on 13th August, were 25.3 and 23.7 respectively. Clearly, these samples consisted mainly of wandering non-breeders.

The only other study of weights of a species of Hydrobatidae is that of Harris (1969) for Oceanodroma castro, and O. tethys. Unfortunately, for both species, his samples were small. He found that in O. castro, the weights of adults increased as the birds started incubation, and he considered that this increase was due to an increase in the number of birds with food stored in the stomach. There was no indication that adults were building up large fat reserves before returning to the colony. Weights decreased again when the birds had small young. He could find no significant changes in weight of adults before laying, failed breeders, or non-breeders. In O. tethys, he could find no significant changes in weight with date, or breeding condition, except that incubating birds, presumably with stored food, tended to be heavier than non-breeders.

(11) Interchange between the Storm Petrel colonies on Skokholm and on Skomer

The only large colony of Storm Petrels within 100 miles of Skokholm is on the island of Skomer, 2½ miles to the north. As described in Appendix IX, work on Skomer during the present study has shown that this colony probably contains in excess of 500 breeding pairs, and perhaps as many as 1,000. Of 580 petrels netted on Skomer in August 1969 and early June 1970, 94 (16%) had previously been ringed on Skokholm, 93 as full-grown birds, and one as a chick. Furthermore, of 414 birds netted on Skomer in 1969, 40 (10%) were recovered on Skokholm later that year. (32 of these had been ringed on Skomer, and 8 had been ringed on Skokholm earlier that year.)

Since a Storm Petrel which has occupied a burrow seldom visits any other part of the colony, the birds which visited both colonies must have been mainly wandering non-breeders. Inspection of the dates of ringing of the 93 full-grown birds which were recovered on Skomer suggested this to be the case.(table 42). In addition, of the total of 77 birds caught on both Skokholm and Skomer in the same season, 53 (69%) still retained traces of old down on the brood patch in August, a characteristic of wandering non-breeders. The bird which was ringed as a chick on Skokholm (in 1966), was recaptured on Skokholm on 30th August 1969, and then recovered on Skomer two days later. This bird also had a downy brood patch, and was probably in its first season on land at the age of three.

Examination of the birds caught on Skomer one or more years after being ringed on Skokholm suggested that most of these birds had occupied a burrow on Skomer, and would eventually breed there, if they had not already done so. All of the birds ringed in 1963, 1966, and 1967, and 18 of the 21 birds ringed in 1968, were considered from their age, condition of brood patch, or presence of food in the stomach, to be either breeding, or spending a non-breeding season in occupation of a burrow, on Skomer in 1969 or 1970. The 20 birds ringed on Skokholm in 1969 and recovered on Skomer in early June 1970 were probably non-breeders with burrows.

In only ten cases of movement from Skokholm to Skomer was there any indication that the bird in question had spent more than one season visiting

Table 42. Date of ringing of Storm Petrels ringed on Skokholm, and recovered on Skomer.

Date of ringing	Number of individuals ringed in each year 1963	1966	1967	1968	1969	Total excluding 1969
May 1-15	0	0	0	0	0	0
May 16-31	0	1	0	1	1	2
Jun 1-15	0	0	1	2	1	3
Jun 16-30	0	0	0	1	3	1
Jul 1-15	1	0	0	1	17	2
Jul 16-31	0	0	1	2	39	3
Aug 1-15	0	2	0	6	0	8
Aug 16-31	0	1	0	7	3	8
Sep 1-15	0	0	0	1	1	1
Sep 16-30	0	0	0	0	0	0
Totals	1	4	2	21	65	28

92% of petrels recovered on Skomer were ringed between mid-June and mid-September, i.e. during period of abundance of non-breeders in their first season on land.

Skokholm. Three birds were ringed in late summer 1968, recaptured on Skokholm in early summer 1969 (24th May, 5th June, and 7th July respectively), and finally recovered on Skomer in August 1969. The other seven birds were ringed on Skokholm before 21st June (1 in 1966, 1 in 1967, 3 in 1968, and 2 in 1969), when only breeding birds and non-breeders in their second season on land are normally present at the colony. In all ten cases, it it likely that the birds had returned to Skokholm as prospecting non-breeders, and had either failed to locate a suitable burrow, or had deserted because of excessive disturbance. In one case, this was known to have occurred. The petrel occupied a burrow in the study area on Skokholm for a short period in late May and early June 1967, but then deserted, presumably as a result of my interference. The bird was not caught again on Skokholm, but was netted on Skomer in August 1969. It was then at least five years old, and presumably therefore breeding.

In none of the cases of interchange was there any indication that a petrel recovered on Skomer had previously bred on Skokholm, or indeed had spent more than two seasons visiting Skokholm before moving. It is concluded therefore, that the interchange between Skokholm and Skomer is due almost entirely to visits by non-breeders in their season of wandering in the year prior to prospecting for a burrow. A few birds may visit both colonies in their second season on land, perhaps as a result of failure to occupy a burrow successfully, but once a bird has become established as a breeder on one of the islands, it rarely, if ever, visits the other.

Some extent of the mixing between the populations of non-breeders from the two islands can be gained from rough estimates of the proportion of non-breeders, ringed on Skokholm in July 1969, to unringed non-breeders in samples taken on both islands later in the season. It was estimated that 42 per cent of the non-breeders visiting Skokholm during the second half of July 1969 were ringed. The proportions of ringed to unringed non-breeders, in samples of non-breeders taken on Skomer on 2nd August and from 18th to 23rd August, and on Skokholm from 25th August to 11th September, were 33%, 22%, and 18% respectively. A decline in the proportion of ringed to unringed birds as the season progresses was to be expected, because of the constant turnover of wandering non-breeders in the population (see table 30). Hence, there is probably completely random mixing of the non-breeders from the two islands.

Current evidence indicates that some interchange occurs between widely separated colonies; details of ringing and recovery of birds showing movement between colonies more than 10 miles apart are given in Appendix IV. Movement is largely by wandering non-breeders, which may visit several colonies during their season of wandering, but there has been one undoubted case of a bird changing colonies after it had bred. Birds tend to visit those colonies in the vicinity of their natal colony, there being few recoveries of birds more than 250 miles from where ringed. Finally, there is some indication that some colonies are visited by wandering non-breeders more frequently than others, the numbers of birds visiting the colony not being related solely to the size of the breeding population (Dennis, 1969).

Interchange between colonies has also been reported in Oceanodroma leucorhoa (Gross, 1947; Spencer, 1959 and 1967), Puffinus tenuirostris (Serventy, 1961), and P. puffinus (Harris and Saunders, in prep.). In the two species of Puffinus, the situation is clearly very similar to that in H. pelagicus, most of the movement between colonies occurring during early life.

Section III : Annual Mortality and Post-fledging Survival

(1) Causes of mortality at the colony

From 1963 to 1969, records of all Storm Petrels found dead on Skokholm have been entered in the daily log of the observatory, and during the present study, whenever possible, the cause of death was also given (table 43). The number of petrels found dead at the colony each season varied between 26 and 139 (average 60).

(i) Predation

Over 90 per cent of all petrel corpses found on Skokholm were the result of predation by gulls Larus spp or Short-eared Owls Asio flammeus. Predation by owls varied greatly from year to year. The species does not breed on Skokholm, but usually several pairs breed on Skomer. In 1966, no Short-eared Owls were observed on Skokholm during the breeding season, and few, if any, petrels were taken, whereas in 1967, a single owl was present on the island for much of June, July, and August, and accounted for 85 of the petrel corpses in that year. In 1968, no owls visited the island during the early part of the season, but during August, September, and October, one or more individuals made sporadic visits to the island, and took a small toll of petrels. In 1969, visits by owls were more frequent, although there was no indication that any birds were permanently resident on the island. The remains of 27 owl kills were found in July and August.

Predation by Short-eared Owls occurs regularly on Skomer. A sample of 151 owl pellets collected on Skomer in 1967 by J. Frazier, and examined by the author, contained remains of 21 Storm Petrels. Frazier also collected 18 wings or pairs of wings of petrels which had been killed by owls. To what extent the petrel remains on Skomer refer to petrels caught on Skokholm and transported to Skomer by the owls is not clear. Most of the remains attributed to owls on Skokholm were pluckings, whereas more than half of the remains on Skomer were in pellets. Hence, it is possible that the owls were killing petrels on Skokholm, returning to Skomer, and subsequently regurgitating the pellets there. That owls do make feeding trips between the islands is shown by the fact that one of the four owl pellets found on Skokholm contained remains of a vole Clethrionomys sp, a genus of mammals which is absent from Skokholm, but present on Skomer, and also by

Table 43. Incidence and causes of mortality of Storm Petrels found dead on Skokholm between 1963 and 1969.

Date	Number found dead	CAUSES OF MORTALITY: 1966 to 1969 ONLY Killed by owl *Asio flammeus*	Killed by owl or gull	Killed by *L. marinus*	Killed by *L. argentatus*	Killed by *Larus* sp.	Dug out of burrow	Whole corpse Cause ?
Apr 16-30	0	0	0	0	0	0	0	0
May 1-15	3	0	0	0	0	1	0	0
May 16-31	18	2	1	0	0	4	2	1
Jun 1-15	57	12	2	3	0	5	0	0
Jun 16-30	86	19	0	7	6	15	2	0
Jul 1-15	78	16	2	8	1	14	1	3
Jul 16-31	74	30	3	6	0	2	1	2
Aug 1-15	37	15	1	1	1	4	0	0
Aug 16-31	23	11	1	0	0	0	2	0
Sep 1-15	31	15	0	0	1	5	0	0
Sep 16-30	13	1	0	0	0	1	0	0
Oct 1-15	5	2	0	0	0	0	0	0
Oct 16-31	3	1	1	0	0	0	0	0
Totals	428	124	11	25	9	51	8	6

the fact that four of the pellets found on Skomer contained remains of petrels which had been ringed on Skokholm. Although two of these had been ringed as non-breeders, and might therefore have visited Skomer of their own accord, two were established breeders on Skokholm.

The effect of owl predation on the large population of petrels on Skokholm is perhaps negligible. However, on Skomer, where the breeding population of petrels is probably between 500 and 1,000 pairs, and as many as five pairs of owls are present throughout the season, predation pressure may be much more severe. This is probably the explanation for the absence of breeding petrels from sites on the top of the island, and their restriction to the gullies and scree slopes low down on the cliffs, in terrain less suitable for hunting owls.

The only other serious predator of petrels on Skokholm is the Great Black-backed Gull _Larus marinus_. The numbers of this species have been controlled, so that at the present time, not more than about fifteen pairs attempt to breed annually. From the distribution of petrel corpses and gull pellets, it would seem that certain gulls have favoured stretches of wall or boulder heaps which they patrol at night, presumably pouncing on petrels as they enter or leave their burrows. There is very little predation on petrels by Herring Gulls _L. argentatus_ and Lesser Black-backed Gulls _L. fuscus_, (of which there are some 3,000 pairs on Skokholm), though a few battered corpses have been found lining gulls' nests.

Relatively few petrel remains were found in August, when the wandering non-breeders are at their most abundant, suggesting that this class of birds, which probably do not alight on the surface, are rarely taken by predators. Of 18 ringed petrels taken by predators during the present study, 3 were known to be breeding birds, a further 4 were five or more years of age, and 8 more were considered to be either breeding birds, or non-breeders with burrows; thus not more than 3 were wandering non-breeders. Proportionately, the individuals most vulnerable to predation are presumably non-breeders prospecting for burrows at the colony. 5 of the 18 ringed birds were probably in this category.

Predation of Storm Petrel chicks at fledging would seem to be negligible. The majority of gulls leave Skokholm in August or early September, and few owls have been reported after the end of September. In the seven years 1963 - 1969, only 21 corpses were found during the period of fledging (mid-September to the end of October), and of the nine corpses found during the present study, none were young birds.

Serious predation on Storm Petrels by Great Black-backed Gulls, possibly causing a decline in the breeding population, has been reported from the Scilly Isles (Parslow, 1965) and the Inner Hebrides (Gordon, 1965). Gull predation of a less serious nature has been reported from the Channel Islands (Long, 1965). Lockley found large numbers of petrel corpses at nests of Little Owls Athene noctua on Skokholm and Skomer, and suggested that the small population of petrels on the latter island was prevented from increasing by the depredations of the owls (Lockley, 1938; Lockley, in Hibbert-Ware, 1938). The very poor success of the small colony of petrels on Bardsey Island has also been attributed to predation by Little Owls (Bardsey Bird Observatory Reports, 1962 - 1967). Little Owls were removed from Skokholm by Davis in 1954, and have not since recolonized the island. Feral cats have been reported as predators on petrels in the Shetland Isles (Bruce, 1952; Dennis, 1969). As Harris (1965a) has suggested, predation by gulls, and to a lesser extent owls, would appear to be a regular feature of Storm Petrel breeding ecology. However, in the absence of accurate censuses, the true effects of the predation are not known for any colony.

Several other species of Hydrobatidae suffer regular predation on the breeding grounds. Ainslie and Atkinson (1937), Gross (1935), and Huntington (1963), described predation on Oceanodroma leucorhoa by L. marinus, and to a lesser extent L. argentatus. Gross also mentioned predation by dogs, cats, and rodents, on islands in the Bay of Fundy, and suggested that this might be responsible for the decline in numbers of petrels at some of the colonies in the area. Williamson (1948) found that feral cats were an important predator on O. leucorhoa in the Faroes. Nelson (1966) and Harris (1969) found evidence of heavy predation on Oceanodroma castro and O. tethys by Short-eared Owls Asio galapagensis on the Galapagos Islands. Harris was able to watch owls taking O. tethys by day, and thought that non-breeders which were prospecting for burrows were taken more frequently than other classes. A variety of species have been shown to prey upon Pelagodroma marina, including the skua Catharacta skua (Richdale, 1943; Warham, 1958), the gulls Larus pacificus and L. novaehollandiae (Warham, 1958), and hawks of the genus Buteo (Jones, 1937).

(ii) Parasitism and disease

There was no indication that parasitism or disease were important causes of mortality in Storm Petrels on the breeding grounds. A few individuals carried feather lice (Mallophaga), apparently all of one species, Halipeurus pelagicus; and one individual had a small tick (Ixodidae) attached at the base of the bill; Generally, however, Storm Petrels appeared to be relatively free of ectoparasites. During the nestling stage, chicks often became infested with the red mite Dermanyssus gallinae. These occurred in small numbers on most healthy chicks, but reached infestation levels on some poorly-fed and weak chicks, and may have accelerated death by starvation in a few cases. Richdale (1943) and Roberts (1940) found that Mallophaga were the only common ectoparasites of Pelagodroma marina and Oceanites oceanicus, respectively.

A few Storm Petrels had signs of blistering on the webs of the feet, reminiscent of the early stages of the virus disease, puffinosis, which causes considerable mortality of Manx Shearwater chicks on Skokholm (Harris, 1965). However, none of the petrels found dead during the present study showed any signs of blistering, and the presence of healed scars in a number of birds suggested that the cause of the blistering was not lethal.

(iii) Other causes of mortality

Eight very battered corpses of Storm Petrels were found at the entrances of burrows of shearwaters, Puffins, or rabbits. As discussed previously, there is little overlap between the nest-sites of Storm Petrels and those of other species, so that mortality as a result of inter-specific competition for burrows must be negligible for the population as a whole. The six petrels listed as "others" in table 43 included one bird which was found drowned in a water tank at the observatory, and one which was found trapped in a crevice in a wall. The four other corpses were intact, and the cause of death could not be determined.

(2) Causes of mortality at sea

There have been no reports of avian predation on petrels in the open ocean, and this would seem unlikely, as the predatory gulls are almost entirely inshore feeders. However, there is some indication that predatory fish take some petrels, although this may be unintentional. Of 10,189 Storm Petrels handled in 1967, 1968, and 1969, 41 (0.4%) had major leg or foot injuries. In 9 individuals, one of the tarsi had been broken, and had healed in an unnatural position; in 9 individuals, one of the feet, or part of a foot, was missing; and in 23 individuals, the whole of one tarsus and foot was missing. Minor injuries, such as slight deformities of the foot, or holes in the webs, were much more frequent. There was no indication that the affected birds were greatly incapacitated by their injuries. Six birds with a leg missing were retrapped a year later, two were retrapped two years later, and one was retrapped three years later. Both Harris (1969) and Allan (1962) found that several per cent of individuals of Oceanodroma castro suffered from leg injuries, and that these injuries did not appreciably affect the breeding success of the birds concerned.

The nature of many of the injuries suggested that the foot or tarsus had been cleanly chopped off, and as Harris suggested, it seems likely that most injuries were made by predatory fish. The petrels' habit of pattering their feet on the surface whilst feeding would render them vulnerable to this form of predation. Ritchie (1966) actually witnessed a shark capturing a Wilson's Petrel Oceanites oceanicus as it pattered along the surface, and it would seem likely that a small number of Storm Petrels suffer a similar fate.

Bad weather, and the rough seas associated with it, are no doubt responsible for some mortality in the Storm Petrel. However, this species does not seem susceptible to large scale "wrecks", such as are occasionally reported in Oceanodroma leucorhoa in the North Atlantic (e.g. Boyd, 1954). Those few Storm Petrels driven ashore in Europe during autumn gales are mainly birds of the year, weakened through food shortage, and possibly also disoriented. The collection of bird skins at the British Museum contains fourteen Storm Petrels found dead in Britain away from breeding colonies. All were birds of the year, picked up dead in October or November, when juveniles from the northern colonies are on their southward migration.

The frequency with which petrels are unable to complete the moult of the remiges during the winter months (see section IV) suggests that feeding conditions in the winter quarters, and during migration, may be poor. The class of birds most likely to be affected by food shortage are young birds. Ringing recoveries suggest that there is relatively high mortality of juvenile Puffinus puffinus soon after arrival in the winter quarters off the coasts of Brazil and Argentina, and Harris (1966) has suggested that shortage of food immediately after the breeding season, and especially during the southward migration, may be an important mortality factor in affecting the survival of the young. The migration southwards in autumn may likewise be a critical period for juvenile Storm Petrels.

Seven petrels ringed on Skokholm have been recovered dead away from the island, five on the west coast of France, and two in the Bristol Channel Four of these birds were ringed as chicks, and were recovered 3, 11, 15, and 22 months after fledging, respectively. Thus four of the 433 petrels ringed as chicks on Skokholm have been recovered dead within two years of fledging, whereas only three of the 12,450 birds ringed when two or more years of age have subsequently been found dead. Although the number of birds found dead is very small, these figures do suggest that mortality at sea is higher during the first two years of life than in subsequent years.

(3) Sources of error in estimates of annual mortality

Several methods of estimating the annual mortality of a species depend on the determination of the rate at which marked individuals disappear from a given sample. This assumes that disappearance of an individual indicates that the individual has died, an assumption which is clearly not always valid. During the present study, three causes of disappearance of ringed adults, other than mortality, have been recognized.

(i) Desertion or natural shift of marked birds from burrows; in spite of searches nearby, it is clear that some of the survivors were overlooked.

(ii) Possible avoidance of nets due to experience of being caught (see appendix VIII).

(iii) Ring loss. This is likely to have been negligible from birds ringed with monel rings since mid-summer 1958, but birds marked before this date, with softer aluminium rings, lost them within five or six years. Consequently, in the present analysis, birds ringed with aluminium rings have been ignored unless subsequently re-ringed with monel rings, in which case, the birds are regarded as having been ringed in the year of re-ringing.

(4) The annual mortality of adult Storm Petrels

Only twenty-nine Storm Petrels, ringed on Skokholm have subsequently been found dead, so that it has not been possible to determine the annual mortality directly from the incidence of deaths in the years after ringing. Determinations of annual mortality have therefore been based on the disappearance of marked birds from particular samples, thus involving the various sources of error outlined above. Calculations have been based on (i) the disappearance of marked birds from burrows, and (ii) the disappearance of marked birds from netted samples.

(i) Disappearance of marked birds from burrows

Davis (1957) found that of 45 Storm Petrels which bred successfully in one year, 42 returned to their burrows in the next. In the present study, of 74 successful breeders, 67 returned to their burrows in the following year. Taken together, these figures represent a survival from one year to the next of 92%. However, the survival refers only to that period between the end of one breeding season, and the early part of the next, i.e. a period of about seven or eight months. The mortality of 8% therefore excludes most of the mortality during the breeding season.

The handling of adults in burrows for marking purposes was generally restricted to the pre-egg stage, between late May and Late June. This was therefore the period during which most desertions occurred. Once the egg had been laid, the petrels were disturbed as little as possible, and desertions were rare. Thus by considering the disappearance of adults between laying and return to the colony in the following year, much of the disappearance caused by my interference has been eliminated, though the calculated mortality is only for a period of about eleven months.

Of a total of 141 successful and failed breeders in 1967 and 1968, 103 were recovered in their original burrows in the following year, and a further 22 were known to be alive from recaptures elsewhere. This gives a minimum survival over eleven months of 88.7%. Assuming that the mortality in the pre-egg stage, after re-occupation of the burrow, is not substantially higher than at other times of the year, the annual mortality of breeding adults cannot be higher than 12.5%.

(ii) Disappearance of marked birds from mist-netted samples

Because of inconsistencies in the trapping effort in the years preceding the present study, it has not been possible to analyse the ringing and re-trapping data at any one site with a view to determining adult survival over a number of years. A rough estimate has been obtained from the survival of eighty petrels ringed at Crab Bay in May and June 1959. 19 of these birds were recaptured in the years 1967 - 1969. It was estimated that only 80 per cent of the breeding birds in Crab Bay were caught, suggesting that a further five of the birds ringed in 1959 were probably missed. Survival of 24 birds from 1959 to 1967 represents a mean annual survival of 86%. This figure is also only a minimum, since some of the eighty birds ringed in 1959 would have been non-breeders which eventually settled elsewhere.

Any estimate of adult survival based on ringing and retrapping effort at one locality is subject to large errors because of small samples. An improved estimate can be obtained by calculating the average rate of disappearance of marked birds from the entire population. Because of the very poor effort on the west half of the island before 1966, only the ringing and retrapping on the east half of the island has been analysed. The total effort in the years 1958 to 1969 is summarized in table 44, and the stages in the calculations are given in tables 45 and 46.

When initially trapped, a number of individuals will have been non-breeders in their first season on land. These birds will have been prospecting for burrows one, and possibly also two, years after ringing. Since prospecting non-breeders show a greater tendency to wander than adults, and probably suffer a higher mortality (see page 91), the inclusion of these birds in the samples will result in a bias towards underestimating the survival of adults. The proportions of marked birds in the population one and two years after initial capture have therefore been excluded from the calculation of adult survival.

The corrected proportions of marked birds in the population 3 - 11

Table 44. Total ringing and retrapping effort on east half of Skokholm, 1958-1969.

Year	Number of petrels caught	Number of Storm Petrels recaptured			
		1966	1967	1968	1969
1958	90	5	8	7	6
1959	312	23	31	26	22
1960	57	6	6	5	5
1961	148	9	13	10	9
1962	117	16	15	14	13
1963	367	28	50	50	30
1964	385	62	62	54	38
1965	273	52	66	65	38
1966	1038	-	292	234	155
1967	1374	-	-	407	278
1968	1408	-	-	-	443
1969	1400	-	-	-	-

Table 45. Percentage of Storm Petrels marked in one year, which were retrapped in each 100 birds caught in a later year.

Year of marking (n)	Year of retrapping (m) 1966	1967	1968	1969
1958	0.54	0.65	0.55	0.48
1959	0.71	0.72	0.59	0.50
1960	1.01	0.77	0.62	0.63
1961	0.59	0.64	0.48	0.43
1962	1.32	0.93	0.85	0.79
1963	0.78	1.05	1.03	0.58
1964	1.55	1.17	1.00	0.71
1965	1.83	1.76	1.69	0.99
1966	-	2.05	1.60	1.07
1967	-	-	2.10	1.45
1968	-	-	-	2.25

Note: The numbers of birds trapped in each of the years 1958-1968 ($n_1 - n_{11}$), which were retrapped in each of the four years of the present study ($m_1 - m_4$), have been expressed as proportions of those birds trapped in year n. These proportions have then been converted into the proportions which were retrapped per 100 birds trapped in year m, thereby eliminating the effects of variations in the trapping effort in the years $m_1 - m_4$.

Table 46. Average percentage of marked Storm Petrels which were retrapped in each 100 birds caught 1-11 years after marking.*

Years after marking	Average percentage of those marked per 100 birds caught in year of retrapping
1	2.06
2	1.59
3	1.18
4	1.09
5	0.81
6	0.77
7	0.69
8	0.58
9	0.62
10	0.53
11	0.48

* averages taken from four years of retrapping 1966-1969 (see table 45) to eliminate some of variations in trapping effort in years 1958-1968.

years after initial capture are plotted on logarithmic scale in figure 19. The best fit to the points has been obtained from a simple regression analysis. The mean annual survival obtained from this line is 89.5% with 95% confidence limits of 88.8% and 90.2%. This gives a mean annual mortality of 10.5 $\pm$ 0.7%, and a mean expectation of further life of 9.0 years, range 8.4 - 9.7. The sources of error given on page 95 may slightly bias this result, but fluctuations in the population size over the period 1958 - 1969 should not affect the calculations, and variations in the trapping effort, and the proportions of non-breeders in the samples, should, on the whole, cancel one another out.

Taking all calculations into consideration, it is concluded that the annual mortality of the Storm Petrel is within the range 9 - 12%, and probably between 10 and 11%.

If, as Lack (1954) has suggested, the probability of survival of an adult is independent of age up to the age at which very few birds are left, a population of Storm Petrels will include a number of individuals surviving for considerably longer than the mean expectation of life. In fact, if survival is truly independent of age, 5 per cent of adult Storm Petrels should survive for 27 years, and 1 per cent should attain an age in excess of 40 years. In view of the necessity for almost continuous flight in feeding and during migration, a slight deterioration in fitness could cause a marked increase in the mortality rate. Clearly, the possibility of an effect of senility on adult survival cannot be ignored. Austin and Austin (1956) have argued that senility probably occurs in the Common Tern Sterna hirundo, a sea-bird which, like the Storm Petrel, has a low annual mortality, and depends on its powers of flight for feeding.

Few Storm Petrels have been recorded at ages of more than 10 years because of the poor quality of the rings used in earlier years. However, 19 birds, which were formerly ringed with aluminium rings and later ringed with monel rings, are known to have survived for 11 years, and a further 4 for 12 years, 2 for 13 years, and singles for 14, 15, and 19 years, respectively. The last bird, ringed on 15th June 1950, was probably in at least its second season at the colony in 1950, i.e. was three or more years of age when ringed, and can therefore be assumed to have been at least 22 years old

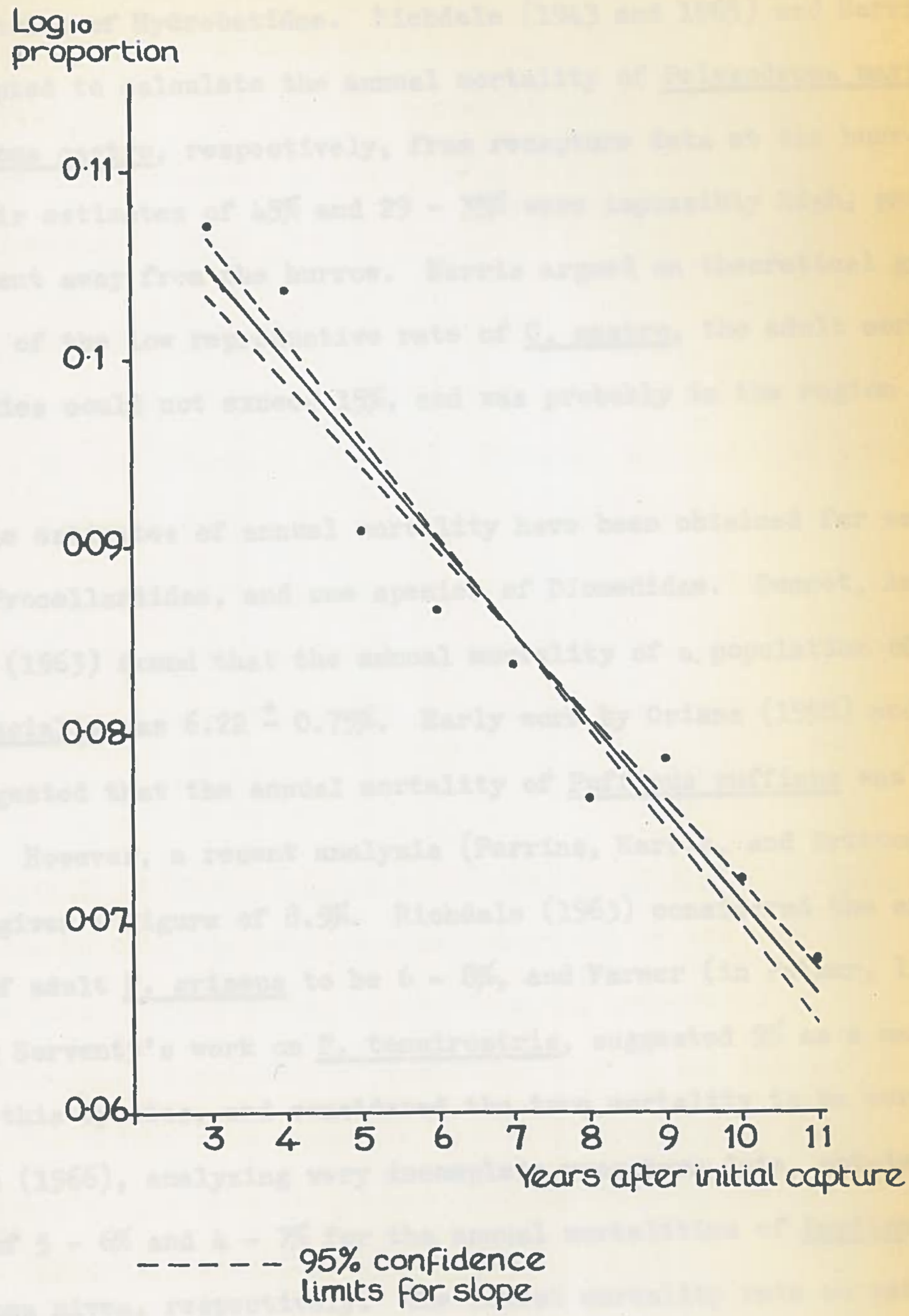


Figure 12. Rate of disappearance of marked Storm Petrels from population on Skokholm.

The Y axis gives a measure of the proportion of birds marked in one year which are present in the population in a later year (see text).

when recaptured in 1969.

(5) The annual mortality of other species of Procellariiformes

No satisfactory estimate has yet been made of the annual mortality of any other species of Hydrobatidae. Richdale (1943 and 1965) and Harris (1969) attempted to calculate the annual mortality of Pelagodroma marina and Oceanodroma castro, respectively, from recapture data at the burrow. However, their estimates of 45% and 29 - 35% were impossibly high, probably due to movement away from the burrow. Harris argued on theoretical grounds that in view of the low reproductive rate of O. castro, the adult mortality of this species could not exceed 15%, and was probably in the region of 5 - 7%.

Reliable estimates of annual mortality have been obtained for several species of Procellariidae, and one species of Diomedidae. Dunnet, Anderson, and Cormack (1963) found that the annual mortality of a population of Fulmarus glacialis was 6.22 ± 0.75%. Early work by Orians (1958) and Harris (1966a) suggested that the annual mortality of Puffinus puffinus was as low as 6 or 7%. However, a recent analysis (Perrins, Harris, and Britton, in prep.) has given a figure of 8.9%. Richdale (1963) considered the annual mortality of adult P. griseus to be 6 - 8%, and Farner (in Palmer, 1962), summarizing Serventy's work on P. tenuirostris, suggested 9% as a maximum figure for this species, and considered the true mortality to be more like 5%. Hudson (1966), analyzing very incomplete recapture data, obtained estimates of 5 - 6% and 4 - 7% for the annual mortalities of Daption capensis and Pagodroma nivea, respectively. The lowest mortality rate as yet discovered for any wild bird is that for Diomedea epomophora. Richdale (1952) found an annual mortality of only 3% in a very small population of Royal Albatrosses. This estimate was considered to be a little lower than the mortality in a stable population, since the population under investigation was increasing.

Thus all six estimates of adult mortality available for Procellariidae are less than 10%, and the one estimate for a species of Diomedidae is considerably less than this. As Hudson (1966) has pointed out, within the Procellariiformes, the larger species tend to have the lowest mortality. Similarly, the larger species have longer periods of immaturity than the smaller species (summarized in Lack, 1968). It appears therefore that within the Procellariiformes, there is a tendency for the three parameters of size, period of immaturity, and adult survival, to be correlated. A relatively high mortality rate is to be expected in the small storm petrels, which have short periods of immaturity (see page 82). As predicted, the present estimate of 10 - 11% for the annual mortality of H. pelagicus is the highest reliable estimate of annual mortality so far obtained for a species of Procellariiformes.

(6) Post-fledging survival

The above considerations establish that the annual mortality of adult Storm Petrels is approximately 10 - 11%. However, as shown previously, Storm Petrels do not normally breed for the first time until four or five years of age. Any mortality during the period of immaturity will reduce the recruitment rate of the population, and hence, for an understanding of the population dynamics of the species, some estimate of the mortality during immaturity is essential.

(i) The mortality between fledging and first return to the colony

It should be possible to determine the extent of the mortality between fledging and first return to the colony from the proportion of birds ringed as chicks which were subsequently recaptured back at the colony. Unfortunately, very few chicks were ringed on Skokholm before 1963, and the retrapping effort was so low that it has not been possible to use the recovery of these birds in mortality estimates.

A total of 37 chicks were ringed on Skokholm in 1963 and 1964. These were found on the walls around the observatory at the time of fledging. During the four seasons 1965 - 1968, 18 (49%) of these chicks were retrapped back at the colony. The tendency for young birds to return to the area of their natal burrow, which in this case corresponds to the area of greatest retrapping effort, has undoubtedly contributed to the success of the recapture rate. However, it seems likely that some of the survivors were missed, since ten birds were retrapped only once. Thus a survival of 49% can be regarded as only a minimum figure for this group of birds.

Ten chicks were ringed in 1965, all in the main shearwater colony on the south-west tip of the island. Because of the large number of shearwaters present in this area, mist-netting was seldom possible, and indeed none of the chicks ringed in 1965 were retrapped there. As only two of this group were recaptured elsewhere, it seems likely that several of the survivors were missed.

During 1966 and 1967, chicks were ringed at a wide variety of sites around the island, and it is clear that even for the 1966 chicks, which were available for recapture in two years, a high proportion of the surviving birds were missed. Nevertheless, of 82 chicks ringed in 1966, 24 were recaptured on Skokholm in 1968 or 1969, and a further two were recovered elsewhere. Of the 59 chicks ringed in 1967, 12 were recaptured on Skokholm in 1969, and another was found dead in France fourteen months after fledging. Recapture data suggested that in 1968 and 1969, about one third and one half, respectively, of all non-breeders visiting the colony were caught. On this basis, it has been estimated that 30 of the chicks ringed in 1966 were present at the colony in 1968, and 36 in 1969. Including the individual caught on Bardsey Island (Caerns.) in 1969, the number of 1966 chicks surviving to the age of three years becomes 37, giving a survival from fledging to this age of 45%. Similarly, it has been estimated that 24 of the chicks ringed in 1967 visited the colony in 1969, giving a survival of 41%. This figure is clearly too low since some of the 1967 chicks would not have returned to the colony for the first time until 1970.

Obviously, the data are insufficient to provide any reliable estimate of survival from fledging to first return to the colony. However, the figures obtained from small samples of chicks ringed in four seasons suggest a survival to the age of two or three years well in excess of 40%, and probably over 50% in some seasons. A summary of the recapture data is given in table 47.

Accurate estimations of the survival from fledging to first breeding have not been made for any species of Hydrobatidae, and indeed are available for only two species of Procellariiformes. Serventy (1967) found that over a period of eleven years, the survival of Puffinus tenuirostris from fledging to the immediate pre-breeding stage varied from 22% to 59%, with a mean at 37%. Perrins, Harris, and Britton (in prep.) found that the

Table 47. Survival of Storm Petrels from fledging until return to colony, as determined from number of ringed chicks which were recaptured two or more years after fledging.

Year of ringing	Number of chicks ringed	Number recaptured back at colony	Years available for capture	% surviving at least until first return
1963	20	10	5	50
1964	17	8	4	47
1965	10	2	3	20
1966	82	26*	2	32
1967	59	12	1	20

* including two recovered elsewhere two or more years after fledging.

survival of P. puffinus from fledging to about four years of age was approximately 40%. These authors considered that much of the predation on Manx Shearwaters on Skokholm occurred during the years of prospecting, and that the mortality rate of non-breeders which were successfully established in burrows was not significantly higher than that of breeding birds.

(ii) The survival of fledglings in relation to date of fledging

At present, the data is insufficient to determine if, on average, early fledged chicks survive better or worse than late fledged chicks. Most of the chicks ringed before 1966 were caught at the time of peak fledging, so that samples of late fledged chicks are very small. Furthermore, marked differences in the timing of the breeding season from year to year prevent the pooling of several years' data. It has therefore been possible to analyse only the data from chicks ringed in 1966 and 1967. Because of the smallness of the samples, each year class of chicks has been divided into two equally-sized categories, viz. those which fledged before, and those which fledged after, the mean date of fledging in the year concerned. The survival of these two groups, for both years, is shown in table 48. In neither season was there any significant difference between the survival of early and late fledged chicks. In 1966, the difference fell ~~just~~ well short of significance (χ^2 = ~~3.6~~ 2.8) for better survival of early fledged chicks, whereas in 1967, the results suggest a better survival of late fledged chicks.

A decline in post-fledging survival as the season progresses would not be expected for three reasons. Firstly, the Storm Petrels on Skokholm fledge, on average, three or four weeks earlier than those raised at colonies in the Faroes and south-west Iceland, much further to the north (page 136). If late fledged chicks from Skokholm regularly suffered a higher mortality rate than early fledged chicks, due to a deterioration in the feeding conditions and/or weather conditions at the time of departure and during the southward migration, it is difficult to understand how Storm Petrels could survive at much higher latitudes, where the fledging period is several weeks later, and the weather conditions are more severe. Secondly, as shown in section I, there is no indication that feeding conditions deteriorate around Skokholm until at least the end of October, by

Table 48. Post-fledging survival of the Storm Petrel in relation to fledging date; 1966 and 1967 chicks only.

Fledging date	1966 Number fledged	1966 Number recaptured	1966 %	1967 Number fledged	1967 Number recaptured	1967 %
Before mean date of fledging*	41	17	42	30	4	13
After mean date of fledging	41	9	22	29	9**	31
Total	82	26	32	59	13	22

* mean date of fledging in 1966 was 30 September/1 October, and in 1967 was 6 October.

** including one bird recovered dead fourteen months after fledging.

which time most chicks have fledged. Thirdly, it is clear that the growth of the chicks, and the feeding regimen of the parents have become adapted to ensure that chicks fledge at as good a weight as possible, rather than as early as possible. Parents will continue to feed retarded chicks long after the end of the normal nestling period, suggesting that there is no high premium on early departure from northern waters.

Bad weather conditions at the time of fledging may be an important cause of post-fledging mortality in some seasons. In 1967, the peak period of fledging, in the first week of October, coincided with a period of gales, and it seems likely that birds fledging at this time would have suffered a higher mortality than chicks fledging earlier or later in the season, when conditions were more amenable. Variations in weather conditions could therefore account for differences in the survival of early and late fledged chicks, both within, and between, seasons.

(iii) The survival of fledglings in relation to the weight at fledging, and the rate of growth achieved during the nestling period

The amount of food reserves with which a chick fledges might be expected to exert a strong influence on the individual's changes of survival during the immediate post-fledging period, when the petrel must become efficient at feeding itself. The mean weight at fledging of 18 chicks which were known to have survived to an age of two years was 34.7 ± 3.5 gm. (range 25.0 - 38.0), whereas the mean weight at fledging of 48 chicks which were not subsequently recaptured was 32.3 ± 4.3 gm (range 16.0 - 39.0). Thus chicks which survived were on average about 7% heavier than those which were not known to have survived. The difference in weight between the two classes was significant at the 95% level ($t = 2.3$, p = between 0.05 and 0.02). This difference is maintained at the same level of significance when chicks with fledging weights of less than 29.0 gm. are ignored, indicating that the low mean weight of the missing birds was not due simply to the presence of a few exceptionally light birds with a very poor chance of survival. It is concluded, therefore, that heavy fledglings, on average, survive better than light-weight birds. Perrins, Harris, and Britton (in prep.) found a similar situation in *Puffinus puffinus*, the weight of chicks known to have survived to return to the colony being, on average, 8 - 9% higher than that of chicks which were not known to have survived.

As discussed in section I, the weight at which a chick fledges is not closely related to the rate of growth which the chick achieved during the nestling period. It might be expected, therefore, that the regularity of feeding during the chick stage, and the duration of the nestling period, are relatively unimportant with regard to subsequent post-fledging survival. Unfortunately, there have been very few recaptures of chicks for which growth curves were obtained. Out of a total of 32 chicks weighed daily in 1966 or 1967, 15 had good rates of growth, 10 were slightly retarded, and 7 were very retarded. Eight of these chicks were known to have survived for at least two years; 4 had good rates of growth as chicks, 2 were slightly retarded, and 2 were very retarded. These results suggest therefore that a good rate of growth may not be of major importance with regard to post-fledging survival, providing that the ultimate weight attained is normal.

(7) <u>The mortality between first return to the colony and first breeding</u>

The majority of immature Storm Petrels spend two seasons at the colony before breeding for the first time. During the first season on land, the petrels do not alight on the surface, and are therefore much less vulnerable to predation than adults. However, it is likely that they are still less efficient at feeding than adults, and therefore more prone to starvation in periods of food shortage. To some extent these two factors will tend to counteract one another, and it is therefore considered that the overall mortality rate of non-breeders during the year between first return and first occupation of a burrow will be similar to that of adults. The mortality rate of non-breeders during the prospecting period at the start of the second season at the colony is likely to be higher than that of adults, because of the increased risk to predation, but thereafter, it will probably not differ substantially from that of adults.

As yet, it has not been possible to obtain a direct estimate of the mortality of non-breeders over the period of about 21 months between first return and first breeding. However, perhaps as much as half of this mortality will have been included in the estimate of survival from fledging to first recapture, since many of the birds recorded as surviving until first return were not initially retrapped until three or four years of age. For example, 45 per cent of the chicks ringed in 1963 were caught in 1966 or later, and an estimated minimum of 45 per cent of the chicks ringed in 1966 were alive in 1969. Mortality additional to that included in the mortality between fledging and first return will therefore refer to the mortality during a period of between 21 months (for petrels caught immediately on arrival at the colony), and 9 months (for petrels caught for the first time in the late summer of their second year at the colony). It is here considered that this additional mortality will on average be between 12 and 20 per cent. Assuming therefore a survival of 45 - 50 per cent from fledging to first capture back at the colony (see above), and 80 - 88 per cent from first capture to first breeding, it is estimated that the overall survival from fledging until first breeding in the Storm Petrel is approximately 36 - 44 per cent.

(8) An attempted construction of a life table for the Storm Petrel

It has been possible to obtain rough estimates for the annual mortality of adult Storm Petrels, the survival of immatures from fledging to first breeding, and the reproductive output of the population in terms of young fledged per breeding pair. Using these three parameters, a life table has been constructed (table 49). On this analysis, the numbers of young birds entering the population as breeding birds each year is slightly less than the losses due to mortality of adults. In view of the possible sources of error in the calculations, this disagreement must not be taken as evidence that the birds breeding in the study area are unable to maintain their numbers. However, there are reasons for believing that the walls on the top of the island are suboptimal sites for petrels (see General Discussion). A life table for petrels breeding in secure sites low down on the cliffs, where there is little predation and no interference from rabbits, shearwaters, or Puffins, may be quite different.

Table 49. Life table for population of Storm Petrels on Skokholm.

[a] Recruitment rate, and annual mortality of adults

[i]	Chicks reared to fledging per breeding pair*	0.50 ± 0.05
[ii]	Survival from fledging to first breeding	40 ± 4%
[iii]	Annual mortality of adults	10.5 ± 1.5%

[b] Life table

		Number of individuals
a.	Adults of breeding age	200
b.	Chicks fledged	50 ± 5
c.	Birds surviving to age of breeding	20 ± 4
d.	Losses from adult population	21 ± 3

* Davis [1957] found that on average 0.59 young were fledged per breeding pair in three good seasons. During four years of present study [1966-1969], average numbers of young fledged per breeding pair were 0.50, 0.27, 0.49 and 0.46, respectively. Low success in 1967 was thought to be exceptional. All figures are considered too low due to my disturbance, which resulted in a high proportion of newly-formed and inexperienced pairs in samples. It is concluded that in an undisturbed population, the average overall breeding success is in the region of 0.5 young fledged per breeding pair.

Section IV : The Moult of the Storm Petrel

The moult of the Procellariiformes is poorly known, and for few species have the details of its timing and sequence been described. Information pertaining to the moult of H. pelagicus is particularly sparse. Witherby et al. (1940) stated that there is a complete moult from September to May, some birds not completing their moult until June or July, though in others, the moult is just finishing in November. Mayaud (1950) was unable to find any evidence of moult on the breeding grounds, and from his examination of specimens collected on migration or in the winter quarters, concluded that the adults start moulting after breeding, and may finish this as early as November, or not until March or April. Harris (1966) found that body and wing moult had started in some birds on Skokholm during the chick stage in August and September.

In 1966, birds were checked for primary moult only. In 1967 and 1968, the stage of moult of the remiges and rectrices was described in detail, and when time permitted, the presence or absence of moult in the body feathers, wing-coverts, and tail-coverts, was also recorded. In 1969, only the presence or absence of moult in the primaries and secondaries were recorded.

(1) The sequence and timing of the moult

Appendix table 11 shows the occurrence of moult in samples taken throughout the period during which birds are present at the colony. The data for 1967 and 1968 are shown in simplified form in figure 20. With the exception of a few birds completing the moult of their primaries, all birds arriving in April and May possess a complete set of primary, body, and tail feathers. Apart from the white areas on the tail and tail-coverts, the pale underwing-coverts, and the pale tips to the greater wing-coverts, the entire plumage is sooty black. In very fresh plumage, pale fringes are discernible on some of the body feather, particularly those of the under-parts, but these disappear rapidly as a result of abrasion. The pale grey tips to the greater coverts are very pronounced, forming a pale wing-bar which is almost as prominent as that of juveniles at the time of fledging. As the season progresses, the plumage loses its blackness, so that just prior to the onset of moult in July and August, the feathers have faded to various shades of

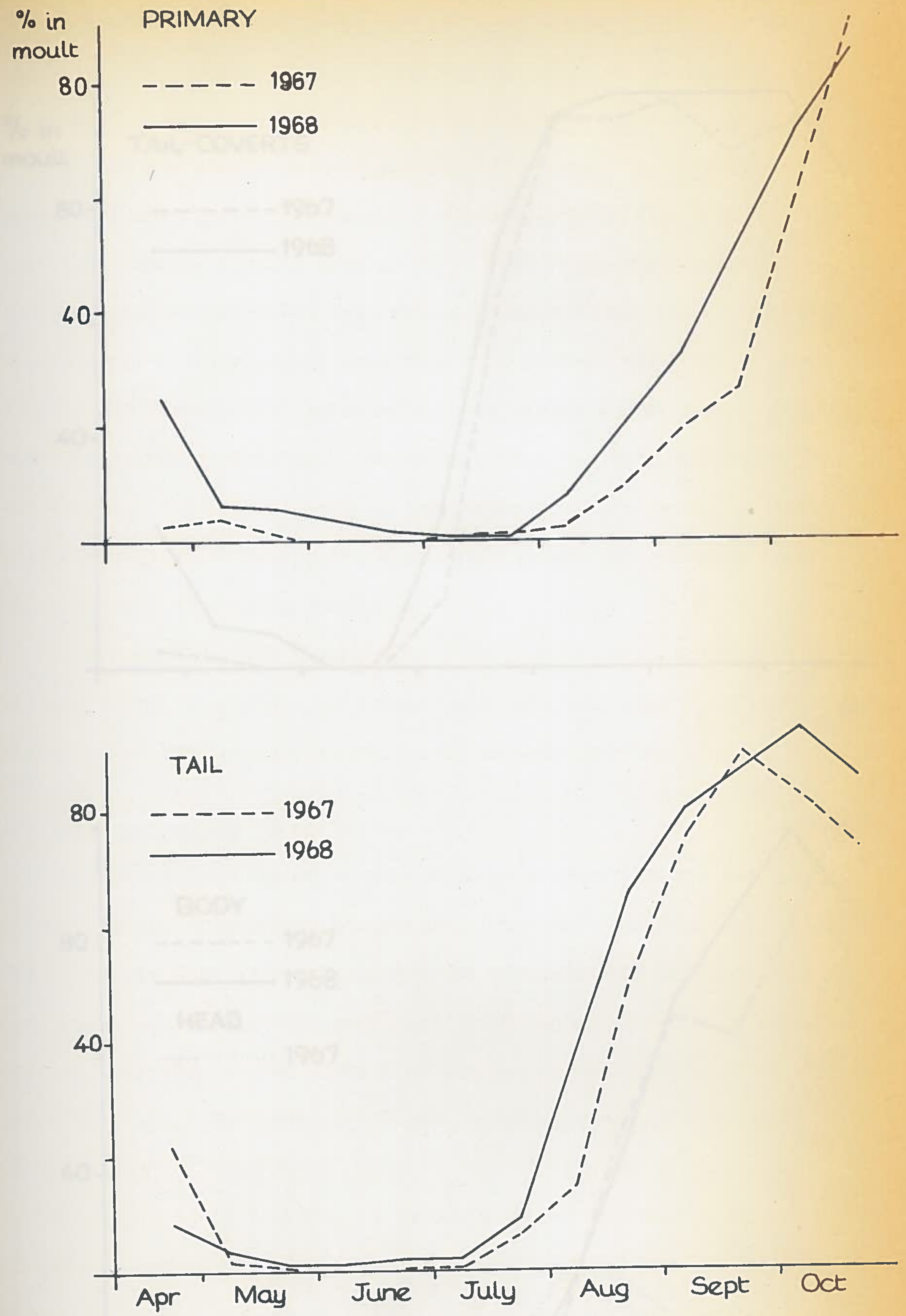


Figure 20. Occurrence of moult in samples of Storm Petrels mist-netted at night: 1967 and 1968.

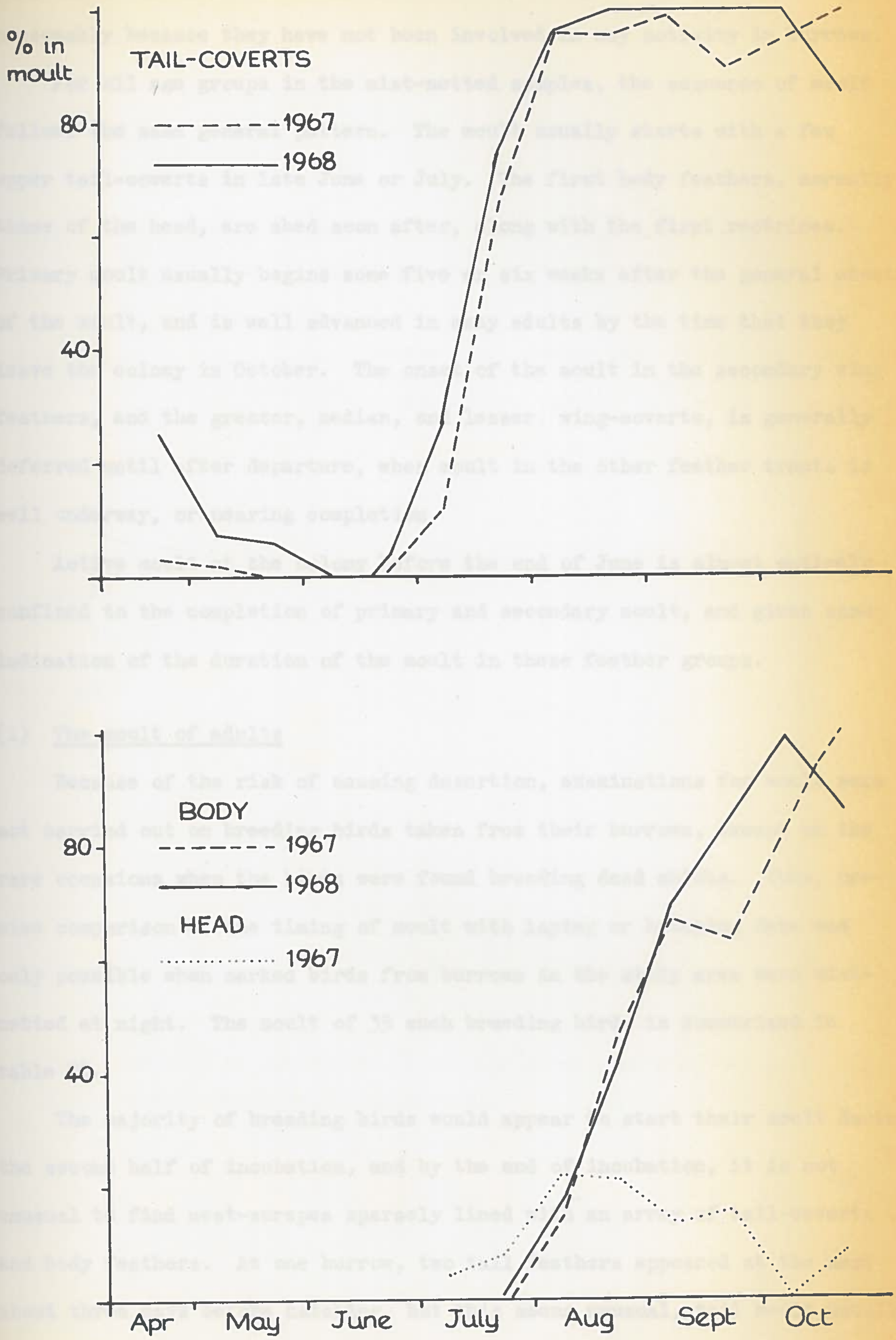


Figure 20 (continued)

brown. In many individuals, at this time, all traces of the pale wing-bar have disappeared. Non-breeders, arriving during July and August, show a slightly lesser degree of wear than breeding birds at the same time of year, presumably because they have not been involved in any activity in burrows.

For all age groups in the mist-netted samples, the sequence of moult follows the same general pattern. The moult usually starts with a few upper tail-coverts in late June or July. The first body feathers, normally those of the head, are shed soon after, along with the first rectrices. Primary moult usually begins some five or six weeks after the general onset of the moult, and is well advanced in many adults by the time that they leave the colony in October. The onset of the moult in the secondary wing feathers, and the greater, median, and lesser wing-coverts, is generally deferred until after departure, when moult in the other feather tracts is well underway, or nearing completion.

Active moult at the colony before the end of June is almost entirely confined to the completion of primary and secondary moult, and gives some indication of the duration of the moult in these feather groups.

(i) The moult of adults

Because of the risk of causing desertion, examinations for moult were not carried out on breeding birds taken from their burrows, except on the rare occasions when the birds were found brooding dead chicks. Thus, precise comparison of the timing of moult with laying or hatching date was only possible when marked birds from burrows in the study area were mist-netted at night. The moult of 39 such breeding birds is summarized in table 50.

The majority of breeding birds would appear to start their moult during the second half of incubation, and by the end of incubation, it is not unusual to find nest-scrapes sparsely lined with an array of tail-coverts and body feathers. At one burrow, two tail feathers appeared at the nest about three days before hatching, but this seems unusual, tail moult usually commencing shortly after hatching. The onset of primary moult is more variable in its timing. One bird, taken off a day-old chick, had already started its primary moult, but primary moult normally starts much later in the nestling period, in a few birds not until the chick is almost due to

Table 50. Occurrence of moult in adult Storm Petrels* in relation to date of laying and date of hatching.

Days after laying	Number of birds examined	Number in primary moult	Number in tail moult	Number in tail-covert moult	Number in body moult
1-10	7	0	0	1	0
11-20	4	0	0	0	0
21-30	4	0	0	3	0
31-hatching	3	0	0	3	1
Days after hatching					
1-10	8	2	2	8	4
11-20	4	0	2	4	3
21-30	2	0	1	2	2
31-40	3	1	3	3	3
41-fledging	3	1	3	3	3

* Birds breeding in burrows in study area which were mist-netted at night during incubation or nestling periods.

fledge.

A more general picture of the moult of breeding birds has been obtained from inspection of mist-netted birds. Table 51 shows the occurrence of moult in birds assumed to be adults, in 1968. By mid-September, over 90 per cent of adults had started to moult their tail and body feathers, and about 30 per cent had begun the moult of their primaries. At the time of peak fledging in early October, 70 per cent of breeding birds were in primary moult.

Since adults leave the colony when their chicks fledge, samples taken after the onset of fledging in late September become biased towards late breeders. Thus eleven birds caught on 21st October 1967, and seven birds caught on 25th October 1968, were undoubtedly all late breeders with chicks nearing the age of fledging. All were in body and tail-covert moult, with the exception of one individual, which had completed the moult of these feathers. Primary moult had started in sixteen (89%) of the birds, tail moult in fourteen (78%), and secondary moult in three (17%). The advanced state of the primary moult, and the onset of secondary moult in some individuals, suggest that the moult of these feather tracts may begin relatively earlier in the breeding cycle in late breeders than in early breeders.

Only five failed breeders have been examined during the short period between loss of egg or chick, and departure from the colony. All were in advanced tail-covert moult and one was in body moult, as typical of successful breeders at the same time of year. One bird, which had lost its egg three days after laying, started its tail moult less than sixteen days after laying, suggesting that some failed breeders, at least, start their moult earlier than adults still engaged in breeding. An earlier moult in failed breeders has been shown to occur amongst the Procellariiformes in *Puffinus lherminieri* (Harris, 1969a), *Fulmarus glacialis* (Wynne-Edwards, 1939; Fisher, 1952), and *Daption capensis* (Beck, 1969).

(ii) The moult of non-breeders

As described in section II, petrels which have spent a non-breeding season in occupation of a burrow leave the colony in July or early August, and hence cannot be examined for moult after this date. Only fourteen known non-breeders from burrows have been examined during July and August.

Table 51. Occurrence of moult in adult Storm Petrels engaged in rearing chicks*, 1968 data only.

Date	Number of birds examined	% in primary moult	% in tail moult	% in tail-covert moult	% in body moult
Aug 1-15	44	0	21	96	21
Aug 16-31	32	2	63	100	66
Sep 1-15	55	29	91	100	93
Sep 16-30	0	-	-	-	-
Oct 1-15	52	71	94	100	98

* Samples taken before 15th September consist of birds which regurgitated large amounts of food during handling. All birds caught after 1st October are assumed to be adults rearing chicks.

Six of these had not yet started moult, seven were moulting their tail-coverts only, and one bird, caught on 17th August, had just commenced its primary moult. Apparently these birds leave the colony as moult commences.

Wandering non-breeders visit the colony from late June or early July until late September. Table 52 summarizes the occurrence of moult in birds identified as wandering non-breeders, in 1968 and 1969. In early July, 52 per cent of these birds had already started the moult of their tail-coverts, and by early August, 45 per cent were in tail moult (c.f. 10 and 21 per cent respectively of breeding adults at this time). The body moult appears to start several weeks later, at about the time when the first primaries are shed, and thus considerably later than that of adults, which follows soon after the onset of tail-covert moult. Only five non-breeders were found moulting their secondaries and wing-coverts; hence this must normally take place at sea, some time after departure from the colony.

Figure 21 shows the frequency of primary moult in samples of breeding birds, and in the whole sample, for the four seasons of the study, and in samples of wandering non-breeders only, in 1968 and 1969. In all years, primary moult commenced two to four weeks earlier in the whole sample than in breeding birds. This was clearly due to non-breeders starting their moult approximately three weeks earlier than breeding birds in 1968 and 1969. During the three years 1967 - 1969, the first non-breeders with primary moult were recorded on 4th August, 1st August, and 22nd July, respectively. In 1966, checking commenced only at the beginning of August; however, from a comparison with 1969, it would appear that active moult first commenced on about 20th July. The earliest dates for the onset of primary moult in breeding birds were: 1966, 23rd August; 1967, 20th August; 1968, 20th August; and 1969, 19th August.

It has been possible to determine the approximate rate of growth of the innermost primaries, and the interval between shedding of these feathers (see page 113). Hence it has been possible to calculate the approximate date of onset of moult for all individuals in any state of moult. Of 565 birds for which the date of onset of primary moult could be calculated, three had started in June (20th, 24th, and 26th), one in the first week of July, four in the second week, and three in the third week. Since no

Table 52. Occurrence of moult in non-breeding Storm Petrels in their first season on land*, 1968 data only.

Date	Number of birds examined	% in primary moult	% in tail moult	% in tail-covert moult	% in body moult
Jul 1-15	42	0	2	52	0
Jul 16-31	29	0	7	69	0
Aug 1-15	242	12	45	96	15
Aug 16-31	146	29	72	100	26
Sep 1-15	64	50	74	98	53

* Identified as non-breeders from condition of brood patch, or lack of site attachment.

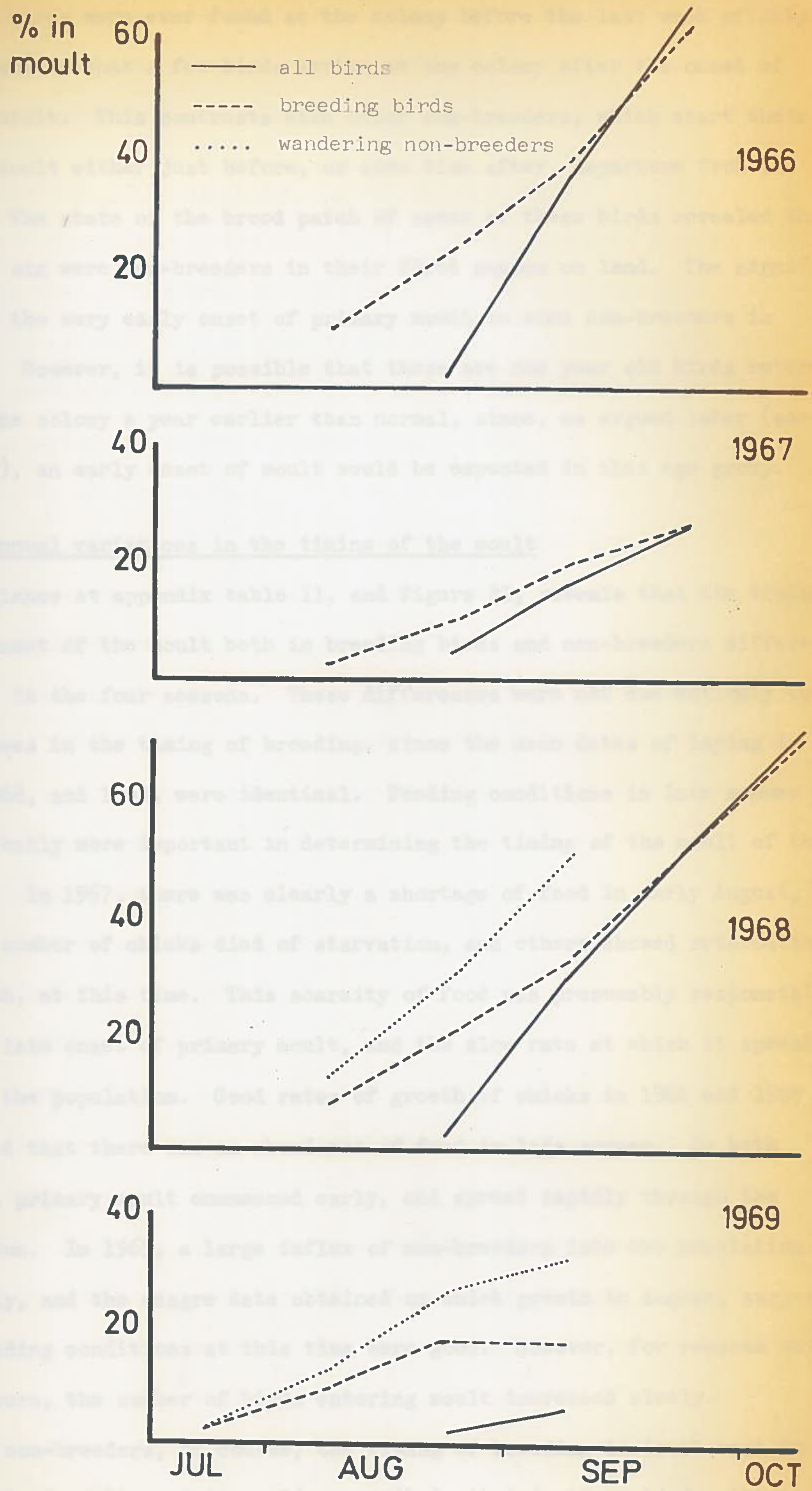


Figure 21. Onset of primary moult in Storm Petrel 1966-1969.

moulting birds were ever found at the colony before the last week of July, it is possible that a few birds arrive at the colony after the onset of primary moult. This contrasts with other non-breeders, which start their primary moult either just before, or some time after, departure from the colony. The state of the brood patch of seven of these birds revealed that at least six were non-breeders in their first season on land. The significance of the very early onset of primary moult in some non-breeders is obscure. However, it is possible that these are one year old birds returning to the colony a year earlier than normal, since, as argued later (see page 131), an early onset of moult would be expected in this age group.

(iii) Annual variations in the timing of the moult

A glance at appendix table 11, and figure 21, reveals that the timing of the onset of the moult both in breeding birds and non-breeders differed somewhat in the four seasons. These differences were not due entirely to differences in the timing of breeding, since the mean dates of laying in 1967, 1968, and 1969, were identical. Feeding conditions in late summer were probably more important in determining the timing of the moult of the remiges. In 1967, there was clearly a shortage of food in early August, since a number of chicks died of starvation, and others showed retardation of growth, at this time. This scarcity of food was presumably responsible for the late onset of primary moult, and the slow rate at which it spread through the population. Good rates of growth of chicks in 1966 and 1968 suggested that there was an abundance of food in late summer. In both seasons, primary moult commenced early, and spread rapidly through the population. In 1969, a large influx of non-breeders into the population in late July, and the meagre data obtained on chick growth in August, suggested that feeding conditions at this time were good. However, for reasons which are obscure, the number of birds entering moult increased slowly.

In non-breeders, of course, the timing of breeding is irrelevant to the onset of moult, and it would seem likely that in these birds, the moult begins as soon as feeding conditions permit. The timing of moult in breeding birds seems to be related both to the timing of breeding, and the feeding conditions. Thus, whereas the onset of the general moult in the tail-coverts and body feathers is relatively fixed to the second half of incubation, and hence related to the timing of breeding, the onset of the moult in the remiges is more variable, and probably determined by the feeding conditions in late summer.

(2) The pattern of moult in the remiges and rectrices

In the Storm Petrel, the moult of the primaries starts several weeks later than that of the body and tail feathers. It has therefore not been possible to use the state of primary moult as an indication of the stage of moult in general; a method first adopted by Miller (1961) and subsequently used by a number of workers. Furthermore, a large part of the moult occurs at sea in the winter quarters. In view of the possibility of different rates of moult during the migration, and in the winter quarters, a simple index of the stage of moult obtained from birds on the breeding grounds would be of little value.

The state of the moult of primary, secondary, and tail feathers was recorded in detail for as many birds as possible. The following scoring system was used for the various stages of growth of individual feathers:

0 old feather

1 feather missing

2 feather protruding in pin

3 feather in the "brush" stage

4 feather $\frac{1}{4}$ to $\frac{1}{2}$ grown

5 feather $\frac{1}{2}$ to $\frac{3}{4}$ grown

6 feather $\frac{3}{4}$ to almost completely grown

7 feather new

With minor exceptions, these stages were found to represent equal time intervals in the growth of a feather. The feathers of the body, tail-coverts, and wing-coverts, were examined for the presence or absence of moulting feathers, no further details being taken. The pattern of moult in these feather tracts is described briefly in Appendix V.

(i) The moult of the primaries

As in all species of Procellariiformes, the Storm Petrel possesses eleven pairs of primaries. These are here numbered from the carpal joint outwards, following Stejneger (1885). The feathers are moulted in descendent sequence, i.e. from the innermost outwards. The eleventh primary, being minute and concealed under the primary coverts, has been ignored in the present study. The onset of primary moult is marked by the dropping of primary one. The first three primaries are shed in rapid succession, in some individuals the third falling before the new first primary has appeared externally. Successive primaries are shed at increasing intervals until at least the fifth. Non-breeders often depart before the onset of the moult, and rarely after the first primary has been completely renewed. Similarly, early breeding birds, leaving the colony in late September, depart either before, or during the early stages of primary moult. Late breeders, still feeding chicks at the end of October, may have completely renewed the first three primaries before departure. The greater part of the moult of the primaries is undertaken at sea during the migration and in the winter quarters, although a few birds may still be completing the growth of the outermost primaries on arrival at the colony in April, May, or June.

In the three seasons 1966 - 1968, 565 birds were examined in detail during the early stages of moult in August, September, and October. At least half of these were non-breeders just starting their moult, and only a small proportion were breeding birds with well grown chicks. Consequently, very few birds were caught in an advanced state of moult. The numbers of birds examined which were renewing one or both of their 4th, 5th, or 6th primaries were 39, 10, and 1, respectively. In the spring of 1967 and 1968, a total of 73 birds were examined before the moult of their outermost two primaries had been completed.

Generally, the left and right wings are moulted symmetrically, except in the early stages, when the primaries are shed in rapid succession, and slight differences between the two wings are frequent. Of 50 birds with four or more feathers involved in the moult, 39 were almost perfectly bilaterally symmetrical. Just before the completion of moult in spring, corresponding feathers rarely differ by even one point on the scoring system.

(a) <u>The rate of feather replacement in the early stages of primary moult</u>

Information on the growth rate of individual feathers is available from 22 birds caught twice during the moult. The data are sufficient for calculation of the growth rates of primaries 1, 2, and 3 only. On average, feather 1 grew so as to gain one point on the scoring system in 5.7 days, and growth was usually completed in 32 to 36 days (extremes of 28 and 41). Feather 2 gained points at a slightly slower rate (mean for one point 6.4 days), complete renewal taking 36 to 42 days. The relative growth of feather 3 was considerably slower (mean for one point 8.6 days), the period for complete renewal being 45 to 55 days. Feathers 2 and 3 are longer than feather 1 by approximately 8 and 16 mm. respectively, so that the growth rates of the feathers, in terms of increase in length per day are similar (ss table 53). The meagre evidence suggests that feather 4 gains points at an even slower rate, taking as long as 55 to 60 days for complete renewal. The growth rate of this feather would then be less than that of the previous feathers. Thus as the moult proceeds, the time taken for complete replacement of individual primaries increases with successive feathers, with the result that the growth rate remains fairly constant for the first three primaries, and perhaps declines for feather 4.

Much of the variation in growth rate between corresponding feathers in different individuals is clearly due to variation in the duration of the missing stage. The shedding of an old feather is generally accepted as being caused by the growth of the new feather in the feather papilla (Jacobs, 1935). The duration of the missing stage is thus dependent on the stage of growth of the new feather at which the old feather is dislodged. Any excessive strain on an old feather at this time might result in premature shedding. For example, a petrel caught on 10th August 1966 with the first primary on the left wing missing was recaptured 37 days later with the new primary still in the pin stage, while another, caught on 11th August 1968, had not started its primary moult, and yet, three days later, had the first primary in pin.

The interval between shedding of successive primaries has been estimated by comparing the relative stages of growth of moulting feathers within individual wings. The full data and calculations of intervals up to the shedding of primary 5 are presented in Appendix VI, and the results are summarized in table 54. As the moult proceeds, the average intervals increase markedly, from about three days between feathers 1 and 2, to about 25 days between feather 4 and 5. Because of the progressive increase in

Table 53. Growth rates of individual primaries in moult of Storm Petrel*.

Primary	Length in mm.	Period for renewal, in days	Rate of growth, in mm./day
1st	42	32-36	1.2-1.3
2nd	50	36-42	1.2-1.4
3rd	58	45-55	1.1-1.3
[4th	65	55-60	1.1-1.2]**

* Growth rates of individual primaries determined from 22 petrels examined twice during renewal of a single feather.

** Estimates very approximate owing to insufficient data.

Table 54. Stage of moult at which primaries 2 to 5 are shed, and intervals between shedding of successive primaries, in primary moult of Storm Petrel.

Primary being shed.	Stage in growth reached by other primaries already in moult: Primary already in moult	Stage in growth reached by other primaries already in moult: Primary score	Days after onset of moult	Days after shedding of previous primary	Average no. of days after shedding of previous primary*
2nd	1st	1	1-6	1-6	2.9
3rd	1st	2-3	7-20	6-17	8.8
	2nd	2-3			
4th	1st	5-6	23-34	9-26	17.8
	2nd	4-5			
	3rd	2-3			
5th	1st	7	47-66	10-40	24.8
	2nd	7			
	3rd	5-6			
	4th	2-4			

* For calculation of mean interval between shedding of successive primaries, see appendix VI.

interval between shedding of successive feathers, as the moult proceeds, the number of feathers actively in moult at any one time decreases from three, or occasionally four, in the early stages, to two feathers by the time that primary 3 has completed its growth.

For a bird such as the Storm Petrel, which is continuously on the wing for the greater part of the year, the ability to fly efficiently throughout the moult is of great importance. A rapid synchronous, or almost synchronous, moult, as may occur in some of the Procellariidae which dive for food (see Meinertzhagen, 1956), would not be possible, hence the extended duration of moult. The shorter inner primaries, by virtue of their size alone, are less important than the outer ones in propulsion and the production of lift in flight. Primaries 1 to 3 are shed in rapid succession, so that all individuals pass through a stage during which there is an effective total lack of these three primaries. By the time that the fourth primary has been shed, the first and second primaries have almost, or entirely, completed their growth, and are able to assist in flight. As the moult proceeds, the number of missing feathers decreases, and, since the outer primaries are longer than the inner ones, the loss in effective wing area remains fairly constant. The reduction in wing area, expressed as square centimetres of primary vane missing, has been calculated for all birds in moult (table 55). There seems to be an upper limit to the loss of wing-area at about 14 sq. cm, which is presumably the most that can be tolerated at a time when petrels are feeding chicks, or starting their autumn migration.

Information on the moult of the Storm Petrel away from the breeding grounds is very scanty. Of the seven British Museum skins collected off the African coast, four were juveniles, and not in moult. The other three were adults moulting their primaries. An undated bird, collected off West Africa, was moulting primaries 3, 4, and 5. This was presumably collected during its southward migration in autumn or early winter. Another undated bird, collected off South Africa, was moulting primaries 7, 8, and 9, while a bird collected off Cape Town on 14th April was moulting primaries 8, 9 and 10 (reductions in wing-area of 14.5, and 13.3 sq. cm. per wing, respectively).

Table 55. Loss of effective wing area during early stages of primary moult of Storm Petrel in sq.cm. of primary vane missing.

Stage in moult	Number of wings checked	Loss of effective wing area in sq.cm. 0.1 -2.0	2.1 -4.0	4.1 -6.0	6.1 -8.0	8.1 -10.0	10.1 -12.0	12.1 -14.0	14.1 -16.0	16.1 -18.0	Mean
Feather 1 in moult	247	0	247	0	0	0	0	0	0	0	3.3
Feather 2 in moult	461	0	1	4	456	0	0	0	0	0	7.1
Feather 3 in moult	178	1	0	9	20	38	110	0	0	0	10.1
Feather 4 in moult	57	0	1	0	9	22	4	13	7	1	10.4
Feather 5 in moult	17	0	0	0	2	3	4	6	1	1	11.2
Feather 6 in moult	1	0	0	0	0	1	0	0	0	0	9.6

(b) The completion of primary moult in spring

The occurrence of primary moult in spring and early summer in 1967 and 1968 is shown in table 56, and the scores of all feathers still in growth, in table 57. In all cases, the moult was very near completion, only the last one or two feathers being affected. Only twelve birds had still to complete the growth of a ninth primary, and in 51 of the 73 birds in moult, primary ten was more than three-quarters grown on both wings. The fact that no birds were caught at an earlier stage of moult, despite the presence of moulting birds in the population as late as July, suggests that return to the colony in spring may be deferred until the moult is almost completed. The slow build-up in numbers of petrels at the colony in the second half of April and early May in 1968, and the relatively high frequency of primary moult as late as mid-June, were no doubt due to the late onset of moult in the poor autumn of 1967, and subsequent late completion.

Only three birds were caught twice during the completion of their primary moult, at intervals of 15, 16, and 24 days, respectively. In each, both tenth primaries increased from 5 to 6 on the scoring system. This represents growth rates of 0.9, 0.8, and 0.6 mm. per day, respectively; which are considerably lower than those of the first four primaries.

Since the majority of birds completing their moult in spring are clearly adults, (one caught as late as 9th June was known to be at least seven years old), one can only conclude that the moult of the primaries takes so long that those birds starting in late October are unable to complete their moult until the following May or June.

(c) The duration of the primary moult

No individual was caught both in early and in late stages of primary moult, and so it was not possible to determine accurately the duration of the primary moult in any individual. However, since probably all breeding birds have started their primary moult by the end of October, and a number of these are still completing their moult in late May, a period of seven months would seem to be required for complete renewal of the primaries. Thus early breeding birds, starting their moult in late August or early September, might be expected to complete their moult in late March or early April, some weeks before returning to the colony.

Table 56. Occurrence of primary moult in Storm Petrel in spring; 1967 and 1968.

Date	1967 Sample	1967 Number in moult	1967 % in moult	1968 Sample	1968 Number in moult	1968 % in moult
Apr 16-30	41	1	2	12	3	25
May 1-15	55	2	4	128	8	6.3
May 16-31	420	3	0.7	564	31	5.5
June 1-15	117	0	0	428	15	3.5
Jun 16-30	295	0	0	244	3	1.2
Jul 1-15	233	1	0.4	540	2	0.4
Jul 16-31	338	2	0.6	263	1	0.4

Table 57. Primary scores in 138 wings* of Storm Petrels with some active moult in spring.

Primary	Score of feather 1	2	3	4	5	6	7
8th	0	0	0	0	0	0	138
9th	0	0	0	0	0	19	119
10th	0	0	2	4	41	91	-

* 73 birds with some active primary moult; in 8 individuals, the moult in one of the wings had been completed, hence only 138 wings with active moult.

It has been shown that both the interval between shedding of successive feathers, and the period required for complete renewal of individual feathers, increase as the moult proceeds, until at least the stage at which feather 5 has just been shed. As a result, there is a progressive decline in the overall rate of progression of the moult. If this decline were to continue, it is clear that the moult could not be completed in seven months. However, it seems reasonable to suppose that the decline in the rate of moult prior to departure from the colony may be an adaptation to meet the requirements of the forthcoming migration, and that subsequent moult in the winter quarters occurs at a greater rate. The two birds collected in the winter quarters off South Africa support this. A further slowing down in the rate of moult might occur in those individuals failing to complete their moult before the migration in spring. This would account for the very slow rate of growth of the tenth primary in birds in moult at the colony in spring. The advantage of a slow rate of moult during migration would be twofold. Firstly, an increase in the interval between shedding of successive feathers would reduce the number of feathers in moult at any one time, and thereby minimize the loss of effective wing-area. Secondly, a decrease in the growth rate of individual feathers would lessen the burden on the energy resources during migration through the relatively poor feeding areas in tropical seas. In the winter quarters, when the petrels can devote the whole of their time to feeding, a greater rate of moult should be possible.

(d) Primary moult in other species of Hydrobatidae

In all species of Procellariiformes for which information is available, the primaries are moulted in descendent sequence from 1st to 11th (summarized in Mayaud, 1931 and 1950; and Stresemann and Stresemann, 1966). However, the timing of the moult in relation to the breeding cycle, migration, and moult in other feather tracts, varies considerably between species (see discussion). Within the Hydrobatidae, information is available for five species excluding H. pelagicus.

Oceanites oceanicus undergoes a complete moult of the primaries at sea in the winter quarters, those birds wintering off the eastern sea-board of North America finishing their moult by about the end of August before the southward migration. No moult of the remiges has been found on the breeding grounds. (Murphy, 1918; Roberts, 1940; Mayaud, 1950; and Beck, in press.)

Oceanodroma castro has a more prolonged moult, commencing in some breeding birds during the late stages of breeding, though never before the chick is well grown. Most of the moult occurs outside the breeding season, however a few birds are still completing their moult on return to the colony, at the start of the next breeding season. (Allan, 1962; Harris, 1969). Harris suggested that in the Galapagos Islands, where breeding at intervals of less than a year would clearly be possible, the great duration of the moult might govern the interval between breeding cycles.

Harris (1969) working on O. tethys in the Galapagos Islands, found that in this species there is a complete moult of the primaries at sea, outside the breeding season. He caught only two individuals in primary moult. These were non-breeders just starting the moult of their primaries at the end of the period of flighting of non-breeders in the hot season. Four birds taken in Galapagos waters in April, May, or June, were just completing primary moult, and were presumably adults returning to the colony prior to breeding.

O. leucorhoa does not appear to start its primary moult whilst on the breeding grounds, but undergoes a complete moult at sea (Huntington, in Palmer, 1962; Mayaud, 1950). Birds driven ashore in Western Europe after severe gales in September or October are commonly in the very early stages of primary moult, indicating that the moult must begin soon after departure from the breeding grounds, and before the southward migration. (Boyd, 1954).

Pelagodroma marina appears to defer its moult until arrival in the winter quarters, the moult then occurring rapidly, so that it is completed before the return to the breeding grounds in the following spring. (Mayaud, 1950; Bourne, in Palmer, 1962).

Thus in all species, except perhaps P. marina, the primary moult commences shortly before, or very soon after, the end of the breeding season, and in two species, individuals occasionally return to the breeding grounds before the moult has been completed. An extended primary moult would be expected in all species of Hydrobatidae, since they feed almost entirely whilst on the wing.

(ii) The moult of the secondaries

Whereas all Procellariiformes have eleven pairs of primaries, the number of secondaries varies greatly. In general, the number of secondaries increases with length of ulna, from eleven pairs in Oceanites spp to 38 - 48 in Diomedia spp (Stresemann and Stresemann, 1966). In the larger species, intraspecific variation is common; in Puffinus puffinus, for example, the number of secondaries varies from 19 to 22 per wing. (Mayaud, 1931). Individual variation amongst the Hydrobatidae has been recorded for Oceanodroma leucorhoa, which may possess 13 or 14 secondaries in each wing (Mayaud, 1950). During the present study, it was discovered that although most Storm Petrels have 13 secondaries, about one per cent have a 14th in one, or more rarely both, wings. As in other species, the inner three pairs of secondaries are commonly referred to as the tertials. As is normal practice, the secondaries are here numbered centripetally, from the carpal joint inwards. Most Storm Petrel replace their secondaries at sea during the winter, but a few birds have been found in the initial or final stages of secondary moult in autumn and spring respectively.

In late June 1967, the presence of two "generations" of secondaries in some wings was recognized; thereafter as many birds as possible were checked for this. Feathers of the most recent generation were sooty-black, and showed little sign of abrasion, while those of the older generation were brown, often with bleached quills, and tatty vanes. The differences between "old" and "new" feathers became more conspicuous as the season progressed. New feathers showed almost no sign of wear even as late as October, whereas the old feathers degenerated rapidly as the barbs and barbules disintegrated. The proportions of birds which had two generations of feathers in at least one wing, in samples taken in 1967, 1968, and 1969, are shown in table 58. Very approximately, about half the petrels had some old secondaries in one or both wings. The number of old feathers in the affected wings are shown in table 59. 95 per cent of the wings examined had less than four old feathers, and in only one wing was there as many as seven unmoulted feathers.

The most likely explanation for the presence of these two generations of feathers in a single wing is that the birds concerned were unable to complete the replacement of their secondaries in the previous winter. Old

Table 58. Proportion of Storm Petrels with interrupted secondary moult in samples taken throughout breeding season: 1967-1969.

Date of sample	1967 Sample size	1967 % with interrupted moult	1968 Sample size	1968 % with interrupted moult	1969 Sample size	1969 % with interrupted moult
Apr 16-30	0	-	12	67	0	-
May 1-15	0	-	128	62	0	-
May 16-31	0	-	562	64	0	-
Jun 1-15	0	-	438	71	0	-
Jun 16-30	0	-	244	72	351	54
Jul 1-15	95	45	540	70	445	52
Jul 16-31	327	46	261	67	514	39
Aug 1-15	102	41	444	55	174	39
Aug 16-31	414	38	255	56	848	41
Sep 1-15	147	54	257	62	743	42
Sep 16-30	19	53	0	-	0	-
Oct 1-15	0	-	52	75	0	-
Oct 16-31	11	64	7	86	0	-
Annual means		43.7		64.9		44.1

Table 59. Number of old secondaries in 3,416 wings of Storm Petrels in which moult of secondaries has been interrupted.

Number of old feathers in wing	Number of wings
1	1597
2	1224
3	422
4	132
5	33
6	7
7	1
more than 7	0

feathers would therefore be at least six months older than any of the new ones, and would attain an age of not less than eighteen months by the end of the breeding season. This would account for the very obvious differences in wear between the old and new feathers, and the rapid degeneration of the old feathers in late summer. The possibility of there being two moults of the secondaries during the winter, the first complete, and the second often incomplete, can be discounted, since the feathers of the first generation would not be more than three months older than those of the second, and would therefore not show such an obvious difference in wear as has been observed.

Rather than continue moulting on the breeding grounds, the majority of petrels which fail to complete the moult before returning to land interrupt it. Any feather already growing is completed, but no further old feathers are shed. The completion of growth of feathers already in moult may occur after the return to land, a number of birds having been caught in spring with one, or occasionally two, feathers in the last stages of growth. Evidence presented below indicates that active moult in autumn commences with the replacement of the old feathers first, after which a new moult cycle is instigated. It was clear, from 525 birds which were checked for secondary moult in two consecutive seasons, that there was no significant tendency for some individuals to complete their moult more frequently than others, and hence, that the completion of secondary moult in one winter in no way affects an individual's chances of completing its secondary moult in the following winter.

As shown previously, although most adult petrels start their primary moult before their chicks have fledged, and rarely after the end of October, a number are unable to complete this moult before returning to the colony in the following spring. The primaries are obviously of supreme importance in flight, and it is probably imperative that the outermost primaries, which are moulted last in the sequence, be replaced each year. Those individuals which failed to complete the moult of the primaries before returning to the colony might therefore be expected to show a higher incidence of interrupted secondary moult, than those which did complete it. Of 62 birds in active moult of the primaries in spring 1968, 56 (90%) had failed to complete the moult of the secondaries. The difference between this figure, and the proportion of breeding birds as a whole which failed to complete secondary moult (66%) is highly significant (χ^2 = 15.9, p = less than 0.001).

Clearly those individuals which have difficulty in completing the moult of the primaries before the beginning of the breeding season are usually unable to complete the moult of their secondaries. Similarly, it might be expected that in seasons following a late primary moult, there would be a higher proportion of birds with interrupted secondary moult than in seasons following an early primary moult. The results of the present study indicate that this is the case. Primary moult started and ended early in the winter of 1966/67, and only 48 per cent of breeding adults had failed to complete the moult of their secondaries before the 1967 breeding season. The following primary moult was late, and in 1968, 66 per cent of breeding adults showed interrupted secondary moult. The primary moult in the winter of 1968/69 was again early, although not as early as in 1966, and as predicted, the proportion of adults with interrupted secondary moult in 1969 (54%) was intermediate between the figures for the two previous years.

(a) <u>The sequence of secondary moult</u>

Although very few birds have been caught in active secondary moult, an examination of the patterns of old and new feathers within individual wings has enabled the sequence of moult to be determined. There was a slight tendency for the left and right wings of birds with interrupted moult of the secondaries to have the same number of old feathers, and similarly for the old feathers to be the same in the two wings. However, marked differences were not uncommon; hence in the following considerations, individual wings have been treated as the units, rather than individual birds. Figure 22 shows the frequency with which each secondary remained unmoulted. It is evident that the secondaries are not moulted in a straightforward ascendent or descendent sequence. (Secondaries 11, 12, and 13, (the tertials) have been ignored, since, as shown below, these are moulted as a group at the onset of secondary moult, and are always completely renewed during each moult cycle.) It has been assumed that old feathers are those which would have been moulted last in the previous cycle, if this had gone to completion. Hence, wings with only one old feather should reveal which feather is

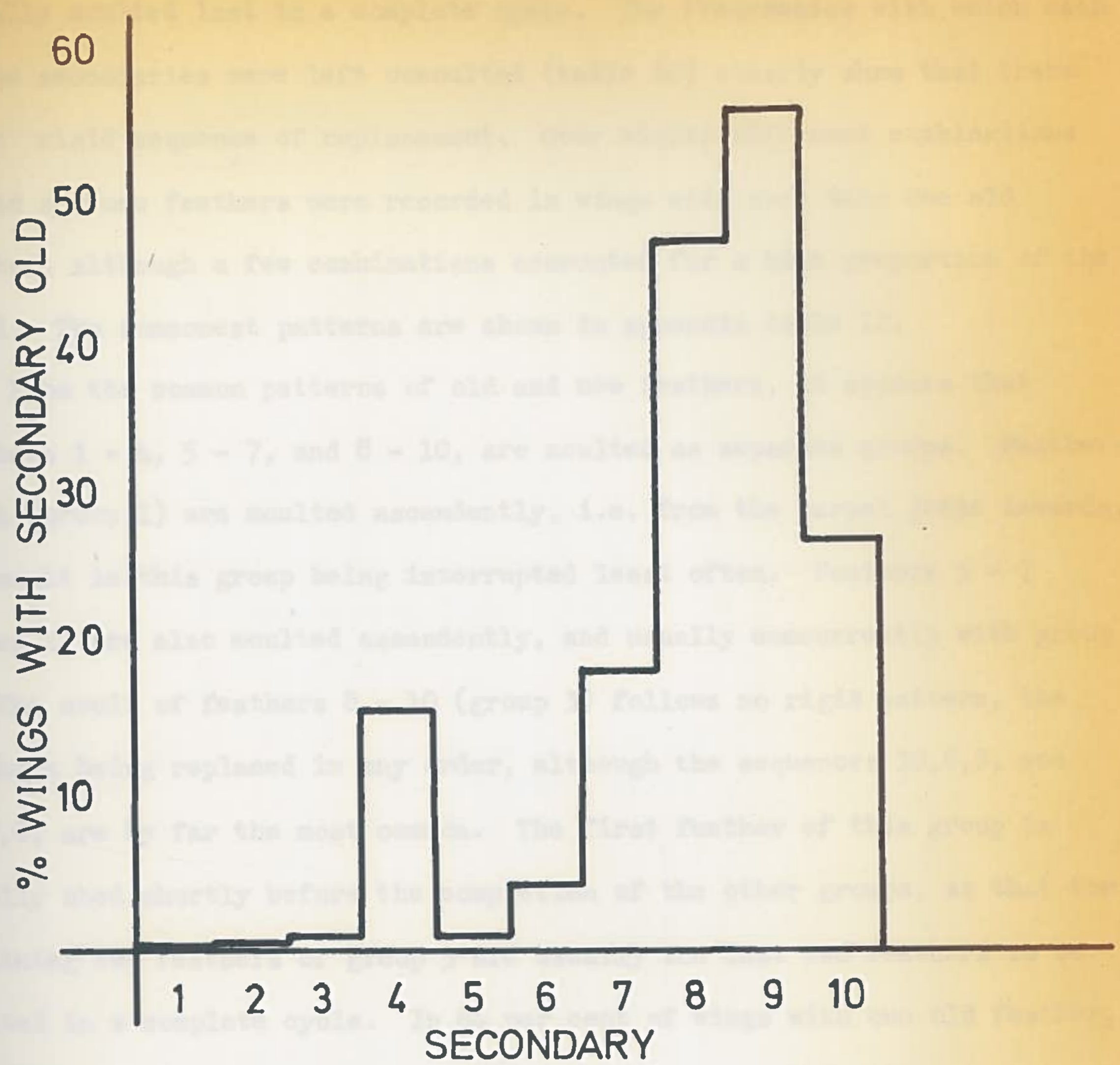


Figure 22. Frequency with which each secondary remained unmoulted in 449 wings of Storm Petrel in interrupted secondary moult.

Note: These frequencies are the average frequencies for the two seasons 1967 and 1968. There were slight differences between the seasons, particularly in the frequencies with which feathers 8 and 10 were old. Clearly, the frequency with which each feather occurs old in the population, following an incomplete moult, will be affected by the completeness of the previous moult. If all birds completed this first moult, interrupted moult in the following year would result in only the last feathers in the basic sequence being left unmoulted (c.f. situation in wandering non-breeders, page 123), whereas, if most birds failed to complete the first moult, interrupted moult in the following year would result in a relatively high frequency of old feathers other than those normally moulted last.

normally moulted last in a complete cycle. The frequencies with which each of the secondaries were left unmoulted (table 60) clearly show that there is no rigid sequence of replacement. Over eighty different combinations of old and new feathers were recorded in wings with more than one old feather, although a few combinations accounted for a high proportion of the total. The commonest patterns are shown in appendix table 12.

From the common patterns of old and new feathers, it appears that feathers 1 - 4, 5 - 7, and 8 - 10, are moulted as separate groups. Feathers 1 - 4 (group 1) are moulted ascendently, i.e. from the carpal joint inwards, the moult in this group being interrupted least often. Feathers 5 - 7 (group 2) are also moulted ascendently, and usually concurrently with group 1. The moult of feathers 8 - 10 (group 3) follows no rigid pattern, the feathers being replaced in any order, although the sequences 10,8,9, and 10,9,8, are by far the most common. The first feather of this group is usually shed shortly before the completion of the other groups, so that the remaining two feathers of group 3 are usually the last two feathers to be moulted in a complete cycle. In 84 per cent of wings with one old feather, and 67 per cent of wings with two old feathers, the old feathers were in group 3.

The patterns of old and new feathers which do not at first appear consistent with the suggestion that groups 1 and 2 are moulted in rigid ascendent sequence are explicable if it is assumed that a new moult cycle always commences with the replacement of feathers which were not shed in the previous cycle. For example, if feather 4 is not replaced in one moult, but is replaced first in the following moult, the feathers of group 1 will then be moulted in the sequence 4,1,2,3. Failure to complete this second moult will result in feather 3 remaining unmoulted during the following breeding season. A further incomplete moult will result in feather 2 being the old one for a season. Similarly, feathers 6 and 5 may occur as the only old feathers in group 2 after, respectively, two and three consecutive years of incomplete moult in that group. Similar changes in the sequence of moult must occur in group 3, and obviously more frequently, because of the greater regularity with which this group fails to complete its moult. (This alone cannot explain the apparently random sequence of moult in group 3, as will

Table 60. Old secondaries in 1597 wings of Storm Petrels in which moult of secondaries had been interrupted when only one feather remained unmoulted.

Secondary which was old	Number of wings with feather old	% of total
Feather 1	0	0
Feather 2	0	0
Feather 3	1	0.1
Feather 4	64	4.0
Feather 5	6	0.4
Feather 6	13	0.8
Feather 7	167	10.5
Feather 8	455	28.5
Feather 9	684	42.8
Feather 10	207	13.0

Note: It is assumed that old feathers are those which would have been replaced last if the moult had not been interrupted.

be shown later.) To explain the relative frequencies of the patterns of old and new feathers, it must be assumed that once a complete moult of the secondaries has been achieved, the following moult cycle commences with feathers 1 and 5, and follows the "basic" sequence.

To test this hypothesis, the patterns of old and new feathers in 432 wings which were checked for secondary moult in both 1967 and 1968 have been examined in detail. Of these, 159 had a complete set of new feathers in 1967, and showed interrupted secondary moult in 1968. All adhered to the normal pattern of old and new feathers in groups 1 and 2, but maintained the random pattern of old and new feathers in group 3, indicating that the previous moult had followed the basic sequence, and supporting the conclusion that, following a complete moult, the moult of the secondaries of groups 1 and 2 follows a rigid ascendent sequence. A further 97 wings contained some old feathers in both 1967 and 1968. In no individual wing was the same feather old in both years, supporting the conclusion that following an interrupted moult, the moult commences with the replacement of those feathers which had not been replaced in the previous moult. No bird failed to complete group 1 in both years, but four birds failed to complete group 2. In two of these, feather 7 was old in 1967, and feather 6 in 1968; in one bird, feather 6 was old in 1967, and feathers 5 and 7 in 1968; and in the fourth bird, feathers 5 and 6 were old in 1967, and feather 7 in 1968.

It is therefore concluded that the moult of the secondaries of birds with interrupted moult during the breeding season begins with the feathers of the earlier generation, and then follows the basic sequence. If this moult is complete, the following moult cycle reverts to the basic sequence, the feathers of groups 1 and 2 being replaced in the orders 1 - 4, and 5 - 7 respectively, regardless of the order in which they were replaced in the previous moult.

(b) Secondary moult in non-breeders

Examination of those birds assumed to be wandering non-breeders has shown that, compared with adults, only a small proportion fail to complete the moult of the secondaries prior to returning to the colony (table 61). In all three seasons 1967 - 1969, between 30 and 33 per cent of non-breeders were in interrupted moult, as compared with 48 - 66 per cent of breeding

Table 61. Proportions of adult Storm Petrels, and non-breeders in their first season on land, with interrupted moult of secondaries during breeding season, 1967-1969.

	1967		1968		1969	
	Sample size	% with interrupted secondary moult	Sample size	% with interrupted secondary moult	Sample size	% with interrupted secondary moult
Breeding birds	268	48	1258	66	896	54
Non-breeders	215	30	405	31	578	33

birds. The greater proportion of adults in interrupted moult is presumably related to their need to start migrating north at an earlier date in order to breed, whereas non-breeders, returning to the colony in late June, July, or August, may linger in rich feeding areas in spring and early summer before visiting the colony.

The combinations of old and new feathers in the wings of non-breeders are shown in appendix table 13. Adherence to the basic sequence is much stronger than in old birds. As argued below, it seems reasonable to suppose that young petrels undergo only one moult at sea prior to their first return to the colony at the age of two years. Assuming that in all individuals the first moult of the secondaries follows the basic sequence, any feathers left unmoulted, on the rare occasions when the first moult is incomplete, should correspond to those feathers which are moulted last in the basic sequence. As can be seen in appendix table 13, in only one wing of 204 examined was there any deviation from the basic pattern. In this wing, feather 3 was old, suggesting that the bird had failed to complete the moult of group 1 in two consecutive years. This bird was presumably therefore a non-breeder returning to the colony for the first time at three years of age.

The patterns of old and new feathers in birds ringed as chicks support these conclusions. Interrupted moult was present in nine of the wings of 21 petrels examined when two years old. In all cases, feather 9 was old, in four cases feather 8 was also old, and in one case, feathers 8, 9, and 10, were old. In known three year olds with interrupted moult, there was a greater frequency of old eighth and tenth secondaries, plus several old fourth and seventh secondaries. One bird, with feathers 5, 6, and 7 old in one wing, and feathers 5, and 6 old in the other, had presumably failed to moult feathers 8, 9, and 10, and 7, 8, 9, and 10, in its first moult, and then failed to complete the moult of group 2 in its second moult.

(c) Active moult of the secondaries

(i) The onset of moult in autumn

Only eleven birds have been found in active moult of the secondaries at the colony in autumn. The details of the moult of these eleven birds are shown in appendix table 14. The tertials, which were in moult in nine birds, appear to be dropped in rapid succession, without rigid order, although there was a tendency for feather 11 to be shed first. The other feathers which were in moult were mainly old feathers which had not been replaced in the previous cycle. However, seven birds were moulting their fifth secondaries, suggesting that in the normal cycle the onset of secondary moult is marked by the loss of the first feather in group 2. Nine of the eleven birds had failed to complete the moult of their secondaries in the previous cycle, which strongly suggests that those birds with interrupted moult might start their secondary moult slightly earlier than birds with a complete set of new feathers.

All birds in active secondary moult were also in primary moult, and in only four wings were there less than four primaries new or in growth. The moult of the other feather tracts was similarly well advanced in all birds, and in two individuals, the moult of the body feathers and tail-coverts had been completed.

The five birds caught in active secondary moult in October were undoubtedly breeding birds, as was one caught in moult on 11th September, and retrapped on 4th October. However, the other five birds, caught in secondary moult between 22nd August and 6th September, were clearly non-breeders from the condition of their brood patches. This again suggests that non-breeders commence the moult of their remiges earlier than breeding birds.

(ii) The completion of moult in spring

During April, May, June, and July, 1968 (the only year in which birds were examined for active secondary moult in spring), 247 petrels were found completing active moult of the secondaries. The occurrence of active secondary moult in the population, and the frequency with which each secondary was still in growth, are shown in tables 62 and 63, respectively. The proportion of birds completing active secondary moult remained fairly constant throughout May and June, but then decreased rapidly in July and August. The feathers involved generally corresponded to those feathers which are thought to be replaced last in the normal cycle (c.f. figure 22). However, feather 4 was in active moult much more frequently than might be expected. As mentioned earlier, the feathers of group 1 are least often left unmoulted in birds which show interrupted secondary moult. (Of 6,400

Table 62. Occurrence of active moult in secondaries of Storm Petrels in spring, 1968.

Date	Number of birds checked	Number of birds in moult	% in moult
Apr 16-30	12	7	58
May 1-15	128	18	14
May 16-31	562	87	16
Jun 1-15	438	71	16
Jun 16-30	244	36	15
Jul 1-15	540	21	4
Jul 16-31	261	4	2
Aug 1-15	444	3	1
Aug 16-31	255	0	0

Table 63. Frequency with which each secondary was in active moult in Storm Petrels in spring, 1968.

Secondary	Number of wings with feather in moult	% total
1	0	0
2	3	1
3	27	8
4	207	64
5	2	1
6	4	1
7	5	2
8	12	4
9	50	15
10	39	12
Total	349	

wings examined in 1968, the moult of group 1 was interrupted in 569 (9%), that of group 2 in 821 (13%), and that of group 3 in 2760 (43%)). The fact that active moult in spring is much commoner in group 1 than in the other groups therefore suggests that the completion of moult in group 1 is more important, birds continuing the moult of this group into the early part of the breeding season if necessary. This is presumably because the secondaries of group 1, adjoining the innermost primaries, are the most important in flight.

Normally, not more than one feather was in active moult in any wing; of 326 wings examined, only 19 had two feathers in growth, and only two had three feathers in growth. Furthermore, nearly all feathers in active moult were nearing the completion of their growth. Of 349 growing feathers, 329 (94%) were more than half grown, and only 5 were less than a quarter grown. This, coupled with the fairly constant proportion of birds in active moult throughout May and June, suggests that return to the colony in spring is deferred in late moulting birds until active moult has almost ceased. A similar conclusion was reached with regard to the completion of primary moult, although in that case the moult is never interrupted.

(d) <u>The rate and duration of the secondary moult</u>

The only data available on the growth rate of individual secondaries was obtained from one bird caught twice in active moult in autumn, and 26 birds caught twice in active moult in spring. The autumn bird, examined first on 11th September 1968, and retrapped 23 days later, was actively moulting seven secondaries on the first occasion, and six on the second (see appendix table 14). The five feathers which were in moult on both occasions had on average increased by three points on the scoring system, i.e. had completed half of their growth, in 23 days, suggesting a period of between 40 and 50 days for the complete renewal of a single feather. The birds caught in spring showed a much slower rate of growth of individual feathers. In ten birds, a feather had increased by one point on the scoring system in 12 - 17 days (average 15). However, in five individuals, a feather increased by one point in between 35 and 40 days, and in six birds a feather had not increased in score at all in between 33 and 49 days. Clearly there is great individual variation in the rate of feather growth in spring; in some individuals the rate of growth was equivalent to complete replacement in as little as 90 days, whereas in others growth appeared to have almost ceased.

The growth rates achieved at the breeding colony in spring and autumn might differ appreciably from those achieved in the major period of active moult in the winter quarters. However, the normal growth rates of individual feathers, the interval between shedding of feathers, and the rate of progression of moult cannot be determined until large numbers of petrels have been examined in active moult in the winter quarters. The occurrence of some active moult in autumn, and again in spring, cannot be taken as an indication that the renewal of the secondaries normally occupies most of the period between breeding seasons. In many birds, the renewal of "old" feathers might take place some time before the onset of the basic moult cycle. Alternatively, active moult of the secondaries might occur only sporadically throughout the winter months, perhaps depending on the feeding conditions at the time.

The complex sequence of moult, involving four foci from which moult waves may arise independently, has presumably evolved to enable petrels to moult several secondaries simultaneously, without leaving any large gaps in the secondary series. Seven of the eleven birds in active moult in autumn were moulting three or more secondaries in one wing. This adaptation should greatly reduce the duration of the moult. However, as shown above, approximately half of the population is unable to complete the moult of the secondaries in the six or seven months between breeding seasons, and some individuals are unable to replace more than four or five feathers. It is clear, therefore, that petrels do not continue the moult of their secondaries throughout the winter at a rate comparable to that achieved in autumn. It is possible that rapid moult, involving the replacement of several feathers simultaneously, is restricted to periods when food is abundant, and that during the greater part of the winter and during the northward and southward migrations, the rate of moult is greatly reduced.

(e) The secondary moult of other species of Procellariiformes

Interrupted secondary moult has not hitherto been recorded in the Procellariiformes, with the exception of an isolated individual of

H. pelagicus described by Mayaud (1950). In the majority of species, replacement of the secondaries occurs at sea, outside the breeding season, and in only a few species has the sequence of moult been determined. Mayaud (1950) described the sequence of moult in Oceanodroma leucorhoa and Oceanites oceanicus from museum specimens obtained at sea during the winter. Both species moult their secondaries in a sequence very similar to that of H. pelagicus. The feathers are moulted in four groups, so that several widely separated feathers may be in moult at the same time. Group 4 consists of the three innermost secondaries (the tertials), group 1 consists of the outermost four secondaries, and the other two groups share the remainder. In O. oceanicus, group 2 consists of feathers 5 and 6, and group 3, feathers 7 and 8. In O. leucorhoa, the groups consist of feathers 5 - 7, and 8 - 10, or 5 - 8, and 9 - 11, depending on whether there are 13 or 14 secondaries in the wing. Replacement of all groups occurs during the moult of the primaries. There are minor differences between the species in the relative timing of the moult of the various groups, and in the sequence of moult in group 4. In both species, however, the feathers of group 3 appear always to be moulted in descendent sequence, whereas in H. pelagicus, the moult of this group follows no rigid sequence.

In only one species of storm petrel has active moult of the secondaries been recorded on the breeding grounds. Harris (1969), working on Oceanodroma castro, found a single bird with one secondary in growth (feather 4), and one secondary still old (feather 5). This individual was an adult which had recently arrived on the breeding grounds at the start of the breeding season.

Mayaud (1931 and 1950) has described the sequence of secondary moult in three species of Procellariidae; Puffinus puffinus mauretanicus, P. gravis, and P. griseus. These species moult their secondaries in five groups simultaneously. As in the Hydrobatidae, the outermost group consists of feathers 1 - 4, and the innermost group, the three tertials. Stresemann and Stresemann (1966), summarizing the moult of the Procellariiformes, concluded that this moult regimen, i.e. simultaneous replacement from a focus in feather 1 and several more foci, is typical of the order. As suggested above, the advantages of such a moult regimen are presumably that it facilitates a rapid moult, without leaving any large gaps in the secondary sequence which might seriously reduce aerodynamic efficiency.

(iii) The moult of the tail feathers

All Hydrobatidae have twelve rectrices, though some large Procellariiformes have more (*Fulmarus* 14, *Macronectes* 16) (Stresemann and Stresemann, 1966). The rectrices are here numbered in pairs from the central tail feathers (1) to the outermost (6).

The occurrence of tail moult in the mist-netted samples is summarized in appendix table 11, and figure 20. Tail moult usually commences in late July or August, though exceptionally as early as the last week of June, or as late as early October. In a few breeding birds, all tail moult occurs on the breeding grounds during the breeding season, but in the majority, and in all non-breeders, the tail moult is completed after departure from the colony.

(a) The sequence of tail moult

During 1967 and 1968, 29 birds were found with one or two tail feathers in moult in April, May, or early June. Of the 40 tail feathers in active moult, 32 (80%) were central feathers (pair 1, 60%; pair 2, 20%), and 30 (75%) were at least three-quarters grown. Since the tail is usually moulted centrifugally (see below), the growth of these feathers cannot have been due to birds completing a moult cycles initiated in the previous autumn; rather it seems that a few adults start a new cycle of tail moult prior to their return to the colony, replace one or two feathers and then interrupt the cycle until mid-summer.

In the general moult in late summer, the two sides of the tail are usually moulted symmetrically, or nearly so. The commonest sequences of replacement in the early stages of moult are shown in appendix table 15. The basic pattern is centrifugal moult from the innermost pair outwards, with the exception that the outermost pair is replaced after the second. Thus the commonest sequence of moult is 1,2,6,3,4,5. Other sequences may arise as a result of the replacement of some feathers in spring, or the replacement of the second or third feather before the first. 69 per cent of birds had started their tail moult in autumn with the replacement of the innermost pair. However, of the remaining 31 per cent, only about 7 or 8 per cent moulted the first pair at a later stage, suggesting that about 23 - 24 per cent of the birds renew this pair in spring. Unfortunately, since tail feathers showed little sign of wear even as late as mid-summer, it was impossible to differentiate between feathers which had been renewed in spring, and feathers which had been renewed in the previous autumn. Thus it was not possible to estimate directly the proportion of individuals which start their tail moult prior to returning to the colony. However, since renewal of the first pair comprises about 60 per cent of all spring moult, it would seem that approximately 40 per cent of all petrels renew some tail feathers in advance of the normal cycle. The reason for this is not known.

(b) The rate and duration of tail moult

Information on the growth rate of individual tail feathers is available from 50 birds examined twice while moulting. In individuals which showed moult in one or more of the three innermost pairs, each feather increased by one point on the scoring system every 5 or 6 days, giving a period for complete renewal of 30 to 36 days; this represents a growth rate of approximately 1.7 mm. per day. The meagre data available suggest that the outer three pairs of tail feathers grow at a similar rate; this is in contrast to the situation in the primaries, where the outer feathers grow more slowly than the inner ones.

The interval between shedding of successive feathers is very variable. Feathers may be shed almost simultaneously, or only after the growth of the previous feather has been completed. On average, however, feathers 1 to 5 are shed at intervals of between 20 and 30 days, feather 6 being replaced at the same time as feather 2 or feather 3. Thus the number of feathers simultaneously in growth within one side of a tail is usually one or two, and rarely three. The duration of the complete moult cycle, calculated from growth rates of individual feathers and the intervals between shedding of successive feathers, is about four months. Birds starting their moult in mid-July should therefore complete it in mid November, after departure from the colony. Hence, those few breeding adults which had completed tail moult by early October, only three months after the first appearance of moulting birds in the samples, are likely to have been birds which moulted part of the tail in spring.

(c) The tail moult of other species of Procellariiformes

The replacement of tail feathers in other species of Procellariiformes is very poorly known. According to Murphy (1918) and Roberts (1940), the replacement of the tail feathers in Oceanites oceanicus generally occurs from the central pair outwards, though Mayaud (1950) thought that there was no regular sequence in this species. All three authors agree that the tail moult commences some time after the onset of primary moult during the southern winter, and is completed before the return to the colony in spring. The sequence of tail moult in Oceanodroma leucorhoa has not been described, although in this species, as in H. pelagicus, the moult commences some time before the onset of primary moult, and before the departure from the colony in autumn (Mayaud, 1950). Both Allan (1962) and Harris (1969), working on O. castro, found tail moult sporadically throughout the breeding season, but could discern no orderly pattern in the replacement of the feathers. In those few species of Procellariidae examined by Mayaud (1931 and 1950), no precise sequence of tail moult was recognizable, and asymmetry within the tail was frequent.

(3) The moult of juveniles

Young Storm Petrels, fledging in late September or October, do so with a completely new set of feathers, at a time when all other age classes which have visited the colony are in heavy moult. Very few young petrels return to the colony until they are two years old. By this time, their moult cycle is similar to that of adults, except that it commences about a month earlier. The condition of their plumage in July and August is similar to that of older birds, suggesting that they have already moulted, the moult starting approximately 12 months previously, i.e. about ten months after fledging. Evidence from a small number of museum skins of H. pelagicus and Oceanodroma leucorhoa (Mayaud, 1950), and of Oceanites oceanicus (Murphy, 1918) suggests that none of these species moults soon after fledging. Mayaud described a series of juveniles of O. leucorhoa, collected between 15th September and 5th December, amongst which he found some birds in fresh plumage, obviously birds of the year, and others in very worn plumage, just starting the moult of their primaries, which he suggested were one year old birds starting their first moult.

In the weeks after fledging, a young petrel has not only to learn to fend for itself, but also to undertake a long migration. Since the plumage is already new, there would seem no point in a juvenile increasing its energy requirements still further at this critical time, as well as reducing its flying efficiency, by moulting in its first autumn. It is concluded, therefore, that juvenile Storm Petrels undergo their first moult when slightly less than a year old.

A very small number of individuals caught in August were moulting far more primaries than the majority of non-breeders (page 109). These birds might be exceptional non-breeders returning to the colony in their first year of life, since early primary moult is to be expected in one year old birds for the following reason. All the primaries of a nestling reach their full length simultaneously, but during moult, the innermost primary is replaced some six months before the outermost. Unless the important outer primaries are to remain unmoulted for eighteen months, the innermost primaries must be shed before they are one year old. The innermost primaries of older birds, immediately prior to moult (i.e. when almost twelve months old), show pronounced wear, and hence it seems likely that the outermost primaries of juveniles would be very worn at an age of eighteen months. However, if juveniles started their first moult in June or early July, the outermost primaries would be replaced when not more than fifteen months old. The second moult, commencing at the end of July or in August, would replace the primaries after fourteen months. A third cycle, this time of thirteen months, would then bring the moult into phase with that of adults. A similar moult regimen might be expected to occur in the other feather tracts, so that the synchronously produced feathers of the fledgling might be replaced in a series of sequential moults without any of the feathers being retained for much more than a year. The early onset of moult, essential for this regimen, might at least be partially responsible for the failure of virtually all the one year old birds to return to the colony.

(4) <u>Discussion</u>

The timing of the moult in relation to breeding and migration has been described for about twenty species of Procellariiformes. Marshall and Serventy (1956a) were the first to point out that many of the Procellariiformes could be divided into two groups with regard to the timing of the moult. In some long-distance, transequatorial migrants, the moult of the remiges and rectrices, and often also the body feathers, is deferred until after migration. These species have a second summer in rich feeding areas, and are able to moult the wings and tail rapidly during their stay in the winter quarters. In species which do not undertake a long migration after breeding, but merely disperse in the adjoining seas, the moult commences during the late stages of the breeding cycle, or immediately afterwards. In all species studied, failed breeders and non-breeders start their moult earlier than successful breeders.

Those species which do not undertake a lengthy migration can be subdivided into those which breed in highly seasonal environments at high latitudes, and those which breed in relatively seasonless tropical and subtropical seas. The former usually have highly sychronized breeding seasons, and start their moult during the incubation or nestling periods, completing it by autumn. Hence, the high energy demands of both breeding and moult are fitted into the short summer period when food supplies are most abundant (Beck, 1969, and in prep.). The latter usually start their moult at the end of the breeding cycle, and complete it shortly before the onset of the next breeding season. Harris (1969b), working on the Procellariiformes breeding in the Galapagos Islands, showed that the moult of Puffinus lherminieri, Oceanodroma castro, and O. tethys, occupied almost the entire period between breeding cycles. Schreiber and Ashmole (1970) found a similar situation in Pterodroma alba and Puffinus nativitatis on Christmas Island (Pacific Ocean). In P. alba, as in P. lherminieri and O. castro, some adults start their primary moult whilst feeding chicks. Harris suggested that in P. lherminieri, and possibly also in O. castro, the duration of the moult determined the interval between breeding cycles. The three common regimes of moult and migration are summarized in table 64.

H. pelagicus does not readily fit into any of these categories. The Storm Petrel breeds late in a highly seasonal environment in north temperate regions, and migrates to tropical and south temperate seas. However, the

Table 64. Regimes of breeding, migration and moult in Procellariformes.

	BREEDING GROUNDS	MIGRATION	MOULT	SPECIES	REFERENCE
1	Temperate and high latitudes	Trans-equatorial	Moult of remiges and retrices, and often also body, deferred until arrival in winter quarters	Puffinus gravis Puffinus griseus Puffinus tenuirostris Puffinus p. puffinus Oceanites oceanicus Pelagodroma marina	Mayaud,1950; Meinertzhagen,1956 Mayaud,1950 Marshall & Serventy,1956 & 1956a Harris, 1966 Roberts,1940; Mayaud,1950; Beck (in press) Browne in Palmer,1962; Mayaud, 1950
2	Temperate and high latitudes	Dispersal in adjoining seas	Moult starts on the breeding grounds, and is usually completed in autumn	Fulmarus glacialis Thalassoica antarctica Daption capensis Puffinus p. mauretanicus Pterodroma lessoni Pagodroma nivea	Wynne-Edwards,1939; Fisher,1952 Biermann & Voous,1950 Biermann & Voous,1950; Beck,1969 Mayaud,1931. Warham,1967 Brown,1966; Beck,1969
3	Tropical	Dispersal in adjoining seas	Moult occupies the whole period between breeding cycles	Puffinus nativitatis Puffinus lherminieri Pterodroma alba Oceanodroma castro Oceanodroma tethys	Schreiber & Ashmole,1970 Harris,1969a Schreiber & Ashmole,1970 Allan,1962; Harris,1969 Harris,1969
Hydrobates pelagicus	Temperate	Trans-equatorial	Moult starts on breeding grounds and occupies whole of period between breeding cycles		

moult may begin during incubation, and by the end of the breeding season, most adults have almost completed the moult of the body feathers, tail-coverts, and tail, and replaced the inner two or three primaries. However, the moult of the remiges proceeds at a very slow rate, and is often not completed by the beginning of the next breeding season.

The long duration of the moult, and the frequency with which this is not completed, suggest that during the winter months, Storm Petrels have difficulty in obtaining sufficient food. Although the wintering grounds of the Storm Petrel are poorly known (see page l), it is clear that the petrels winter in warmer seas than most long-distance migrants. There is abundant evidence which suggests that warm seas have poorer and less predictable supplies of plankton than cold seas.

It is concluded that the Storm Petrel finds such an abundance of food in late summer that it is able to undergo heavy moult, and to breed, at the same time, whereas at all other times of the year, food is too scarce for heavy moult to be possible. Poor feeding conditions in the winter quarters are presumably responsible for the failure of up to two-thirds of the adult population to complete the moult of the secondaries before the following breeding season. Flexibility in the rate of moult of the remiges enables the birds to adjust their rate of moult to the changing conditions of food availability during the period between breeding seasons.

General Discussion

The factors relating to the onset and termination of breeding in those species of bird with an annual cycle have been discussed by Lack (1954 and 1968), and Perrins (1970). Lack argued that each species has presumably evolved the timing of its breeding so that it raises most offspring, and concluded that where only one brood is possible in the year, as in the Procellariiformes, laying will be timed so that the young are in the nest in the most favourable period for feeding them. However, Lack added that in a number of species this required modification. Perrins considered that an important factor in determining the timing of breeding in many species may be the availability of food for the female just before laying, particularly, perhaps, in species which lay large eggs or large clutches. A shortage of food at this time may prevent the females from forming eggs, and thus laying at the time which would result in the young being in the nest at the most favourable time for feeding them. In particular, Perrins thought that this was the case in the Manx Shearwater Puffinus puffinus, and perhaps several other species of Procellariiformes.

In species breeding at high latitudes, climatic factors may be very important in restricting the period when breeding is possible. In some species, breeding must begin as soon as the breeding grounds become snow-free, in order that the chicks might fledge before the end of the short summer. Roberts (1940) considered that the ratio of snowfall to ablation may be a critical factor in limiting the breeding distribution of Oceanites oceanicus in Antarctica. In tropical seas, the situation is entirely different. In general, tropical seas are much poorer in plankton than cold seas, and in some regions there are no marked seasonal fluctuations in the abundance of the food supply; rather, the food supplies may be erratic and unpredictable. Breeding may be possible at all times of the year, and may therefore occur on a non-annual cycle, the interval between breeding seasons being determined by the length of time required to raise young to independence and to perform a complete moult. (Ashmole, 1963a; Harris, 1969a and b; Schreiber and Ashmole, 1970). Schreiber and Ashmole (1970), discussing the breeding seasons of sea-birds on Christmas Island (Pacific Ocean), considered that species with a more or less rigidly defined annual cycle were responding to slight seasonal changes in the availability of food, whereas others, with cycles of less than twelve months, were responding directly to irregular fluctuations in the food supply. These authors also suggested that social interaction and the effects of predation may be important in bringing about synchronous breeding in some species.

A consideration of various aspects of the breeding biology of the Storm Petrel suggest however, that, for this species, Lack's original explanation requires little modification. The breeding season is very protracted on Skokholm where eggs have been laid between 28th May and 20th August. This fact alone would suggest that birds are not breeding as early as possible, since it is difficult to believe that some females would still have found insufficient food to produce an egg at a time when others are already feeding small chicks. Furthermore, work on Skokholm has not revealed any marked differences in breeding success between early and late breeding Storm Petrels, or any deterioration in the feeding conditions until at least the end of October, almost a month after the date of peak fledging. This suggests that there is no particular advantage to be gained by breeding early, and indeed that breeding might be possible on Skokholm even later than is the case, at least with regard to the availability of food.

It is suggested therefore, that the ultimate factor determining the timing of the breeding season of the Storm Petrel on Skokholm is the availability of food for the young, breeding being timed so that the young are in the nest at the time when food is most abundant. Clearly, the food in the seas around Skokholm is sufficiently constant from late July to the end of October to enable parents to raise chicks at any time during this period, with equal success. Probably, however, late breeding is disadvantageous in that it overlaps with the moult to too great an extent. Most breeding birds start to moult their body feathers during the second half of incubation, their tail feathers shortly after the egg has hatched, and their primaries late in the nestling period. However, in late breeders, the moult of the remiges commences at an earlier stage in the breeding cycle, suggesting that it is advantageous to start the moult of the wing feathers as early as possible, and therefore take advantage of the abundance of food in late summer. Too early breeding, however, although allowing more time for the moult at the end of the breeding season, may be disadvantageous in that the chicks hatch before the food supply has become sufficiently abundant and reliable.

Information on the timing of breeding at other colonies of Storm Petrels is very imprecise. However, it is clear that the laying season commences progressively later with increasing latitude, from about the third week of May, in the Western Mediterranean (40 deg. N), to late July, in the Westmann Islands, Iceland (63.5 deg. N) (table 65). The late date of breeding at the northern colonies, with chicks in the nest in September, October, and November, supports the conclusion that the feeding conditions and weather conditions in the North Atlantic do not deteriorate, as far as Storm Petrels are concerned, until long after most chicks from the Skokholm colony have fledged. Although the late breeding of the northern populations may be related in part to the late flush of plankton, another important factor is probably the greater risk from predation during the light nights in mid-summer. It will presumably be advantageous to time the breeding season so that the period when frequent visits to the burrow are most essential, viz. the first two or three weeks after hatching, falls after the period of nights when there is no true darkness. This possible role of night-length in determining the timing of breeding has been suggested by Williamson (1948), and Andrew and Sandeman (1953), who thought that the late breeding of <u>H. pelagicus</u> and <u>Oceanodroma leucorhoa</u> in the Faeroes and Hebrides ensured some protection from predation by gulls and other predators. Myrberget, Johansen and Storjord (1969) also thought that the light nights in mid-summer may be an important factor influencing the timing of breeding of <u>O. leucorhoa</u> and <u>H. pelagicus</u> at the colonies in the Lofoten Isles, Norway (67 deg. N). Limitation by light nights may also offer an explanation for the late onset of breeding at the colony on Skokholm, since pairs which laid in late May would be feeding chicks at the end of June and in early July, when night-length is shortest, and, as shown in section III, predation is highest.

The nature of the proximate factor, or factors, which determine the onset of breeding in the Storm Petrel is not known. Annual variation in the mean date of laying (extremes in the seven years for which data are

Table 65

Main laying period of Storm Petrel at colonies from Mediterranean to Iceland.

Colony	Latitude	Period when most eggs laid	Source
Western Mediterranean	40	4th week of May, first two weeks of June	Géroudet, 1965
Channel Islands	49.5	End of May and June	Smith, 1879
Scilly Isles	50	Middle of June	Joy, 1912; Robinson, 1920
Skokholm	52	Last two weeks of June, first week of July	
Roanninish, N.W. Ireland	55	Last week of June, first two weeks of July	Wilson, 1959
Hebrides	58	First three weeks of July	Gordon, 1920 & 1921; Gordon, 1931 & 1939
Orkneys	59	3rd and 4th weeks of July	Robinson, 1920
Faeroes	62	Late July and early August	Williamson, 1948
Westmann Islands, Iceland	63.5	Late July and August	Sutton, 1961; M. Green, pers. comm.

available; 18th June and 26th June) suggest that day-length is not the sole factor, although it might play a part. The increase in plankton in early summer may be important, since this would presumably give some indication of the timing of the flush of plankton in late summer. Individual variation in response to whatever proximate factors are involved would explain the tendency for some birds always to breed early in relation to the mean date of laying, and others always to lay late (see page 23).

It has been established for a number of species of birds that females breeding for the first time lay at a later date than older birds (see Perrins, 1970). Such is the case in H. pelagicus (see page 23). Perrins (1966 and 1970) and Lack (1968) have suggested that, in those species in which the onset of breeding is determined by the availability of food for the female just before laying, the late breeding of young females may be due to their finding it harder to obtain enough food to form the egg. However, Coulson (1966) has shown that in Kittiwakes Rissa tridactyla retention of the mate plays a much bigger part than actual age in causing older birds to breed earlier. Experienced birds which have paired with each other for the first time breed later than those of the same age which have mated in previous years, suggesting that a change of mate has a prolonged effect upon the birds' breeding physiology. A similar situation may exist in the Storm Petrel; newly-formed pairs which contain at least one experienced bird either breed later than experienced pairs which have bred together in previous years, or not at all (see page 23). Clearly, late breeding in newly-formed pairs in which both partners have previously bred can hardly be due to the female's inability to obtain sufficient food to form an egg any earlier. If, as Coulson has suggested, the date of laying is influenced by physiological and psychological factors associated with the status of the pair, it seems reasonable to suppose that the pairs containing two birds which have had no previous experience of breeding would breed even later. It is therefore considered that the late breeding of Storm Petrels breeding for the first time is more likely to be due to the birds' lack of experience in pairing, rather than to their inability to obtain sufficient food to produce the egg.

Lack (1966) considered the low reproductive rates of Procellariiformes to be the result of a series of adaptations, evolved through natural selection, enabling these birds to raise as many young as possible as quickly as possible under difficult feeding conditions. Thus, he considered that the clutch of one has been evolved because the parents can normally raise only one chick. The unusually slow rate of growth of the young is thought to be an adaptation to a slow feeding rate by the parents due to the food supplies being irregular, and distant from the colony, and to the need for the young to build up fat reserves to allow for periods of starvation. Lack also considered that the long incubation period has perhaps been evolved because the easiest way to evolve a slow rate of nestling growth may be to retard the whole period of development. It is possible, however, that the long incubation period is advantageous in itself if, as Matthews (1954) suggested, a slow rate of development in the egg is more resistant to chilling than a rapid one. Finally, Lack (1968) argued that in the species with deferred maturity, those individuals which start to breed at the normal age for their species leave, in the end, more offspring than those which start when younger. He supposed that breeding at an earlier age than the normal is unlikely to produce young, and diminishes the birds' own chances of survival; possibly, also, in the years before breeding the individuals perform activities which help them raise young effectively later.

These views are considered here to provide an adequate explanation for the low reproductive rate in H. pelagicus. Several features of the species' breeding biology suggest that a clutch of one is the maximum that the species can raise successfully under normal conditions. It is unlikely that a Storm Petrel would be able to incubate two large eggs successfully. Norman and Gottsch (1969) found that pairs of Puffinus tenuirostris, given a second egg, on average hatched 0.4 eggs per pair, as compared with 0.8 eggs per pair by pairs with only one egg. Presumably, petrels could have evolved a clutch of two small eggs. However, the hatching success of the single large egg of the Storm Petrel is low, and many of the chicks which hatch do so with insufficient food reserves to enable them to survive until the first feed (see page 32). This suggests that the size of the egg is an extremely important factor influencing the immediate post-hatching survival of the chick. Two small eggs, with reduced hatching success and poor survival of the chicks, might therefore result in a lower overall production than a single large egg.

More convincing is the difficulty that many pairs have in rearing even one chick. In the four seasons of the present study, about half of the observed chicks were retarded in some way, especially during the first two weeks after hatching. In the poor breeding season of 1967, about a quarter of the chicks died of starvation, and of the remainder, about two-thirds suffered some retardation of growth. Poorly fed and retarded chicks are unable to accumulate large reserves of food, and therefore succumb rapidly during periods of food shortage. It is clear that a twofold increase in the size of the brood would result in a great increase in the proportion of retarded chicks, and hence a great increase in the mortality of chicks during periods of food shortage. Furthermore, it seems likely that the extra food-gathering required of the parents in raising a second chick might weaken them to such an extent that their chances of survival would be lowered. In a species with a low annual mortality, and hence great expectation of further life, a slight increase in annual mortality may outweigh the advantage of even a relatively large increase in the reproductive rate (see Slobodkin, 1961, page 54). In the Storm Petrel, with a mean expectation of further life of about nine years, an increase of 10 per cent in the annual mortality of adults would offset a twofold increase in clutch-size, even if it is assumed that the breeding success, in terms of young fledged per egg laid, remains the same.

No attempt was made during the present study to raise the brood size artificially by giving parents a second chick. However, at two burrows, one of the parents disappeared during the nestling period. In one instance, the chick died five days later, after two nights without food, but in the other, the chick was fed by the surviving parent on alternate nights for seventeen days. During this period the chick's weight remained between 7.5 gm and 10.0 gm, and all growth ceased. The chick was unable to build up any food reserves, and died when 28 days old. In this case, it seems that one parent had been able to provide just enough food to meet the maintenance requirements of the chick, but not enough for any growth.

"Twinning" experiments have been attempted with several species of Procellariiformes. Rice and Kenyon (1962), Huntington (in Lack, 1966), Harris (1969) and Norman and Gottsch (1969) found that in the four species, Diomedea immutabilis, Oceanodroma leucorhoa, Oceanodroma castro, and Puffinus tenuirostris, respectively, pairs given a second chick shortly after their own chick hatched did not raise more young to fledging than control pairs. On the other hand, Harris, Perrins, and Britton (in prep.) found that in one season at least, pairs of Puffinus puffinus given broods of two raised almost twice as many chicks to fledging as normal pairs, and that the mortality between fledging and the first return to the colony was not significantly higher in "twins" than in control chicks. However, these authors have provided some circumstantial evidence which suggests that females might have difficulty in obtaining sufficient food to produce more than one egg.

The growth rates of chicks of the Storm Petrel and other species have been discussed in an earlier section (page 43). It was shown that the rate of growth of the nestlings is closely tied to the rate of feeding, and hence to the availability of food. A more rapid rate of growth, although perhaps possible during periods of good feeding, would be disadvantageous in that it would not allow chicks to lay down large reserves of food.

Storm Petrels normally breed for the first time when four or five years of age, although a few individuals may breed at three, and a few not until six. The young do not normally return to the colony during their first year of life, although they may return to the seas around the colony. It was suggested (page 131) that a possible reason for the failure to return in the first season was the need to start the moult early (in June or July), so that none of the feathers of the juvenile plumage were retained for much more than twelve months. During the second year of life, petrels normally return to the colony for a short period in late summer without alighting on the surface, or entering burrows. It was suggested (page 67) that during this season, non-breeders gain valuable experience of flighting at the colony, the general topography of the breeding grounds, and the location of the feeding areas, without exposing themselves to the additional risk of predation if they alighted. In the following year, the petrels return to the colony earlier in the season, prospect for a burrow, and if successful, endeavour to obtain a mate. It is probably during this season that petrels are most vulnerable to predation. Clearly, in the absence of breeding responsibilities, the petrels may confine their activity at the colony to periods of dark nights when the risk from predation will be low, and to periods when there is an abundant food source locally.

Non-breeders, in their year of prospecting for burrows, arrive at the colony several weeks after adults; indeed a number of non-breeders are occupying burrows for the first time in July, when most adults are incubating. Lack (1968) has suggested that it might be advantageous for birds prospecting for burrows to return to the colony later than adults, since this prevents young birds from occupying sites from which they will later be ousted by the returning owners. Thus late arrivals may have a better chance of obtaining a burrow than other subadults which returned earlier and risked competing for occupied sites. Similarly, young females prospecting for mates will have a better chance of locating an unmated male if they return after the older females. It was suggested that the few birds breeding for the first time at three years of age were females which had been able to locate an experienced male which had lost its mate of previous years. Males returning late to the colony, and then having to locate a burrow and attract a mate, would perhaps have insufficient time in which to breed in that season.

After a season spent in occupation as a non-breeder, most young petrels return in the following year to the same burrow, with the same mate, and breed. However, the success of breeding in this first year is considerably lower than that of experienced breeders (page 57). The reasons for this are obscure. However, it is likely that birds breeding at an earlier age than normal would be even less successful. This might be especially the case if breeding at an earlier age than normal were achieved by omitting the non-breeding season spent in occupation of a burrow, since there is some evidence which suggests that breeding success may be related to the previous experience of the pair together (see page 58 , and Coulson, 1966).

Clearly, in a long-lived species, the proportionate gain in reproductive output by breeding one year earlier than normal would be small, particularly if the breeding success is lower than at the normal age. A slight increase in mortality as a result of the increased risk from predation, and greater stress imposed on a young bird attempting to breed before it is fully efficient at feeding, could easily offset this gain. It is likely that birds which bred a year earlier than normal would be more successful in the following year than birds of the same age which were breeding for the first time. Richdale (1957) showed that Yellow-eyed Penguins *Megadyptes antipodes* breeding unsuccessfully at two were more successful at three than those breeding for the first time at three. However, even if it is assumed that Storm Petrels which breed at three are as successful as birds breeding for the first time at four, and are subsequently as successful as older birds, if, by breeding at three, they suffered an increase of 5 per cent in the mortality between fledging and the age of four, they would on average leave less offspring than birds which bred for the first time at four.

Wynne-Edwards (1955 and 1962) considered that the clutch-size of one, slow rate of development, and deferred maturity of Procellariiformes have been evolved to reduce the reproductive rate to balance the low annual mortality, and thereby prevent increase in the population to the point at which the food resources become limiting. Similarly, he considered the flightings of petrels at the colony to be a form of epideictic display in which adults and non-breeders could acquire information about the total size of the population, and adjust their reproductive rate accordingly. However, it seems that the reproductive rate of many species of Procellariiformes, including *H. pelagicus*, is the maximum that the species can achieve under present conditions. Furthermore, as argued in section II, several features of the flightings of petrels at the colony suggest that birds would not be able to assess the breeding strength of the colony by such means. This therefore raises the question of what does limit the numbers of Procellariiformes.

Ashmole (1963) considered that since pelagic birds outside the breeding season scatter over immense areas of ocean, it is very unlikely that they could at such times be in direct competition for food. He therefore postulated that the numbers of sea-birds are most likely to be regulated in a density-dependent way by competition for food during the breeding season, when the birds are concentrated together by the need to nest in secure sites.

He argued that breeding colonies deplete the food in the seas around them, so that, as the populations increase and competition becomes more intense, the adults have to fly further out for each meal, and hence fewer adults succeed in raising chicks. Ashmole added however that food is less likely to be important in controlling population size in temperate than in tropical seas, as there is a large flush of marine life in the temperate seas in summer. Furthermore, Lack (1966), following Bailey (1968), pointed out that the areas where food for sea-birds is plentiful are localized at all times of the year, so that for some species, shortage of food might be severe in winter.

Rowan (1965) considered that competition for food during the breeding season was unlikely to limit the population of Puffinus gravis on Nightingale Island (Tristan da Cunha group) because of the great mobility of the adults and the ability of the chicks to survive for long periods without food. She thought that the foraging ranges in the breeding and non-breeding seasons were of about similar size, and concluded that food shortage would have to be extreme and very widespread before competition became more acute in the breeding season than out of it. Furthermore, she found no indication of periodic breeding failures through starvation of chicks, which would be expected if the food supplies were limiting in the breeding season.

Several features of the breeding biology of the Storm Petrel suggest that the numbers of this species are not limited by competition for food in the breeding season. Both adults and non-breeders with burrows are heaviest in May and June, despite making frequent visits to the colony at night, and spending as much as one day in three in the burrow, suggesting that food is not critically short. Furthermore, although many chicks were retarded in all seven seasons for which data are available, actual mortality of chicks from starvation occurred in only one, indicating that food is rarely in such short supply that the reproductive output is affected. More important, however, is the fact that almost the entire moult of the body and tail feathers, and a part of the moult of the remiges, are undertaken during the second half of incubation, and when the chicks are in the nest. This implies that food is much more abundant in late summer than at any other time of the year.

Critical periods for food shortage are much more likely to occur outside the breeding season, and particularly during the migrations through the tropics. On average, about half of the adult population of Storm Petrels are incapable of completing the moult of the remiges in the seven months between breeding seasons, despite having evolved a sequence of replacement in the secondaries which enables several feathers to be moulted simultaneously without serious reduction in aerodynamic efficiency, and having completed much of the moult while breeding. This inability can only be because the birds are having difficulty in obtaining sufficient food to provide the energy for moult. It is difficult to believe that Storm Petrels, foraging widely, and taking only those prey items that are available to them at, or within an inch or two of, the surface, will deplete the total population of their prey to the extent that they will be in direct competition with each other for food, or indeed will have any marked effect on the fluctuations in their food supply. It is possible, however, that petrels may effectively compete for food by influencing each other's chances of surprising prey items near the surface. This would occur if the disturbance caused by a petrel catching a fish results in the other fishes in the area diving, and therefore ceasing to be available to other petrels foraging in the immediate vicinity.

Clearly, intraspecific competition for food outside the breeding season, perhaps operating more through intraspecific interference during feeding than through reduction in the total stock of food, could, in theory, limit the numbers of petrels in a density-dependent manner. The overwinter losses of adult Storm Petrels are so low (not more than 8 per cent (see section III)), that it is difficult to visualise density-dependent mortality operating on these birds. It seems likely, therefore, that if there is any density-dependent mortality due to food shortage, this will affect young birds, which are probably less efficient at feeding than adults, and hence influence the recruitment rate of breeding birds into the population, as has been suggested by Harris (1966) for Puffinus puffinus. However, competition for the available prey could occur only in years when the food is both scarce, and restricted in its distribution, so that petrels have to congregate in large numbers in the areas where it is available. But there are no references in the literature to Storm Petrels congregating in the winter quarters in anything like the densities which must be postulated if competition for food is to occur. It is therefore considered unlikely that, at the present time, the numbers of Storm Petrels are limited in a density-dependent manner by competition for food at any time of the year.

For several species of Procellariiformes, there is clear evidence of intraspecific competition for nest-sites (Rowan, 1952; Warham, 1960; Allan, 1962; Harris, 1969). Rowan (1965) estimated that eggs laid on the surface by Puffinus gravis on Nightingale accounted for about 10 per cent of all eggs laid, and concluded that a large number of birds were being prevented from raising chicks because of the shortage of nest-sites. In Oceanodroma tethys (Harris, 1969) and O. castro (Allan, 1962; Harris, 1969), the low breeding success was due almost entirely to severe intraspecific competition for nest-sites, and Allan thought that many birds were being prevented from breeding because of this. Lack (1966) suggested that competition for nest-sites could not itself regulate the numbers of a species, since it would merely result in a steadily increasing proportion of non-breeders in the population. He argued that this increase would continue until the total community of breeding birds and non-breeders combined reached a density-dependent limit set by some other factor such as food. However, this would be true only if the non-breeders which were unable to occupy burrows were immortal. If the number of nest-sites is limited, the number of breeding pairs, and hence reproductive output of the population, is also limited. Thus the number of non-breeders entering the population each year will be relatively constant. However, as the total number of non-breeders in the population increases, the number dying each year from density-independent causes will also increase. Hence the limit to the population size will eventually be set when the annual mortality of breeding birds and birds unable to occupy burrows is equal to the annual input of young birds into the population.

Competition for nest-sites could therefore limit the numbers of a species without there being any density-dependent mortality at any stage in the life cycle. The absolute size of the population would then be set by the number of available nest-sites, the reproductive output, and the mean density-independent mortality of adults and non-breeders combined. However, in addition, in natural situations competition for nest-sites could affect both the success of breeding and the mortality of non-breeders in a density-dependent manner. As the population increases, competition for nest-sites will become more intense, as more and more birds compete for the same burrows, resulting in a decline in the breeding success of those birds which are able to obtain a burrow (as in O. tethys and O. castro). As breeding success declines, the number of non-breeders entering the population, and hence the total population, will decline, thereby eventually reducing the severity of the competition for nest-sites.

As the number of birds unable to occupy burrows increases, the number which must spend several years prospecting, and the number occupying unsuitable and exposed sites on the edge of the colony, will also increase. It was suggested that non-breeders prospecting for burrows are much more vulnerable to predation than other classes (page 91). Furthermore, it is likely that birds occupying exposed sites would be at a greater risk from predation than those in secure sites. Most of the predation on Storm Petrels on Skokholm occurs along the walls, and on the rocky outcrops on the top of the cliffs, whereas there is very little in the main breeding sites of the petrels in boulder beaches and scree slopes low down on the cliffs. It was suggested (Appendix IX) that the absence of petrels from the top of Skomer Island is due not to the lack of sites, but to the large number of predators present. In two areas on Skokholm, Storm Petrels breed in atypical sites in dense colonies of rabbits and shearwaters. Clearly breeding losses and adult mortality due to interspecific interference would be more severe than in the typical sites, where the petrels do not compete with other species for burrows.

The fact that there may be an unlimited supply of suboptimal sites (i.e. nest-sites in which the reproductive output is insufficient to cover losses due to adult mortality) available to the birds does not invalidate the conclusion that the population is limited by the availability of nest-sites. It is sufficient that the number of optimal sites (i.e. nest-sites in which the reproductive output equals or exceeds the losses due to adult mortality) is limited. The number of birds which may breed in suboptimal sites will be determined by the number of birds which are unable to obtain burrows in the optimal sites. Hence it is not necessary to suppose that the surplus of young birds from the optimal sites is prevented from breeding, but merely that they are forced to breed in suboptimal sites.

This is probably the situation on Skokholm. There was little indication that many birds were being prevented from breeding on the top of the island, although it is possible that this was the case in the dense colonies low down on the cliffs. Work in the study area suggested that there was no shortage of nest-sites for petrels in the walls, and there were certainly many colonies of shearwaters and rabbits in which few if any petrels were breeding. However, the walls and burrows on the top of the island are clearly suboptimal sites for petrels. The fact that some petrels were breeding in them is therefore taken as indication that there is a shortage of optimal sites.

To test this hypothesis, a model for the limitation of numbers of a petrel population by competition for nest-sites has been constructed. As far as possible, this has been based on estimates of the breeding success and of the annual mortality of the different age classes obtained during the present study. It is assumed that:

(i) there are 4,300 optimal sites always fully occupied, and an unlimited number of suboptimal sites. (On Skokholm about 4,300 pairs breed in secure sites low down on the cliffs.)

(ii) the breeding success at optimal sites is 0.5 young fledged per pair, and at suboptimal sites is 0.45 young fledged per pair.

(iii) the survival between fledging and return to the colony as a prospecting non-breeder is the same for chicks raised in both types of site (45%).

(iv) non-breeders from optimal sites suffer a mortality of 12% during their year of prospecting for a burrow, those from suboptimal sites a mortality of 17%.

(v) the annual mortality of breeding birds in optimal sites is 9%, that of breeding birds in suboptimal sites 10%.

(vi) non-breeders which were raised in optimal sites, and which were unable to obtain a burrow in these sites in their first year of prospecting, move to suboptimal sites in the following year, and spend a season prospecting there. All other non-breeders spend only one season prospecting for a burrow before breeding.

The calculations are given in appendix table 16. On this model, the population will stabilize at 6,320 pairs, i.e. when there are 2,020 pairs breeding in suboptimal sites. It should be noted that only 78 birds each year are unable to locate a burrow in their first season of prospecting. (If a few birds are unable to obtain a burrow in a suboptimal site in their first season of prospecting, or if some birds prospecting in optimal sites spend more than one season prospecting there before moving to suboptimal sites, the population will stabilize at a slightly lower level.) It was estimated in Appendix VIII that on Skokholm approximately 1,450 pairs of petrels occupied sites in the walls, in shearwater colonies, or in rocky outcrops on the top of the island. A further 450 pairs were breeding in exposed sites on the top of the cliffs. The close agreement between the observed number of pairs breeding in suboptimal sites (1,900) and the number that would be expected to do so on the above model (2,020) is taken as support for the conclusion that the numbers of Storm Petrels on Skokholm are limited by competition for optimal nest-sites, and the associated effects of this on breeding success and mortality of non-breeders.

In at least two species of Procellariiformes in which there is intense competition for nest sites, there are large areas of apparently suitable, and yet unoccupied, ground close at hand (O. tethys, Harris, 1969; P. gravis, Rowan, 1965). Rowan therefore concluded that in P. gravis, although shortage of nest-sites may limit the size of individual colonies, it could not limit the total population of the species. However, if birds in some areas are being prevented from breeding as a result of competition for nest-sites, the absence of birds from other areas nearby suggests that these latter sites are in some way unsuitable. The tendency amongst colonial sea-birds for young birds to return to their natal colony to breed, and for adults to return to nest-sites which they have occupied in previous years (discussed by Lack, 1966), probably explains why, when competition for burrows becomes intense, birds do not move away immediately to unoccupied areas nearby. It must be assumed that on the whole it is more advantageous for a bird to attempt to occupy a burrow in an already overcrowded colony, even though it may have to spend several years prospecting before finally obtaining one, than to move to a completely "unknown" area elsewhere, where its own chances of survival may be smaller.

It is tentatively suggested that competition for nest-sites may limit the numbers of many species of Procellariiformes, and perhaps also of other species of sea-bird, which nest in holes or crevices on small, inaccessible islands. Lack (1968) has drawn attention to the tendency in some groups of sea-birds for similar species, where they occur together, to nest in different sites. He quoted, as examples, the six species of Alcidae on Bear Island, and the five species of Procellariiformes on Whero Island, New Zealand (Richdale, 1965). Lack argued that such segregation of nest-sites has presumably been evolved through interspecific competition for nest-sites in the past, and must be periodically reinforced by competition at the present day (Principle of competitive exclusion, see Lack, 1954). If interspecific competition for nest-sites occurs, then it follows that intraspecific competition must also occur, and to a more serious degree, since the requirements of conspecifics will be more similar than those of congenerics.

Clearly, in a species which is limited by competition for nest-sites, and in which there is a surplus of mature birds unable to obtain a burrow, even occasional large losses or disasters as a result of density-independent mortality or breeding failure would not appreciably reduce the number of breeding pairs, since any vacated burrow would soon be occupied by mature birds from the non-breeding population. In colonies in which the surplus of mature birds are able to breed in suboptimal sites, any large reduction in the population should become evident first in the number of pairs in the suboptimal sites. Thus, for monitoring trends in the populations of sea-birds which are limited in this way, precise counts of the number of breeding pairs in optimal habitats may be very misleading; ideally, estimates of the non-breeding population, or the number of birds breeding in suboptimal sites around the fringe of the colony are required.

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APPENDICES

Appendix I

Calculation of the true size of the feeds given to chicks

The difference between evening and morning weights of chicks which had been fed is less than the actual weight of the food received by an amount equal to the weight lost in the fourteen hours between weighings. To determine the actual size of feeds, from the overnight increases in weight, it was therefore necessary to take into account the rate of loss of weight between feeds. Davis (1957) undertook a series of weighings at midnight to determine the actual size of the feeds, in an endeavour to establish the relationship between overnight increase in weight and size of feed. He found what he considered to be a fairly constant relationship between feed-size and overnight increase, and calculated the size of feeds for chicks of all ages from this.

The present study has shown that the relationship between actual size of the feed and overnight increase in weight is very complex, and that the calculation of feed-sizes from a single average relationship gives poor results. During the three seasons 1966 - 1968, a total of 40 chicks were weighed twice daily, in the morning and in the evening. For each of these, it was therefore possible to determine the change in weight overnight, and the loss during the following day. The rate at which a chick, which had been fed, lost weight was not related solely to the size of the previous night's feed, but also to the following factors:-

(i) the age of the chick. Up to the age of about thirty days, younger chicks lost weight more slowly than older chicks.

(ii) the weight of the chick, which is in part dependent on the feeding during several previous nights. Chicks which had been fed well for several nights lost weight more rapidly than chicks of the same age which had been poorly fed.

(iii) the stage of development of the chick. Retarded chicks lost weight more slowly than normal chicks of the same age and weight.

Young chicks, after small feeds, or older chicks, after one or more nights without food, may lose as little as 0.5 gm. in weight in ten hours, whereas older chicks, after large feeds, may lose ten times this amount in the same period.

The loss in weight of a chick after a feed follows the usual pattern of a steadily smaller decrease in each succeeding hour; hence the weight lost during the period between evening and morning weighings will also depend on the time at which the feed is given. Feeds may be given at any hour of the night. During early August 1966, 50 chicks were weighed in the evening, at 0200 hrs. BST., and at the usual time in the morning. Ten were not fed at all, 10 received all their food before 0200 hrs and 8 all their food after this time, and the remaining 22 were fed in both periods of the night. As there was no way of determining at what time, or times, the food was given, for the present calculations it has been assumed quite arbitrarily that all feeds were given at 0200 hrs. BST., $7\frac{1}{2}$ hours before the morning weight was taken. Although apparent feed-sizes will be too high for chicks fed after 0200 hrs., and too low for chicks fed before, on average these errors should cancel out.

Inspection of the rate at which chicks which had not been fed lost weight after their previous feed revealed that approximately half as much weight is lost in the first half of the night as in the previous day (i.e between 0930 and 1930 hrs.). The weight lost between acceptance of the food and the morning weighing has been calculated directly for the ten chicks which had received a complete feed by 0200 hrs. The loss in weight between 0200 and 0930 hrs. was approximately the same as that between 0930 and 1930 hours. Hence, the amount of food given on any one night is approximately equal to the overnight increase in weight, plus an amount equal to half the weight lost during the previous day, plus an amount equal to the weight lost during the following day. Feed-sizes have been calculated in this way for all chicks which were weighed twice daily. The average relationship between feed-size and overnight increase, according to age, is shown in figure 23, to afford comparison with the single relationship produced by Davis.

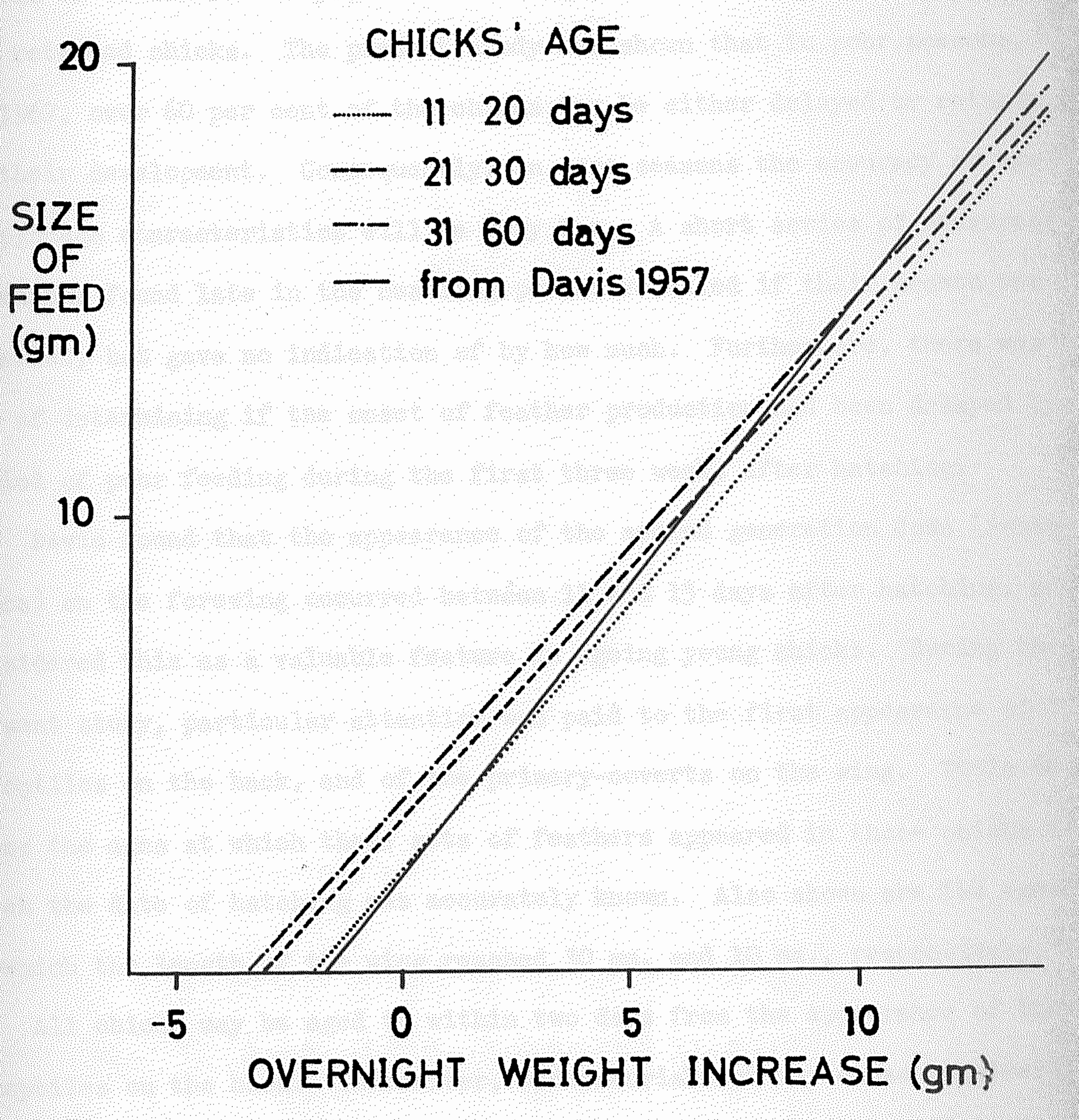


Figure 23. Relationship between actual size of feeds and overnight increase in weight of chicks of Storm Petrel.

Appendix II

The ageing of chicks on the development of the plumage

Davis (1957) described the development of the plumage and soft parts of the Storm Petrel chick in some detail in the hope that it would be practicable to compile a growth chart for ageing chicks. However, the large variation in growth rate enabled him to age only about 80 per cent of the chicks to within five days, the remaining 20 per cent consisting of underfed and retarded chicks. The present study has shown that in poor seasons, such as 1967, over 60 per cent of the chicks may be either delayed or retarded in their development. Consequently, in some seasons the accuracy of ageing on plumage characteristics will be very low. A short series of measurements of chicks found late in the nestling period revealed if their growth was retarded, but gave no indication of by how much. Furthermore, there was no way of determining if the onset of feather production had been delayed by a period of poor feeding during the first three weeks after hatching.

Davis found that the appearance of the second generation down (mesoptiles) on the forewing occurred between 11 and 15 days after hatching, and considered this as a valuable feature in ageing young chicks. During the present study, particular attention was paid to the first appearance of the mesoptiles on the back, and of the primary-coverts on the wing. Table 66 gives the ages at which these sets of feathers appeared in those chicks for which the date of hatching was accurately known. Also shown are the ages at which the length of the wing reached 30 mm. and 10 mm., respectively.

All chicks may be aged to within two days from the appearance of the mesoptiles on the back. Thereafter, undernourishment may cause considerable retardation of growth, so that only a proportion of the chicks may be aged with reasonable accuracy. 80 per cent of the chicks could be aged to within plus or minus three days from the appearance of the primary-coverts in pin, to within plus or minus four days from attainment of a wing-length of 30 mm., and to within plus or minus five days from attainment of a wing-length of 100 mm. However, the total spread in ages at these stages in development were 13, 14, and 29 days, respectively. As described by Davis, the loss of down prior to fledging is very variable, and therefore of little use in determining either the age of the chicks, or the proximity of fledging.

Table 66

Age of chicks of Storm Petrel at which (a) mesoptiles appear on back, (b) primary coverts appear in pin, (c) wing-length attains 30mm., (d) wing-length attains 100mm.

a/ Age at which mesoptiles appear on back.

	Age in days							
	6	7	8	9	10	11	12	Total
Number of chicks	0	1	8	19	8	4	0	40

b/ Age at which primary coverts appear in pin.

	Age in days														
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Total
Number of chicks	2	4	3	11	4	7	6	2	0	1	0	2	3	0	45

c/ Age at which wing-length attains 30mm.

	Age in days														
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	Total
Number of chicks	2	0	6	9	7	6	4	4	1	2	1	1	3	1	47

d/ Age at which wing-length attains 100mm.

	Age in days															
	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65...
Number of chicks	1	0	4	1	8	2	6	3	3	6	1	3	2	1	0	1

	...66	67	68	69	70	71	72	73	74	75	76	77	78	Total
Number of chicks	0	0	2	1	1	0	0	0	0	0	0	0	1	47

Some chicks have lost almost all their down by the 55th day, a week or more before fledging, whereas others may retain large areas of down on the underparts until after departure from the colony.

Appendix III

The proportion of wandering non-breeders in the mist-netted samples of Storm Petrels

In their first season at the colony, young Storm Petrels make irregular nocturnal visits to the colony in late summer, but do not enter burrows. Several criteria have been found for distinguishing these so-called wandering non-breeders from older birds. It was shown in section II that the non-breeders differ from older birds in showing no special attachment to any particular part of the island, having a somewhat different brood patch cycle, and being on average lighter in weight, and shorter in the wing. Two of these criteria, viz. the difference in the brood patch cycles and the difference in weights, have been used to estimate the numbers, and hence proportions, of non-breeders in the mist-netted samples.

From mid July until mid September, about 70 per cent of wandering non-breeders are identifiable on the condition of their brood patch (see page 79). The remainder, passing through a completely bare stage in the brood patch cycle, are indistinguishable from older birds. By making an allowance for these non-breeders with bare brood patches, the total numbers, and hence proportions, of non-breeders in the samples can be calculated. The results are shown in table 67a.

Throughout their stay at the colony, wandering non-breeders are, on average, 1.5 - 2.5 grams lighter than breeding birds and non-breeders which have occupied a burrow (see page 85). Thus, the mean weight of a sample of birds containing some light-weight wandering non-breeders will be less than that of a sample of older birds by an amount which is directly proportional to the number of wandering non-breeders in the sample. To arrive at an estimate for the mean weight of all birds with burrows, it has been necessary to determine the ratio of prospecting non-breeders to breeding birds in the population. In section II, it was shown that about 30 per cent of birds found in burrows were non-breeders. However, this figure was thought to be too high for a variety of reasons. On the other hand, from a consideration of the annual mortality rate of adults and the recruitment rate necessary to maintain a stable population, it was concluded that the number of non-breeders in occupation of a burrow prior to breeding for the

Table 67

Proportion of wandering non-breeders in mist-netted samples of Storm Petrels on Skokholm, throughout the season, as calculated from: a/ brood patch data; b/ mean weight of samples; c/ proportion of ringed to unringed birds in areas where proportion of ringed to unringed adults is known.

Date of samples	a/ Brood patch data		b/ Mean weights			c/ Proportions ringed**		
	% with some old down	% non-breeders in sample	Mean wt. of birds in burrows* (gms.)	Mean wt. all birds (gms.)	% non-breeders in sample+	Total caught	No. of new unringed birds	% non-breeders in sample
May 16-31	-	-	29.1	29.1	0	-	-	-
Jun 1-15	-	-	28.5	28.2	10	-	-	-
Jun 16-30	-	-	28.2	27.8	15	217	49	23
Jul 1-15	-	-	27.9	27.5	15	1054	361	34
Jul 16-31	19.5	28	27.6	26.6	43	3103	1512	49
Aug 1-15	31.5	45	27.4	26.2	59	491	246	50
Aug 16-31	29.5	42	27.3	26.5	39	1108	517	47
Sep 1-15	17.5	25	27.3	27.1	11	1039	395	38
Sep 16-30	10.5	15	27.1	26.9	10	61	6	10
Oct 1-15	0	0	26.9	27.1	0	-	-	-

* Approximately 30% of wandering non-breeders have bare brood patches, hence proportion of non-breeders in sample = proportion with some

Table 67 (... cont.)

old down plus a correction factor for those with bare brood patches.

ˇ Mean weights of all birds in burrows have been calculated from mean weight of breeding birds and mean weights of non-breeders in burrows (see table 41), assuming that they occur in population in the ratio of 4 : 1 (see text).

+ Mean weight of wandering non-breeders at all times of the year is taken as 25.3gm. (see table 41).

** Total caught refers to number of petrels caught in areas where proportion of ringed to unringed adults is known (from samples taken in May or early June). Number of new unringed birds refers to number of unringed birds which have arrived in samples, and caused a reduction in the proportion of ringed to unringed birds. Numbers of new arrivals have been calculated for each area separately, and then summed to give total number of wandering non-breeders which are present in samples.

first time should be equal to approximately 11 - 13 per cent of the adult population (see Appendix VIII). This figure is likely to be slightly less than the proportion of non-breeders in the population because some birds, which are unable to obtain a suitable burrow, or a mate, in their first season of prospecting, must spend a further year at the colony as non-breeders. It has therefore been assumed, for the present calculations, that about 20 per cent of the birds in burrows are non-breeders and that the ratio of breeding birds to non-breeders with burrows is 4 : 1. From this ratio, and the known weights of the two classes of birds, it has been possible to give figures for the mean weights of all birds in burrows at different times of the year. It should be noted that, with the departure of prospecting non-breeders in August, the mean weight of birds with burrows becomes equal to that of breeding birds.

The mean weight of wandering non-breeders was obtained directly from the weights of birds identified as belonging to this class on the condition of their brood patch, or lack of site attachment (see page 73). From mid-July until mid-September, the mean weight of these birds was constant at 25.3 grams. Knowing the mean weight of wandering non-breeders and the mean weights of all birds in burrows, it has been possible to calculate the proportion of wandering non-breeders in any sample from a consideration of the mean weight of that sample. The results are shown in table 67b.

One further characteristic of wandering non-breeders can be used to determine the proportion of this class of petrels in the netted samples. Clearly, except for the very small number of birds ringed as chicks, all birds returning to the colony for the first time will be unringed. However, as a result of the intensive ringing during the present study, a high proportion of breeding birds and non-breeders in their second season at the colony were marked. Table 68 shows the proportion of ringed to unringed birds in samples taken at various localities in May/June and July/August during the four seasons of the study. (Birds ringed in the season of sampling are regarded as being unringed). In all instances where figures are available, the proportion of ringed birds in late summer was lower than in early summer. By comparing the proportion of ringed birds in a sample taken in late summer with the proportion of ringed birds in samples taken

Table 68

Percentage of Storm Petrels ringed at most important net-sites on Skokholm, in May and June, and July and August, 1967-1969.

Net-site	1967		1968		1969	
	May/Jun	Jul/Aug	May/Jun	Jul/Aug	May/Jun	Jul/Aug
Met. field	56	29	70	40	88	63
Observatory	85	38	90	51	86	-
Coal corner	65	28	67	61	66	-
Knoll	65	-	52	27	70	32
North pond	35	11	62	44	62	-
Medicine wall	-	-	37*	24	71	29
Potholes	23	21	50	26	-	-
Northern rocks	-	8*	25	12	52	19
Winch	-	16	71	34	57	-
Gantry	36	6	39	17	38	16
Crab bay	48	26	62	47	47	42
Crab bay gut	-	7*	24	12	32	29
South g. point	-	8*	21	16	-	27
Frank's point	-	-	-	7*	33	14
Head	-	-	23	-	38	35
Quarry	3*	2	20	14	54	37
Quarry point	-	18	-	26	37	27
Bluffs	-	-	17*	2	34	16
Wall's end	-	11	42	26	50	22
Heligoland	34	-	71	53	77	57

* Net-site used for first time.

At all sites for which data are available in both early and late summer in any year, proportion of ringed to unringed birds in samples taken in July/August is less than that in samples taken in May/June, due to influx in late summer of unringed non-breeders.

at that site in May or early June, it has been possible to calculate the number, and hence proportion, of new arrivals in the late summer sample. By summing all the data for the four years, an average for the proportion of wandering non-breeders present at various times of the year has been obtained (table 67c).

The proportion of wandering non-breeders in the mist-netted samples, as calculated by the above three methods, is shown in figure 24. In view of the many assumptions and approximations in the calculations, the results of the three methods agree with one another surprisingly well.

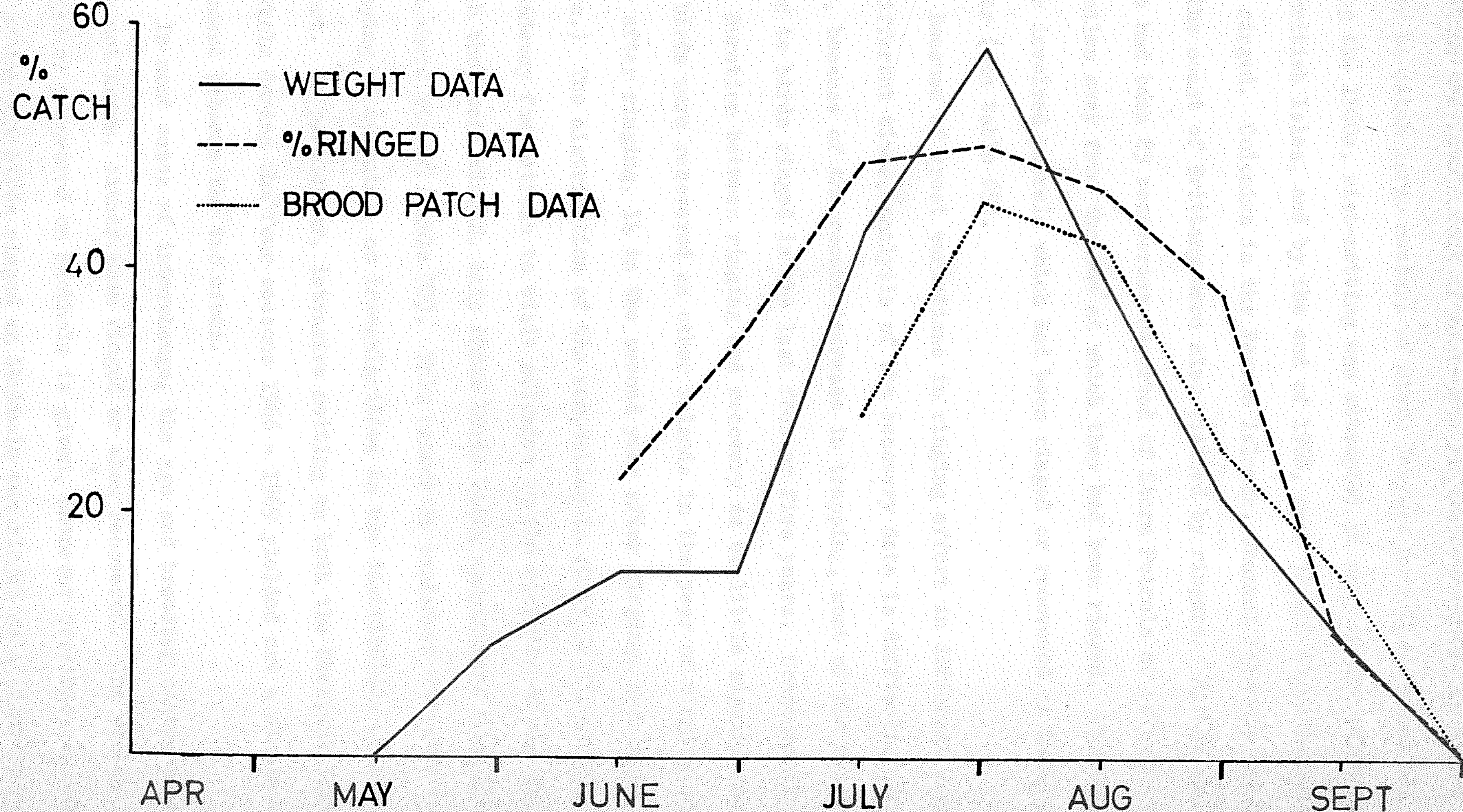


Figure 24. Proportion of wandering non-breeders in samples of Storm Petrels mist-netted at night.

Appendix IV

Interchange between widely-separated colonies of the Storm Petrel

With the development of mist-nets in the late 1950s, it became a simple matter to catch large numbers of Storm Petrels in flight at any big colony. During the 1960s, mist-netting was attempted at some twenty colonies around the British Isles, and by the end of 1968, over 38,000 Storm Petrels had been ringed. Colonies in the Faeroe Islands, Channel Islands, and islands off the coast of Brittany were also visited by ringers. By the end of 1969, there had been 83 recoveries reported of Storm Petrels at colonies more than ten miles away from the one at which they had been ringed. Nineteen of these involved petrels which had been ringed or recovered on Skokholm or Skomer (see table 69).

Because of great variations in ringing effort in different areas and at different times, analysis of the recovery data is difficult. In particular, because of the recent increase in trapping, most of the recoveries refer to birds ringed in the last four or five years. Consequently, the mean duration between ringing and recovery is of little significance. (20 birds were recovered on other islands in the year of ringing, 34 in the year after ringing, 14 in the second year after ringing, and 14 in subsequent years.) The distribution of the recoveries is shown in figure 25. There is a tendency for petrels to visit colonies in the vicinity of the island on which they were ringed, only three birds being caught more than 250 miles from where ringed (table 70). This cannot be explained entirely by the grouping of colonies, or irregularities in the distribution of the ringing effort. In particular, intensive netting on both the Shetland Isles and Skokholm during the four seasons 1966 - 1969 yielded not a single case of movement between the two areas.

In most cases of interchange, the age and breeding status of the birds were not known, either when ringed or when recovered. The status of birds ringed or recovered on Skokholm is given, whenever possible, in table 69. One of the six birds ringed on Skokholm was ringed as a chick and was therefore of known age. Of the other five, only two were examined in detail, and as both had bare brood patches nothing could be said of their breeding status. The majority of the birds recovered on Skokholm were considered

Table 69

Interchange between colonies involving Storm Petrels ringed or recovered on Skokholm or Skomer.

Ring number	Date ringed	Where ringed	Date recovered	Where recovered	Status on Skokholm or Skomer
AA.1168	20.8.56	Skokholm	25.4.62	Annet, Scilly Isles	?
661554	15.8.66	do.	18.8.66	Bardsey, Caerns.	?
663470	11.9.66	do.	12.8.69	do.	Pullus
673123	11.6.67	do.	15.8.69	do.	?
674480	10.8.67	do.	6.6.68	Inishtearaght, Kerry	?
698839	29.6.69	do.	?.?.69	Bardsey, Caerns.	?
2112092	3.8.69	Skomer	12.8.69	do.	Wandering non-breeder
737945	26.5.63	Annet, Scilly Isles	10.5.65	Skokholm	Breeder
do.			29.6.67	do.	do.
Illegible	Pre-'65	Burhou, Channel Isles	11.8.68	do.	do.
B.919?	6.7.63	do.	4.10.68	do.	do.
BB.11637	4.7.66	Inishglora, Mayo	23.8.67	do.	Prospecting n-b?
Paris 389250*	5.7.66	Île de Molène Finistère	6.7.69	do.	Breeder?

Table 69 (... cont.)

Ring number	Date ringed	Where ringed	Date recovered	Where recovered	Status on Skokholm or Skomer
P.2051	22.7.66	Burhou, Channel Isles	27.8.67	do.	Prospecting n-b?
P.1519	28.7.66	do.	6.6.69	do.	Breeder
652365	28.7.66	Annet, Scilly Isles	20.6.68	do.	?
HC.38282	13.8.66	Bardsey, Caerns.	9.9.69	do.	?
HH.46632	11.8.67	do.	6.7.68	do.	N-b in burrow
670010	22.8.67	Annet, Scilly Isles	18.7.68	do.	Prospecting n-b?
do.			2.6.69	do.	Breeder?
do.			2.9.69	do.	do.
690222	1.7.68	Inishvickillaun, Kerry	30.6.69	do.	Prospecting n-b?
2100346	8.8.68	do.	30.6.69	do.	do.

* incubating egg when ringed.

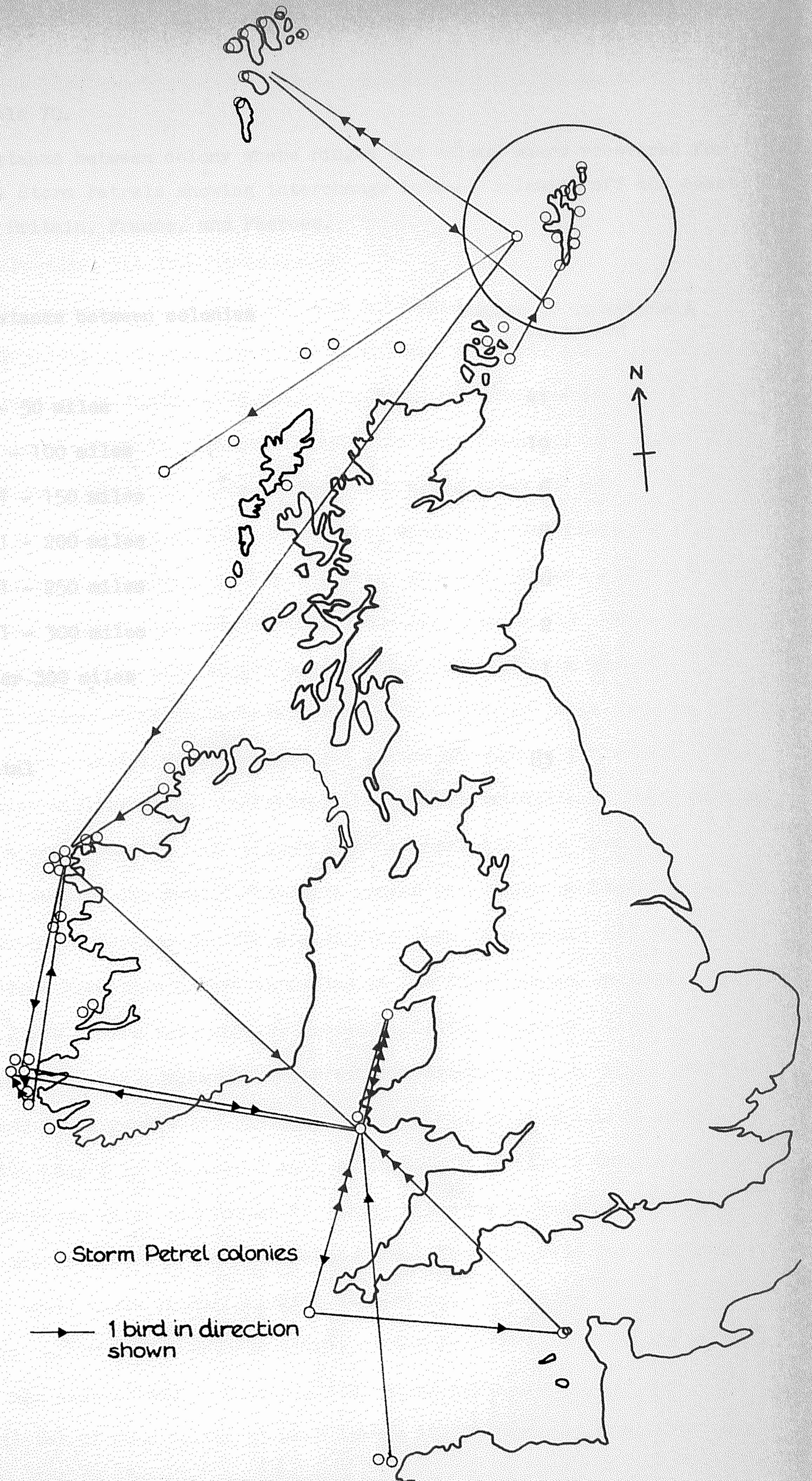


Figure 25. Movement of Storm Petrels between breeding colonies.
For movements within Shetland Isles, see Dennis,1969

Table 70.

Distance between colony where ringed and colony where recovered for all Storm Petrels showing interchange between colonies off the coast of Britain, France, and Faeroes.

Distance between colonies	Number of individuals recovered
0 - 50 miles	41
51 - 100 miles	19
101 - 150 miles	6
151 - 200 miles	8
201 - 250 miles	6
251 - 300 miles	2
over 300 miles	1
Total	83

to be either breeding or prospecting for burrows. Five birds were known to be at least five years of age, and one bird, which was ringed on Bardsey (Caerns.) on 11th August 1967, was found in a burrow in the study area on Skokholm on 6th July 1968. The bird spent a short period in occupation as a non-breeder, but finally deserted.

It was shown in section II that interchange between Skokholm and the nearby colony on Skomer ($2\frac{1}{2}$ miles north) was almost entirely restricted to non-breeders in their first season on land, and that once a petrel had occupied a burrow it remained faithful to that locality. It seems likely, therefore, that those birds which wander to colonies at some distance from those on which they will breed are also wandering non-breeders. The dates of ringing and recovery of birds showing movement between widely-separated colonies suggest that this is indeed the case (table 71). More than 90 per cent of the birds were ringed between 21st June and 15th September, the period during which non-breeders visit the colony in large numbers. (Dates of recovery show a much more general spread throughout the season, with somewhat earlier peaks, indicating that the distribution of dates of ringing is not merely due to more trapping being carried out in late summer than at other times of the year.) The bird ringed as a chick on Skokholm was recovered on Bardsey on 12th August 1969 when three years old, and might therefore have been a bird wandering in its first season on land.

A few of the interchanges between colonies, however, indicate that wandering is not completely restricted to non-breeders in their first season on land. The recoveries include two birds ringed in the last week of May, and two ringed in the second week of June. It is likely that these were non-breeders which had failed to occupy a burrow in their second season on land and as a result had moved elsewhere. There is also one undoubted case of an adult Storm Petrel changing its colony. This bird was found incubating an egg on Île de Moléne, Finistére, on 5th July 1966. On 6th July 1969, the bird was mist-netted on Skokholm (225 miles north). The presence of large quantities of food in the stomach leaves little doubt that the bird was in occupation of a burrow and probably breeding on Skokholm in 1969. However, in view of the faithfulness of adults, particularly successful breeders, to burrows in which they have previously bred (see section I), there can be

Table 71.

Dates of ringing and dates of recovery of all Storm Petrels showing interchange between colonies of the coasts of Britain, France, and the Faeroes.

Date ringed or recovered	No. caught in year of ringing	No. caught 1 year after ringing	No. caught 2 years after ringing	No. caught 3 or more years after ringing
Apr 16-30	0	0	0	1
May 1-15	0	0	1	0
May 16-31	2	0	0	0
Jun 1-15	2	1	2	2
Jun 16-30	3	5	2	0
Jul 1-15	13	12	2	4
Jul 16-31	15	10	4	4
Aug 1-15	37	4	3	0
Aug 16-31	22	2	0	1
Sep 1-15	3	0	0	0
Sep 16-30	3	0	0	0
Oct 1-15	0	0	0	1

little doubt that a change of colony by adults is very rare.

Dennis (1969), discussing the series of interchanges between colonies in the Shetland Isles, pointed out that movements tend to occur in certain directions. For example, 37 birds which were ringed on Foula were found at other colonies, but only two birds ringed elsewhere in Shetland were recovered on Foula. On Mousa, the situation was reversed. No birds ringed on this island were found at any other colony, but six birds ringed elsewhere were recovered there. It is likely that non-breeders which have not yet developed any strong attachment to a particular colony will tend to congregate on those islands nearest to the feeding grounds. The islands of Foula and Fair Isle, situated well to the west and south, respectively, of the main Shetland group, might therefore attract a large proportion of those non-breeders feeding further out in the Atlantic. Certainly, from the apparently small size of the breeding population on Fair Isle, and the large numbers of petrels netted there, it would appear that this island attracts many non-breeders from other colonies. On the other hand, Foula is not only a "visiting" colony, as this island has one of the largest breeding colonies of petrels in the Shetlands. Unfortunately, the nature of the terrain in which the petrels breed would make accurate censusing well-nigh impossible (personal observation). The relatively sheltered islands of Mousa and Fetlar, lying off the east coast of the mainland of Shetland and the island of Yell, respectively, might be less readily accessible to non-breeders.

Interchange between colonies has also been recorded, though rarely, in Oceanodroma leucorhoa (Gross, 1947; Spencer, 1959 and 1967), and there have been occasional records of birds visiting Storm Petrel colonies outside the breeding range of the species (Dennis, 1969). A single Leach's Petrel was mist-netted on Skokholm on 15th July 1966, 435 miles SSE of the nearest breeding colony in the Outer Hebrides. In no other species of Hydrobatidae has ringing been carried out on a sufficient scale to determine whether or not wandering between colonies is of general occurrence in the family. However, interchange between colonies has been well documented for two species of Procellariidae. Serventy (1961) found that although the majority of young Puffinus tenuirostris returned to their natal colony to breed, a few apparently settled in other colonies nearby. Eight birds ringed as chicks in his study area were recovered at colonies on nearby islands. Four of these were still non-breeders when recovered, and may therefore have subsequently returned to their natal colony to breed. However, the other four birds were of breeding age when recovered, suggesting a permanent change of colony. Serventy also reported two instances of adults changing their breeding colony, although the distance moved in both cases was less than a mile.

Harris and Saunders (in prep.) have discussed the interchange between colonies in Puffinus puffinus. They found considerable interchange between the colonies on Skokholm and Skomer, and considered this to be mainly due to wandering of non-breeders. However, one bird which was ringed as a chick on Skomer was found incubating an egg on Skokholm. 37 shearwaters which had been ringed as chicks were subsequently recovered at colonies more than ten miles from the natal colony. 23 of these were recovered between two and four years after fledging and were therefore still non-breeders, probably making only casual visits to the colonies, since three were subsequently recovered back at the natal colony. However, in eight instances, the birds were six or more years old when recovered, and presumably therefore breeding on the second island. 28 shearwaters which had been ringed as full-grown birds, presumably non-breeders, were recovered at other colonies.

The evidence therefore suggests that in H. pelagicus, P. puffinus, and P. tenuirostris (and probably also in O. leucorhoa), much of the wandering between colonies occurs in the first few years of life. Once a bird has occupied a burrow and bred, it thenceforth remains faithful to that site. Although young birds may visit several colonies during their first season on land, they usually return to their natal colony to breed. It is clear, however, that a few birds may change colonies after occupying a burrow as a non-breeder, or even after breeding. As Serventy (1967) suggested, it seems likely that those non-breeders which fail to obtain a burrow or a mate at their natal colony may move to another colony. Adults perhaps change colonies only after repeated breeding failure.

Appendix V

The moult of the wing-coverts, tail-coverts, and body feathers of the Storm Petrel

(1) Wing-coverts

The primary coverts are moulted concurrently with the primaries, each covert being replaced during the early stages of moult of its respective primary. The greater, median, and lesser wing-coverts are moulted at sea during the period of active moult of the secondaries. A few birds have been found moulting one or two coverts in autumn, whilst others have been found completing the moult of these feathers in spring. Until further information from birds in the winter quarters becomes available, the pattern of moult in these feather tracts cannot be determined.

(2) Tail-coverts

The occurrence of moult of the tail-coverts in the population is shown in appendix table 11, and in text figure 20. The upper tail-coverts are moulted first, the moult commencing in breeding birds during the second half of incubation. In the youngest class of non-breeders visiting the colony, the onset of the moult seems to be coincident with arrival at the colony in July. The moult of the under tail-coverts commences two or three weeks after the onset of the moult of the upper tail-coverts, usually at about the time of the onset of tail moult. In both sets of tail-coverts, the moult begins in the central posterior feathers, and then proceeds forwards and outwards until it eventually merges with the wave of moult which is by this time affecting the body feathers.

Data from birds retrapped twice during the course of the moult suggest that complete replacement of the upper tail-coverts takes about 40 days, and that of the under tail-coverts, about 60 days. A few non-breeders caught in early September and a few breeding birds caught in October had completed the moult of their tail-coverts; however, it appears that completion usually occurs shortly after departure from the colony. A few individuals have been found moulting tail-coverts in spring, well in advance of the general onset of the moult. This is presumably in some way connected with early tail moult, those birds which replace some tail feathers in spring also replacing a few tail-coverts at the same time.

(3) Body feathers

Replacement of the feathers of the body (dorsal, ventral, lumbar, shoulder, and crural tracts) and those of the head (capital tract) are here treated separately, because of certain peculiarities of the head moult, although in practice they are both part of the single cycle of body moult. The occurrence of head and body moult in the population is shown in appendix table 11, and text figure 20. The feathers of the head are moulted first, usually in July or early August, and are replaced rapidly, those of the forehead growing almost synchronously. The moult of the feathers of the body commences two or three weeks later, usually beginning in the shoulder tract, and then spreading rapidly through the dorsal tract and tracts of the underparts. Once started, however, the moult is slow and irregular, relatively few feathers being involved at any one time. Within each feather tract, replacement does not seem to follow any precise pattern, although further information would be desirable here.

The completion of body moult in all classes of birds usually occurs after departure from the colony. An adult caught on 25th October 1968 had apparently completed its body moult, and several other birds caught in October had very few old feathers remaining in the plumage. In these individuals, there was a striking contrast between the fresh sooty-black plumage of the body and head, and the worn and faded primaries and wing-coverts. It would seem, therefore, that the body moult in breeding birds is completed in about three and a half months. The body moult of non-breeders is unusual in that it occurs at a later stage in the general cycle than is the case in breeding birds, the body moult of non-breeders commencing at about the time that the first primaries are shed.

The moult of the head feathers, occurring at the beginning of the body moult, is completed in as little as three or four weeks, after which all birds possess a completely black forehead and crown. On arrival at the colony in April and May, the majority of adults still possess dark heads, although a few individuals show signs of abrasion in the feathers of the forehead. As the season progresses, the abrasion of the head feathers proceeds to a very variable degree, so that immediately prior to the onset of moult there is enormous variation in the colouration of the head feathers, particularly those above the base of the upper mandible. In some individuals, the whole of the forehead and anterior half of the crown becomes bleached to a light sandy-brown; in others the pale area is restricted to a more or less clearly defined "saddle" above the base of the upper mandible; and in others the forehead shows no greater signs of abrasion than the rest of the body feathers.

The proportion of birds with noticeable pale areas on the head in mid-summer in all four seasons of the present study was approximately 50%. There was no sex difference or age difference in the degree of fading. It was however found that birds showing a marked degree in one year tended to show fading in subsequent years. Of 189 birds with pale foreheads in one year, 161 (85%) had pale foreheads in the following year. Thus the proportion of birds with pale foreheads in a sample of birds which had previously had pale foreheads is significantly higher than in the population as a whole (χ^2 = 52.7, p = less than 0.001).

The reason for the excessive fading of the head feathers of some birds is not known. Abrasion resulting from the burrowing activities of those birds digging a new burrow, or enlarging an old one, may be responsible in some cases. However, this could account for only a small proportion of birds with pale foreheads, since many non-breeders which have not yet occupied a burrow show the feature.

Appendix VI

Calculation of the interval between shedding of successive feathers in the primary moult of the Storm Petrel

The interval between shedding of successive primaries during the moult of the primaries was estimated by comparing the relative stages of growth of the moulting feathers within individual wings. In all wings examined, the stage of development of each moulting feather was compared with that of all other feathers in the same wing. The results are presented in table 72. The data were sufficient for a complete analysis of feathers 1, 2, and 3, only. Feathers 6 to 11 have been ignored, since only one bird was found with any of these feathers in moult in autumn. In table 72a, feather 1 is taken as a basis for comparison. The vertical columns constitute the stages of growth of this feather, and the horizontal columns constitute the stages of growth of the feathers with which the stage of growth of feather 1 is to be compared. The figures in the body of the table refer to the number of wings which were found with any particular combination of growth stages in two feathers. For example, from table 72a, it can be seen that when feather 1 scored 1 (538 wings), feather 2 scored 0 (245 wings) or 1 (293 wings), and feather 3 scored 0 (525 wings) or 1 (13 wings). This gives mean scores for feathers 2 and 3 of 0.54 and 0.02, respectively, when feather 1 is in the missing stage. The mean scores of feathers 2 to 5, for all stages in the growth of feather 1, are shown in table 73a.

In tables 72b and 72c, feathers 2 and 3 form the bases for comparison. The mean scores of other feathers at the various stages of growth of feathers 2 and 3 are shown in tables 73b and 73c respectively. The mean scores from tables 73a, 73b, and 73c are shown graphically in figure 26. The x axis represents the score of the feather with which the others are to be compared and the y axis represents the mean scores of these feathers. The curves which best fit the points relating to the individual feathers have been drawn by eye.

In an ideal system of scoring the stage of moult of an individual feather, equal increments in feather score should connote equal periods of time, and the curves for individual feathers should therefore appear as straight lines. That they do so on this analysis confirms that the scoring

Table 72.

a/ Stage of growth of primaries 2, 3, 4 and 5 at each stage in growth of primary 1, in primary moult of Storm Petrel.

		Stage in growth of primary one.						
Primary	Stage	1	2	3	4	5	6	7
2	0	245	2	0	0	0	0	0
	1	293	81	1	0	0	0	0
	2	-	124	36	4	0	0	0
	3	-	-	19	26	3	0	0
	4	-	-	-	4	22	4	0
	5	-	-	-	-	8	19	4
	6	-	-	-	-	-	2	15
3	0	525	146	19	3	1	1	0
	1	13	50	21	3	3	2	0
	2	-	11	16	28	20	12	3
	3	-	-	0	0	9	6	9
	4	-	-	-	0	0	3	6
	5	-	-	-	-	0	1	1
4	0	538	206	54	29	22	11	3
	1	0	1	2	3	4	8	11
	2	-	0	0	2	7	6	4
	3	-	-	0	0	0	0	1
	4	-	-	-	0	0	0	0
5	0	538	207	56	34	33	25	17
	1	0	0	0	0	0	0	1
	2	-	0	0	0	0	0	1
	3	-	-	0	0	0	0	0

b/ Stage of growth of primaries 3, 4 and 5 at each stage in growth of primary 2, in primary moult of Storm Petrel.

		Stage in growth of primary two.						
Primary	Stage	1	2	3	4	5	6	7
3	0	359	85	1	0	1	0	0
	1	16	62	10	4	0	0	0
	2	-	16	36	17	10	1	0

Table 72 (... cont.)

Stage in growth of primary two.

Primary	Stage	1	2	3	4	5	6	7
3	3	-	-	0	9	18	6	1
	4	-	-	-	0	1	7	13
	5	-	-	-	-	1	2	12
	6	-	-	-	-	-	0	7
4	0	374	163	41	18	10	0	1
	1	1	0	4	5	11	7	6
	2	-	0	2	7	10	7	18
	3	-	-	0	0	0	2	5
	4	-	-	-	0	0	0	3
	5	-	-	-	-	0	0	0
5	0	375	163	47	30	30	15	23
	1	0	0	0	0	1	0	5
	2	-	0	0	0	0	1	5
	3	-	-	0	0	0	0	0

c/ Stage of growth of primaries 4 and 5 at each stage in growth of primary 3, in primary moult of Storm Petrel.

Stage in growth of primary three.

Primary	Stage	1	2	3	4	5	6	7
4	0	91	74	8	2	1	0	0
	1	2	13	8	7	2	1	0
	2	-	2	9	12	7	2	0
	3	-	-	0	1	4	1	0
	4	-	-	-	0	0	3	3
	5	-	-	-	-	0	1	1
	6	-	-	-	-	-	0	2
5	0	93	89	24	21	8	2	1
	1	0	0	1	0	4	2	4
	2	-	0	0	1	2	4	0
	3	-	-	0	0	0	0	1

Table 73.

a/ Mean scores of primaries 2, 3, 4, and 5 at each stage in growth of primary 1, in primary moult of Storm Petrel.

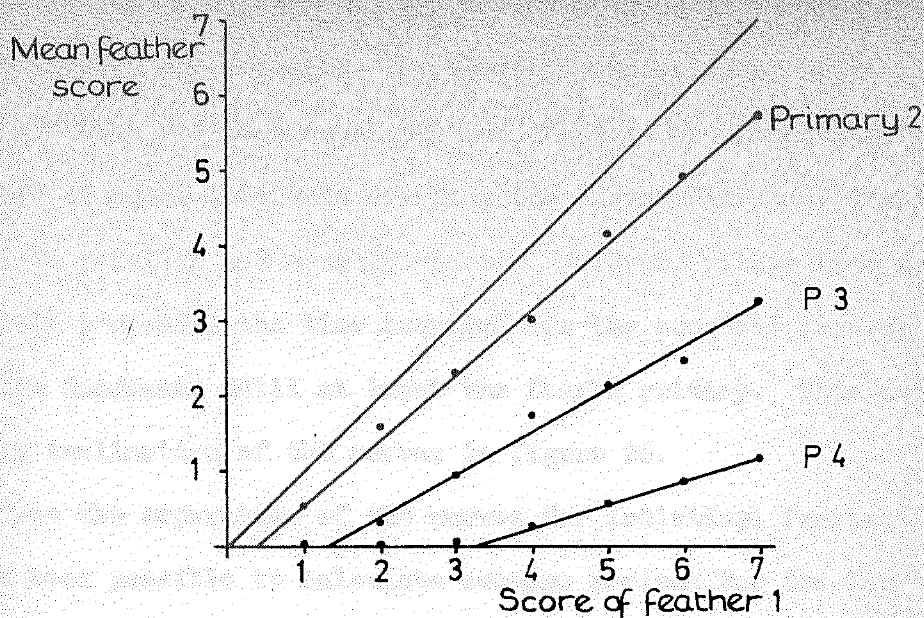
	Stage in growth of primary one.						
Primary	1	2	3	4	5	6	7
2	0.54	1.59	2.3	3.0	4.2	4.9	5.8
3	0.02	0.4	1.0	1.7	2.1	2.4	3.3
4	0	0.01	0.04	0.2	0.6	0.8	1.2
5	0	0	0	0	0	0	0.2

b/ Mean scores of primaries 3, 4, and 5 at each stage in growth of primary 2, in primary moult of Storm Petrel.

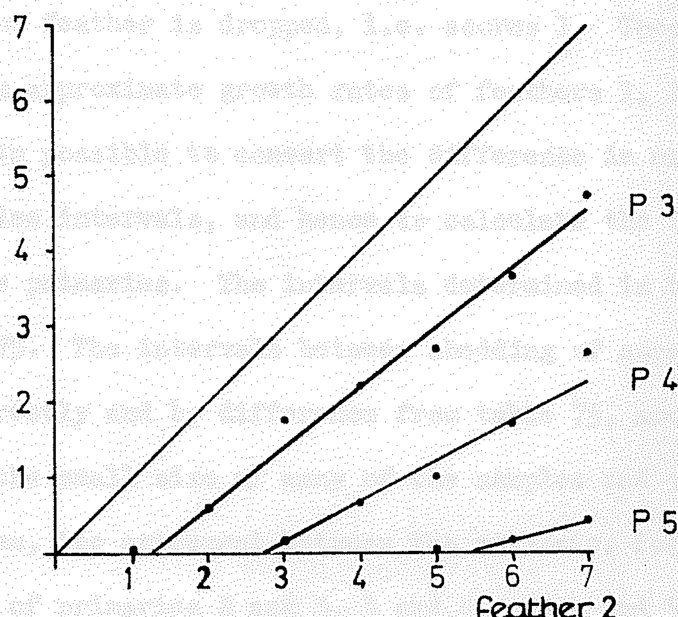
	Stage in growth of primary two.						
Primary	1	2	3	4	5	6	7
3	0.04	0.6	1.7	2.2	2.7	3.6	4.8
4	0	0	0.2	0.6	1.0	1.7	2.6
5	0	0	0	0	0.03	0.13	0.5

c/ Mean scores of primaries 4 and 5 at each stage in growth of primary three, in primary moult of Storm Petrel.

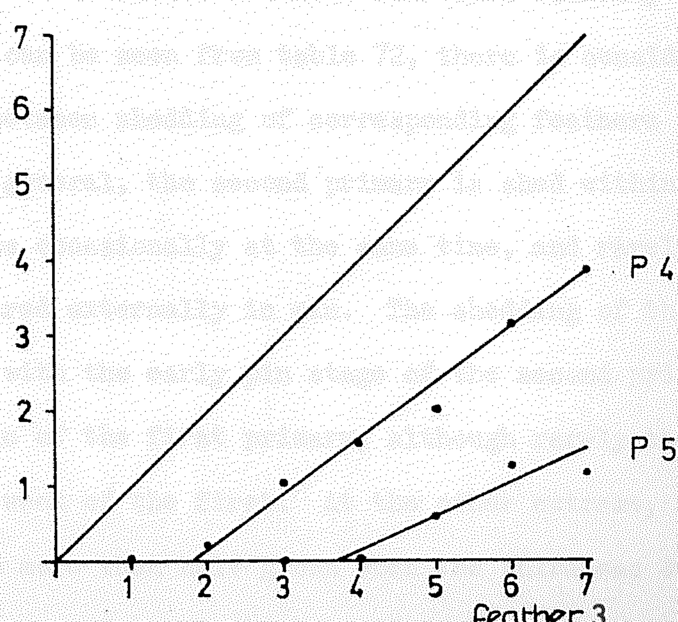
	Stage in growth of primary three.						
Primary	1	2	3	4	5	6	7
4	0.02	0.2	1.0	1.6	2.0	3.1	4.8
5	0	0	0.04	0.1	0.6	1.3	1.2



[a] Mean scores of primaries 2, 3, and 4, at each stage in growth of primary 1, in moult of Storm Petrel.



[b] Mean scores of primaries 3,4, and 5, at each stage in growth of primary 2.



[c] Mean scores of primaries 4 and 5, at each stage in growth of primary 3.

system adopted was suitable. Furthermore, in an ideal moult situation in which the feathers take equal periods of time to complete their growth and are shed at equal intervals of time, the curves for the individual feathers should be parallel and equally spaced. However, it has been shown that as the moult proceeds, the time required for the complete renewal of successive feathers increases until at least the fourth primary. This accounts for the varying inclination of the curves in figure 26.

From the separation of the curves for individual feathers in figure 26, it has been possible to calculate average periods for the interval between shedding of successive feathers up to the fifth. This has been achieved by calculating from table 72 the mean scores of feathers 1, 2, 3, and 4 at which a subsequent feather is dropped, i.e. scores 1. These are shown in table 74. As the approximate growth rates of feathers 1, 2, 3, and 4 are known, it has been possible to convert the difference in mean scores of two primaries into time intervals, and hence to calculate the interval between shedding of these primaries. The intervals determined in this way are presented in table 75. The intervals between shedding of successive feathers, obtained both directly and by difference from table 75, are shown in table 76. In view of the small size of many of the samples and the coarseness of the scoring system, the agreement between the estimates for the intervals between shedding of primaries 2 and 3, 3 and 4, and 4 and 5, is surprisingly good. The results clearly indicate that, as the moult proceeds, the interval between shedding of successive feathers increases markedly.

However, as can be seen from table 72, there is considerable variation in the interval between shedding of corresponding feathers in different individuals. In general, the second primary is shed within a few days of the first, perhaps occasionally at the same time, and rarely after the first primary has appeared externally in pin. The shedding of the third primary usually coincides with the early pin stage of the second primary and the late pin or brush stage of the first primary, although rarely the third primary is shed within a week of the first. At the other extreme, in one bird the first primary was more than half grown when the third was dropped. The fourth primary is usually shed when the first is just completing its growth, and the second is half to three-quarters grown. The fifth primary is shed

Table 74.

a/ Mean scores of primaries 1, 2, and 3, when primary 2, 3, or 4 is in missing stage i.e. scores 1, as determined from figure 26a.

	Mean scores of primaries 1, 2, and 3.		
Missing primary	1	2	3
2	1.5	-	-
3	3.1	2.4	-
4	6.5	5.4	3.0

b/ Mean scores of primaries 2 and 3, when primary 3, 4, or 5 is in missing stage i.e. scores 1, as determined from figure 26b.

	Mean scores of primaries 2 and 3.	
Missing primary	2	3
3	2.3	-
4	4.8	2.9
5	7+	5.9

c/ Mean scores of primaries 3 and 4, when primary 4 or 5 is in missing stage i.e. scores 1, as determined from figure 26c.

	Mean scores of primaries 3 and 4.	
Missing primary	3	4
4	3.3	-
5	6.3	3.3

Table 75.

a/ Mean intervals between shedding of primaries, determined from table 74a.

b/ Mean intervals between shedding of primaries, determined from table 74b.

c/ Mean intervals between shedding of primaries, determined from table 74c.

a			b			c		
Interval between	Days	Ref.*	Interval between	Days	Ref.	Interval between	Days	Ref.
1 and 2	2.9	a	2 and 3	8.3	g	3 and 4	19.4	l
1 and 3	12.1	b	2 and 4	24.0	h	3 and 5	45.3	m
1 and 4	31.6	c	2 and 5	38+	-	4 and 5	22.5	n
2 and 3	8.9	d	3 and 4	16.0	j			
2 and 4	28.1	e	3 and 5	41.9	k			
3 and 4	17.3	f						

* Letter reference to intervals used in calculations of intervals between shedding of successive feathers in table 76.

Table 76.

Mean interval between shedding of successive primaries, in early stages of primary moult of Storm Petrel.

Successive feathers	Source	Interval between shedding in days
1 and 2	a*	2.9
2 and 3	g	8.3
	b-a	9.2
	d	8.9
3 and 4	f	17.3
	j	16.0
	c-b	19.5
	e-d	19.1
	h-g	15.7
	l	19.4
4 and 5	n	22.5
	k-j	25.9
	m-l	25.9

* letter reference to intervals calculated in table 75.

after the second has completed its growth, and when the third is about three-quarters grown. In the bird with a sixth primary in moult, this was in the pin stage when primaries 1 to 4 had completed their growth, and feather 5 was three-quarters grown.

Appendix VII

Plumage aberrations

Approximately two per cent of the Storm Petrels examined on Skokholm during 1967 and 1968 had some white or partially white feathers in the normally dark parts of the plumage. This was quite distinct from the pronounced fading of the head feathers described in appendix V. True albinism was largely restricted to one or two remiges; of 55 birds with some white in the plumage, 34 had one or two white primaries only, and 7 had one or two white secondaries only. In 13 birds, the albinism was more extensive, affecting a few feathers of the scapulars (shoulder tract), and belly and flanks (ventral tract). One bird had a very striking broad white pectoral band, although the rest of the plumage was normal. Only one bird could be regarded as a partial albino. This had white tips to most of the body and wing feathers, the belly and under tail-coverts were mainly white, and a total of eight primaries were wholly white. The rest of the plumage was a light sandy-brown in colouration.

When one or more primaries were affected, these were usually the innermost. The first primary accounted for 67 per cent of all white primaries and the second primary for a further 18%. Albinism appeared to be restricted to adult petrels. 14 of the 55 birds with some white in the plumage were known to be of breeding age, and a further 36 were considered to be adults from date of capture, site tenacity, or condition of the brood patch. 10 birds were caught both in 1967 and 1968. Seven of these had the same amount of white, or more, in the second year, and only one bird had no white feathering in the second year, indicating that white feathers are usually replaced by white feathers.

Perhaps the most interesting feature of the albinism was its uneven distribution in the population. No less than 17 of the birds with some white feathering were caught at the net-site in the Quarry. Considering only those birds caught in April, May, or June, when there are few non-breeders about to confuse the situation, of 562 birds caught in the Quarry, 14 (2.5%) had some white feathers in the plumage, whereas of 1,824 birds caught elsewhere, only 21 (1.2%) had any white feathering. ($\chi^2 = 5.1$, $p = 0.025$). If, as seems likely, the presence of white feathers is restricted to "old" birds, a possible explanation for the uneven distribution of birds with some white in the plumage could be that the mist-netted samples taken in the Quarry contain a higher proportion of old birds than samples taken elsewhere. The Quarry is undoubtedly one of the best breeding sites, since the burrows are not subjected to any disturbance from rabbits, shearwaters, or Puffins. No evidence was found of any predation by owls, and predation by gulls was less severe than in other parts of the colony. Competition for burrows at a very favourable site would result in few young birds being able to settle, and a low adult mortality on the breeding grounds would result in a higher average age.

Alternatively, if the presence of white feathers in the plumage is controlled genetically, it is possible that the difference in proportions in different parts of the island reflects a difference in the frequency of the controlling gene, or gene complex. Differences in gene frequencies could be maintained over short periods of time by the faithfulness of young birds to the locality of their natal burrow.

The sporadic presence of white feathers in the otherwise dark parts of the plumage has been recorded in several species of Hydrobatidae. Baptista (1966) and Harris (1969) recorded this on Oceanodroma castro and O. tethys in the Galapagos Islands, and Trimble (1968) described two striking cases of partial albinism in Oceanites oceanicus. Murphy and Snyder (1952) considered the white feathering of some O. oceanicus to be an example of the "pealea" phenomenon; the tendency amongst certain genera of storm petrels for the underparts to become mottled.

Appendix VIII

The size of the colony of Storm Petrels on Skokholm

The censusing of populations of burrowing Procellariiformes is notoriously difficult. Most species breed in large, densely-crowded colonies on remote islands which are often difficult of access, and many visit the colony only at night. Some species, particularly species of Hydrobatidae, breed in crevices in cliffs or amongst boulders where they are totally inaccessible to the observer. Fortunately, on Skokholm, all the major breeding areas of the Storm Petrel were readily accessible, so that it was possible to attempt a census of the breeding population.

A count of burrows containing churring birds gives little indication of the number of breeding pairs, since nightly checks of the walls in the study area revealed that even during the peak period for churring not more than 20 - 30 per cent of the burrows known to be occupied by breeding pairs contained churring birds on any one occasion. Many burrows contained several pairs of petrels breeding in close proximity to each other, so that it was often difficult to determine the number of occupied burrows at even one site. In some of the larger caves amongst boulders at the base of the cliffs, the density of churring birds on a night in early June was such that it was impossible for an observer to pin-point individual birds. The situation was further complicated since prospecting non-breeders may visit several burrows in the same season, churring in each. Once established in a burrow, they churr regularly throughout their stay, continuing long after breeding birds have ceased. The greatest difficulty, and that which precluded the possibility of any reasonable estimate being obtained from counts of occupied burrows, was simply that of locating the burrows. The churring of a Storm Petrel in occupation of a burrow is often inaudible from more than five yards, and birds churring from deep underground are easily overlooked against the background of nocturnal cries of shearwaters on dark nights and Oystercatchers Haematopus ostralegus on light nights.

The obvious alternative to direct counts of occupied burrows is the use of a mark-release-recapture method on the adults frequenting the colony. However, the present study has shown that the aerial activity of breeding birds at the colony is extremely non-random. As shown in section II, breeding birds are particularly faithful to the locality of their burrow, and are rarely caught in any other part of the colony. Ringing at one locality, however intense, will sample an insignificant proportion of petrels breeding more than 100 yards away. On the other hand, non-breeders arriving at the colony in large numbers in late June or July show no site attachment and wander about the island in an apparently random fashion. Consequently they are more susceptible to capture than breeding adults, and in late summer may comprise more than half of the mist-netted samples. As shown in section II and appendix IV, some of these non-breeders are casual visitors from other colonies, perhaps visiting Skokholm for a few nights only. Furthermore, there is a constant turnover in the population of non-breeders visiting the colony. Petrels which arrive in late June may depart again before the end of July, whereas others, arriving in late July or early August, may continue to visit the colony until mid-September.

Conventional mark-release-recapture methods are therefore only of any value when applied to samples taken before the arrival of these wandering non-breeders in late June. The estimates derived from the trapping at any particular site will relate to the number of petrels breeding in the vicinity of the nets, and are therefore difficult to interpret unless the precise limits of the area sampled can be determined. This has been possible in some of the smaller bays, or heaps of boulders, where it is clear that the nets have effectively sampled the entire sub-colony. However, at the majority of sub-colonies, this has obviously not been the case. Intensive netting in a large bay at the south-west corner of the island has shown that two nets erected at the top of a scree slope were sampling an almost entirely different population from that sampled by a net erected only 20 yards further down the same slope.

Harris (1966) and Perrins (1968) have used mark-release-recapture methods to estimate the numbers of Manx Shearwaters Puffinus puffinus breeding on Skokholm. Harris calculated the number of young reared to fledging from the number of fledglings ringed and the proportion of ringed to unringed fledglings amongst those killed by gulls. Since the breeding success in that season was known, the total population of breeding pairs could be calculated. Perrins' method was similarly based on the ringing of young. He colour-ringed several hundred chicks in the burrow and then calculated the total number of chicks fledged from the proportion of colour-ringed to unringed fledglings in those caught on the surface at the time of fledging. Neither of these methods could be used to estimate the number of Storm Petrels on Skokholm because of the immense difficulties encountered in locating chicks both in the burrow and on the surface at fledging.

At present, therefore, no satisfactory single method is available for censusing the population of Storm Petrels on Skokholm. In order to obtain some estimate for the size of the population, it has been necessary to take into account data from several sources and to employ a considerable amount of intuitive guesswork based on local knowledge.

As a first step in estimating the size of the Skokholm colony, it was necessary to determine the distribution of breeding birds, and to obtain some measure of the relative abundance of petrels at the different sites. This was achieved in three independent ways. An initial survey of the distribution of petrels was carried out in mid-June 1967. During a period of light nights between 7th and 18th June, the entire coast of the island was explored and sample counts taken of the number of birds in flight over the colony. At each of 128 sites on the cliffs, the number of petrels observed in 90 seconds was recorded. (The counts at the major sites are given in table 77, column 2.) Although the number of birds observed per unit time was affected by the time of night at which the observations were made, the light intensity, and the nature of the background against which the birds were viewed, the results gave a reasonable indication of which sites were the most important for breeding petrels.

A better indication of the relative densities of breeding pairs was obtained from the trapping effort. Mist-netting was carried out at all major breeding areas on the island. The total catch at each site has been expressed as the number of birds caught per 30 feet of net per night (see table 77, column 6).

Finally, the number of occupied burrows located at each site was recorded irrespective of whether these contained breeding birds or non-breeders (see table 77, column 3). The distribution of the 980 burrows located during the present study is clearly biased towards those sites

Table 77

An estimate of the number of breeding pairs of Storm Petrels on Skokholm, and the sources of evidence on which the estimate has been based.

1 Locality	2 Counts of flying birds	3 No. of burrows located	4 M.R.R. estimates	5 Nights netting	6 Average catch/ 30ft. net	7 No. of breeders ringed	8 No. of breeders alive in 1969	9 % breeders ringed by 1969	10 No. of breeders sampled by nets	11 Estimated no. of breeding pairs	12 Maximum no. of pairs	13 Minimum no. of pairs
1 Observatory	-	19	-	13	4	106	79	85	90	25	30	20
2 Knoll	-	32	-	11	11	150	130	66	167	45	55	35
3 Bunkhouse	-	6	-	2	21	27	24	-	-	5	10	4
4 Met Field	-	37	-	25	6	303	246	93	262	85	100	70
5 Medicine Wall	-	24	180	14	25	183	170	83	196	50	60	40
6 N. of Hel.	-	13	-	10	7	118	102	80	124	30	45	20
7 S. of Hel.	-	9	-	11	9	81	73	80	88	25	30	20
8 Coal Corner	-	42	-	12	6	141	113	80	139	50	60	40
9 Winch	-	0	-	12	3	91	74	75	93	15	20	10
10 Gantry	3	5	-	17	24	118	97	50	162	30	40	20
11 North Haven top	4	0	-	1	10	13	10	-	-	0	0	0
12 North Haven Gut	14	20	-	1	21	15	13	-	-	40	50	30
13 Neck Gate	5	10	-	2	12	33	26	-	-	25	30	20

Table 77 (... cont.)

1	2	3	4	5	6	7	8	9	10	11	12	13
14 Rat Island	15	8	-	1	6	3	2	-	-	20	25	15
15 Little Neck	1	0	-	1	7	20	18	-	-	20	25	15
16 Dumbell Bay	10	15	-	2	8	9	7	-	-	30	40	25
17 Peter's Bay	3	5	-	2	22	26	21	-	-	20	30	15
18 Tunnel	6	2	-	1	9	5	4	-	-	10	15	5
19 Hog Bay	4	0	-	1	5	10	8	-	-	20	30	15
20 East Stream	-	2	-	1	3	5	4	-	-	10	15	5
21 Spy Rocks	1	0	-	4	9	40	37	67	51	25	30	20
22 Crab Bay	9	20	180	22	15	452	386	69	538	200	225	175
23 Crab Bay Gut	17	50	150	5	85	192	173	50	314	150	175	125
24 Theatre	2	0	-	1	9	10	9	-	-	15	20	10
25 South Gallery Point	3	3	-	1	27	30	30	-	-	30	40	25
26 Gallery Rocks	23	20	-	4	46	94	80	33	210	100	125	75
27 Frank's Gully	30	10	-	4	37	84	72	33	186	100	125	75
28 Frank's Point	3	10	-	9	55	329	316	33	894	200	250	150
29 Frank's Rocks	12	25	-	1	61	25	22	-	-	100	125	75
30 Half Way Wall S.	5	4	-	1	16	16	14	-	-	25	30	20
31 Garden Rocks	7	2	-	1	7	5	4	-	-	25	30	20

Table 77 (... cont.)

1	2	3	4	5	6	7	8	9	10	11	12	13
32 South Crags	-	15	-	1	8	24	20	-	-	45	55	35
33 Pigsty Wall	-	25	-	1	6	41	36	-	-	40	50	30
34 North Pond	-	23	-	9	5	136	101	72	124	50	60	40
35 Potholes	6	5	-	7	16	158	123	-	-	50	70	30
36 Northern Rocks	13	40	-	10	50	370	328	50	550	250	300	200
37 N. Plain Wall N.	1	7	-	1	8	4	3	-	-	75	90	60
38 Little Bay Point	5	2	-	2	72	114	88	-	-	50	70	30
39 Hard Point	1	2	-	1	10	16	14	-	-	20	30	15
40 Purple Cove	0	0	-	1	1	0	0	-	-	0	0	0
41 Fossil Cove	4	25	-	1	65	54	48	-	-	60	70	50
42 Wall's End	10	30	220	8	32	315	269	66	385	200	250	175
43 West Gate	3	5	50	4	12	26	24	-	-	25	40	20
44 Bluffs	25	30	-	4	49	237	224	23	587	300	350	250
45 Warden's Rest	10	6	-	1	22	56	50	-	-	100	125	75
46 Quarry Point	23	30	-	7	39	435	385	52	644	300	350	250
47 Quarry Top	100+	150+	1000	28	56	1516	1306	66	1899	1000	1100	900
48 Quarry Bottom	45	30	-	1	50	91	81	-	-	1000	1250	750

Table 77 (... cont.)

1	2	3	4	5	6	7	8	9	10	11	12	13
49 Main	6	10	190	5	12	127	118	56	182	125	150	100
50 Lighthouse	3	0	-	2	4	8	7	-	-	20	30	10
51 Wall Rock	6	10	120	4	21	90	82	33	207	110	120	100
52 Dip Gully	3	12	-	5	44	97	85	33	174	75	100	50
53 Winter Gully	5	15	-	3	25	42	34	-	-	40	50	30
54 Winter Pond	0	0	-	1	7	5	4	-	-	0	0	0
Other areas	-	115	-	0	-	-	-	-	-	740	900	575
Totals	-	980	-	-	-	6696	5791	-	-	6200	7495	4970

which were visited most frequently, notably the walls in the study area. The efficiency of direct counts of occupied burrows for determining the number of breeding pairs in an area was clearly highest in the study area, although even there, intensive mist-netting indicated that not more than a third of the occupied burrows had been located in some stretches of wall. Taking into consideration the varying efficiency of the searches, it was thought that approximately 400 pairs of petrels were breeding in the 1,440 yards of wall in the study area, although only 230 burrows were actually located. This would give a breeding density of 0.3 pair per yard. Other walls which were of similar suitability for petrels, and which were outside the study area, totalled 890 yards in length. Assuming an average density of 0.3 pair per yard there also, the number of breeding pairs in these walls would be about 250. The searches for burrows at other sites were clearly far too inefficient for any direct estimation of the number of breeding pairs to be obtained.

Apart from the walls, the flat grassy top of the island has few rocky areas suitable for petrels. Some petrels, probably less than 100 pairs, breed around the rocky outcrops in the centre of the island. However, in two areas, large numbers of petrels have adopted atypical nest-sites, and breed in burrows in the level ground at the top of the cliffs. These two areas are the areas of greatest density of shearwater burrows, which honeycomb the ground to such an extent that the general topography of the surface is not altogether unlike that of a boulder beach. Estimation of the numbers of petrels in these areas was particularly difficult. Location of burrows by their distinctive odour, or by the presence of a churring bird, was almost impossible because of the large numbers of shearwaters in the vicinity. Mist netting was also impossible because of interference from these birds, except on very light nights. A rough indication of numbers has been obtained from ringing and recapture data, but as it was clear that the nets were not sampling the whole of the population breeding in one of the shearwater colonies, the estimate for this area (main/wall rock) may be much too low.

More than three-quarters of the petrels breeding on Skokholm occupy sites on the cliffs or in the bays. Here the counts of occupied burrows did little more than indicate which sites were important, and which held few if any petrels. Estimates for the number of breeding pairs were obtained in a few of the smaller and more discrete sub-colonies from mark-release-recapture data. Otherwise, estimates are based largely on the nature and extent of the areas, and comparison with other areas for which a reasonably accurate estimate was available.

A valuable guide in estimating the number of petrels breeding in areas at which mist-netting had been carried out has been the total number of birds ringed at that site, and the resulting proportion of ringed birds in the population. As shown in appendix III, it was possible to determine the proportion of non-breeders in the late summer samples from examinations of brood patches, the mean weights of the samples, and changes in the proportion of ringed to unringed birds in the community. Thus it has been possible to obtain an estimate for the total number of breeding birds ringed at each net site. Assuming an annual mortality of adults of 10 - 12 per cent (see section III), the number of ringed birds still alive in 1969 could be calculated. From the proportion of ringed to unringed adults in the last sample taken at each site in 1969, it has been possible to obtain an estimate of the number of breeding birds in the area sampled by the nets.

Using the various sources of information outlined above, it has been possible to give a rough estimate of the number of breeding pairs of Storm Petrels in each part of the island. The details of the estimates for the various parts of the island are given in table 77, the important features of which are summarized in table 78. It must be stressed that the estimates have not been obtained in any strict mathematical fashion, but are those figures which are considered by the author to be the most reasonable on the basis of the evidence available. It is concluded that the breeding population of Storm Petrels on Skokholm numbers about 6,200 pairs, and is not less than 5,000 or more than 7,500. The approximate distribution of the breeding pairs is shown in figure 27.

The numbers of non-breeders at the colony

Young Storm Petrels normally return to the colony when two years old, and first breed when four. In their first season at the colony, the petrels make irregular nocturnal visits to the island without entering burrows,

Table 78.

Number of Storm Petrels ringed, number of occupied burrows located, and an estimate of the total number of breeding pairs on Skokholm, 1966-1969.

Locality	No. of birds ringed	No. of ringed breeders alive in 1969	No. of burrows located	No. of nights netting	Estimated no. of pairs	Min. no. present	Max. no. present
Walls of study area	1647	1074	230	108	405	320	500
Other walls	206	141	66	18	250	200	300
Inland rocky outcrops	73	45	4	6	100	80	120
Crab Bay shear-water colony	600	386	20	22	200	175	225
Main/Wall Rock shearwater colony	252	207	20	11	500	420	580
Quarry	2181	1387	180	29	2000	1650	2350
Quarry Point	918	385	30	7	300	250	350
Bluffs	435	224	30	4	300	250	350
Wall's End/ West Gate	697	293	35	12	225	195	290
Fossil Cove	60	48	25	1	60	50	70

Table 78 (... cont.)

Locality	No. of birds ringed	No. of ringed breeders alive in 1969	No. of burrows located	No. of nights netting	Estimated no. of pairs	Min. no. present	Max. no. present
Northern Rocks	748	328	40	10	250	200	300
North Haven Gut	19	13	20	1	40	30	50
Crab Bay Gut	316	173	50	5	150	125	175
Frank's Gully and Gallery Rocks	254	152	30	8	200	150	250
Frank's Point and Frank's Rocks	1130	338	35	10	300	225	375
Winter Gully	69	34	15	3	40	30	50
Dip Gully	345	82	12	5	75	50	100
Remainder of cliffs:							
i. Lighthouse to Purple Cove	219	50	26	1	200	150	250
ii. Purple Cove to North Haven	622	235	19	12	180	110	250
iii. North Haven to Winch	98	52	45	7	180	140	230
iv. Winch to Frank's Point	686	144	30	20	145	100	200

Table 78 (... cont.)

Locality	No. of birds ringed	No. of ringed breeders alive in 1969	No. of burrows located	No. of nights netting	Estimated no. of pairs	Min. no. present	Max. no. present
v. Frank's Point to Lighthouse	0	0	18	0	100	70	130
Totals	11,575	5,791	980	-	6,200	4,970	7,495

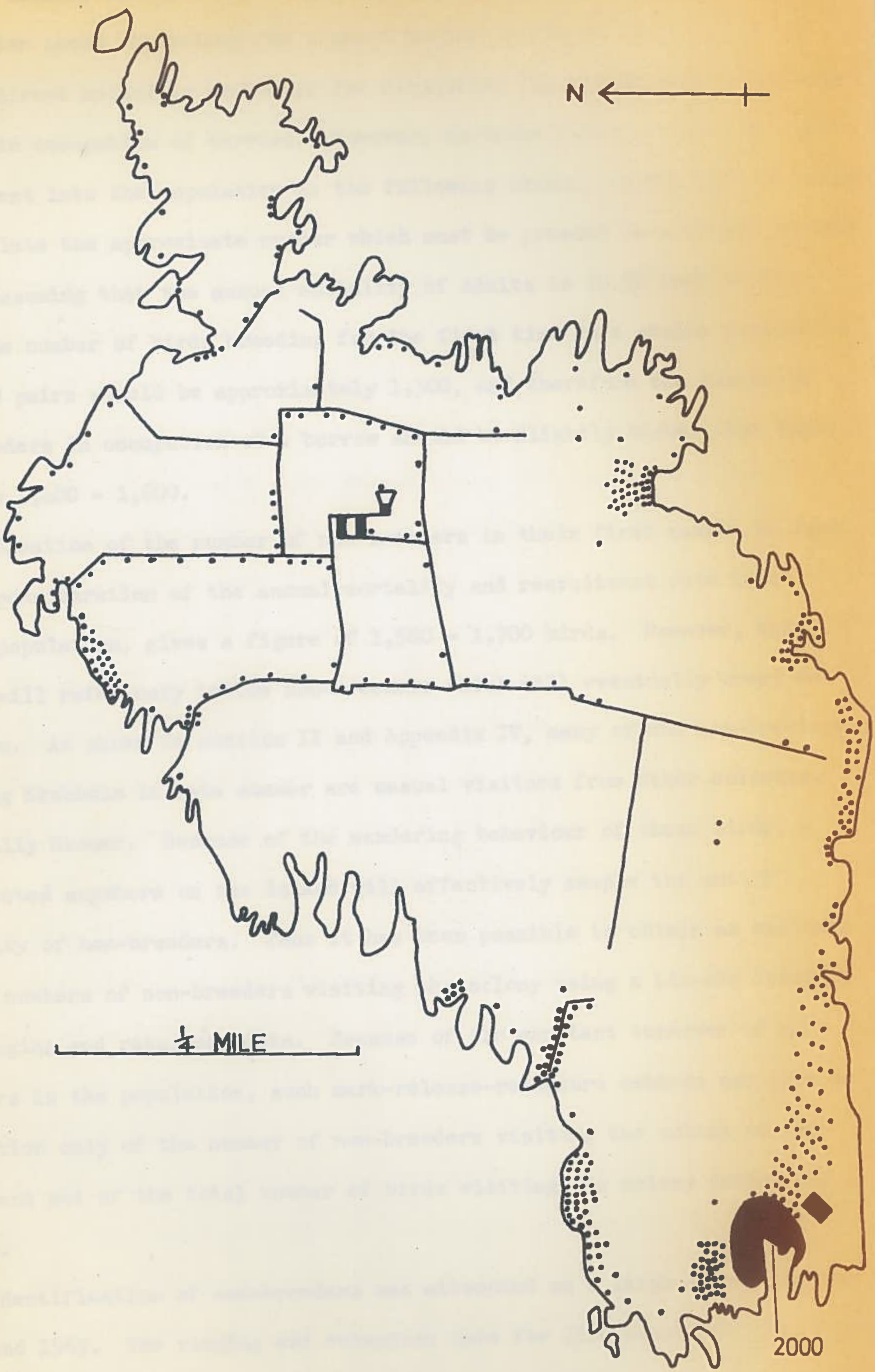


Figure 27. Approximate distribution of breeding pairs of Storm Petrels on Skokholm.

Each dot represents ten pairs.

during a short period in late summer. In their second season on land, non-breeders usually occupy a burrow for several weeks in June and July, and then wander about the colony for a short period in August.

No direct method is available for estimating the number of non-breeding petrels in occupation of burrows. However, as these birds account for the recruitment into the population in the following season, it has been possible to calculate the approximate number which must be present in a stable population. Assuming that the annual mortality of adults is 10.5% (see section III), the number of birds breeding for the first time in a stable population of 6,200 pairs should be approximately 1,300, and therefore the number of non-breeders in occupation of a burrow should be slightly higher than this; probably 1,400 - 1,600.

Estimation of the number of non-breeders in their first season on land, from a consideration of the annual mortality and recruitment rate in a stable population, gives a figure of 1,500 - 1,700 birds. However, this figure will refer only to the non-breeders which will eventually breed on Skokholm. As shown in section II and Appendix IV, many of the non-breeders visiting Skokholm in late summer are casual visitors from other colonies, especially Skomer. Because of the wandering behaviour of these birds, a net erected anywhere on the island will effectively sample the entire community of non-breeders. Thus it has been possible to obtain an estimate of the numbers of non-breeders visiting the colony using a Lincoln Index on the ringing and recapture data. Because of the constant turnover of non-breeders in the population, such mark-release-recapture methods can give an indication only of the number of non-breeders visiting the colony at one time, and not of the total number of birds visiting the colony during the season.

Identification of non-breeders was attempted on a large scale only in 1968 and 1969. The ringing and recapture data for 1968 suggested that there were approximately 1,800 non-breeders at the colony in late July, 3,900 in the second half of August, and 1,600 in early September. In 1969, the figures were 2,800 - 3,100 in late July, and 2,800 in late August and early September. Since most of the non-breeders present in the second half of July have left the colony by the end of August, it would appear that not less than 4,000 - 5,000 non-breeders visited Skokholm during each of these two years. It was argued that a stable population of 6,200 pairs should contain only about 1,500 - 1,700 non-breeders in their first season at the colony. The total number of non-breeders without burrows will be slightly higher than this, since there will be some birds which are unable to obtain a burrow in their first season of prospecting, and must therefore spend two seasons as wandering non-breeders. However, it is clear that at least half of the 4,000 - 5,000 wandering non-breeders visiting Skokholm each year are casual visitors from other colonies.

The total community of Storm Petrels on Skokholm reaches a peak in late July and early August, after the first influx of wandering non-breeders, and before the failed breeders and non-breeders with burrows have started to leave. Assuming a breeding population of 6,200 pairs, at its peak the community will contain 12,400 breeding birds, 1,400 - 1,600 non-breeders with burrows, and 3,000 - 5,000 wandering non-breeders, i.e. about 17,000 - 19,000 birds. The size of the community has also been calculated from the total ringing and retrapping effort. During the four seasons 1966 - 1969, a total of 11,575 birds were ringed, and a further 638 birds, which had been ringed before 1966, were retrapped. Allowing for the mortality of birds ringed prior to 1969, it has been estimated that about 11,200 birds ringed on Skokholm were alive in 1969. Probably about 2,000 of these were ringed as casual visitors from other colonies, and were therefore not available for recapture on Skokholm in 1969. Thus an estimated 9,000 ringed birds should have been present at the Skokholm colony in 1969. The recapture rate in 1969 suggested that by the end of the year, about half of the island's breeding birds had been ringed, and likewise that about half of the non-breeders visiting the colony in that season had been ringed. This suggests a total community of about 18,000 birds, which is taken as evidence that the estimate of 6,200 pairs for the breeding population is probably considerably more accurate than the limits of 5,000 and 7,500 imply.

<u>The source of the strange non-breeders visiting the Skokholm colony</u>

It appears that between 2,000 and 3,000 of the non-breeders visiting the Skokholm colony during late summer are visitors from other colonies, wandering during their first season on land. As shown in section II, there is considerable, and perhaps total, intermingling of the populations of wandering non-breeders on Skokholm and the nearby island of Skomer. However, the size of the Storm Petrel colony on Skomer (500 - 1,000 pairs, see appendix IX) is insufficient to account for more than 100 - 300 of the strange non-breeders visiting Skokholm each season.

The colony of Storm Petrels on the island of Bardsey, 75 miles to the north-north-east, is very small. Breeding was first proved in 1953 (Norris 1954) and since then, only about a dozen burrows have been discovered. Apparently much of the island is unsuitable for petrels, lacking boulder beaches and scree slopes (M. P. Harris, pers. comm.). Clearly this colony is not important as a source of visitors to Skokholm. The Storm Petrel colonies in the Isles of Scilly undoubtedly provide some of the wandering non-breeders visiting Skokholm. Parslow (1965) suggested a figure of 1,500 pairs for the colony on Annet, and mentioned smaller numbers on several of the small outlying islands. The large colony on Burhou in the Channel Islands probably accounts for many of the non-breeders on Skokholm. Arthur (1962) estimated the total community at something over 10,000 individuals, although his estimate, based on a mark-release-recapture method, may be grossly inaccurate. Breeding of the Storm Petrel has been reported on a number of islands off the coast of Brittany, but the total population appears to be relatively small.

Probably the most important source of the visitors to Skokholm is the islands off the coasts of Cork and Kerry, in south-west Ireland. Ruttledge (1966) listed large colonies of Storm Petrels on Great Skellig (4,000 pairs), Inishvickillaun (7,600 pairs), Inishtooskert (3,000 - 5,000 pairs), Inishnabro (1,000 pairs), and Inishtearaght ("vast numbers"), and small colonies on a number of other islands. Although most of these estimates are little more than guesses, it is clear that a very large number of petrels breed in the area. The fact that only one bird ringed on Skokholm has subsequently been recovered at an Irish colony is likely to be a consequence of the small amount of ringing at these colonies, rather than a lack of movement between these colonies and Skokholm.

Colonies further to the north, in northern Ireland, Scotland, and the Faeroes, probably provide very few of the non-breeders visiting Skokholm, since as yet there has been no proven case of movement in either direction between Skokholm and any of the well-worked Scottish colonies.

Previous estimates of the Storm Petrel colony on Skokholm

The present estimate of about 6,200 pairs of Storm Petrels breeding on Skokholm is far in excess of any previously made. In 1931 and 1932, Lockley (1932) attempted to census the population by counting occupied burrows. He wrote as follows: "to arrive at an estimate of the number of nests on the island, as far as possible those in the hedge-walls were counted carefully. They amounted to just over two hundred. The nests on the cliffs and elsewhere were roughly calculated at 300, giving a minimum of 500 breeding pairs." Lockley and Buxton (1947) considered that the population in the 1940s numbered about 600 pairs, but gave no indication of how this estimate had been obtained. In 1949, Conder and Keighley (1950) attempted to census the population by counting occupied burrows which they located by smell. Their results agreed with those of Lockley, and they concluded that the population numbered about 500 pairs. Davis (1957) did not attempt any detailed census, but agreed that the population was in the region of 500 pairs in the mid-1950s. He added that the influx of non-breeders into the population in late summer might raise the total community to about 1,500 birds. No further references to the number of Storm Petrels on Skokholm appeared in the literature until 1964, when Harris (1964) concluded that since 913 individuals had been mist-netted during the 1963 breeding season, the population was probably much higher than had previously been thought.

Thus from 1931 until at least 1956, there was nothing in the literature to suggest that more than 500 or 600 pairs of Storm Petrels bred on Skokholm. It would therefore appear that the population has increased by about tenfold in a period of about twenty years. However, it seems likely, for a variety of reasons, that the earlier estimates were grossly inaccurate. The censuses were based on counts of occupied burrows which were located by listening for churring birds, or sniffing for the distinctive aroma of petrels. As the present study has shown, both of these methods are very inefficient in areas which are easily investigated, such as the walls, and totally impracticable in the dense colonies amongst boulders. Furthermore, it seems that previous workers have assumed that the majority of petrels breed in the walls, or under boulders on the top of the cliffs, there being practically no references to petrels breeding in boulder beaches or scree slopes low down on the cliffs. The subcolony in the Quarry, numbering about 2,000 pairs, appears to have been completely overlooked. Clearly, there had been little, if any, exploration of the cliffs at night during the period of peak churring in June.

Until the late 1950s, no efficient means were available for catching large numbers of petrels in flight. Consequently, it was not possible to census the population by mark-release-recapture methods. However, from the advent of mist-nets in 1958 until 1965, netting was attempted at only eleven sites, seven of which were by the walls around the observatory, and no attempt was made to net low down on the cliffs, or at the bottom of any of the bays. Consequently, most of the major breeding areas of the petrels were never visited.

Two pieces of evidence suggest that the breeding population of Storm Petrels has not changed markedly since the first censuses were made. Firstly, counts of occupied burrows made by Lockley in 1931 and 1932 and by Conder and Keighley in 1949 are similar to those made in the same areas during the present study. Lockley, in two seasons of searching, located just over 200 burrows in the walls, as compared with about 300 in the four seasons of the present study, whilst Conder and Keighley found about 30 burrows in a heap of boulders at Quarry Point, the same number as was found between 1966 and 1969. Mist-netting at this site during the present study suggested that the actual number of pairs breeding in the boulders was about 300.

The second source of evidence comes from a comparison of the average rate of capture at mist-netting sites used regularly since 1958. The comparable catch-sizes and rates of capture are summarized in table 79. These figures certainly do not indicate any large increase in the abundance of petrels in the ten years 1958 - 1967, especially when it is remembered that the rates of capture obtained during the present study were often enlarged by the use of an amplified tape-recording of petrel churring at the net site, and by the use of a greater length of net than in previous years. The table reveals quite clearly a drop in the rate of capture at those sites

Table 79.

Average rate of capture of Storm Petrels at seven net-sites on Skokholm in years 1959-1964 compared with average rate of capture during period 1966-1969.

		1959 - 1964			1966 - 1969		
Net-site	Year	No. of nights netting	Total catch	No. of birds /hour	No. of nights netting	Total catch	No. of birds /hour
Crab Bay	1959	9	266	10.0	22	1220	9.2
Quarry	1960	1	54	16.7	28	3104	18.5
Crab Bay	1961	3	78	8.7	22	1220	9.2
Main	1962	2	119	10.0	5	230	7.7
Winch	1963	10	337	8.7	12	189	2.7
Gantry	1963	5	194	9.2	17	800	7.8
North Pond	1963	4	77	6.3	9	344	6.3
Observatory	1963/64	5	75	5.0	13	213	2.7

which were used most frequently, viz. Winch and Observatory. A similar decline in the rate of capture at sites used regularly was noticed at several localities during the course of the present study, suggesting that the birds breeding locally were learning the whereabouts of the nets, and avoiding them on their way in to their burrows.

To sum up, it appears that the earlier workers had obtained very low estimates for the number of Storm Petrels breeding on Skokholm because of their incomplete coverage of the island, and ignorance of the preferred breeding sites and whereabouts of the main concentrations of petrels. It is concluded that there is no valid reason for believing that the population has increased since the first censuses were made. Indeed, there is some evidence which suggests that the population has remained relatively stable for at least twelve years up to 1969. That the early estimates were so inaccurate merely emphasises the difficulties encountered in estimating petrel populations.

Appendix IX

The size of the colony of Storm Petrels on Skomer

For a long time it has been known that Storm Petrels breed on the island of Skomer, two and a half miles to the north of Skokholm. Apart from casual observations at night and a few limited searches for occupied burrows, no work has been done at the colony and, prior to this study, no mist-netting had been attempted. The population has always been regarded as very small, probably in the region of 20 - 30 pairs (Buxton and Lockley, 1950). However, mist-netting carried out during the present study has revealed that the colony on Skomer is very much larger than was previously thought.

The island was first visited on 2nd August 1969 and mist-nets were erected in a deep gully, known as Tom's House, near the south-west tip of the island. The catch of 174 birds, although including a number of visiting non-breeders from Skokholm (see section II), contained about 80 birds which were thought, from the condition of their brood patches and presence of food in the stomach, to be breeding birds or non-breeders with burrows. In view of the success of this first visit, netting was again attempted on Skomer between 18th and 24th August 1969 at five sites around the island. Although the weather conditions were poor for netting, a total of 240 birds were trapped, including at least 90 breeding birds. To establish more precisely the number of breeding birds in certain areas, the colony was again visited on 6th and 7th June 1970, at a time when only breeding birds and non-breeders prospecting for burrows are present at the colony. Netting was carried out at four sites including Tom's House, and two sites which had not been visited in 1969. A total of 194 birds were trapped, the catches at each site ranging from 44 to 57 birds.

A crude mark-release-recapture analysis of the ringing and retrapping data from Tom's House and another site which had been visited in both 1969 and 1970 suggested breeding populations of 140 and 50 pairs respectively in the areas covered by the nets. There can be little doubt that the other two sites visited in 1970 held at least 50 pairs each, and that the three sites visited only in 1969 held between 10 and 30 pairs each. Thus it seems that at least 350 pairs of Storm Petrels breed in the seven sites visited in the two years. A number of other suitable areas for petrels were discovered during the exploration of the cliffs by day, including a large scree slope at the west end of the island, which was found to be inaccessible without the aid of a rope. Consequently, the figure of 350 pairs must be taken only as an absolute minimum for the breeding population on Skomer.

Until the entire island has been explored thoroughly and the distribution and relative densities of breeding petrels determined, it is not possible to give any meaningful estimate of the size of the Skomer colony. However, I would tentatively suggest that the colony contains not less than 500, and possibly more than 1,000, pairs of Storm Petrels. What is clear is that the colony is considerably smaller than that on Skokholm. Considering the large size of Skomer (approximately three times as large in acreage as Skokholm), this might at first sight seem surprising. However, Skomer differs from Skokholm geologically in being composed principally of igneous rocks. These hard rocks are less prone to crumbling than the Old Red Sandstone of Skokholm and as a consequence there are relatively fewer scree slopes, crevices in the cliffs, and boulder beaches, than on Skokholm. Furthermore, avian predators are considerably more numerous than on Skokholm. there being over 200 pairs of Great Black-backed Gulls <u>Larus marinus</u>, several pairs of Short-eared Owls <u>Asio flammeus</u>, and until recently, one or two pairs of Little Owls <u>Athene noctua</u>. All three species have been recorded taking large numbers of Storm Petrels (see section III). This is probably the explanation for the absence of petrels from the walls on the top of the island, many of which would appear to be suitable for breeding.

APPENDIX TABLES

Appendix table 1.

Duration of pre-egg stage of Storm Petrel

Burrow no.	Year	1st visit (p.m.)	Egg laid (a.m.)	Duration of stage (days)	Status of pair c.f. previous year
2	1967	2 Jun	26 Jun	23	Same pair
16	"	29 Apr	23 Jun	54	Probably same pair
22	"	9 May	25 Jun	46	do.
23	"	3 Jun	30 Jun	26	Pair breeding for first time
37	"	9 May	25 Jun	46	One of pair new
61	"	13 May	17 Jun	35	?
78	"	1 Jun	7 Jul	35	Same pair
80	"	24 May	24 Jun	30	do.
86	"	27 May	27 Jun	30	do.
88	"	6 May	30 Jun	54	Experienced pair from nearby burrow
4	1968	9 May	30 Jun	51	Probably same pair
7	"	14 May	4 Jul	50	One of pair new
9	"	13 May	22 Jul	60	Same pair
13	"	14 May	24 Jun	40	do.
14	"	30 Apr	25 Jun	55	do.
18	"	13 May	30 Jun	47	do.
23	"	18 May	1 Jul	43	do.
24a	"	13 May	9 Jul	56	do.
30	"	14 May	21 Jun	37	Pair breeding for first time
33a	"	12 May	28 Jun	46	Same pair
34	"	18 May	28 Jun	40	do.
37a	"	16 May	28 Jun	42	One of pair new
60b	"	14 May	24 Jun	40	Same pair
72	"	12 May	20 Jun	38	do.
74c	"	11 May	22 Jun	41	do.
89	"	16 May	29 Jun	43	Pair breeding for first time

Average duration of the pre-egg stage: 42.7 ± 9.4 days

Appendix table 2

Frequency of night visits to burrow, in pre-egg stage of Storm Petrel, as determined from checks at entrance of burrow.

	Days before laying						
	70-61	60-51	50-41	40-31	30-21	20-11	10-1
Nts. possible	230	230	230	230	230	230	230
Nts. with visits	2	10	46	104	144	164	155
% of nts. visited	1	4	20	45	63	71	67

Appendix table 3

Day-occupation in pre-egg period of the Storm Petrel, at burrows in which pair remained intact from first occupation to laying.

1967					1968				
Burrow no.	Both birds	One bird	Total days	Duration of pre-egg stage	Burrow no.	Both birds	One bird	Total days	Duration of pre-egg stage
2	2	4	6	24	3	4	8	12	
4	4	1	5		4	1	4	5	51
7	5	0	5		7	3	4	7	50
8	2	1	3		9	2	8	10	60
9	4	6	10		13	3	2	5	40
12	4	1	5		16	3	1	4	
13	4	0	4		18	2	8	10	47
14	2	5	7		20c	1	1	2	
16	3	3	6	54	21	4	3	7	
18	6	5	11		23	1	0	1	43
22	2	2	4	46	24a	2	1	3	56
31	3	3	6		24b	1	2	3	
34	1	4	5		30	2	0	2	37
67	4	3	7		34	1	4	5	40
72	1	3	4		37a	1	2	3	42
78	4	1	5	35	60b	6	1	7	40
80	0	1	1	30	72	1	2	3	38
88	1	3	4	54	74c	4	1	5	41
					89	6	3	9	44
		Totals for both years				100	101	201	

Appendix table 4

Frequency of day-occupation in pre-egg stage of Storm Petrel.

Days before laying	Days in occupation	Possible days	%
60-56	1	185	1
55-51	0	185	0
50-46	2	185	1
45-41	5	185	3
40-36	6	185	3
35-31	16	185	9
30-26	22	185	12
25-21	24	185	13
20-16	41	185	22
15-11	42	185	23
10-6	23	185	13
5-1	15	185	8

Appendix table 5

Laying season of Storm Petrel on Skokholm: 1954-1956 (from Davis, 1957) and 1966-1969.

	1954-56 (Davis)	1966	1967	1968	1969
Mean date of laying	23 Jun	18 Jun	26 Jun	26 Jun	26 Jun
5-day period during which most eggs laid (ending)	5 Jul	20 Jun	30 Jun	25 Jun	30 Jun
Earliest known egg	28 May	3 Jun	12 Jun*	11 Jun*	28 May*
Latest known egg	20 Aug	19 Jul	1 Aug	29 Jul*	1 Aug*
Spread of laying (days)	84	46	50	48	65
80% eggs laid in period	10 Jun-5 Jul	7 Jun-2 Jul	16 Jun-16 Jul	17 Jun-13 Jul	11 Jun-10 Jul

* female mist-netted with egg in oviduct.

Appendix table 6

Frequency of brooding of chick at 55 burrows of Storm Petrel.

a/ Frequency of brooding in relation to age.

	Age in days													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Number of chicks brooded	55	54	54	50	41	42	21	17	12	7	7	3	4	3
% brooded	100	98	98	91	75	76	38	31	22	13	13	5	7	5

b/ Number of days on which chick was brooded.

	Number of days brooded											
	1	2	3	4	5	6	7	8	9	10	11	12
Number of chicks	0	1	0	3	5	16	14	10	4	1	1	0
% of chicks	0	2	0	6	9	29	26	18	7	2	2	0

Appendix table 7

Frequency of feeding between hatching and day 60 at 54 burrows of Storm Petrel.

		Age of chicks						
		1-10	11-20	21-30	31-40	41-50	51-60	Total
1966	Nights available	76	80	80	86	88	81	491
	Nights fed	64	66	66	74	74	65	409
	%	90	83	83	93	93	78	83
1967	Nights available	111	175	187	192	205	208	1078
	Nights fed	89	129	143	156	171	160	848
	%	80	74	77	81	83	77	79
1968	Nights available	207	257	244	240	240	239	1427
	Nights fed	166	221	207	217	194	189	1194
	%	80	86	85	90	81	80	84
Total	Nights available	394	512	511	518	533	528	2996
	Nights fed	319	416	416	447	439	414	2451
	%	81	81	81	86	82	78	82

Appendix table 8

Condition of brood patch of Storm Petrels mist-netted at night: 1967-1968.

Date	Sample size	% downy	% losing down	% bare	% vasc.	% with old & new down	% growing down	% new down
Apr 21-30	12	100	0	0	0	0	0	0
May 1-10	68	71	28	2	2	0	0	0
May 11-20	201	37	62	2	2	0	0	0
May 21-31	659	28	58	15	7	0	0	0
Jun 1-10	231	8	60	32	5	0	0	0
Jun 11-20	396	9	41	50	11	0	0	0
Jun 21-30	512	2	29	69	12	0.2	0.4	0
Jul 1-10	738	1	25	71	13	0.7	2	0
Jul 11-20	665	1	20	70	13	3	7	0
Jul 21-31	509	0.8	15	68	6	4	16	0
Aug 1-10	796	0.4	25	34	10	6	31	0
Aug 11-20	762	0.1	17	24	2	13	44	2
Aug 21-31	472	0.2	11	15	5	15	52	7
Sep 1-10	220	0	3	5	1	15	49	29
Sep 11-20	227	0	3	2	1	10	41	44
Sep 21-30	0	-	-	-	-	-	-	-
Oct 1-10	53	0	0	0	0	0	17	83
Oct 11-20	0	-	-	-	-	-	-	-
Oct 21-31	18	0	0	0	0	0	0	100

Appendix table 9

Condition of brood patch of adult Storm Petrels mist-netted at night, including:

(a) all birds examined before 11th May, or after 30th September.

(b) all birds recaptured two or more years after ringing.

(c) all birds which regurgitated food.

Date	Sample	% downy	% losing down	% bare	% vasc.	% with old & new down	% growing down	% new down
Apr 21-30	12	100	0	0	0	0	0	0
May 1-10	68	71	28	2	2	0	0	0
May 11-20	44	39	59	2	5	0	0	0
May 21-31	201	19	64	17	9	0	0	0
Jun 1-10	71	3	58	39	9	0	0	0
Jun 11-20	97	0	44	56	8	0	0	0
Jun 21-30	75	0	28	71	16	0	0	0
Jul 1-10	130	0	16	78	19	0	5	0
Jul 11-20	79	0	6	89	20	0	5	0
Jul 21-31	60	0	2	63	17	0	35	0
Aug 1-10	105	0	2	24	12	1	73	0
Aug 11-20	48	0	2	10	6	2	83	2
Aug 21-31	236	0	0	10	2	0	77	13
Sep 1-10	233	0	0	0	1	0	51	49
Sep 11-20	123	0	0	0	0	0	35	65
Sep 21-30	0	-	-	-	-	-	-	-
Oct 1-10	53	0	0	0	0	0	17	83
Oct 11-20	0	-	-	-	-	-	-	-
Oct 21-31	18	0	0	0	0	0	0	100

Appendix table 10

Mean wing-lengths and weights of Storm Petrels mist-netted during breeding season.

Date of sample	Mean wing-lengths (in mms.)		Mean weights (in grams)	
	Sample size	Mean wing-length	Sample size	Mean weight
Apr 16-30	49	118.7	60	30.2
May 1-15	149	120.2	230	29.5
May 16-31	824	120.0	1008	29.1
Jun 1-15	458	120.1	617	29.2
Jun 16-30	404	119.8	315	27.8
Jul 1-15	1137	119.8	778	27.5
Jul 16-31	906	119.8	634	26.6
Aug 1-15	1464	119.4	673	26.2
Aug 16-31	1001	119.2	812	26.5
Sep 1-15	369	119.7	272	27.1
Sep 16-30	63	119.9	118	26.9
Oct 1-31	37	120.0	72	27.3
Totals	6861	119.7	5589	27.6

Appendix table 11

Occurrence of moult in mist-netted samples of Storm Petrels.

	--1966--		----	----	----	----	----	----	-1967-	----	----	----	----	----
	Primary		Primary		Secondary		Tail		Tail covt.		Body		Head	
Date	No*	%*	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Apr	-	-	41	2	-	-	41	22	41	3	41	0	41	0
May	-	-	55	4	-	-	55	2	55	2	55	0	55	0
May	-	-	420	1	-	-	276	1	276	0	276	0	276	0
Jun	-	-	117	0	-	-	117	0	117	0	117	0	117	0
Jun	-	-	295	0	-	-	295	1	295	1	295	0	295	0
Jul	-	-	233	1	233	52	233	1	233	13	233	0	233	4
Jul	-	-	338	1	338	52	338	6	338	65	338	0	338	8
Aug	414	10	111	3	111	44	111	14	111	96	111	14	111	22
Aug	582	15	713	9	494	41	521	50	538	95	438	45	513	21
Sep	115	39	147	19	147	43	147	75	147	99	147	67	147	14
Sep	51	61	19	26	19	53	19	90	19	90	19	63	19	16
Oct	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oct	-	-	11	91	11	64	11	73	11	100	11	100	11	9

Appendix table (... cont.)

	----	----	----	-1968-	----	----	----	----	----	----	-1969-		----	----
	Primary		Secondary		Tail		Tail covt.		Body		Primary		Secondary	
Date	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Apr	12	25	12	83	12	8	12	25	12	8	-	-	-	-
May	128	6	128	61	128	3	79	8	79	0	-	-	-	-
May	564	6	564	65	564	1	47	6	47	0	-	-	-	-
Jun	428	4	428	74	428	1	230	0	230	0	-	-	-	-
Jun	244	1	244	73	244	2	124	3	124	0	-	-	351	54
Jul	540	1	540	69	540	2	340	27	112	0	445	0	445	52
Jul	263	1	263	67	263	8	263	75	263	1	514	2	514	39
Aug	708	8	571	55	427	37	427	96	427	17	174	9	174	39
Aug	443	20	443	55	243	65	243	100	243	41	848	17	848	41
Sep	270	32	270	62	270	79	270	100	270	70	743	18	743	42
Sep	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oct	52	71	52	75	52	94	52	100	52	98	-	-	-	-
Oct	7	86	7	86	7	86	7	86	7	86	-	-	-	-

* Number of individuals checked.   * % of birds in moult.

Appendix table 12

Combinations of old feathers in wings with 2, 3, 4, and 5 unmoulted secondaries in Storm Petrel.

2 secondaries old (sample 1224)		3 secondaries old (sample 422)		4 secondaries old (sample 132)		5 secondaries old (sample 33)	
Old feathers	% with these old	Old feathers	% with these old	Old feathers	% with these old	Old feathers	% with these old
4. 7	3	4. 7. 8	7	4. 6. 8. 9	5	4. 7. 8. 9. 10	58
4. 8	5	4. 7. 10	9	4. 7. 8. 9	10	5. 6. 7. 8. 9	9
4. 9	4	4. 8. 9	12	4. 7. 8. 10	7	others	33
4. 10	4	4. 8. 10	5	4. 7. 9. 10	14		
7. 8	6	4. 9. 10	8	4. 8. 9. 10	18		
7. 9	6	7. 8. 9	15	7. 8. 9. 10	22		
7. 10	3	7. 8. 10	4	others	24		
8. 9	49	7. 9. 10	5				
8. 10	7	8. 9. 10	18				
9. 10	10	others	18				
others	3						

Appendix table 13

Combinations of old feathers in wings of non-breeding Storm Petrels in interrupted secondary moult.

1 secondary old (sample 81)		2 secondaries old (sample 89)		3 secondaries old (sample 23)		4 secondaries old (sample 10)	
Old feathers	% with these old	Old feathers	% with these old	Old feathers	% with these old	Old feathers	% with these old
1	0	3. 9*	1	4. 7. 8	4	4. 7. 8. 9	40
2	0	4. 7	2	4. 7. 9	4	4. 7. 9. 10	20
3	0	4. 9	1	4. 7. 10	9	4. 8. 9. 10	10
4	4	4. 10	2	4. 8. 10	4	7. 8. 9. 10	30
5	0	7. 8	7	4. 9. 10	9		
6	0	7. 9	2	7. 8. 9	4		
7	6	7. 10	5	7. 8. 10	13		
8	15	8. 9	71	7. 9. 10	13		
9	54	8. 10	3	8. 9. 10	39		
10	21	9. 10	6				

* The single exception to the basic sequence of moult (see text).

Appendix table 14

Active secondary moult in Storm Petrels in autumn 1967-1968.

Ring no. of bird	Date of capture	Wing	Secondary scores												
			1	2	3	4	5	6	7	8	9	10	11	12	13
646550	21.10.67	Right	0	0	0	0	0	0	0	0	0	0	1	0	0
		Left	0	0	0	0	0	0	0	2	0	0	0	3	3
687387	22.8.68	Right	0	0	0	0	0	0	6	6	0	4	0	0	0
		Left	0	0	0	0	0	0	0	5	0	5	0	0	0
687743	28.8.68	Right	0	0	0	0	6	0	0	0	0	7	1	0	0
		Left	0	0	0	0	7	0	0	0	0	3	5	0	0
687424	6.9.68	Right	0	0	0	0	4	0	0	0	0	0*	4	5	0
		Left	0	0	0	0	0	0	0	0	0	0*	0	0	0
687918	11.9.68	Right	0	0	0	0	2	0	0	0	5	4	0	2	7
		Left	0	0	0	0	2	0	0	2	0	2	0	0	0
do.	4.10.68	Right	0	0	0	0	4	0	0	0	7	7	0	3	7
		Left	0	0	0	0	5	0	0	6	0	6	0	3	0
698006	3.10.68	Right	0	0	0	0	0	0	5	0	4	0*	7	2	2
		Left	0	0	0	0	0	0	0	0	0*	0	6	0	7
646060	4.10.68	Right	0	0	0	2	0	0	0	6	0	0	5	0	5
		Left	0	0	0	1	0	0	0	0	4	0	5	0	2
675419	25.10.68	Right	0	0	0	0	0	0	0	0	0	0	7	0	0
		Left	0	0	0	0	7	0	0	0	0	0	7	0	0
698023	25.10.68	Right	0	0	0	0	3	0	0	0	0	0	0	0	0
		Left	0	0	0	0	0	0	4	0	0	0	0	0	0
2112638	30.8.69	Right	0	0	0	0	2	0	1	0	0	0	4	0	0
		Left	0	0	0	0	1	0	0	0	0	0	5	0	0
2112841	2.9.69	Right	0	0	0	0	1	0	0	0	0	0	0	3	0
		Left	0	0	0	0	1	0	0	0	0	0	0	4	0

* very old feather, i.e. unmoulted feather of previous generation.

Appendix table 15

Sequences of replacement of feathers in early stages of tail moult of Storm Petrel.

One feather in moult		Two feathers in moult		Three feathers in moult	
Feather in moult	% tails examined*	Sequence of moult	% tails examined*	Sequence of moult	% tails examined*
1	67	1 - 2	30	1 - 2 - 6	59
2	20	1 - 3	22	1 - 3 - 6	18
3	9	1 - 6	18	1 - 6 - 2	12
6	2	2 - 6	10	2 - 3 - 6	6
4	1	3 - 6	6	3 - 1 - 6	6
5	1	2 - 1	4	others	0
(sample = 706)		1 - 4	2	(sample = 17)	
		3 - 1	2		
		3 - 2	2		
		others	4		
		(sample = 135)			

* Because of asymmetry in some tails, each half of a tail has been regarded as one tail.

Appendix table 16. A model for the limitation of a petrel population by competition for nest-sites.

	Optimal sites (4,300)	Suboptimal sites (unlimited)
Breeding success (young fledged per pair)	0.5	0.45
Survival of young from fledging to prospecting	45%	45%
Mortality in year of prospecting	12%	17%
Annual mortality of adults	9%	10%
Young fledged per year	2150	45 (per 100 pairs)
Young returning as prospecting non-breeders	968	20.3
Young surviving to breeding age	852	16.8
Losses of adults per year	774	20
Surplus/deficit in population	+ 78	- 3.2
Surplus surviving after second year of prospecting (in suboptimal sites)	64.5	

Hence a surplus of 64.5 breeding birds enter population in suboptimal sites each year.

Population will stablize when deficit from population breeding in suboptimal sites is equal to immigration of breeding birds from optimal sites, i.e. when population in suboptimal sites is 2,020 pairs $(\frac{64.5}{3.2} \times 100)$

Hence total population will stabilize at 6,320 pairs.

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Note: Between 1967 and 1969, an average of 94 petrel corpses were found on the top of the island each year. Therefore probably at least 100 were killed each year. About 70 were thought to be adults, the rest mainly prospecting non-breeders. About 2,000 pairs breed on the top of the island. Therefore, mortality due to predation is sufficient to account for 1.75% adults, and 6.2% prospecting non-breeders. (It has been assumed that the mortality of adults in suboptimal sites is 1% greater than that of adults in optimal sites, and that of prospecting non-breeders, 5% greater than that of the same class of birds in optimal sites.)

Birds in suboptimal sites are thought to have lower breeding success than birds in optimal sites because of interference from shearwaters, rabbits and Puffins. (Birds breeding in the walls, where there are few shearwaters and rabbits, and no Puffins, are probably almost as successful as birds in optimal sites.)

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