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THE BIOLOGY OF WILSON'S STORM PETREL,  
*Oceanites oceanicus* (Kuhl), AT SIGNY ISLAND,  
SOUTH ORKNEY ISLANDS

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*British Antarctic Survey*



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*The authors would like to dedicate this paper to Dr. Brian Roberts, Research Associate of the Scott Polar Research Institute, Cambridge, in appreciation of his invaluable pioneer study of Wilson's petrel and his continuing work in the field of Antarctic ornithology.*

# THE BIOLOGY OF WILSON'S STORM PETREL, *Oceanites oceanicus* (Kuhl), AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS

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## ABSTRACT

OBSERVATIONS on the ecology of Wilson's storm petrel at Signy Island over three seasons are described and compared with studies of storm petrels in other parts of the world. The reproductive cycle is similar to that of other storm petrels, but the abundant food supplies in Antarctic waters in summer may allow *O. oceanicus* to form a proportionately large egg more quickly, incubate in shorter spells and allow the young to grow faster. Egg-laying and breeding success are greatly influenced by snowfall.

A detailed account of the breeding cycle is given. Before laying, females depart to sea for a variable period (mean 11 days) while the males maintain nightly visits to the nests. Individual females vary from one year to another in the time they take to form the egg; this is partly responsible for the spread in egg-laying. It is shown that, at Signy Island, eggs are laid up to 1 month later than at higher latitudes. The average incubation period lasts 38–44 days, but it may be lengthened by temporary desertions. Chicks are brooded for up to 3 days, and finally leave the nest at an average age of 60 days.

Overall breeding success during the study period was very low. 65 per cent of eggs laid failed to hatch, 58 per cent through chilling or desertion by the parents when nests became blocked by snow. Drift snow blocking the nests prevented some females from laying and, in two seasons, entombed chicks in the critical early stages before they had laid down fat reserves. 1966–67 was the most successful season, with 73 per cent of chicks hatched leaving the nest, whereas in the two subsequent seasons none was fledged.

The difficulties of estimating population size by mist-netting are discussed; non-random sampling invalidated the use of this method for *O. oceanicus*. However, a comparison of mist-net catches over the three seasons showed a 40 per cent decline in the number of birds in flight over the colony in 1967–68. Extrapolation from the study colony gave an estimated total population for the island of approximately 200,000 pairs.

Adult survival in a small sample of ringed birds was high—90·8 per cent per annum. Since the average output of young in the colony was not enough to offset the annual losses of adults, the population may be maintained by immigrants. The main causes of adult mortality are discussed.

Seasonal variation in body weight was marked, culminating in a rapid increase at the end of the season, which was probably due to the deposition of fat reserves before migration. In the north–south cline of increasing wing/tail length, the South Orkney Islands population falls between those of South Georgia and continental Antarctica. Comparison of the measurements of different populations affords little justification for the recognition of more than the two zonal races *O. o. oceanicus* and *O. o. exasperatus*.

Skua predation forces *O. oceanicus* to breed in small crevices, but its weak build and inability to clear snow and ice make these inaccessible until the spring melt has cleared the nest. Hence, indirectly because

of its small size, *O. oceanicus* breeds later than the larger and more strongly built petrels on the island. Although this scarcely allows the breeding cycle to be fitted into the summer, egg-laying is not synchronous, mainly because of individual variability in the time needed to form the egg. This variability is presumably favoured by natural selection because in some years, heavy snowfalls in mid-season might kill the newly hatched chicks of early breeders, whereas eggs laid later would be only temporarily deserted. In other seasons, with no snow in mid-summer but substantial falls in autumn and early winter, the young of early breeders would probably survive while those of later breeders would perish.

Other topics discussed include brood-patch development, intermittent breeding, food and feeding, and moult.

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## I. INTRODUCTION

ALTHOUGH Wilson's storm petrel, *Oceanites oceanicus* (Plate I), is one of the smallest Antarctic sea birds, it is possibly the most abundant. Very large numbers breed on the Antarctic Peninsula wherever snow-free areas of land provide suitable nesting crevices. Smaller numbers are found around the coastline of continental Antarctica. Extremely little detailed breeding information was available until the publication in 1940 of Roberts' important study, carried out during the 1934-37 British Graham Land Expedition at the Argentine Islands, west Graham Land.\* Two notable discoveries had, however, been made earlier. The Antarctic expeditions at the turn of the century (e.g. Borchgrevink, 1901; Clarke, 1906) reported that breeding took place under severe climatic conditions, often with heavy mortality of eggs and young, while Murphy (1918) demonstrated that birds migrated from breeding grounds in the far south to wintering areas in the tropics and Northern Hemisphere.† Roberts' monograph synthesized all this earlier breeding information and also summarized fully all that was known concerning the remarkable migration of the species. Since then, the breeding ecology of *O. oceanicus* has received little more than cursory attention and the small amount of new data which has accumulated has not amplified or altered Roberts' (1940) findings in any important respect.

The breeding grounds listed by Roberts (1940) include the entire ice-free coastline of the Antarctic continent, South Georgia, the South Shetland Islands and South Orkney Islands south of the Antarctic Convergence, and Iles Kerguelen, the Falkland Islands and archipelagos of Tierra del Fuego and southern Chile to the north. In addition to these localities, breeding has now been confirmed for Heard Island (Downes and others, 1959), and the South Sandwich Islands (personal communication from P. J. Tilbrook), but there is still no unequivocal proof of breeding for Bouvetøya (Holgersen, 1945) and Iles Crozet (personal communication from Dr. J. Prévost). Paulian (1953) mentioned an adult female with well-developed gonads caught at night on board ship off Ile Amsterdam but, as he saw no more birds during a year's residence on the island, regular breeding seems most unlikely. *O. oceanicus* has not yet been recorded from Marion or Prince Edward Islands or their immediate vicinity (personal communication from E. M. van Zinderen Bakker, Jr.).

The study described in this paper was carried out at Signy Island, South Orkney Islands (lat. 60°43'S., long. 45°38'W.), the main centre for biological research by the British Antarctic Survey since 1962. The work covered the three seasons between December 1966 and April 1969, and was carried out by both authors in 1966-67 and 1967-68 and by D.W.B. alone in 1968-69. Although many nests at Signy Island were situated beyond reach within deep fissures and holes between boulders, enough were accessible to make detailed observations feasible. Birds were readily extracted from holes using a miniature "puffin hook", about 10 cm. long made of fine flexible wire. Over 70 accessible sites were found and their occupants ringed in 1966-67. Nests were examined twice daily (around noon and around midnight, local time) during the pre-egg and incubation stages from November to March, and daily until mid-May during the development of the young. As described in a previous paper on the black-bellied storm petrel, *Fregetta tropica* (Beck and Brown, 1971), members of the pair were distinguished by spots of yellow or blue quick-drying paint applied to the forehead. Sexing was by relative cloaca size, confirmed wherever possible by the condition of the cloaca after egg-laying (Serventy, 1956). Unlike British storm petrels, *Hydrobates pelagicus* (Davis, 1957), birds tolerated the considerable disturbance involved in extraction for marking, ringing and examination during the pre-egg period without deserting the nest. However, during incubation, birds were handled as little as possible as they tended to leave the egg unattended for long periods.

\*Since this report was completed, a detailed account of the reproductive cycle of Wilson's petrel at Terre Adélie in 1967-68 has been published by Lacan (1971). While the breeding data presented in this paper agree generally with our findings at Signy Island, there are some important differences. Birds at Terre Adélie lay approximately 3 weeks earlier, incubate in shorter spells of just over 1 day and the fledging period is considerably shorter (mean period at Terre Adélie 48 days; mean period at Signy Island 60 days). The mean maximum weight reached by chicks at Terre Adélie is also slightly higher (76 g.) than at Signy Island (73 g.). Overall breeding success was 31 per cent, similar to the highest success rate (33 per cent) in 1966-67 at Signy Island.

†After this paper had been completed news was received that a Wilson's petrel (ring number BB18083) ringed at Signy Island on 3 February 1970 had been recaptured 4 months later near Ambrose Channel light vessel, off the coast of New Jersey State, U.S.A. This is the first recovery in winter quarters of a Wilson's petrel ringed in the Antarctic.

In April 1967, marker stakes at 20 nests were fitted with 20 cm. engraved metal scales (Plate IIIa and b); these provided information on seasonal snow accumulation and dispersal. This information was used to obtain an index of snow levels throughout the colony. When the weather permitted during December and January, mist-nets were used to capture birds flying over the breeding colony at night. These birds provided weights and measurements and information on development of the brood patch.

## II. HABITAT AND NEST SITE

SIGNY ISLAND, the fourth largest island in the South Orkney Islands group, is almost 20 km.<sup>2</sup> in area, with a rugged hilly terrain which rises to a maximum elevation of 276·5 m. The main features of the island have been described by Holdgate (1967). Approximately half of the island's surface is free of ice and snow in mid-summer, the remainder being covered by a permanent ice cap. Despite its northerly position, the climate is distinctly polar, owing to the dominating influence of the Weddell Sea, and it is typical of the maritime Antarctic zone, as defined by Holdgate (1964). With frequent precipitation, almost invariably falling as snow, and with mean temperatures for the warmest month (February) of about 0° C and for the coldest month (July) approximately -10° C, the climate resembles that of the northern part of the Antarctic Peninsula, approximately 600 km. to the south-west. Strong westerly and north-westerly winds predominate throughout the year and the frequency of complete cover by low cloud is high.

The study area at Signy Island consisted of low-lying expanses of broken rock and moss slopes at the head of Factory Cove (Fig. 1), extending in an arc from immediately behind the present British Antarctic Survey station huts to include some of the steeper scree slopes at the foot of Factory Cove bluffs (Plate IIa and b). The ground occupied by the colony sloped toward the north and west but it was sheltered from prevailing winds by the high ground on the western side of the cove, and from easterlies by the ridge culminating in Observation Bluff.

The area behind the station huts contained a fairly localized colony, bounded on the south and east by stony slopes offering few nest sites and on the north by the sea and station huts. Approximately 275 m. to the south-west, this colony is linked to the larger populations inhabiting Factory Cove bluffs, but mist-netting showed that there was scarcely any interchange of breeding or visiting birds between the two areas. Some work on *O. oceanicus* has been carried out in this same colony in earlier years. In 1960-61, R. Pinder marked 25 accessible sites behind the old station hut and ringed their occupants. Some recoveries were made at these sites in subsequent seasons but by 1966, only six sites remained occupied, the others having been deserted or destroyed by the increased traffic and building operations associated with the expansion of the station in 1963-64. However, a number of birds from these disused sites were known to have dispersed to nearby holes or were known from mist-netting to be still breeding within the general area of the colony although their nests were not found.

Mist-net samples suggested that the population inhabiting Factory Cove bluffs was large, as the proportion of ringed to unringed birds caught was always low. Furthermore, the broken cliffs and scree falls offered many suitable nesting sites. Of 86 marked nests studied, 42 were located in the lower slopes of these bluffs while the remaining 44 were distributed over the flatter ground behind the station buildings.

As described by Roberts (1940), the usual nest site is a natural cavity beneath rocks. Almost all the nests studied at Signy Island were of this type, located in holes below large boulders, in fissures in rock walls or in the interstices between rounded boulders partly embedded in soil and moss (Plate IIIa and b). Most nest chambers were within 30 cm. of the surface and many were only 15 cm. from the entrance; in no case was the hole so shallow that the sitting bird could be seen by day without the aid of a torch. By contrast, at Adelaide Island, Marguerite Bay, many nests were seen in exposed situations in the lee of large boulders. In most cavities at Signy Island, where the floor was composed of soil or decomposed moss, a small cup had been excavated. Signs of excavation were seen at the beginning of the season, although the birds were rarely disturbed while digging or seen with soiled webs or claws (cf. the dove prion *Pachyptila desolata* (Tickell, 1962)). In some *O. oceanicus* nests, eggs were lost through partially sinking into the loose damp material on the nest floor and these eggs were usually deserted soon after the birds could no longer incubate satisfactorily.

Away from the vicinity of the station, nest-lining material was either not used or consisted of a few dead lichen stems, occasional feathers and fragments of moss, as mentioned by Roberts (1940). By con-

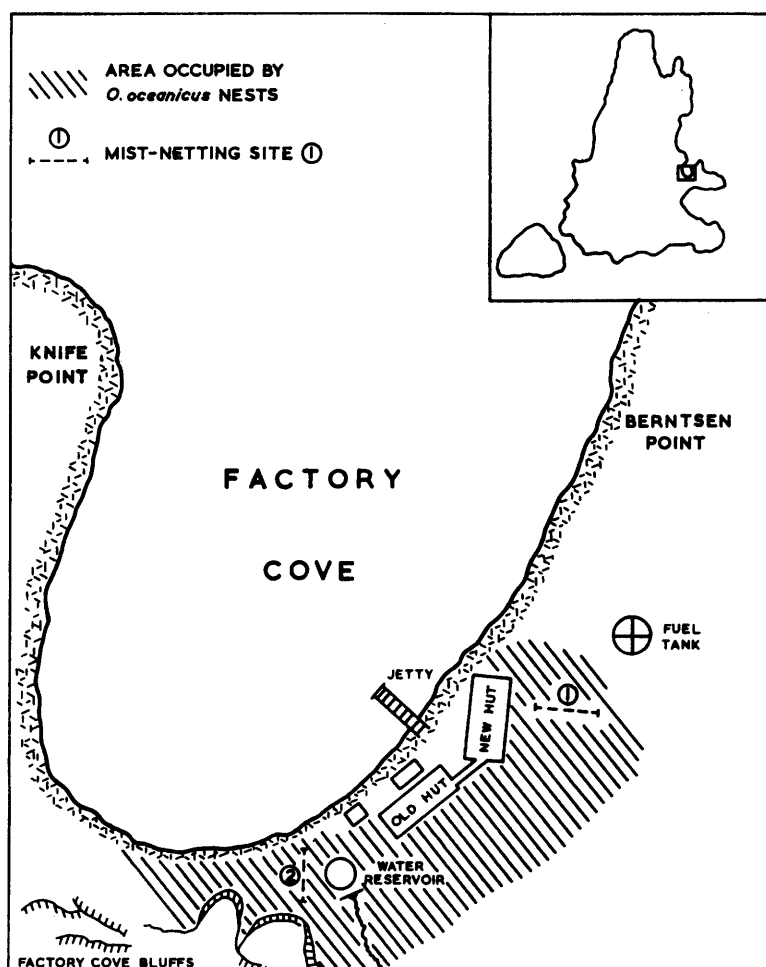


FIGURE 1

Sketch map of Factory Cove showing the study area. The inset shows the position of this area in relation to the rest of Signy Island.

trast, two nests among rocks close to the station hut contained substantial linings made up of scraps of paper, strands of wood wool from packing cases and pieces of celluloid film. All these items had been dragged into the holes by the birds and were not merely blown in by the wind. Pinder (1961) described similar appropriation of artificial materials during the 1960-61 breeding season, while in February 1969 at Adelaide Island, Marguerite Bay, several nests were lined with sledge-dog hair and in some cases a well-constructed cup had been formed.

In some parts of Signy Island, including Factory Cove bluffs, substantial moss mats up to 1 m. thick are found, but searching failed to locate any *Oceanites* nests in the natural cavities in these mats. This contrasts with the situation in the Argentine Islands, where Roberts (1940) found four colonies in burrows excavated in moss banks, and the accessibility of these nests was a major factor prompting his detailed study of the species there. Short burrows or natural cavities in soil are also used in the Cape Horn area (Reynolds, 1935), while burrows in volcanic ash were used at Deception Island, South Shetland Islands, in 1969.

In view of Allan's (1962) success with nest boxes for Madeiran storm petrels, *Oceanodroma castro*, on Ascension Island, ten similar nest boxes were constructed and sited beneath boulders in a scree slope on Factory Cove bluffs. The boxes were rectangular, approximately 30 cm. in length with a 10 cm. section, and were fitted with an inspection lid. Decomposed moss was put in to form a natural floor and a cup roughly fashioned at the rear of the box. However, in spite of the care taken in siting and construction, no birds used the boxes.

### III. THE BREEDING CYCLE

#### A. PRE-EGG STAGE

##### 1. Arrival

Wilson's storm petrels return to their Signy Island breeding grounds in November after a 7 month absence during the southern winter. First sightings over 18 seasons (recorded in unpublished station reports) are remarkably constant, falling mainly within the period 4–13 November. Exceptionally early individuals were reported on 26 October 1955 and 19 October 1965. The population returns gradually over the 2 weeks following the first arrivals and in most years a large proportion of birds has returned by the end of November. As in *Fregetta tropica* (Beck and Brown, 1971), there is no correlation between the date of arrival and the date at which the sea ice breaks out (cf. the cape pigeon, *Daption capensis* (Pinder, 1966)). As Roberts (1940) pointed out, there is little difference in arrival dates at the various breeding localities, despite wide differences in latitude and climate (Fig. 4). Hence, birds breeding at high latitudes on the Antarctic continent, e.g. Davis station, Princess Elizabeth Land, presumably leave their northern wintering grounds somewhat earlier than birds breeding 2,083 km. farther northward at Iles Kerguelen.

Wilson's petrels usually arrive at Signy Island during the main melt of winter snow and ice but, in some years, snowdrifts in low-lying sheltered parts of the study area persist until December or even January. This occurred in 1966–67 following a "hard" winter with deep snow; several pairs were prevented from breeding in that season because their holes remained blocked by snow after the normal egg-laying period. Generally, however, the bulk of the population arrives about the same time as, or after, burrows become accessible. During periods of rapid melt in November/December, a number of holes were made temporarily uninhabitable by melt water trickling through the nest chambers, but most sites were in well-drained situations and quickly dried out.

Most ringed birds were first recognized when they appeared in the nest at night. A few, however, were caught in mist-nets up to 1 week before (in one case 3 weeks before) their appearance in the nest hole. This confirms Roberts' (1940) opinion that birds do not visit their nests immediately on arrival. In 21 *Oceanites* nests where the pairs of the previous season were re-established, the male was identified first at 11 sites, the female at six sites and both birds appeared together for the first time at four sites. This preponderance of males in the first recorded arrivals is to be expected, since males spend more time at the nest than females during the pre-egg period and are thus more likely to be observed (see later). Mist-net totals during the first weeks of the arrival period showed males and females present in roughly equal numbers, so both sexes probably arrive on the breeding grounds at the same time.

#### NIGHT ATTENDANCE AT

	50/49	48/47	46/45	44/43	42/41	40/39
Number of possible night visits†	18	19	22	26	35	36
Percentage of night visits nests occupied*	0	0	9.1	11.5	14.3	5.6
Percentage of night visits when male present	0	0	4.5	7.7	8.6	2.8
Percentage of night visits when female present	0	0	0	0	5.7	0
Percentage of night visits when both male and female present						
Percentage of night visits when unidentified individuals present	0	0	4.5	3.8	5.7	5.6

\* Includes occasions when visiting birds present as well as rightful occupants.

† Nights of drift preventing view of occupants excluded from analysis.



Birds visited the nest in the pre-egg period almost exclusively at night, i.e. between the hours of 21.00 and 03.00 hr. local time in the near-continuous daylight in December. During the three seasons, birds were found in the nest during daylight hours in the pre-egg period on only two occasions. It is difficult to reconcile this dearth of day visits at Signy Island with Roberts' (1940) observations in the Argentine Islands where birds visited nests fairly frequently by day before laying. A possible explanation could be the apparent lack of predation on *Oceanites* by brown skuas, *Catharacta skua*, in the Argentine Islands, whereas skua predation at Signy Island may be a significant factor in the mortality of adult storm petrels (p. 39).

Details of night attendance before egg-laying by the occupants of 30 sites are shown in Fig. 2 and summarized in Table I. The earliest arrivals appeared in the nest holes more than 40 days before laying. At 26 sites the interval between first occupation of the nest by a known member of the breeding pair and the subsequent laying date was 34.4 days. Although arrival dates were similar, this interval was rather shorter in 1967-68 (mean 29.8, range 14-44 days) than in 1968-69 (mean 39.0, range 28-45 days). After the first visits to the nest, the frequency of visits by members of the pair and by strange individuals increased steadily, reached a peak about 2-3 weeks before laying and remained at a high level until the egg was laid. Visits by each sex individually and also by the pair reached a peak between 13 and 18 days before laying, and just before the female's pre-laying exodus (see later). Copulation almost certainly took place during this period before the female departed. It is also interesting to note that the visiting frequency by unidentified (mostly strange) individuals, after gradually rising in the weeks following arrival, dropped considerably over this same period of intense activity by the breeding pair prior to the female's departure. The number of such visits then rose once more toward the end of the exodus period when the breeding male was the sole occupant of the nest.

## 2. Pre-laying exodus

Throughout the pre-egg period, nest visits by the female were less frequent than those by the male (Table I). Visits by females fall off markedly between 5 and 12 days before laying, when they depart to sea in order to form the egg. The pre-laying exodus, which is characteristic of all the smaller Procellariiformes studied in sufficient detail, is not conspicuous in this species. This is because only one member of the pair departs and the spread in laying dates means that different pairs are not in phase. The mean length of the pre-laying exodus (interval between last recorded visit by the female and her return or subsequent laying date) at 31 nests was 10.7 days (range 6-18 days) over the three seasons. The exodus period or time taken to form the egg is evidently quite variable and, as shown in Table II, this variability does not appear to be correlated with either the date of laying or with the constancy of the pair-bond. At nests 2 and 31, where the same pairs bred in all three seasons, the exodus period varied between 8

## TABLE II. THE PRE-EGG PERIOD

Pre laying															
31	30/29	28/27	26/25	24/23	22/21	20/19	18/17	16/15	14/13	12/11	10/9	8/7	6/5	4/3	2/1
	36	37	39	40	38	39	40	42	43	46	55	55	56	57	56
3	38.9	56.7	53.8	70.0	42.1	64.1	82.5	83.3	72.1	56.5	70.9	61.8	57.1	57.9	50.0
0	27.8	45.9	33.3	52.5	36.8	46.1	70.0	64.3	51.2	50.0	56.4	50.9	48.2	50.9	42.8
8	16.7	21.6	25.6	27.5	23.7	38.5	37.5	57.1	39.5	21.7	20.0	10.9	1.8	0	0
	11.1	16.2	15.4	20.0	18.4	23.1	27.5	40.5	23.2	15.2	12.7	3.6	1.8	0	0
3	2.8	13.5	15.4	17.5	2.6	10.2	7.5	2.4	4.6	4.3	7.3	7.3	8.9	10.5	12.5
										← Pre-laying exodus →					

SEASON	DAYS BEFORE LAYING																																																					
	45	44	43	42	41	40	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0								
1966-67	2	-																																																				
	15	-																																																				
	*17	♂				♂	♀	♂											♂																																			
	26																																																					
	31																																																					
	60																																																					
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♂ MALE PRESENT BUT NO EGG  
 ♀ FEMALE PRESENT BUT NO EGG  
 E EGG ONLY  
 S NEST HOLE BLOCKED BY DRIFT SNOW  
 X UNIDENTIFIED BIRD PRESENT  
 - BIRD NOT PRESENT AT TIME OF OBSERVATION

FIGURE 2

\* The pair at this nest laid two eggs in 1966-67 (see p. 22 for details).

TABLE II  
PRE-LAYING EXODUS IN RELATION TO LAYING DATE AND STATE OF PAIR-BOND

Season 1966-67				1967-68				1968-69			
Nest number	Exodus period (days)	Pair-bond	Laying date	Nest number	Exodus period (days)	Pair-bond	Laying date	Nest number	Exodus period (days)	Pair-bond	Laying date
64*	6	—	13 Jan.	10*	9	Same pair	7 Jan.	4	8	Same pair	8 Jan.
2†	8	—	26 Jan.	26*	10	Same pair	7 Jan.	47	8	—	9 Jan.
26*	8	—	18 Jan.	13B	10	—	24 Jan.	31†	9	Same pair	31 Dec.
23	8	—	10 Jan.	2†	11	Same pair	7 Jan.	45	9	New female	1 Jan.
31†	9	—	3 Jan.	4*	11	Same pair	17 Jan.	46	9	—	1 Jan.
62*	9	—	31 Dec.	34	11	Same pair	20 Jan.	13C	10	—	5 Jan.
32	9	—	29 Dec.	7	12	Same pair	12 Jan.	10*	10	Same pair	11 Jan.
15	10	—	13 Jan.	64A	13	—	4 Jan.	29	12	New female	15 Jan.
60	10	—	16 Jan.	62*	14	Same pair	6 Jan.	43	12	New male	17 Jan.
				31†	16	Same pair	16 Jan.	55	14	—	12 Jan.
				64*	18	Same pair	9 Jan.	2†	17	Same pair	2 Jan.
MEAN	8.6			MEAN	12.3			MEAN	10.7		

\* Indicates same pair bred in two seasons.

† Indicates same pair bred in three seasons.

The difference between the means for 1966-67 and 1967-68 is significant,  $P < 0.01$ .

and 17 days, and the date of laying between 31 December and 26 January. At nest 45, although a different female was in occupation in 1968–69, the exodus period and laying date were similar to those of nest 31 with an unbroken pair-bond of at least 2 years. These observations suggest that there is considerable individual variation in the amount of time required to form the egg in different years, and/or variation in the time of departure by the females after mating. These variations, perhaps associated with annual changes in feeding conditions, are evidently at least partly responsible for the spread in egg-laying in this species.

Although the length of the pre-laying absence is now known with varying degrees of accuracy for several of the larger shearwaters (*Puffinus puffinus* (Harris, 1966b); *P. tenuirostris* (Marshall and Serventy, 1956)) and fulmarine petrels (*Fulmarus glacialis* (Dunnet and others, 1963); *Daption capensis* (Pinder, 1966); *Pagodroma nivea* (Brown, 1966; Beck, unpublished notes on the snow petrel)), there is little information for small nocturnal petrels. Data for Madeiran storm petrels in the Galapagos given by Harris (1969b) indicate a possible pre-laying absence of about 3 weeks by the female, but as his nest inspections were made by day, the observations are not strictly comparable. Davis (1957) also found that British storm petrels were rarely present in the nest by day during the week before laying but he gave no details of night attendance during this period. The most comprehensive data are those by Tickell (1962) for the dove prion at Signy Island. He showed that female prions were absent from the nest for about 9 days (range 7–14 days) before laying, while the male continued regularly to visit the nest at night in her absence. Tickell concluded that the regular night visits by the male were important in keeping the nest hole free of snow and accessible to the female on her return. His observations also suggest that the continued presence of the male at the nest in this strongly territorial species may help to maintain ownership of the hole by preventing entry by strange birds. In all the larger Procellariidae both sexes depart to sea before laying but, as in the prion, the males of both *O. oceanicus* and *Fregetta tropica* (Beck and Brown, 1971) regularly visit the nest while the female is away at sea. Neither species is territorial but, like the prion, they breed in situations vulnerable to blockage by snowfalls. The chief function of the male's regular presence, therefore, is likewise the necessity for keeping the hole snow-free.

### 3. Nest defence

As well as established breeding birds with nest holes, large numbers of non-breeders form an important part of the population. These birds spend much time visiting occupied sites but no evidence was obtained that the nest was defended against entry by these intruders. This is in marked contrast to the behaviour of *O. oceanicus* observed by Pryor (1968) at Haswell Island and also to the situation in the dove prion, in which nest defence is strongly developed (Tickell, 1962; personal observations). The chief means of proclaiming ownership of a site is the nocturnal calling, which may be heard from November until February and reaches a peak in mid-December before egg-laying. Most of this calling is by single birds in or near the nest site and is seldom heard when two birds are present, or during incubation. The call consists of a rather nasal disyllabic grating sound "aark-aark" repeated monotonously, with an occasional variant "aark-aark-uh-ah-ah-uh-uh" usually terminating a long sequence of calls. Some authors (e.g. Clarke, 1906; Ardley, 1936) have asserted that the species has a whistling call resembling that of *Fregetta tropica* but this is almost certainly the result of confusion between the two species on the breeding grounds. No call other than the nest advertisement "song" is known to us.

Visiting birds were frequently found in company with one of the rightful occupants during our night inspections of the nests and, on several occasions, strange individuals were seen entering sites from which birds were calling, their arrival being apparently accepted without dispute by the occupant. In these circumstances, it is not easy to see how ownership of the hole is re-established and the pair-bond maintained unless, as Davis (1957) pointed out, intruding birds show little site attachment and seldom return to holes they visit. Possibly, individual recognition based on scent may also play a part in re-establishing the pair-bond.

### 4. Courtship and nocturnal activity

As the activities of nocturnal petrels are easily interrupted by torch-light, it is extremely difficult to study their courtship behaviour. Roberts (1940) described mutual allo-preening of the head feathers by a pair of Wilson's petrels inside the burrow and similar behaviour was witnessed by us on 19 December

1967 at Signy Island. On eight occasions between 18 December and 16 January, birds with damp and matted areas of head feathers were seen in nests; these areas may well have been produced by mutual preening, although it is also possible that they may have been produced by the lashing of a krill, *E. superba*, captured at sea before birds came in at dusk to visit their nests. As Roberts (1940) remarked, copulation evidently takes place inside the nest, at least usually. Attempted copulation was recorded twice; a mounted pair was disturbed in a nest on 16 January 1969 while another pair was seen attempting to mate outside the nest on 10 December 1967.

At one nest, birds were easily extracted by hand and the occupants often called when a hand placed in the nest entrance blocked out the light. Birds also nibbled tentatively at the approaching finger-tips until finally grasped, when they would struggle and frequently eject small quantities of thin reddish oil. In some cases the bill-nibbling may have been in response to the scent of other petrels previously handled. Possibly, all birds entering the hole are treated by the occupant as if they are the returning mate and it is their subsequent behaviour and response to head-preening, etc. that determines the course of events. Repeated visits by one or more birds which have just attained sexual maturity, to an adult male which has lost its mate, may explain the few authenticated instances of replacement eggs recorded in storm petrels (p. 22; Harris, 1969*b*; Wilbur, 1969).

In our experience, Wilson's storm petrels do not perform aerial chases (cf. Roberts, 1940) as do certain other nocturnal species, e.g. *Hydrobates pelagicus* (Davis, 1957), and display activity outside the nest is evidently rare, being seen on only two occasions, both in December 1967. Each time three individuals were involved, resting close together on a moss bank at dusk. Their behaviour may be termed "leap-frog display". Essentially, this consisted of a bird springing into the air and either dropping down again on the same spot or on the other side of a neighbouring individual. Only one bird was in the air at any one time, but the rapidity with which each bird followed suit produced an almost comic effect, as if the birds were being jerked up and down like puppets. The participants in these displays were not marked and neither their breeding status nor the function of the display was established.

When visiting their nests, birds do not alight directly at the entrance but fly in circuits of decreasing radius for several minutes before landing nearby. Even then, birds do not enter immediately but only after a pause of about a minute. Circuiting was also seen sometimes in birds leaving the site and may possibly be a means of fixing the position of topographical features near the nest entrance. It is known that the hunting-wasp, *Philanthus triangulum*, uses an analogous circuiting flight to fix the position of its nest burrow relative to nearby landmarks; interference with these flights after re-arrangement of some of these landmarks causes the insect to become disorientated (Van Beusekom, 1948). In Wilson's petrel, precise knowledge of the landscape around the nest would be of value in locating the entrance when it and many nearby features are covered by drift snow. Like the dove prion (Tickell, 1962), Wilson's storm petrels are adept at finding the nest even when it is completely buried under soft snow.

##### 5. Development of the brood patch

During the 1966-67 and 1967-68 seasons, the state of development of the brood patch was recorded in most birds caught at marked nests or in mist-nets. The chief purpose was to determine the rate of de-feathering and duration of full development in relation to the incubation period. Since the function of the brood patch is to transfer heat from the bird to the egg, and in storm petrels the brood patch is large relative to total surface area, the development of the patch in a petrel breeding in a cold climate might be expected to differ markedly from that in species which breed at lower latitudes. Further, as brood-patch development is controlled by hormones associated with reproduction (Bailey, 1952), the state of the patch might provide a guide to the breeding status. For example, when most adults are incubating, birds not yet mature enough to breed might be identified by brood patches which are only partially developed.

A simple numerical scoring system was used to record the state of defeathering of the brood patch as follows: 0—a patch fully covered, with no defeathering; 1—a patch with some down missing but less than one-quarter of patch bare; 2—half the patch bare; 3—three-quarters bare with only a few down tufts remaining; 4—completely bare and down-free. Vascularization and oedematization of the patch were not scored as these features were not seen in the majority of birds examined, the fully developed patch in most birds being smooth and pale pink in colour with no knotted blood vessels evident. The same scoring system was used to record re-growth of the brood patch: 3—denoted a patch with a few developing down-feather sheaths; 2—a patch with substantial coverage of burst sheaths; 1—a patch

completely covered with re-growing down not yet full-length. During the three seasons, over 900 observations on brood patches were made, of which 135 were taken from breeding birds and 788 from birds of unknown breeding status. The following account of these observations is based mainly on mean brood patch scores for 10 day periods in relation to egg-laying. No differences between the sexes or between seasons were found and all the data have therefore been combined.

a. *Breeding birds.* Table III shows mean brood-patch scores for 10 day periods before the egg was laid. The scores show wide variability, some birds arriving on the breeding grounds with completely undeveloped brood patches while others have already lost about half the brood-patch down. Most birds have a fully developed brood patch by the time the eggs are laid, although one or two birds retained small residual down tufts throughout incubation.

TABLE III  
DEVELOPMENT OF THE BROOD PATCH IN BREEDING BIRDS IN RELATION  
TO LAYING DATE

<i>Days before laying</i>	<i>Number of observations</i>	<i>Brood-patch scores*</i>					<i>Mean score</i>
		0	1	2	3	4	
41-50	12	3	3	3	2	1	1.6
31-40	11	2	6	1	1	1	1.4
21-30	23	8	4	6	5	0	1.3
11-20	22	2	2	3	10	5	2.6
1-10	18	0	0	3	4	11	3.4

\* Development of the brood patch is scored on a scale from 0 (undeveloped) to 4 (fully developed).

Few birds were handled during incubation, as already mentioned, and all these, as expected, had fully developed brood patches. Birds which lost their egg apparently began to re-grow the brood patch down after the normal hatching period, 38-45 days after laying (Table IV). On the other hand, in successful breeders where the chick hatched and later fledged, re-growth appeared to be considerably delayed. Of nine birds examined more than 60 days after laying, six were successful breeders with brood patches either fully developed or just beginning to re-grow down. At least three of these birds had chicks within 10 days of fledging, while five had brood-patch scores of 3 or 4 as late as mid-April, a month in which the mean temperature is  $-2^{\circ}\text{C}$  and the mean lowest minimum is  $-12^{\circ}\text{C}$ . This apparent slow rate of re-growth is surprising, since the chick is rarely brooded by the parents for more than 3 days after hatching, except in bad weather when brooding may occur up to the twelfth day. Even though the patch is superficially covered by the belly contour feathering, heat loss through the patch must presumably be substantial in low temperatures. It is difficult to see what advantage there can be in the retention of a fully developed brood patch after hatching except possibly as an emergency source of heat to revive a chick if the down has become waterlogged following a melt of snow. This would only be of value however in the first fortnight when the chick is still small enough to be brooded. Complete re-growth may be protracted, for Bailey (1966) caught a bird with a fully developed brood patch in the Indian Ocean as late as July.

Re-growth of the brood patch usually begins with the development of down-feather sheaths in the centre, later extending in a tract along the mid-line to the edges. The sheaths appear to burst in unison when the central tract has formed, the down on the rest of the patch developing slightly later.

b. *Non-breeders/birds of unknown breeding status.* In order to provide a comparison with breeding birds in the pre-egg stage, the brood-patch scores of non-breeders and birds whose breeding status was unknown have been grouped in 10 day intervals working back from 1 January (Table V), which is a convenient reference point, as egg-laying has just begun by then in most years. The laying season in 1967-68 was 1 week later than in 1966-67 or 1968-69 but brood-patch development was scarcely affected and the data for the three seasons have been combined.

TABLE IV  
RE-GROWTH OF BROOD PATCH IN BREEDING BIRDS IN RELATION  
TO LAYING DATE

Days after laying	Number of observations	Brood-patch score					Mean Score
		0	1	2	3	4	
1-10	13	—	—	—	1	12	3·9
11-20	3	—	—	—	—	3	4·0
21-30	5	—	—	—	—	5	4·0
31-40	3	—	—	1	1	1	3·0
41-50	10	—	—	1	6	3	3·2
51-60	7	—	—	2	5	—	2·7
61-70	1	—	—	—	1	—	(3·0)
71-80	1	—	—	—	1	—	(3·0)
81-90	2	—	—	—	1	1	(3·5)
91-100	4	—	—	—	3	1	3·3
101-110	1	—	—	—	1	—	(3·0)

See Table III for explanation of brood-patch scores.

TABLE V  
DEVELOPMENT OF THE BROOD PATCH AND RE-GROWTH IN NON-BREEDING  
BIRDS IN RELATION TO THE BEGINNING OF LAYING

Days before 1 January	Date of period	Number of observations	Brood-patch score					Mean score
			0	1	2	3	4	
21-30	2-11 December	57	36	10	7	4	0	0·6
11-20	12-21 December	189	44	60	57	22	6	1·4
1-10	22-31 December	240	27	21	48	94	50	2·5
	January	203	7	4	13	59	120	3·4
	February	61	0	0	9	30	22	3·2
	March	38	0	2	9	23	4	2·8

As egg-laying has just begun by 1 January in most years, this date is taken as a reference point in grouping the data. See Table III for explanation of brood-patch scores.

Like the breeding birds, on arrival most non-breeders have low scores, which increase steadily up to the normal time of egg-laying. Once again, however, there is wide variation and 20 per cent of the birds still have brood patches scoring 0 or 1 at the end of December. In January this proportion falls markedly and many birds, which have incomplete brood patches at the beginning of the month, complete development by its end. The great majority of individuals are then indistinguishable from incubating birds. Table V suggests that de-feathering of the brood patch might take about 30 days. A more precise estimate is given by successive brood-patch scores of individuals caught more than once during the pre-egg period (Table VI), which give a mean of just over 3 weeks for complete defeathering. Data for known breeders

TABLE VI  
RATE OF DEVELOPMENT OF THE BROOD PATCH IN BIRDS  
CAUGHT MORE THAN ONCE

Score interval	Number of observations	Observed interval in days																		Mean interval (days)
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
0-1	15			4	1	4	3		3											5.2
1-2	37		2	6	5	6	9	2		1	2	2			1	1				5.9
2-3	43		2	4	7	9	9	2		2	2	2	1		1	2				6.3
3-4	37			5	7	7	6	2	2	3			2	1		1			1	6.5
0-4	132		4	19	20	26	27	6	5	6	4	4	3	1	2	4			1	23.9

are insufficient for separate analysis but the rate of development does not appear to differ from that in non-breeders. Comparable estimates of the rate of re-feathering could not be obtained, as most non-breeders left the island by mid-March with incompletely re-grown brood patches and, as described above, breeding birds had often scarcely started to re-grow the brood-patch down by the time their chicks fledged.

c. *Brood patches and ageing.* It remains to ask whether the state of the brood patch can provide an approximate guide to ageing. As already mentioned, only a small proportion of birds possesses incompletely developed brood patches in late December and early January, when most breeders have begun to lay or are incubating. It is probable that immature birds returning to the colony for the first time or prospecting nest holes on subsequent visits do not become attached to a particular site immediately, but spend some time wandering around the colony. Therefore, the mist-net catches may be expected to contain a higher proportion of sub-adult birds than samples of birds captured in nest holes. Table VII compares mean brood-patch scores for 10 day periods in December and for the whole of January in birds caught in mist-nets and birds caught at marked nests. Known breeding birds have been excluded from the mist-net totals as these would tend to obscure any differences there might be between the two categories. Birds taken at marked sites have slightly higher average scores than those caught in mist-nets, presumably reflecting the higher proportion of mature birds, but the difference is slight and isolated individuals cannot be assigned to either category with any precision. Further evidence that brood-patch development is

TABLE VII  
COMPARISON OF BROOD-PATCH DEVELOPMENT IN NON-BREEDERS  
CAUGHT IN MIST-NETS AND IN NEST HOLES

Days before 1 January	Date of period	Mist-netted birds					Birds caught in holes								
		Number of observations	Brood-patch scores				Mean score	Number of observations	Brood-patch scores				Mean score		
			0	1	2	3			4	0	1	2		3	4
21-30	2-11 December	48	32	6	6	4	0	0.625	12	5	4	3	0	0	0.83
11-20	12-21 December	149	37	47	42	18	5	1.375	57	12	19	17	6	3	1.46
1-10	22-31 December	179	25	12	37	68	37	2.45	83	3	10	15	38	17	2.67
	January	150	7	3	10	48	82	3.30	82	0	1	4	7	70	3.78

See Table III for explanation of brood-patch scores.



unreliable as an indicator of breeding status is provided by a male bird (BB05847) at nest 61 in 1967-68. On 27 November the brood-patch score was 2, on 22 December 3 and the same on 17 January. In spite of the fact that its brood patch did not fully develop in 1967-68, the bird had bred successfully in 1966-67 and was first ringed as a breeder in December 1959. Evidently brood-patch development is of no practical value in the assessment of age and breeding status in this species and similar conclusions may be applicable in other storm petrels.

The only other existing information on brood patches in storm petrels is that provided for the tropical species, *Oceanodroma castro*, by Allan (1962) and Harris (1969b). These authors also found that brood-patch development in non-breeders paralleled that of breeders, that individual variation in de-feathering was considerable but, unlike *Oceanites*, re-growth in some birds began during incubation and birds with chicks were re-growing or had already re-grown the brood-patch down. From his more extensive data, Harris concluded that the minimum time for de-feathering was 12 days (similar to *O. oceanicus*) and for vascularization of the de-feathered patch 7 days. Harris also found that the brood patches of a sample of mist-netted birds were less developed on average than a sample of birds taken from burrows in the same month.

## B. EGG STAGE

### 1. The egg

Wilson's storm petrels lay a single, white elliptical egg, often speckled with faint reddish brown and greyish lilac spots which may form a band around one end. Measurements of 15 eggs from Signy Island nests are shown in Table VIII.

TABLE VIII  
MEASUREMENTS OF *O. oceanicus* EGGS FROM SIGNY ISLAND

Number	Mean length (mm.)	Range (mm.)	Mean width (mm.)	Range (mm.)	Mean fresh weight (g.)	Weight range (g.)
15	34.8	33-36	24.7	24-26	11.0*	10-12.5*

\* Data from eight fresh eggs.

Roberts (1940) considered eggs from different localities were indistinguishable and gave the mean measurements of 20 in various collections as 33.4 mm. by 24.2 mm. (range 28.0-36.0 mm. by 22.5-27.4 mm.). In addition to the Signy Island eggs, we have measured a number in the British Museum (Nat. Hist.) collections. Two eggs collected at Signy Island in 1933 by Ardley fall within the range of measurements given in Table VIII, as do single eggs from Deception Island, South Shetland Islands, and from Cape Adare, south Victoria Land. Nine eggs from Iles Kerguelen are appreciably smaller, however, with mean measurements of 32.8 mm. by 23.5 mm. (range 29.9-34.6 mm. by 22.6-25.2 mm.). This difference reflects a difference in body size between the two populations; the mean wing length of Signy Island birds is 151.4 mm. (see later), while Roberts (1940) and Milon and Jouanin (1953) gave 144.5 mm. and 145.75 mm., respectively, for the mean wing length of Iles Kerguelen birds.

As emphasized by Lack (1966, 1968), many Procellariiformes lay large eggs proportionate to their body weight. This trend is shown in extreme form by the Hydrobatidae where the weight of the egg relative to body weight is very large indeed and exceeds that of any other family of birds. A fresh *O. oceanicus* egg weighing 11.0 g. represents approximately 28.5 per cent of the mean adult weight of 38.2 g. As shown in Table IX, the egg of Wilson's storm petrel is proportionately larger than in any other storm petrel with the exception of the tropical species, *Nesofregatta albigularis*, in which the egg comprises 29.4 per cent of the body weight (Ashmole (*in* Lack, 1968)).

Lack (1968) has suggested that there may be a tendency for tropical petrels to have proportionately larger eggs than petrels breeding at high latitudes and this may be due to the difference in food availability between the two regions. In the tropics, food supplies are generally scarce throughout the year and do not fluctuate seasonally, egg formation may be prolonged and chick survival does not depend on the egg being

TABLE IX  
PROPORTIONATE EGG SIZE IN VARIOUS STORM PETRELS

Species	Locality	Adult weight (g.)	Egg weight (g.)	Egg as percentage of body weight	Reference
a. Warm water					
<i>Oceanodroma tethys</i>	Galapagos	23, 26	5.0, 6.0	21.7–23.1	Harris (1969b)
<i>Oceanodroma castro</i>	i. Ascension Island	44	11.0	25.0	Allan (1962)
	ii. Galapagos	39.8	8.5	21.4	Harris (1969b)
<i>Nesofregatta albigularis</i>	Tropical Pacific Ocean	68	20	29.4	Ashmole ( <i>in</i> Lack, 1968)
b. Cold water					
<i>Hydrobates pelagicus</i>	South Wales	28	7	25.0	Davis (1957)
<i>Oceanites oceanicus</i>	i. Argentine Islands	34	9	26.5	Roberts (1940)
	ii. South Orkney Islands	38.2	11.0	28.5	This report
<i>Pelagodroma marina</i>	New Zealand	47	11.8	25.1	Richdale (1964)
<i>Oceanodroma leucorhoa</i>	New Brunswick	50	10	20.0	Huntington ( <i>in</i> Lack, 1968)
<i>Fregatta tropica</i>	South Orkney Islands	56.5	15.0	26.5	Beck and Brown (1971)

Mean measurements are cited for all species except *Oceanodroma tethys* for which measurements of two individual females and their eggs are given.

laid by a particular date. An unusually large egg formed slowly may therefore be advantageous in providing a food reserve for the newly hatched chick, helping it to withstand food shortages in early development. By contrast, at high latitudes, food is very abundant for a short period in summer but very scarce for the rest of the year. Survival of the young depends on the egg being formed quickly by a set date early in the season when food is still relatively sparse; these pressures may necessitate the laying of a smaller egg than in tropical waters. In support of his thesis, Lack (1968) pointed out that the tropical shearwater, *Puffinus nativitatis*, and gad-fly petrel, *Pterodroma alba*, lay proportionately larger eggs than the shearwaters and fulmarine petrels breeding in cold seas. Furthermore, Harris (1969a) has shown that the tropical Audubon's shearwater, *Puffinus lherminieri*, in the Galapagos also has a proportionately larger egg and newly hatched young than any cold-water *Puffinus* species.

The data set out in Table IX, however, show that this relationship is not found in the storm petrels. Although Lack (1968) stated that the storm petrel, *Oceanodroma castro*, at Ascension lays a proportionately larger egg than its congener *O. leucorhoa* in high latitudes, more precise data for *O. castro* in the Galapagos (Harris, 1969b) show little or no difference from *O. leucorhoa*. Harris' data for the Galapagos storm petrel, *Oceanodroma tethys*, are also similar to those for *O. leucorhoa*. Furthermore, the eggs of the Antarctic storm petrels, *Oceanites oceanicus* and *Fregatta tropica* (Beck and Brown, 1971) are larger than those of all the other species studied, including tropical forms, except for *Nesofregatta albigularis*. It is probable that the formation of a proportionately very large egg in these Antarctic species is made possible by the very rich food supplies available to the laying female in late December (Foxton, 1956, 1964).

## 2. Egg-laying

Egg-laying dates obtained during the three seasons are shown in Fig. 3 in relation to snow levels at the colony over the same period. The snow levels are mean values from readings taken from 20 snow-level gauges attached to stakes marking nests in the colony. The laying period may be protracted, extending from the last week in December until early February in 1966–67, but laying was more synchronous in 1967–68 and 1968–69, extending over 21 days in both seasons. Fig. 3 shows that nest holes at Signy

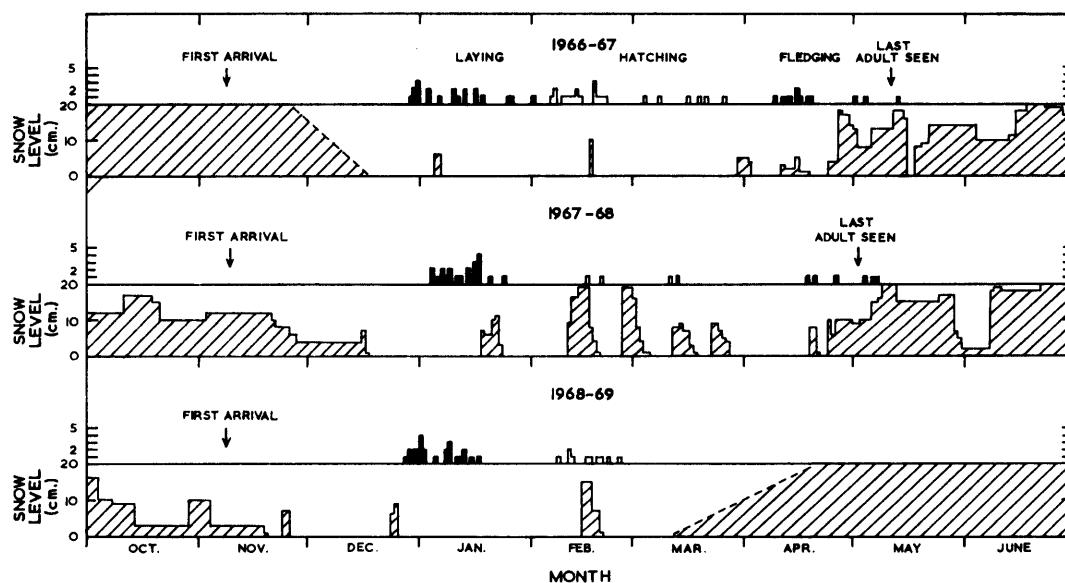


FIGURE 3

The breeding cycle of *O. oceanicus* at Signy Island over three seasons in relation to snow levels in the colony. Laying, hatching and fledging dates are given in the top half of each diagram. Snow levels, given in cm. in the lower half, are means of 20 snow-level readings. Levels for the spring of 1966-67 and autumn of 1969 are approximations based on field notes and not on actual readings. Nests become blocked by snow when levels exceed 5 cm.

Island may be blocked by drift snow for several days at a time, so that an extended laying period may have considerable survival value, as shown by the following observations.

In 1967-68, egg-laying was delayed, the first egg appearing on 4 January and the modal date of laying being a little over 1 week later than in 1966-67 or 1968-69.\* On 18 January there was a substantial snowfall, amounting to 6-10 cm. at the majority of sites, sufficient to block most entrance holes. The following few days brought low temperatures and high winds with the result that most of the holes remained blocked until 22-23 January. The pattern of egg-laying that season had indicated an expected peak about 18-19 January, but in fact only two more eggs were laid after 17 January in the marked nests (Fig. 3). Thus, several pairs were apparently prevented from breeding because the laying female was excluded from the burrow by snow.

The information now available suggests that the timing of the breeding cycle varies with the latitude of the colony, with an earlier season at higher latitudes, as shown in Fig. 4. It can be seen that the earliest recorded dates of laying occur during late November on the Antarctic continent (Mougin, 1968; Pryor, 1968) and become progressively later at breeding stations farther north in Graham Land and the Scotia arc, while the latest recorded date is 7 February at Iles Kerguelen (Hall, 1900). Further information from colonies in southern South America and the Falkland Islands would be desirable, as fresh eggs have been found on 14 December and 1 January at the former locality (Reynolds, 1935; Murphy, 1936). Although dates of first arrival at Iles Kerguelen are somewhat later than at other localities, arrival dates at most breeding stations are very similar irrespective of latitude, as pointed out by Roberts (1940). The difference in the timing of laying is thus apparently brought about by curtailing the time interval between arrival and laying—about 1 month in Signy Island birds. Earlier laying is presumably an adaptation to the shorter season in these latitudes and allows both the adults and fledged young to migrate before the formation of sea ice and rapid drop in temperature in April and May.

Confirmation of a difference in the interval between arrival and laying at low and high latitudes, respectively, is given by a comparison of observations made in 1968-69 at Signy Island and at Adelaide Island, Marguerite Bay (lat. 67°S., long. 68°W.). The first arrival at Signy Island was noted on 8 November and numbers gradually built up until by 20 November approximately 10 per cent of the population had

\* No reason for this delay was found, for in each season birds arrived at much the same time and a comparison of the mean daily temperatures in the pre-egg period revealed no significant differences.

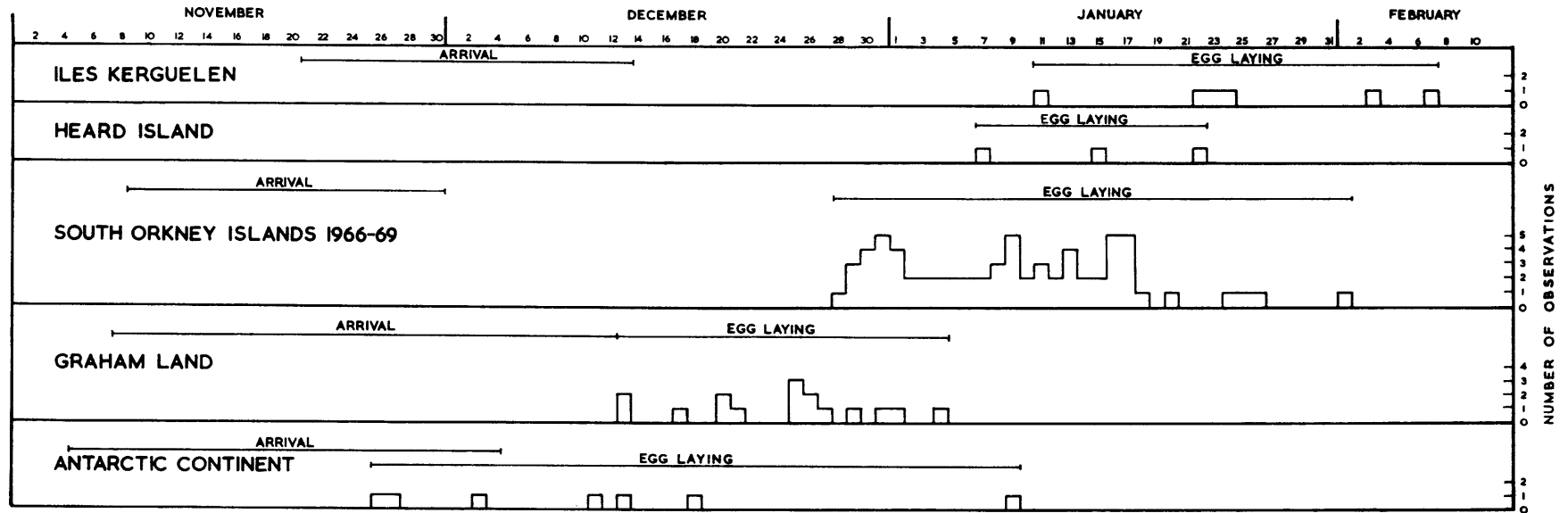


FIGURE 4

Variation of laying season in *O. oceanicus* with latitude. *Data sources.* Iles Kerguelen: Eaton, 1875; Sharpe, 1879; Hall, 1900; Loranchet, 1915. Heard Island: Downes and others, 1959. Graham Land: Gain, 1914; Roberts, 1940; Barlow and Willey, personal communication. Antarctic continent: Wilson, 1907; Falla, 1937; Mougin, 1968; Pryor, 1968.

returned. At Adelaide Island, the first bird was seen on 11 November and by 21 November over 100 birds were present (personal communication from I. Willey). Birds were occupying the breeding colonies at both localities by 12 November. Thus there appeared to be no difference in the time of return of *O. oceanicus* to these two breeding stations more than 1,500 km. apart. As regards breeding dates, the earliest hatching date in three seasons at Signy Island was 6 February. But on that date in 1969, 22 (55 per cent) out of 40 nests examined by D. W. B. at Adelaide Island contained chicks, some of which were up to 14 days old. The timing of the breeding cycle thus ensures that departure of the adults and young from the breeding grounds in Marguerite Bay is completed by the second half of April, whereas the departure of the last birds from the South Orkney Islands may be as much as 1 month later.

### 3. Incubation spells and incubation weight losses

As shown by Roberts (1940) from daily visits to marked nests, incubation was shared equally by both adults in alternating spells of approximately 48 hr. At Signy Island, observations were made twice daily and the mean length of a successfully completed incubation spell was 60 hr (range 36–96 hr.) as shown in Table X. The male usually took the first incubation spell after the egg had been laid and at successful sites each bird generally completed 7–9 spells before the egg hatched.

TABLE X  
INCUBATION SPELLS OF *Oceanites oceanicus* AT SIGNY ISLAND

Spell length (hr.)	Number of observations		
	Male	Female	Total
36	6	8	14
48	29	38	67
60	27	30	57
72	20	28	48
84	13	8	21
96	—	2	2
TOTAL	95	114	209

Total number of spells	Mean duration (hr.)	S.D. (hr.)	S.E.	Range (hr.)
209	60	13.32	0.924	36–96

The change-over of the adults was a fairly rapid process and apparently always took place at night. When birds came to the colony in the late evening, the occupants of sites with eggs were often distinguishable from visiting non-breeders by their behaviour. Birds with eggs came straight in from the sea, usually completed two or three circuits of 6–10 m. radius around their nest site before alighting close to the entrance. They then shuffled forward awkwardly on their tarsi, often using their wings to keep balance, and entered the nest cavity. The time between arrival from the sea and entering the nest was usually between 2 and 3 min. Birds without nests tend to fly about in a more aimless manner.

The behaviour of the birds during the change-over was observed on only one occasion. Observations were made using a torch but this appeared to have no effect on the behaviour of the occupants of the hole. Both birds were present in the nest, the relieving bird having entered a few moments before. Both birds were initially calling and holding each other's bills as though fighting, with one bird continually clawing

the other with one foot. They then broke apart and the relieved bird came to the nest entrance, paused for a few seconds and then flew off. The relieving bird continued to call loudly, following its mate half-way along the tunnel entrance and then remaining. The change-over had lasted for approximately  $1\frac{1}{2}$  min. 10 minutes later the new bird had ceased calling and was standing over the egg as if about to incubate.

At some sites incubation was not continuous, being marked by the absence of the incubating bird during the day, followed by its return at night to resume incubation. This day-time absence was particularly noticeable when the incubation spell continued for longer than the average 60 hr., indicating that these departures from the nest were probably made for feeding. This behaviour was not seen in *Fregatta tropica* (Beck and Brown, 1971) in which incubation was usually continuous.

An attempt was made during the study to obtain a series of measurements of the weight loss incurred by incubating birds. Many birds were intolerant of handling, however, and tended to desert for the remainder of the spell so that only a few observations could be made. In four sets of measurements, the mean weight loss over 24 hr. was 2.75 g. (range 2–4 g.). The mean weight of four birds at the start of an incubation spell was found to be 42 g. and the mean spell length was 60 hr. By the end of the spell the incubating birds had lost on average a little over 16 per cent of their body weight. Assuming a constant weight loss with time, for a maximum recorded spell of 96 hr., the corresponding maximum loss would be 26 per cent of the body weight at the start. These weight losses are similar to those recorded for *Fregatta tropica* (Beck and Brown, 1971).

#### 4. Temperature of the egg during incubation

In 1967–68, a twin-channel automatic recorder and thermistor probe were used to determine the temperature within the egg. The thermistor bead was sealed inside an egg which had been incubated for at least 19 days. The contents of the egg were blown out and replaced with concentrated gelatine solution in which the thermistor bead became embedded when the solution set. The egg was then replaced in the nest and was accepted by the parent birds. Subsequent recordings showed an average incubation temperature of 36° C as registered by the thermistor. Unfortunately, we were not able to measure the body temperature of adult birds, but Roberts (1940) gave the average body temperature of ten adults in the breeding season as 38.8° C (range 36.5–40.5° C) and Mougin (1968) a mean of 38.7° C for three individuals. Confirmation of the incubation temperature registered by the recorder was provided by artificial incubation of another egg which had been deserted after being incubated for 12 days in the nest. This egg was maintained at a constant temperature of 36° C in an incubator. On the twenty-sixth day of artificial incubation the chick was “peeping” and tapping on the inside of the shell but later died in the process of hatching.

#### 5. Incubation period

Over the three seasons the incubation periods of 19 eggs were determined, as shown in Table XI. Since observations were made at night as well as by day, it was possible to take into account the number of times the egg had been temporarily deserted. These desertion periods were caused by (i) the temporary absence of the incubating bird for part of a day as described earlier, (ii) failure of the relieving bird to appear on time, (iii) drift snow sealing the nest entrance, causing the occupant to leave prematurely, thereby disrupting the incubation routine. As recorded by Tickell (1962) for the dove prion, by taking into account the occasions when the egg was not incubated it was possible to distinguish the “real incubation period” from the “apparent incubation period”. In some cases this difference was substantial, for at one nest the apparent incubation period exceeded the real one by almost 12 days (Table XI).

No experiments were carried out to examine the length of time that an egg remained viable when deserted. During late December and early January at Signy Island the air temperature generally remains a little above freezing-point during the day but falls below freezing-point at night. Roberts (1940), however, showed that the temperature inside an *O. oceanicus* burrow in a moss bank was not subject to the marked daily fluctuations of the air outside and remained slightly above freezing-point. Occasional absence of the adults thus does not appear to involve much risk to eggs in good weather conditions, but if fine drift snow accumulated in the hole during bad weather after the bird had left, then the embryo apparently became fatally chilled after only a few hours contact with the snow. Some pairs seemed more prone to desert temporarily than others—one pair deserted quite frequently in 1966–67 and in 1968–69 but hatched the egg after an apparent incubation period of over 50 days in both seasons. On one occasion at this

TABLE XI  
INCUBATION PERIODS OF *Oceanites oceanicus* AT SIGNY ISLAND

1966-67			1967-68			1968-69		
Nest number	"Apparent" period	"Real" period	Nest number	"Apparent" period	"Real" period	Nest number	"Apparent" period	"Real" period
2	51	39½	46	55	47½†	2	54	*
21	41	40½				10	40	*
31	46	42½				31	43	*
32	43	39				45	47	*
35	44	40½				46	46	*
60	47	42½				55	41	*
62	42	39½				64B	41	*
67	38	38				66	44	*
						67	42	*
						Unmarked	41	*

All periods are in days. The difference between "apparent" and "real" periods is accounted for by temporary desertion.

\* Observations insufficiently detailed to establish "real" period.

† Night visits missed during bad weather so true period may have been shorter.

site the egg was deserted for 60 consecutive hours half-way through the incubation period. The pair appeared to be well established, however, and a visiting bird was recorded on only one occasion.

As can be seen from Table XI, the minimum recorded "real" incubation period was 38 days and the maximum a little under 43 days. One period of 47½ days was recorded but no visits were made at night to this nest for 11 days during a period of bad weather. These incubation periods are comparable with the range of 39-48 days given by Roberts (1940), although his results did not take temporary desertions of the egg into account. During 1961-62 at Signy Island two apparent incubation periods of 52 and 53 days were obtained (Jones and Pinder, 1962). During this season drifting snow was reported as affecting the nest sites during the summer; in some cases the females were unable to gain access to the burrows and consequently some eggs were laid out in the open. At Adelaide Island, Marguerite Bay, observations were made at four nest sites during 1968-69 (personal communication from I. Willey). The egg hatched at three sites and two incubation periods of 40 days and one of 41 days were observed (Table XII). These records are in accord with those from Signy Island. The incubation period in *O. oceanicus* is clearly very similar to the length of the period in other Hydrobatidae, e.g. 41 days in *Hydrobates pelagicus* (Davis, 1957); 38 days in *Oceanodroma castro* (Allan, 1962; Harris, 1969b); 42 days in *Oceanodroma leucorhoa* (Huntington in Palmer, 1962; Lack, 1968); 38-44 days in *Fregetta tropica* (Beck and Brown, 1971), and the discrepancies may be attributed to undetected periods of desertion and small sample sizes.

#### 6. Replacement laying

The normal procellariiform clutch of one egg is not usually replaced if lost, but two-egg clutches have been reported in some species (e.g. the cape pigeon (Pinder, 1966) and giant petrel, *Macronectes giganteus* (Warham, 1962)) and re-laying has been suspected but not proven in others (Allan, 1962; Davis, 1957). In the absence of precise information, egg replacement in petrels was doubted and its significance questioned (see for example, Marshall and Serventy, 1956; Warham, 1962; Tickell and Pinder, 1966; Fisher, 1968). Recently, however, Harris (1966b) obtained fairly conclusive evidence of repeat laying in one pair of Manx shearwaters, *Puffinus puffinus*, and also in several pairs of the storm petrel, *Oceanodroma castro*,

TABLE XII  
EGG-LAYING AND HATCHING DATES OF *O. oceanicus*  
AT ADELAIDE ISLAND 1968-69

<i>Nest number</i>	<i>Laying date</i>	<i>Hatching date</i>	<i>"Apparent" incubation period (days)</i>
	1968	1969	
1	26 December	5 February	41
2	13 December	22 January	40
3	26 December	4 February	40
4	20 December	Infertile	—
—	—	5 February	—

in the Galapagos (Harris, 1969*b*). During the present study of *O. oceanicus*, we noted one instance in 1966-67 when a pair apparently produced more than one egg during the season—nest 17 (Fig. 2.).

The nest was first found on 22 December 1966 when an unringed male bird was caught and ringed BB02561. This bird was present on the two following nights and also probably on 26 December. On 27 December two new unringed birds were present but did not appear subsequently. On 28 December, BB02561 was again present and was given a yellow head mark. This bird was absent on the nights of 29 and 30 December but was found incubating an egg on 31 December. Incubation then proceeded intermittently, being shared between Yellow BB02561 and another bird ringed BB05824 and head-marked Blue—the female. The latter was not examined until 9 January when the cloaca was recorded as indeterminate. On 10 and 11 January the egg was deserted and had begun to sink into the soil of the nest cup. Blue and Yellow continued to incubate sporadically or occupy the nest up to 23 January when the egg disappeared. Thereafter, Yellow visited the nest alone on most subsequent nights until 2 February, when a new egg was present at the noon visit and was incubated that night by Yellow. Blue re-appeared on 4 February and a normal incubation routine was established up to 17 February when the hole became almost completely snow-blocked for 2 days. Incubation broke down after the snow melted, Blue appeared only once more at the nest and Yellow's visits became more and more infrequent, finally ceasing after 3 March. On 9 March, while the egg was being removed from the nest, a second very dirty egg was recovered from the rear of the cavity, presumably the egg discarded earlier in the season.

As the female's cloaca was not examined after the appearance of each egg, replacement laying by this pair cannot be claimed as certain, but the absence of the female from the nest in the period immediately before each egg appeared suggests she was then away at sea forming the egg. The period of absence in each case is in accord with the length of the pre-laying exodus recorded at other sites.

#### 7. Egg loss and the effect of snowfall on incubation

53 out of 82 eggs laid in the marked sites in 1966-67 and 1967-68 failed to hatch. The loss of these eggs could be accounted for as follows:

- i. 17 eggs were drifted over with snow and the nest was subsequently deserted by the adults.
- ii. 13 eggs failed when incubation was disturbed by snow blockage. Chilling accounted for some losses. Other eggs became embedded in the nest floor and attempts by the adults to resume incubation were ineffectual.
- iii. 12 eggs disappeared without trace. In most cases the inaccessibility of the nest site ruled out possible predation by a sheathbill, *Chionis alba*. The only explanation that can be given is that the eggs may have been knocked out of sight at the rear of the cavity during change-overs.
- iv. 11 eggs were deserted by the adults at nests unaffected by snowfalls. At five nests the male bird either failed to relieve the female at the proper time or repeatedly left the egg after complet-



ing only a small part of his incubation spell. Both birds consistently failed to complete incubation spells at five other sites, while desertion at one site was caused by the overflow of a nearby melt stream into the nest cavity.

Thus a total of 31 eggs which failed to hatch was lost owing to the direct or indirect effects of drift snow. Furthermore, an unknown number of eggs was lost in 1966–67 and in 1967–68 when drift snow blocked the nest holes and prevented a number of females from entering the hole and laying the egg.

Whenever the general depth of snow in the colony began to exceed 5 cm. or drift snow began to pile up at the nest entrance, there was an increasing tendency for the incubating bird to leave the egg. In a few cases, however, the incubating bird waited until the entrance hole became completely covered before leaving the nest, but we have no records of birds becoming entombed and adult mortality from this cause is probably rare. When eggs and chicks of a long-lived species are periodically at risk due to snowfalls, it is clearly advantageous for the adults to abandon the nest early and attempt to breed in a subsequent season rather than run the risk of becoming trapped in the nest.

Birds, forced by snow to leave their eggs during the day time, generally returned in the evening and sometimes made desultory attempts to dig through to the nest. On the second night after blockage the adults made more determined efforts to reach the nest (Plate IVa). The behaviour of birds was recorded during a heavy snowfall on 26 February 1968. Snow fell heavily all day and by early evening the majority of nests were covered by a soft snow layer at least 20 cm. deep and all entrances were blocked. Very few birds were seen flying over the colony that evening or attempting to dig their way into their nests. On 27 February more snow fell and a 20 kt. [10.3 m./sec.] wind resulted in further drifting. That evening more birds returned to the colony and digging was observed at a number of sites. The birds appeared wary and vulnerable to sudden squalls of wind, flying off whenever there was a particularly strong gust. At several sites birds were not actually digging but were resting on the snow surface near their nest (Plate IVb). One marked nest, together with the site marker, was completely buried under snow to a depth of 30–45 cm., and all nearby distinguishing features were sufficiently obscured that there was little to indicate the position of the nest. The snow was fairly well packed and a slight wind crust was forming on the surface. The male bird began to dig in four places, each one approximating to the corner of a 1 m. square and roughly equidistant from the nest entrance. The bird dug into the snow for a while and then took off and flew for long periods around the site before alighting and resuming excavation. The bird remained at the nest site for about 90 min. before finally abandoning the attempt to excavate a tunnel. The digging spells did not last longer than 10–15 sec. and both the bill and the feet were used to remove the snow. The bird usually balanced on one leg, while digging furiously with the other and using the bill as a probe. On occasions the wing tips were used as supports and both feet were used in digging. When the excavation attempt was finally abandoned, the depth of the deepest hole was about 15 cm. Birds also attempted to dig through to the nest at other sites but none was successful in doing so and all digging attempts were eventually given up and the birds left the colony. On the third night there were few birds present although several individuals had appeared over the slopes during the day. No further attempts at excavation were observed and the snow remained for a further 3 days.

Of the 20 sites which contained eggs and were affected by this snowfall, nine were completely deserted with no record of an occupant at the site after the snow had cleared. Incubation was resumed at the other 11 sites but no eggs hatched, either because the incubation routine never became properly re-established or because the embryo had been chilled by contact with snow. As mentioned earlier, eggs appear to remain viable for some days when merely deserted, but contact with ice or snow is quickly fatal. Tickell (1962) reported similar findings for the dove prion at Signy Island.

### C. CHICK STAGE

#### 1. *Hatching and the fledging period*

The distribution of hatching dates during the three study seasons at Signy Island is shown in Fig. 3. Once the egg became "pipped", the chick usually hatched within 24–48 hr., although one egg at Adelaide Island was observed to be pipped 3 days before the chick emerged.

During 1966–67, 12 fledging periods were determined, with a mean of 60 days and range of 54–69 days. The chick which fledged at 69 days suffered some starvation for its weight curve was much lower than those of other chicks and the peak weight was only 49 g., against a mean peak weight of a little over 73 g. for

seven other chicks. Laws (1948) found an *Oceanites* chick approximately 10 days old on 26 February which fledged on 15 April when about 60 days old, and Roberts (1940) obtained a fledging period of 52 days for one chick in the Argentine Islands. Similarly, Davis (1957) gave a range of 56–73 days for the fledging period of the British storm petrel with a mean value of almost 63 days. The fledging period of *Oceanodroma castro* in the Galapagos is rather longer, averaging 70 days in the hot season and 78 days in the cold season (Harris, 1969b).

## 2. Growth of the chick

Average growth curves for certain linear dimensions are shown in Figs. 5 and 6 and for weight in Fig. 7.

The body of a newly hatched chick is covered with dark grey down. The facial area remains completely bare until growth of the black juvenile feathering commences about the thirtieth day. The eyes which are closed at hatching begin to open from the fifth or sixth day onward. Brooding of the chick takes place during the first 3 days after hatching and in some cases extends to the fifth day. Subsequently, there are occasions when the chick is intermittently brooded by one of the adults until the twelfth day during periods of bad weather. The following description of the general features of the growth of the chick is based on observations made during the first two seasons' work:

- Day 1–10.* The eyes are completely open by the ninth or tenth day. The egg tooth is still present. Initial development of the steel-blue primary quills has begun in some chicks. The soft parts darken and there are the first signs of yellow coloration on the webs of the feet (Plate Va).
- Day 11–20.* The last traces of the egg tooth have disappeared in all chicks by the sixteenth day. The primary quills are approximately 10–15 mm. in length and the black feathers tipped with light grey down are now bursting from the sheaths. The first signs of tail development are evident in the most advanced chicks. The body weight of a little over 7 g. at hatching has continued to increase steadily, reaching a mean value of 36 g. by the twentieth day.
- Day 21–40.* From the thirtieth day onward the body down begins to thin and at the same time formation of the black body contour feathering and the white feathering of the rump and flanks commences. The soft parts continue to darken and are almost black by the fortieth day (Plate Vb and c).
- Day 41–50.* Thinning of the body down and development of the rectrices and remiges continue while growth of the soft parts ceases in this period. The body weight attains a maximum about the fiftieth day and decreases thereafter until the chick departs (Plate Vd).
- Day 51–departure.* Loss of body down continues until all traces have gone when the chick is fully fledged but a few strands persist on the head and flanks in some chicks.

The plumage of the fully fledged chick is similar to that of the adult except that there is usually white speckling on the belly feathers; there are also pronounced white edges and tips on the greater coverts while some chicks also have distinct whitish spots on the lores. The last feature is more variable than the others. Like Roberts (1940), we found no evidence for the existence of two down stages in this species.

## 3. Feeding of the chick

Feeding of the chick may not be shared equally between the adult birds. The male predominates in attending the nest during the chick stage (Table XIII), perhaps to keep the entrance snow-free as he does in the pre-egg period, while the female brings most of the food to the chick. At 10 marked sites containing chicks there were 166 recorded visits by the male, 51 by the female and five by both birds together. Feeding visits were nocturnal, except for three records of day-time feeding.

The mean peak weight attained by seven nestlings was 73.4 g. with a range of 62–81 g. This mean peak weight was 92 per cent (range 63–113 per cent) above the mean adult body weight of 38.2 g. and compares with an almost identical figure for *Fregetta tropica* (Beck and Brown, 1971). These weights are due to large fat reserves which presumably increase the chick's chance of survival during prolonged starvation periods caused by heavy snowfalls, as mentioned by Roberts (1940). Similar large reserves occur in other storm petrels and, as shown in Fig. 8, the average growth curve of *O. oceanicus* chicks closely resembles that of the young of the tropical *Oceanodroma castro* and north temperate *Hydrobates pelagicus*.

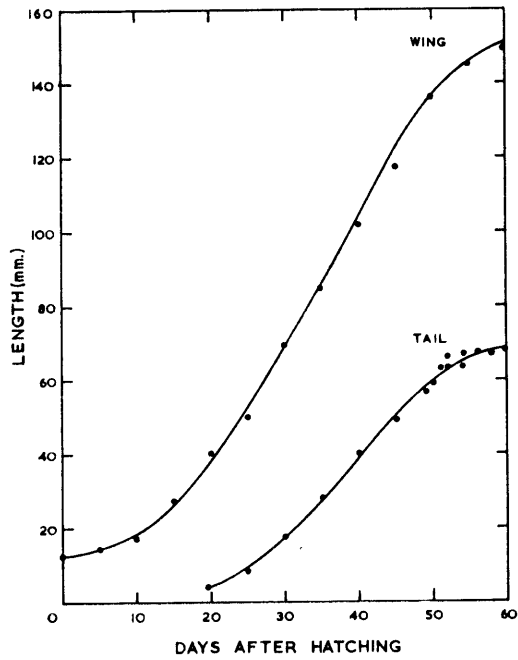


FIGURE 5

Growth of the wing and tail in young *O. oceanicus*.

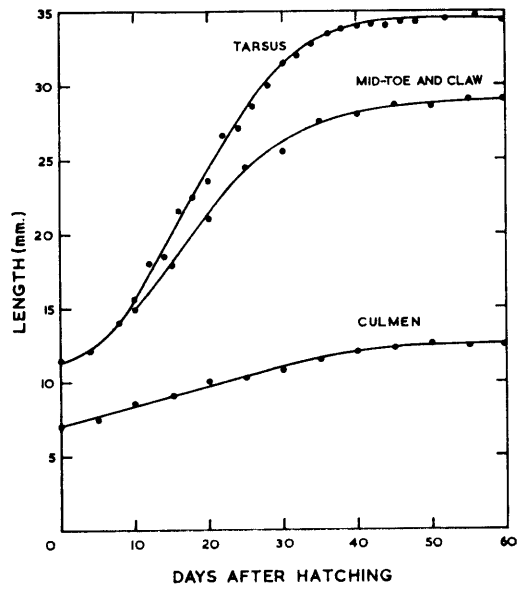


FIGURE 6

Growth of the tarsus, mid-toe/claw and culmen in young *O. oceanicus*.

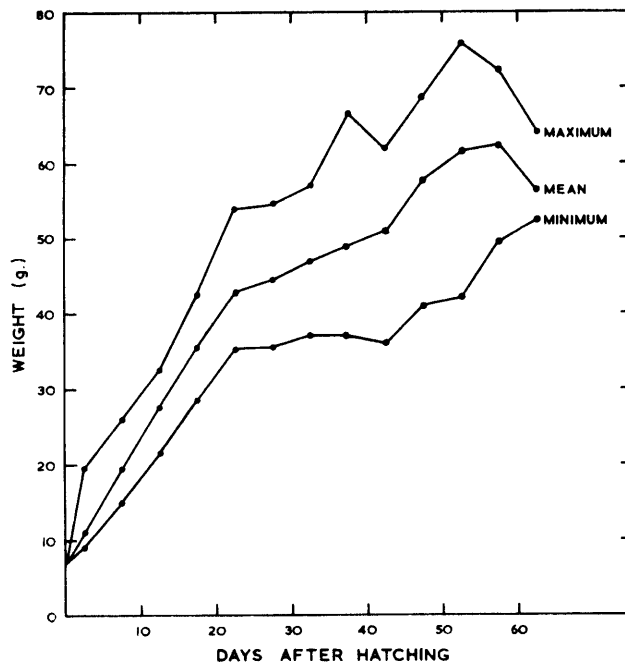


FIGURE 7

Weights of young *O. oceanicus*. Values are calculated from pooled daily weights over 5 day periods.

TABLE XIII  
NIGHT VISITS BY ADULT *O. oceanicus* TO SEVEN CHICKS AT  
SIGNY ISLAND DURING THE FLEDGING PERIOD

Nest	Number of visits				Nights between last visit and chick departure
	Male	Female	Both adults	No adult present	
7	17	2	—	39	4
10	13	5	—	43	Nil
31	14	7	2	37	Nil
32	10	5	—	46	5
34	31	3	1	21	2 or 5
35	16	3	—	37	3
40	19	8	—	41	1

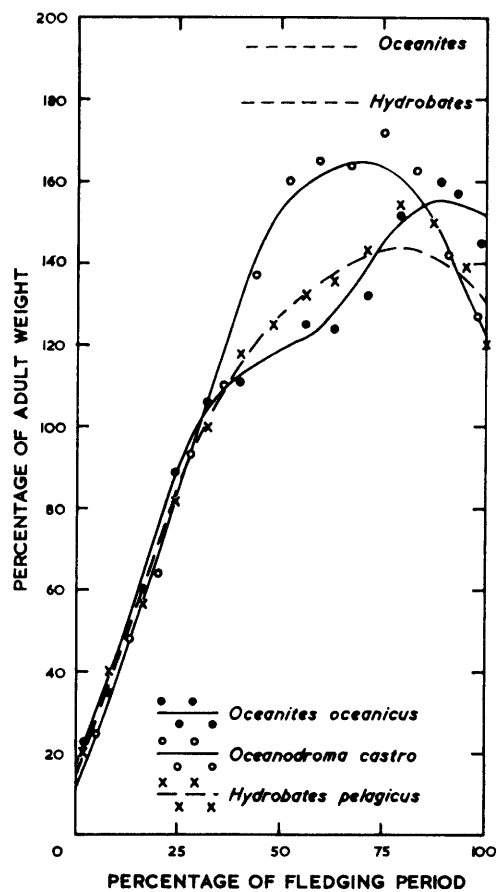


FIGURE 8

Average growth curves for *Oceanites oceanicus*, *Oceanodroma castro* and *Hydrobates pelagicus*. Data for *O. castro* from Allan (1962) and for *H. pelagicus* from Davis (1957). Maximum weights for *Oceanites* and *Hydrobates* are also shown at the top of the diagram.

Chick feeding during the last 10 days in the nest became more sporadic, culminating in a short starvation period of from 3 to 5 days immediately prior to departure (Table XIII). The mean fledging weight of 15 chicks during the two seasons 1966–67 and 1967–68 was 55.3 g. (range 49–64 g.), which is approximately 45 per cent above adult weight. This is higher than in *H. pelagicus* (Davis, 1957), in which chicks depart about 20 per cent above adult weight. There was a significant difference ( $P < 0.05$ ) between the fledging weights in the two seasons (1966–67 mean 57.8 g.,  $N = 9$ ; 1967–68 mean 51.5 g.,  $N = 6$ ), suggesting a difference in the availability of food in the 2 years. Chicks occasionally lost a considerable amount of weight during snowfalls and became torpid. Torpor due to starvation has been commented upon in other storm petrels (Davis, 1957; Allan, 1962; Tickell, 1962; Beck and Brown, 1971). Lengthy periods of temporary starvation due to snowfall, like that of 20 days described by Roberts (1940), were not observed at Signy Island. On Signy Island such periods were either quite brief or so prolonged and severe that entombment and death resulted.

#### 4. Departure

Fledging dates have been recorded between the second week in April and mid-May at Signy Island (Fig. 3). Towards the end of their stay in the nest, the chicks become extremely active and in some cases venture outside the nest cavity and exercise their wings. At one nest in 1966–67 a chick thought to have fledged was found on the following evening near the station hut. When it was returned to the nest, the male was present and initially it treated the chick as an intruder, taking up a crouched posture and ejecting oil—the only instance of threat behaviour we observed in this species. A few minutes later, however, the chick had been accepted by the adult bird and the latter was nibbling the chick's head and bill. The following morning the nest was empty although the night had been cold and windy. Nights with high winds are frequent during April and May, presenting another hazard to be negotiated by the chick as it leaves the nest. On the evening of 7 May 1969 during gale force winds, a recently fledged chick was found floundering in slush ice in Factory Cove. It was kept indoors overnight and released the following day, only to be taken in flight by a Dominican gull, *Larus dominicanus* (personal communication from V. W. Spaul).

Once their chick has left the nest, the adult birds also disappear although visits by male birds and one by a female were recorded at nests where the chick had departed.

#### 5. Chick mortality

The chick is most vulnerable during the first few days in the nest and, during 1966–67 and 1967–68, 7 chicks died or disappeared before their eighth day, while another two disappeared when 51 days old. These two chicks may have been taken by a sheathbill but no trace of down or feathering was found. Chick mortality in each year of the study was as follows:

- 1966–67 22 eggs hatched and 16 chicks successfully fledged.
- 1967–68 3 eggs hatched but no chicks fledged.
- 1968–69 At least 10 eggs hatched but no chicks fledged.

The first season 1966–67 was by far the most successful. Of 49 eggs laid at the marked sites, 22 hatched and of these 16 chicks fledged successfully, an overall success rate of 33 per cent. However, as the two following seasons were totally unsuccessful, the overall breeding success during the period of study was only 11 per cent.

In 1967–68 and 1968–69 all the chicks hatched in the marked nests were entombed by heavy falls of snow. The only chicks to escape in the Factory Bluffs colony were those in unmarked nests in exposed positions higher on the crags, where gusts of wind removed most of the snow as soon as it fell. Thus, in all seasons when there are heavy falls of snow during breeding, probably only those sites located in high exposed positions, i.e. more than 20 m. above M.S.L., are successful in producing fledged young, those in lower positions in the moss and boulder slopes being unproductive in these circumstances. From the comprehensive meteorological and ornithological records kept by the Survey's personnel at Signy Island, it is possible to give some indication of the mortality of eggs and young since the opening of the station in 1947. Seasons when there were heavy snowfalls affecting breeding were as follows:

- 1947–48 Reports of blocking of nest entrances but no high mortality recorded.

- 1955-56 Mortality of eggs and chicks probably high for drift snow occurred throughout December and early January.
- 1958-59 Cold spell in February with high wind, snow and drifting. Heavy mortality as many nests were buried for several weeks. Richards (1959) considered that some birds dug into their nests through almost 1 m. of drift snow, in marked contrast to our observations under similar circumstances (p. 23).
- 1960-61 25 nests marked. A heavy snowfall on 18 January followed by a thaw caused six pairs to desert. When the nests were checked in March, only six contained chicks, of which three were in rock crevices high on Factory Cove bluffs. From three nests on the lower slopes only one chick survived to depart successfully and this was probably because the nest was cleared regularly by the observer.
- 1961-62 From the same 25 sites seven chicks were produced. Some drift snow during late December and early January prevented a number of birds from using their burrows.

Thus, in at least six out of 22 seasons at Signy Island, conditions were such that success was extremely low in the study colony at Factory Cove. It is clear that exposure of the nest site is a vital factor in the breeding success of this species but it is also, unfortunately, a factor which is difficult to quantify. It is not possible to draw any conclusions concerning breeding success in other parts of the island since local conditions are too variable. At present, all one can say is that colonies situated in low-lying areas sheltered by ridges from the prevailing winds are most susceptible to the effects of snowfall. Nests in such colonies may be completely unproductive in one season out of three due to this cause alone.

#### D. BEHAVIOUR OF FAILED BREEDERS

As already mentioned, birds excluded from burrows by heavy snowfalls usually resumed incubation for a while when nests again became accessible, but then deserted the egg although continuing to visit the nest. Similarly, pairs continued to visit the nest intermittently when the incubation routine broke down or where eggs disappeared or sank into the soil of the nest chamber, and few appeared to depart to sea immediately after failure. Observations maintained at failed nests showed that the period of nest visiting after failure was very variable, ranging from 3 to 32 days with a mean of 13.7 days (33 nests). The length of the period was not apparently related to the laying date, the failure date or the number of days incubated before failure. Both sexes visited the nest, the male more often than the female, as in the pre-laying and chick-rearing periods. Birds generally remained faithful to their sites and few visited other nests in this period. Of 26 nests which failed in 1966-67 and 21 nests in 1967-68, birds were known to have wandered to other nests in only three cases; none of these re-occupied the original nest in the following season. However, the proportion of such cases could be higher, as movements from some sites on the edge of the study area could have been missed. Most failed breeders last visited their nests between 22 February and 21 March, thus leaving the island 1-2 months before the departure of successful breeders and their young.

#### E. ACTIVITY OF NON-BREEDING BIRDS

As in most petrel colonies elsewhere, the *O. oceanicus* population studied contained a substantial proportion of non-breeders. These birds were known to include some adults which had been prevented from breeding by persistent winter snows and other former breeders which had lost their mate through separation or death and had not yet found a new partner. Also, after the beginning of egg-laying in December, the number of non-breeders was steadily augmented by failed breeders which had lost or deserted their egg or chick. The majority of non-breeders, however, was presumably young birds which had not yet reached breeding age. From what is known of the age structure of other petrel populations (e.g. Harris, 1966a; Pinder, 1966; Serventy, 1967), it is reasonable to assume that the youngest of these non-breeders would be visiting the colony for the first time, whereas those regularly occupying nest holes would be mainly older birds. The latter would have already spent one or more seasons gaining experience of conditions in the colony and on the feeding grounds, during which time they had acquired a nest hole and in some cases a mate also.

Non-breeders which regularly visit nest holes in the colony are readily recognizable as such, but extremely little is known at present about the younger age classes. In 1966-67, out of 330 birds mist-

netted and ringed, 55 per cent were not recaptured either later that season or in the two subsequent seasons. The status of these birds is obscure and some could have been breeders with a nest outside the study area. However, in a colony of *Hydrobates pelagicus* on Skokholm Island, South Wales, it has been established that young birds do not stay in one area on their return to land at 2–3 years old, but wander extensively, appearing in different areas all over the island on different nights (some also visit neighbouring islands); attachment to a nest site or section of the colony is not developed until the third or fourth year (personal communication from D. Scott). If young *O. oceanicus* returning to the breeding grounds behave similarly, many if not most of the birds caught once only may have been non-breeding immatures less than 3 years old passing through the colony. This question can be resolved only by further trapping and recapture of much larger samples in different parts of Signy Island which include birds of known age.

Fig. 9 shows the proportion of nest holes occupied by non-breeders and by breeders as a percentage of all nests examined in 10 day periods throughout the season. The combined data from 1966–67 and 1967–68 have been used, but observations in 1968–69 were insufficiently detailed. The incidence of eggs and young in the study nests is also shown, together with the percentage of birds caught in the mist-nets once only in 1966–67; the latter possibly represent a younger non-breeding age group than birds in occupation of nest holes, as already mentioned.

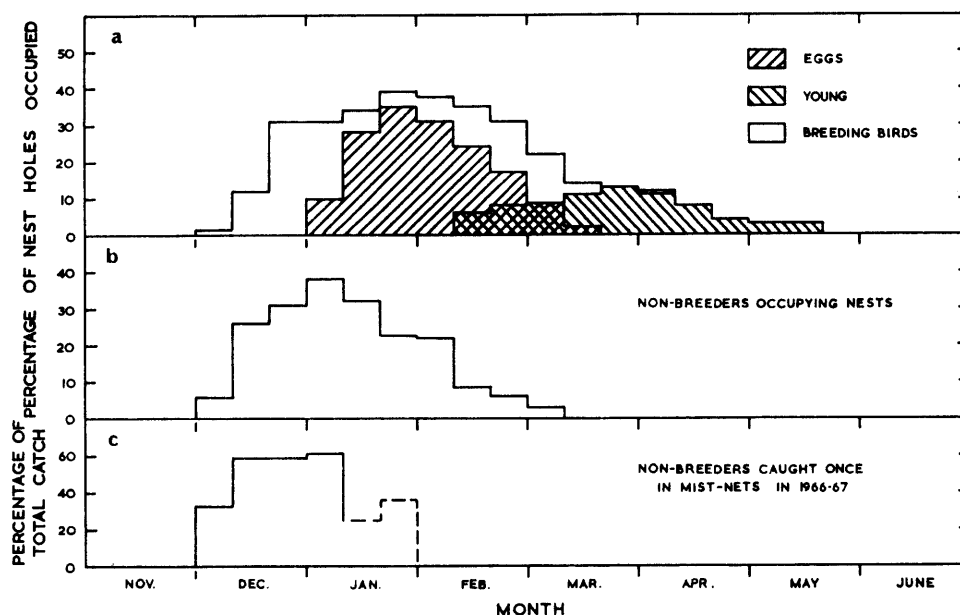


FIGURE 9

The percentages of nests occupied by (a) breeding birds, eggs and young, and (b) non-breeders throughout the season. Data from 1966–67 and 1967–68 have been combined. Also shown is the proportion of non-breeders (c) caught once in mist-net total catches in 1966–67.

It is clear from Fig. 9 that non-breeders occupying nest holes are most numerous in the early part of the season. They arrive at the same time as the breeding birds and numbers build up at the same rate, but their activity reaches a peak in the first week of January, as egg-laying is beginning. This is about 3 weeks earlier than the peak of activity in the breeding birds, which falls in the period 21 January–10 February; by this time the non-breeders have declined to about half their peak number. Most non-breeders have left the island by mid-March. The decrease in the breeding population proceeds more slowly, since pairs which lose their egg or chick continue to visit the nest for a while before departing finally to sea.

The activity of the mist-netted birds caught once is much less clear, as no netting was carried out after 22 January and catches in the period 11–31 January were small, comprising two samples of 12 and 11 birds, respectively. Nonetheless, it is evident that these birds arrive on the breeding grounds at the same time as the breeders and non-breeders, occupying nests and comprise 60 per cent of the mist-net catches

until at least 10 January. Thus, there is no evidence that their behaviour differs markedly from that of the other non-breeding group.

These observations on activity of non-breeders are similar to those of Harris (1969*b*), who found that numbers of non-breeding *Oceanodroma castro* in the Galapagos also reached a maximum early in the season, coinciding with the peak activity period of the returning breeding adults. He pointed out that this differed from the situation in *H. pelagicus* and in the shearwaters, *Puffinus puffinus* and *P. tenuirostris*, in which non-breeders arrive much later than the breeding birds, are most numerous during incubation, and begin to depart only after most young have hatched. Harris discussed possible factors which might influence the timing of visits by young storm petrels to the colonies and considered that food supplies were probably unimportant as, although non-breeders might be less efficient at feeding than breeders, they would require less food and would probably not be at a disadvantage if competing for food with adults feeding young. A more important factor in this *O. castro* colony was predation by owls, and Harris suggested that inexperienced non-breeders, returning in large numbers with the breeding adults, "swamp" the predators and the chances of any one individual being taken are less.

Similar reasoning may explain the timing of visits to the colony by non-breeding *O. oceanicus*. The food supplies in Antarctic surface waters are much richer in the period February–April than in December–January (Foxton, 1956, 1964), when the activity of non-breeders is greatest. Food is therefore unlikely to be an important influence. However, a number of storm petrels are eaten annually by skuas, and to a lesser extent by gulls (see later). As in the Manx shearwater (Harris, 1966*b*), non-breeders probably spend more time in flight or on the surface of the colony visiting different holes, and are correspondingly more exposed to predation than breeders, which do not wander in the colony but fly almost directly to and from their nests. Hence, by returning early with the breeders and staying only a short time at the colony (while the skuas still have eggs and small young (Burton, 1968; personal observations)), the risk of predation may be lessened. It would be interesting to know if the activity of non-breeding *O. oceanicus* is the same at the Argentine Islands, for Roberts (1940) reported that storm petrels there were not attacked by skuas.

#### IV. PAIR-BOND AND SITE ATTACHMENT

##### A. DURATION OF THE PAIR-BOND

Insufficient information was obtained to trace the subsequent history of the pair-bond in the birds ringed by Pinder in 1960–62. Observations made during the present study, however, show that the pair-bond in Wilson's petrel is normally of short duration and may be compared with the situation found in the sooty shearwater, *Puffinus griseus*, by Richdale (1963). Only six out of 35 pairs of Wilson's petrels at the start of the study at Signy Island remained intact and occupied the same nest in all three seasons and only four of these pairs bred in each season.

Table XIV summarizes information on the fate of the pair-bond in the two successive seasons studied, in 46 cases involving breeding birds and in 14 cases non-breeding birds that were keeping company. On average, just over 50 per cent of the breeding pairs remained unchanged from one season to the next, 35 per cent of pairs were broken up by the failure of one or more birds to return, presumably through death, while 13 per cent separated, neither partner returning to occupy the nest although both were known to be still alive. Table XIV also shows that these overall figures mask considerable annual variation, the proportion of pairs remaining intact being much greater in 1966/67–1967/68 than in 1967/68–1968/69. As nests were followed closely each season, it was known precisely how many pair-bonds remained intact. Figures for the categories where the pair-bond was broken are much less accurate, however, for only subsequent recapture shows whether a bird has been missed in a particular season. Thus, the figures for birds not recovered might be lower, particularly for 1967/68–1968/69, and those for separation higher than indicated in Table XIV. The movements of birds displaced by separation are particularly difficult to follow and impossible if birds move to holes inaccessible to observation. The totals for a broken pair-bond are therefore minimal. Table XIV*b*, which examines the pair-bond in birds keeping company in the first season, is subject to the same limitations as those affecting breeding birds. Only 43 per cent of pairs keeping company remained intact and proportionately more bonds were broken by disappearance or separation than in breeding pairs.



TABLE XIV  
FATE OF THE PAIR-BOND IN SUCCESSIVE SEASONS

a. Breeding birds				
Fate of pair-bond in following season	1966/67-1967/68	1967/68-1968/69	Total number of pairs	Per cent
	Number of pairs	Number of pairs		
Still intact	18	6	24	52.2
One bird not recovered	6	7	13	34.8
Neither bird recovered	1	2	3	
Separated—both birds still alive	5	1	6	13.0
b. Pairs keeping company				
Fate of pair-bond in following season	1966/67-1967/68	1967/68-1968/69	Total number of pairs	Per cent
	Number of pairs	Number of pairs		
Still intact	1	1	2	42.9
Intact and breeding	—	4	4	
One bird not recovered	3	2	5	42.9
Neither bird recovered	—	1	1	
Separated—both birds still alive	1	1	2	14.3

The smaller number of intact breeding pairs in 1968-69, following a season when all nests failed in the egg stage, might suggest that the success or otherwise in one season influences the fate of the pair-bond in the next. However, it can be seen from Table XV that, following failure in the first season, as many pairs remained intact as split up. There are few data for successful pairs, however, and the two seasons were so dissimilar that further records are desirable before the question can be settled.

TABLE XV  
FATE OF PAIR-BOND ACCORDING TO BREEDING SUCCESS IN PREVIOUS YEAR

	Same pairs	Split pairs
Successful in previous year	6	3
Unsuccessful in previous year	18	20

Most pair bonds broke down because one partner did not return. In 12 cases where the bond was broken in this way and the surviving bird remained faithful to the nest site, five gained a new mate and produced an egg in the same season that the original partner disappeared. In at least two cases, the new bird was

known to be an experienced adult which had bred in an earlier season at another nest, and the other three may well have been of similar status. Usually, however, no egg is laid since the site is either deserted altogether or the surviving bird spends one or more seasons consorting with a number of different individuals in the original nest. In three cases where the mate failed to return in 1967–68 and the survivor remained faithful to the nest, the latter had not yet bred or acquired a new mate 1 year later.

The behaviour of the surviving partner and the subsequent course of events at the nest depend to some extent on the sex of the bird concerned (cf. Wilbur, 1969). Of ten cases where the male disappeared, the surviving female deserted at five nests (and wandered to other sites) but stayed faithful to the site at the other five nests. On the other hand, the male remained faithful at eight out of nine nests where the female failed to re-appear. This suggests that site attachment is stronger in the male than the female, which is not surprising if, as is likely, the male chooses the nest site. Similar behaviour was found in black-bellied storm petrels at Signy Island (Beck and Brown, 1971); at one nest the female moved away after the male failed to return, while at another, after loss of the female, the male stayed and consorted with a number of females before mating and breeding with one of these birds in the following season.

Hence, pair formation appears to depend on the ability of a male to maintain ownership of a nest hole, where it then meets unmated females of breeding age visiting different sites in search of a partner. Most calling from nest holes came from single birds standing near the entrance and there seems little doubt that its function is to proclaim the single status of the hole owner to potential mates. If the visiting female is an experienced breeder which has lost its partner, pair formation may be relatively brief and breeding may occur in the same season. But where the newcomer is just attaining breeding age, pair formation may be protracted, trios or even quartets of birds may occupy the nest for a season, and final pairing and breeding may be delayed for another year.

#### B. PAIR-BOND AND INTERMITTENT BREEDING

Only between one-quarter and half of the 86 *O. oceanicus* nests under study contained eggs or chicks in any one season. The unproductive nests were occupied with varying degrees of regularity by non-breeding pairs and single individuals. The status of all paired birds, whether breeding or keeping company, from one season to the next is shown in Table XVI. It can be seen that only 37 per cent of breeders in the first

TABLE XVI  
STATUS OF PAIRED INDIVIDUALS RECAPTURED IN FOLLOWING SEASON

<i>Status of pair in first season</i>	<i>Number and status of birds recaptured in second season</i>						
	<i>Total birds recaptured</i>	<i>Breeding with</i>		<i>Keeping company with</i>		<i>Alone at nest</i>	<i>Alive— status unknown</i>
		<i>Same bird</i>	<i>Different bird</i>	<i>Same bird</i>	<i>Different bird</i>		
Breeding	72	26 (36%)	1 (1%)	15 (21%)	3 (4%)	6 (8%)	21 (29%)
Keeping company	21	2 (10%)	5 (24%)	3 (14%)	3 (14%)	2 (10%)	6 (29%)

season bred in the next, another 21 per cent did not breed but kept company with the same mate and another 41 per cent either lost their mate or separated and did not breed. On the other hand, of 21 birds keeping company in the first season, 34 per cent bred in the next, 10 per cent with the same partner. Thus, an observer visiting the colony in two consecutive seasons would find an appreciable proportion of the first season's breeders reduced in status to keeping company, for no apparent reason, in the second season, while some of those originally found keeping company would be breeding. If only casual observations were possible and little more was known of the colony or the status of individuals, it would be possible for our observer to conclude that breeding was intermittent, for birds with apparently ample opportunity to do so were failing to breed.

Intermittent breeding was first suggested by Wynne-Edwards (1939) to occur in Canadian fulmars, *Fulmarus glacialis*, and was later supported by Duffey (1950) working on Scottish fulmars. This was contested by Carrick and Dunnet (1954), who found no evidence to support it in Scottish fulmars. While acknowledging that the majority of non-breeders are probably young birds which have yet to breed, Wynne-Edwards (1962, p. 569) then suggested that, whereas most adults would breed annually in the rapidly expanding British fulmar population, this may not be so in the older and more static populations in arctic Canada.

Richdale (1963), working on the sooty shearwater, found that 29 per cent of his original breeding birds were keeping company in the following season, 15 per cent with the same partner as in the first season. He considered the possibility of intermittent breeding but thought its occurrence highly improbable. Where birds were keeping company with the same partner, he considered that most were failed breeders whose egg-laying he had missed. He also considered that birds keeping company with a new partner could be prevented from breeding by factors such as burrow destruction, late separation or death of the former partner in the critical breeding stages and immaturity of the new partner. As he was working with large numbers of birds which were largely unsexed, he was not able to follow individual cases in detail.

During our observations at Signy Island, 12 *O. oceanicus* pairs bred in 1 year and then kept company at the same nest but without breeding in the following season. All these pairs arrived back on the breeding grounds in time to breed in the second season, none were failed breeders, and all apparently had the opportunity to breed but did not do so. In eight of these cases, however, observations in the next season suggested that non-breeding was caused by the pair-bond breaking down, followed by separation, and this was confirmed by the behaviour in the third season when either both birds deserted the nest or one remained and mated with a new bird. In two cases, these new birds consorted with the original pair in the second season and formed trios. In five pairs, birds visited the nest on only a few occasions before splitting up but, in the other three pairs, both sexes visited the nest frequently for some time before the female disappeared, and later wandered to other sites leaving the male to continue nest visiting for the remainder of the season.

Apart from separation and break-down of the pair-bond, the other main cause of non-breeding appeared to be prevention by snow blockage which affected three pairs. In each case, both sexes visited the nest normally until heavy snowfalls completely blocked the holes for 6 days between 18 and 24 January 1968. At two of these nests, just prior to blockage, the male was visiting alone at night and it is highly probable the female was away on the pre-laying exodus. Presumably, she was unable to enter the nest on return and the egg was laid outside and lost. Visits to the nest after the snow had melted were sporadic. In the following season separation occurred at one nest, while at the second the female did not return and the male bred with a new female, and at the third the pair remained the same but did not breed.

Thus, 11 nests can be explained in terms of either separation or prevented breeding and only one nest remains where genuine intermittent breeding could have occurred. At nest 47, an egg was laid and a chick fledged in 1966-67; in 1967-68 no egg was laid, although the occupants visited the nest regularly throughout the season, and no intruders were recorded; in 1968-69 an egg was laid but its subsequent fate was not followed after 21 January 1969. The male bird was the same in all three seasons but the female was ringed only at the start of the second (non-breeding) season. Thus, there remains the possibility that the female of the second season may have been different from that of the first. Hence, it is clear that, despite appearances, intermittent breeding either does not occur or is rare in Wilson's petrels at Signy Island. Although the history of the South Orkney Islands colonies is not known, there is no reason to think that it is other than an old-established and probably stable population.

## V. MOULT

ADULT birds complete most of their moult between May and October outside the breeding season (Murphy, 1918; Roberts, 1940). Replacement of the flight feathers apparently begins during the northward migration and is completed relatively rapidly in about 4 months in the winter quarters. Birds wintering in the cool seas of the eastern North Atlantic finish replacing the flight feathers by the end of August, rather earlier than birds wintering in the tropical waters of the northern Indian Ocean (Bourne, 1960). The black-bellied storm petrel and dove prion also moult away from the breeding grounds. All three species have

late and protracted breeding cycles filling virtually the whole of the short Antarctic summer, so that after the young depart food is probably too scarce, and/or time too short before winter sets in, for moult to begin at the breeding colony (Beck, 1970).

The situation in *O. oceanicus* forms an interesting contrast with the much more prolonged moult indicated by Stresemann and Stresemann (1966) for the Northern Hemisphere storm petrels, *Hydrobates pelagicus* and *Oceanodroma leucorhoa*. These birds breed in the North Atlantic and migrate south to winter in sub-tropical and tropical waters. In *Hydrobates pelagicus* (and probably in *O. leucorhoa* as well), wing and body moult begins on the breeding grounds while birds are still feeding young (Harris, 1966b). Replacement extends over the entire non-breeding season and some individuals are still re-growing the outermost primaries during the return northward migration (Stresemann and Stresemann, 1966). In these North Atlantic breeding species, moult presumably begins on the breeding grounds because food is still abundant near the colony even at the end of the season and perhaps considerably more abundant than on the migration route or in the winter quarters.

Most adult Wilson's storm petrels handled at Signy Island were inspected for signs of moult, particularly at the beginning and end of the season, but none was in wing or tail moult. However, between 7 February and 19 March 1968, seven individuals were moulting contour feathering. Four birds were of uncertain breeding status with cloacas of the male type, the other three were adult females which were known to have lost their egg or chick. In three of the presumed males, several white rump feathers were bursting from sheaths and others were in pin, while the fourth bird had new feathers sprouting around the brood patch. Two of the females were also renewing feathers around the brood patch while the third bird was in moderate head, nape and rump moult, with some feathers freshly burst from their sheaths. In addition to these records, on 4 February 1969, D.W.B. captured two adult birds at Adelaide Island, which were also renewing contour feathering around the brood patch. One was incubating an egg, while the other was brooding a newly hatched chick. No other birds were found moulting at Adelaide Island out of 40 individuals examined in early February.

## VI. FOOD AND FEEDING HABITS

WILSON'S storm petrels are rarely captured at sea and the few stomachs that have been examined usually contained few identifiable remains. Roberts (1940) summarized the scanty information available at that time. He found only krill, *Euphausia superba*, in Graham Land birds and suggested that this abundant crustacean forms the usual diet at all Antarctic breeding stations. Bierman and Voous (1950) reported numerous fragments of small cephalopods in one bird and cephalopod and isopod remains in another; both birds were collected in the eastern South Atlantic in February. Few birds have been examined on the breeding grounds. One at Iles Kerguelen was found to contain eye lenses and cephalopod jaws (Paulian, 1953), while Mougín (1968) found cephalopods in three out of four stomachs, with whale oil also present in one bird and crustacean remains in another. Falla (1937) recorded an amphipod, *Euthemisto* sp., as the chief food at Iles Kerguelen, but he identified euphausiids and cephalopods in stomachs of birds taken off the Antarctic continent.

At Signy Island, birds captured in mist-nets as they came into the colony at night frequently spat drops of clear reddish oil and sometimes regurgitated partly digested food material before they could be extracted from the net. Many of these food samples were unavoidably lost and systematic collection was not possible. Although specific identifications could rarely be made, euphausiid eyes and limbs predominated in most regurgitations and 20 samples collected in December and January contained almost complete adult and adolescent stages of *Euphausia superba*. It seems therefore that *E. superba* may be the principal prey of Wilson's petrels at Signy Island, as well as at the Argentine Islands (Roberts, 1940) and near the Antarctic continent (Falla, 1937).

The scavenging habits of *O. oceanicus* are well known and detailed accounts have been given by Murphy (1936), Falla (1937) and Roberts (1940). The activities of marine predators provide an intermittent secondary source of food at Signy Island. Parties of storm petrels were frequently seen feeding on scraps left after penguins had been killed by leopard seals, *Hydrurga leptonyx*. On 7 March 1968, a seal was killed in Borge Bay, probably by a killer whale, *Orcinus orca*. Over 300 *O. oceanicus* gathered to feed from the oily slicks seeping from chunks of blubber floating on the sea surface, even though few birds were present in the area earlier (Plate VIa and b). Birds are remarkably quick to take advantage of these temporary

windfalls and large numbers assemble rapidly. This feeding by "local enhancement" (Hinde, 1961) was also seen in other scavenging petrels such as the giant petrel and cape pigeon. At Adelaide Island, D.W.B. observed *O. oceanicus* feeding around the base of grounding icebergs, presumably on organisms brought to the surface by the water turbulence. This source of food is also exploited by cape pigeons (Beck, 1969).

## VII. POPULATION DYNAMICS

### A. POPULATION SIZE AND ITS ESTIMATION

The practical difficulties of measuring the size of the population in small nocturnal petrels are formidable. First, few colonies are small and discrete, hence only a fraction of the entire population present can normally be marked and studied in detail. Secondly, non-breeding sub-adult birds comprise a high proportion of the total numbers present and, as the season progresses, their ranks are continually being swelled by adults which have lost their egg or chick. The numbers of these unemployed birds are particularly difficult to assess as the various age and breeding classes are morphologically indistinguishable. The status of an individual can be defined with certainty only by following the behaviour of that individual throughout the season—an extremely difficult task when large numbers of birds are present. In the case of Wilson's petrel, these problems are increased by the fact that, unlike most Antarctic Procellarii, some mature adults are prevented from breeding every year, either by the loss of their mate or by persistent winter snows excluding them from the nest hole.

Theoretically, an estimate of the population might be obtained by mark/recapture analysis using samples of mist-netted birds. These samples should contain breeding adults, failed breeders visiting their sites, and sub-adult birds either prospecting future sites or visiting the colony for the first time. If the proportions of these classes present are representative of the population as a whole, and if the number of breeding birds is known from counts of nests containing eggs/young per unit area, the number of unemployed individuals is readily calculated. However, this approach cannot be used because mist-netted birds are not a random sample of the whole population.

Because of the uneven rocky terrain, the mist-nets were in all three seasons (Fig. 1) used in two main sites, one immediately south-east of the new hut (site 1), and the other (site 2) straddling the rock/moss slopes below Factory Bluffs. In addition, some netting was carried out around the old hut in order to catch birds originally ringed in this area by R. Pinder in 1960–62. Although the two main sites were only about 200 m. apart and over 400 birds were ringed, only two ringed at one site were recovered at the other. It thus appears that little mixing was occurring and birds were keeping to one sub-area within the general colony.

Recapture proportions in the mist-net catches were low; in 1966–67, out of 256 birds netted and ringed at the two sites up to 30 December, only 46 (18 per cent) were captured later in the season. Of these, 28 were recaptured once only, 15 twice and three birds on three occasions. Most birds recaptured more than once were either breeders or non-breeders owning nest sites very near (within 3 m.) to the net. Furthermore, as mentioned earlier, rather more than half the birds netted and ringed in 1966–67 were not recaptured either later that season or in the two following seasons. This is much too large a proportion to be accounted for in terms of the normal annual mortality (see later) and, together with the bias towards single recaptures, strongly suggests that the birds were not sampled at random by the nets. An additional unexpected source of bias encountered was that ringing itself affected the chances of a bird's subsequent recapture. Some birds extracted from the nets were held by only a strand of net which had slipped through the butt joint of the monel ring. These rings were slightly springy and could not be butted tightly. But for the ring, many of the birds caught would probably have "bounced out" and escaped.

Table XVII shows the proportion of birds recaptured in 1966–67 at mist-net site 2 where most netting was carried out. The largest number of birds ringed on one night was 56 on 15 December, but the maximum number of recoveries from this group on any subsequent night was only four. In order to test whether this group of birds was being sampled at random, the data were treated by the method described by Orians (1958) in his analysis of shearwater recoveries. Comparison of the observed and expected variation in the recovery distribution gave a  $\chi^2$  value of +2.08, which is equivalent to a probability between  $P = 0.03$  and  $P = 0.04$ . Thus the difference between the observed and expected recapture frequencies is

TABLE XVII  
RECOVERIES OF *O. oceanicus* AT MIST-NET SITE 2 IN 1966-67

Date ringed	Dates of recapture										
	1966										1967
	10 Dec.	11 Dec.	13 Dec.	15 Dec.	21 Dec.	25 Dec.	27 Dec.	29 Dec.	30 Dec.	1 Jan.	2 Jan.
1966											
10 December		1	0	0	0	0	1	2	2	0	1
11 December			0	2	2	1	3	0	4	1	1
13 December				0	1	0	1	0	0	1	0
15 December					3	4	4	1	1	3	0
21 December						2	4	4	0	3	1
25 December							0	2	2	0	0
27 December								2	3	2	1
29 December									2	0	0
30 December										0	0
1967											
1 January											2
Total already ringed	—	1	—	2	6	7	13	11	14	10	6
Total unringed	10	23	6	56	35	24	33	27	38	23	13
Total catch	10	24	6	58	41	31	46	38	52	33	19
Percentage of previously ringed in catch	—	4.2	—	3.4	14.6	22.6	28.3	28.9	26.9	30.3	31.6

statistically significant and provides evidence that birds were not being caught at random. Calculations for the other groups of recoveries shown in Table XVII gave similar results. Hence, it is concluded that the total population cannot be assessed on the basis of mist-netting data obtained during this study, because some birds appeared more and others less frequently in the nets than would be expected if sampling were random.

#### B. RELATIVE POPULATION SIZE

Although the deficiencies of the mist-netting data do not allow an estimate to be made of the total population, the data provide a relative measure of the number of birds in flight over the area in the different seasons. The same mist-netting sites were used each year and netting was carried out between 21.30 and 24.00 L.M.T., beginning just after birds began to return to the colony at dusk. The amount of netting that could be done was limited by the weather—fairly calm conditions were necessary, with wind speeds of 10 kt [5.2 m./sec.] or less. During each session, the total number of birds caught (including those released unringed) and the number of hours spent netting were recorded, so that catches could be expressed in terms of unit effort. One 12.2 m. net was generally used, but occasionally an additional 6.1 m. net was also worked. On these occasions, the latter was regarded as having half the catching potential of the larger net and the total number of hours the 12.2 m. net was worked was increased by a factor of half the number of hours the 6.1 m. net was worked to give the number of effective hours spent netting. In order to make valid comparisons between the three seasons, only netting totals for the period between

arrival and the beginning of January have been used, i.e. at the beginning of egg-laying when the largest numbers of birds are present in the colony.

Table XVIII shows the number of birds caught in the nets in each season in relation to the time spent. In 1966-67, 399 birds were caught in 19.2 effective hours of netting. In the following year, 313 birds were

TABLE XVIII  
RELATIVE NUMBERS OF *O. oceanicus* PRESENT IN DIFFERENT SEASONS  
BASED ON MIST-NETTING

Season	Period of mist-netting	Number of hours netted*	Number of effective hours netted*	Number caught	Catch/hr.	Percentage of 1966-67 numbers
1966-67	9 December 1966-6 January 1967	19.2	19.2	399	20.8	100
1967-68	5 December 1967-4 January 1968	22.7	25.9	313	12.1	58.2
1968-69	4-29 December 1968	10.5	10.8	208	19.3	92.7

\* Total of hours netted corrected for additional use of 20 ft. [6.1 m.] mist-net.

caught over the same period of the year in 25.9 hr. Assuming that the netting procedure remained constant and that the same numbers of birds were present in 1967-68 as in 1966-67, the expected number caught in 1967-68 would be 538 by simple proportion. In fact, 313 birds were caught so that the percentage of those actually caught of those expected to be captured is given by

$$\frac{313 \times 19.2 \times 100}{399 \times 25.9} = 58.2 \text{ per cent.}$$

Treating the 1968-69 figures similarly, then 208 birds netted in 10.8 effective hours represents 92.7 per cent of the 1966-67 total.

Thus, there is evidence that in 1967-68 the population at risk to capture by mist-netting was approximately 40 per cent lower than in the previous season but regained this former level in the following 1968-69 season. The very appreciable drop in numbers in 1967-68 was also reflected in the numbers of non-breeding birds visiting or occupying sites. Holes which in 1966-67 were visited by up to eight different individuals were not occupied or scarcely visited in 1967-68. On the other hand, the number of breeding birds was only a little less than in 1966-67 (allowing for annual mortality), with 84 per cent of the 1966-67 breeding birds known to be still alive in 1967-68. Netting conditions were apparently the same in all three seasons and the breeding population remained almost unchanged throughout, so the decline must have occurred in the presumed non-breeders. Severe weather in several earlier breeding seasons, killing all the young, would lower the recruitment rate and cause such a temporary decline in numbers. However, meteorological records for the four seasons before this study began do not support this view. Alternatively, the non-breeders (a) met with some disaster between departure in February/March 1967 and arrival in the following November/December or (b) 40 per cent deliberately stayed away from all breeding grounds in that season or (c) just from the particular colony at Signy Island under study. Losses on migration or in winter quarters caused, for example, by hurricanes would probably take not one but several years to recoup. Thus the rapid return of the population in 1968-69 to the 1966-67 level rules out mass mortality and implies that birds simply did not return to the island or to the colony in 1967-68. At present, it is not possible to distinguish between these alternatives and no reasons can be given to explain this absence; there was no evidence of food shortage either in this species or in other petrels under study.

### C. SIZE OF THE SIGNY ISLAND POPULATION

The area of the study colony was found by pacing to measure approximately 1,486 m.<sup>2</sup> and a careful survey showed that this area contained a total of 184 suitable nest sites, an average nest density of one nest

per 8 m.<sup>2</sup>. Thus, assuming all holes are occupied, the carrying capacity of the area is theoretically 368 paired individuals. However, only a proportion of these sites was occupied and others were inaccessible to observation, so it was not known if birds were present. In all, 70 of the 184 nest sites in the colony were known to have been in use during the three seasons (a density equivalent to one nest per 21 m.<sup>2</sup>), but only some of these produced eggs; 35 in 1966–67, 23 in 1967–68 and 17 in 1968–69.

The total area of the island which is ice-free in summer and also provides suitable nesting habitat for Wilson's storm petrels was found using squared paper to be 4.135 km.<sup>2</sup>. Extrapolation from the 1966–67 sample of 35 eggs produced per 1,486 m.<sup>2</sup> gives a figure of 97,375 eggs (= pairs) for the entire island, assuming that breeding success and nest density is similar in different areas. From mist-netting, it appears that the breeding population forms one-half or less of the total number of birds present, so that the population of the whole island could be about 200,000 pairs.

#### D. ADULT SURVIVAL

##### 1. Survival estimates

One of the chief aims of the mist-netting programme was to recapture as many as possible of the birds ringed between 1959 and 1962 by R. Pinder so that adult survival could be estimated. Pinder's birds were ringed as breeding adults, the majority in nests close to the station huts, and recapturing in subsequent years showed that several birds were still occupying their original nests while others were known to have moved only to nearby sites. Thus, it seemed likely that mist-netting would recapture almost all birds still alive even if some had changed nest sites or if, for reasons mentioned earlier, birds were not breeding but still visiting the colony.

Over the three seasons, 27 out of a possible 56 of these 1959–62 birds were recovered (66 were ringed originally but two had been found dead and eight ringed at three sites on Factory Bluffs have been omitted). Details of the known periods of survival of these 27 birds plus all known to have survived more than 1 year (42) are set out in Table XIX. The survival estimates calculated from these data range from 89 to 92 per cent per annum with a mean of 91 per cent. From the formula  $(2-m)/2m$ , where  $m$  is the adult mortality, the mean life expectancy for these birds is 10.4 yr. These estimates are based on a small sample and are almost certainly too low, for failure to catch only one or two individuals would make a proportionately large difference to the results and, as noted earlier, mist-netting is not a very efficient method of recapturing breeding birds.

Another independent survival estimate is provided by the proportion of breeding birds in marked nests which return in the following season. Of 69 birds which bred in 1966–67 (23 successfully), 58 (84 per cent) were recaptured either in the same nests or by mist-nets in 1967–68. The proportion recaptured in 1968–69 of 37 breeding in 1967–68 was only 70 per cent with 11 birds apparently failing to return. However, all the 1967–68 birds were failed breeders, which may have resulted in more pairs splitting up and moving to other sites with lessened chances of being recaptured. Of the 21 birds which failed to return, two successful breeders identified in April and three failed breeders still present in March probably died away from the breeding grounds; the remaining 16 birds were last identified between December and February and there is no way of telling how many died at the colony and how many at sea in the non-breeding season.

Adult survival estimates are available for several members of the Procellariidae and all exceed 90 per cent per annum—94 per cent for *Fulmarus glacialis* (Dunnet and others, 1963); 92–94 per cent for *Puffinus griseus* (Richdale, 1963); 91–95 per cent for *Puffinus tenuirostris* (Farner, in Palmer, 1962); 93–96 per cent for *Puffinus puffinus* (Harris, 1966a) and 93–96 per cent for *Daption capensis* and *Pagodroma nivea* (Hudson, 1966). There are no comparable estimates available for the smaller petrel species. Davis (1957), over two seasons, recaptured 60 out of 74 breeding British storm petrels in the following season but this 81 per cent apparent survival, like the results given for *O. oceanicus*, is almost certainly depressed by the failure to recapture failed breeders which have moved to new sites. Lack (1966, 1968) quoted 7 per cent for the annual mortality in *Hydrobates pelagicus*, based on Davis' figures for successful breeders only, but this is effectively a measure of over-winter survival and probably underestimates mortality occurring on the breeding grounds.

An overall breeding success of 11 per cent per year means that, if the population is to remain stable, the adult annual mortality cannot exceed 5 per cent and all young fledged must survive to recruitment.



TABLE XIX  
MEAN ADULT SURVIVAL ESTIMATES OF *O. oceanicus* RINGED IN 1959-62

Year of ringing	Known minimum period of survival (yr.)								Accumulated total at risk
	1	2	3	4	5	6	7	8	
1959-60	4	4	2	2	2	2	2	2	4
1960-61	31	23	23	18	18	18	14		35
1961-62	7	7	7	7	7	6			42
TOTAL	42	34	32	27	27	26	16	2	
Proportion surviving	= 42/42	34/42	32/42	27/42	27/42	26/42	16/35	2/4	
	1.0000	0.8095	0.7619	0.6429	0.6429	0.6190	0.4571	0.5000	
If annual survival rate is $S$ , these equal	$S$	$S^2$	$S^3$	$S^4$	$S^5$	$S^6$	$S^7$	$S^8$	
Therefore $S$ equals		0.8997	0.9133	0.8954	0.9154	0.9230	0.8942	0.9167	
Geometrical mean $S = 0.9083$									
Mean annual survival = 90.83% (range 89.42-92.3%)									
Therefore, mean annual mortality $m = 9.17\%$ (range 7.7-10.58%)									
and mean adult life expectancy $\frac{2-m}{2m} = 10.40$ yr.									

However, complete post-fledging survival is exceedingly unlikely and, as already indicated, adult survival is probably of the order of 90-95 per cent per year. Therefore, on the results obtained during this study, the Factory Cove colony has too small an output of young to offset annual losses of adults, and it appears that the colony is either declining or is maintained by immigration from more favourable areas.

Only 15 birds have been ringed as nestlings, 12 during this study, and so far none has been recovered. Hence, there is no information on the age of first breeding or return to the colony in this species. Work on other Hydrobatidae, however, is providing increasing evidence that the storm petrels resemble the larger petrels, such as the shearwaters, in their population parameters. *O. leucorrhoa* has been found breeding once at 3 yr. (Gross, 1947), once at 4 yr. and four times at 5 yr. (Huntington, in Harris, 1969b), while most *H. pelagicus* first return to the colonies at 2 yr. and single birds have bred at 3 and 4 yr. (personal communication from D. Scott). Thus, it seems likely that some *O. oceanicus* might begin to breed at 3 yr. but most individuals would probably begin to lay 1-2 yr. later.

## 2. Causes of adult mortality at the breeding colony

Roberts (1940) considered *O. oceanicus* to be virtually the only Antarctic bird which is not attacked by skuas and giant petrels. He was able to cite only one record of *O. oceanicus* forming the prey of larger birds, that of Priestley (1914), who found a half-digested Wilson's storm petrel in the stomach of a south polar skua, *Catharacta skua maccormicki*, shot at Cape Adare. However, as Tickell (1960) has pointed out, skua predation of storm petrels is a familiar feature both at South Georgia and in the South Orkney Islands and is probably the most significant single cause of adult mortality on the breeding grounds.

Burton (1968), describing the feeding habits of brown skuas at Signy Island, referred to these birds catching Wilson's storm petrels both in flight and on the ground as they are about to enter the nest holes. Station ornithological reports for past seasons contain several references to such behaviour and also mention storm petrel remains in skua pellets and around skua nests. During the present study, two skuas

often visited the petrel colony in the evenings in early December, perching on prominent rocks and watching the incoming petrels, or wandering around the moss slopes investigating nest holes. Attacks were witnessed on several occasions. Sometimes, the skua pursued a bird in flight which escaped by jinking. More often, the skua would glide low over the moss slope and either drop suddenly to the ground on top of a crouching storm petrel or would swoop down, snatch up a petrel in its bill and carry it off. Wilson's storm petrels feeding and flying offshore by day were hardly ever molested but on 18 April 1968, during rough weather, a skua was observed forcing an adult storm petrel down into the sea. It attempted to kill the struggling petrel but was prevented from alighting by the heavy swell. While it hovered overhead, a giant petrel landed and caught and swallowed the storm petrel. It was not possible to assess the impact of skua predation on the petrel population. In all, 450 storm petrels were ringed and only two rings were found in skua pellets; both were from non-breeders. It is to be expected that non-breeding birds spending more time on the surface at the colony would be more susceptible to predation than breeding birds.

Wilson's storm petrels were also preyed upon by Dominican gulls. In December 1967, two pairs of gulls frequented the same stretch of moss bank as the skuas and were probably attempting to catch birds as they came into the colony in the evening. Gulls have twice been seen to take a storm petrel in flight, one being an injured adult and the other a recently fledged chick; probably a mature healthy bird can out-manoeuvre a gull in the air. The remains of a Wilson's storm petrel regurgitated by a Dominican gull on 24 May 1965 and other remains noted in May at gull roosts were probably those of newly fledged young.

Apart from the single observation cited above, predation by giant petrels or sheathbills was not observed and it seems likely that only birds which had been disabled in some way would be attacked by these primarily scavenging species. Exceptionally, Wilson's storm petrels may be taken by leopard seals, for on 23 January 1969 a seal was seen snapping unsuccessfully at *O. oceanicus* pattering on the sea and feeding from an oily slick streaming from a stranded dead fin whale, *Balaenoptera physalus* (personal communication from D. G. Bone).

Finally, possible mortality due to entombment during heavy snowfalls must be considered. As described earlier, all occupants (both breeding and non-breeding) in the study nests at Signy Island deserted the nest when the entrance became snow-blocked and only unfledged chicks were entombed. On the other hand, Mougin (1968) mentioned a bird becoming iced into the nest and Tickell (1956) described a bird which had become stuck while digging a tunnel through drift snow and, although he did not say whether the bird was alive or dead, evidently a few birds die through drift snow blocking their nests.

### 3. Causes of adult mortality away from the breeding grounds

Although Wilson's storm petrels have few natural predators at sea, they are vulnerable to attacks by predatory fish while pattering along the sea-surface in search of food. Roberts (1940) mentioned a bird in the Argentine Islands with a foot missing and noted that birds with one leg missing have been seen in the north Atlantic. One non-breeding bird occupying a nest at Signy Island had lost a leg just below the tarsal joint but it was normal in weight and did not seem inconvenienced by this disability. Also, two birds caught in the mist-nets had damaged feet and webs. In the tropics, predatory fish are numerous and Allan (1962) working on *Oceanodroma castro* on Ascension Island found 3.5 per cent of his birds had damaged feet while Harris (1969b) recorded a 7 per cent incidence of foot injuries in the Galapagos and also noted a bird with a missing leg. Not surprisingly, direct observations of fish predation on birds at sea are rare, so that Ritchie's (1966) record of an *O. oceanicus* being caught by a shark while pattering on the surface is particularly interesting.

While on migration or in winter quarters, Wilson's storm petrels are at times preyed on by raptorial birds, for there are now several reports of peregrine falcons, *Falco peregrinus*, coming aboard ships in mid-ocean and living off storm petrels for several days (Voous, 1961). The storm petrels caught are usually unidentified but the notes of Capt. G. E. Hodges (referred to in *Sea Swallow*, 1957, Vol. 10, p. 20) reported peregrines regularly visiting the ship off the Arabian coast and mentioned "Wilson's petrels (in season) being brought to the truck and eaten by peregrines".

Reviewing the significance and validity of vagrant petrel records, Bourne (1967) emphasized the remarkably small number of reliable records of *O. oceanicus* cast ashore in Europe and in North America, despite the abundance of the species in the North Atlantic from May until September. This is evidently not due to the species preferring the open ocean, for most North Atlantic records between June and August

come from European and American coastal waters (Roberts, 1940), while Bailey (1966) found that the majority of wintering birds in the Arabian Sea during July and August occurred along the edge of the continental shelf, less than 80 km. from land. Bourne (1967) concluded that the species must be well adapted to cope with bad weather and this explanation seems convincing, particularly as the weather conditions usually encountered in the North Atlantic during the northern summer and in the Indian Ocean during the south-west monsoon are much less severe than those on the breeding grounds in the Southern Ocean. Wrecks involving British and Leach's storm petrels have occurred on several occasions (Evans, 1892; Boyd, 1954) but the only one involving *O. oceanicus* seems to be that described by Pearson (1899) and quoted by Roberts (1940), when prodigious numbers died on the coast of North Carolina, U.S.A., during a great storm in August 1893.

### VIII. WEIGHTS OF ADULTS

THERE are still very few detailed studies of sea-bird weights. Richdale's (1947) work on the weights of various Southern Hemisphere petrels and penguins was one of the first modern studies. More recently, Fisher (1967) has provided valuable data on weight variations in relation to reproductive state in the tropical albatross, *Diomedea immutabilis*, while Harris (1966*b*, 1969*a*, *b*) presented information on seasonal weight changes in *Puffinus puffinus*, *P. lherminieri* and *Oceanodroma castro*, respectively. One of the main aims of the present work was to obtain weights from large samples of mist-netted birds in order to follow weight changes throughout the breeding season.

All weights discussed in this section were taken from birds caught at night between 20.00 and 02.00 L.M.T. Most birds were mist-netted on arrival at the colony but some were caught by hand in nest holes. The majority of weights were taken inside the station hut out of the wind. Pesola spring balances supplied by the British Trust for Ornithology were used and weights were taken to the nearest 0.5 g. The balances were checked for accuracy against standard weights at intervals throughout the study. In *Fregatta tropica* (Beck and Brown, 1971), sexual dimorphism in size is marked but in *O. oceanicus* the sexes are alike or differ only slightly in weights and measurements, and for most purposes the data may be combined. This is illustrated in Fig. 10, which shows the frequency distribution of 267 weights obtained from birds mist-netted in December 1966. Although as shown earlier, males spent more time at the nest and are thus more often caught than females, the sexes should be more evenly represented in the non-breeding part of the population which predominates in mist-net catches. The distribution of weights in Fig. 10 is approximately normal and there is no evidence of bimodality consistent with a sex difference in body weight. The wings of a proportion of the birds mist-netted in December 1966 were measured and the relationship between wing length and weight is shown in Table XX. Longer-winged birds appear to weigh a little more than those with shorter wings but the difference is slight; differences between the mean weights for the wing-length groups 141–145 and 156–160 mm. at the extremes of the series are not significant ( $t = 1.16$ ; d.f. = 34).

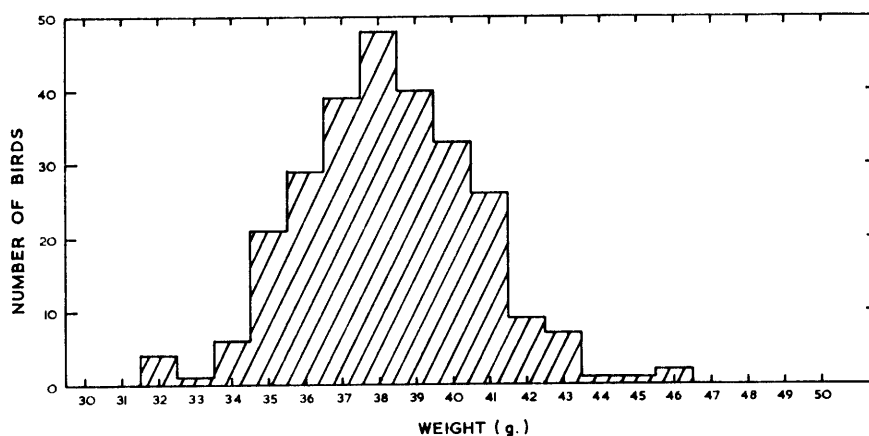


FIGURE 10

The distribution of weights of 267 adult *O. oceanicus* caught in December 1966.

TABLE XX  
WEIGHTS AND WING LENGTHS OF 154 *O. oceanicus*  
CAUGHT IN PERIOD 9-21 DECEMBER 1966

<i>Wing length</i> (mm.)	<i>Number weighed</i>	<i>Mean weight</i> (g.)	<i>S.D.</i>
141			
142	3	37.3	1.99
143			
144	3	39.0	
145	4	39.4	
146	7	38.3	2.34
147	7	38.1	
148	13	37.6	
149	13	38.9	
150	15	37.7	2.12
151	20	37.9	
152	15	39.6	
153	8	39.6	
154	7	38.0	2.89
155	13	38.8	
156	12	39.4	
157	3	41.7	
158	4	39.5	2.89
159	5	39.6	
160	2	40.5	

Over the three seasons 644 birds were weighed and the numbers weighed in different months in each season are analysed in Table XXI. Figures for November/December refer mainly to mist-netted birds, whereas those for February onwards were of birds caught by hand in nest holes. Comparison of the data for the seasons 1966-67 and 1967-68 showed no significant difference between these two seasons; results for the period 1-15 December 1968 were also similar to those obtained in the two previous years. The pattern of weight change was thus identical in the two seasons. The mean weight decreased steadily through December, was lowest in January/February, and then rose sharply through March to April, when birds leave the island approximately 7 g. heavier than when they arrive in November/December. The pooled data for the three seasons are graphed for statistical comparison in Fig. 11. The differences between the mean weight on arrival in November and the mid-season weight in January and the means for March and April at the end of the breeding season are statistically significant (November-March  $P < 0.05$ ; November-January and November-April  $P < 0.000,01$ ).

Weights of breeding birds are examined in Table XXII, which shows the weights of all adults, whose status was precisely known, grouped according to sex and breeding state. During the pre-laying period, females are slightly heavier ( $P < 0.01$ ) than males, but males are very active in this period, returning almost

TABLE XXI  
SEASONAL VARIATION IN WEIGHTS OF *O. oceanicus* AT SIGNY ISLAND

Season	1966-67				1967-68				1968-69				Total			
Month	Number weighed	Mean weight (g.)	Range	S.D.	Number weighed	Mean weight (g.)	Range	S.D.	Number weighed	Mean weight (g.)	Range	S.D.	Number weighed	Mean weight (g.)	Range	S.D.
November	—	—	—	—	3	40.83	39.5-43.5	—	58	39.42	34-45	2.42	61	39.49	34-45	2.41
1-15 December	117	38.60	32-46	2.49	39	39.61	36-44.5	2.26	42	39.76	36-45	2.32	198	39.05	32-46	2.46
16-31 December	150	38.09	32-46	2.32	76	38.68	33.5-45	2.15	—	—	—	—	226	38.29	32-46	2.28
January	75	37.55	33-43	2.29	—	—	—	—	—	—	—	—	75	37.55	33-43	2.29
February	4	40.50	36-43	—	15	37.53	35.5-41	1.29	—	—	—	—	19	38.16	35.5-43	2.11
March	2	41.00	—	—	48	40.45	36-47	2.38	—	—	—	—	50	40.47	36-47	2.33
April	11	46.41	42-50	2.63	3	46.33	—	—	—	—	—	—	14	46.39	42-50	2.38
May	—	—	—	—	1	44.00	—	—	—	—	—	—	1	44.00	—	—

Standard deviations of samples smaller than ten are not shown.

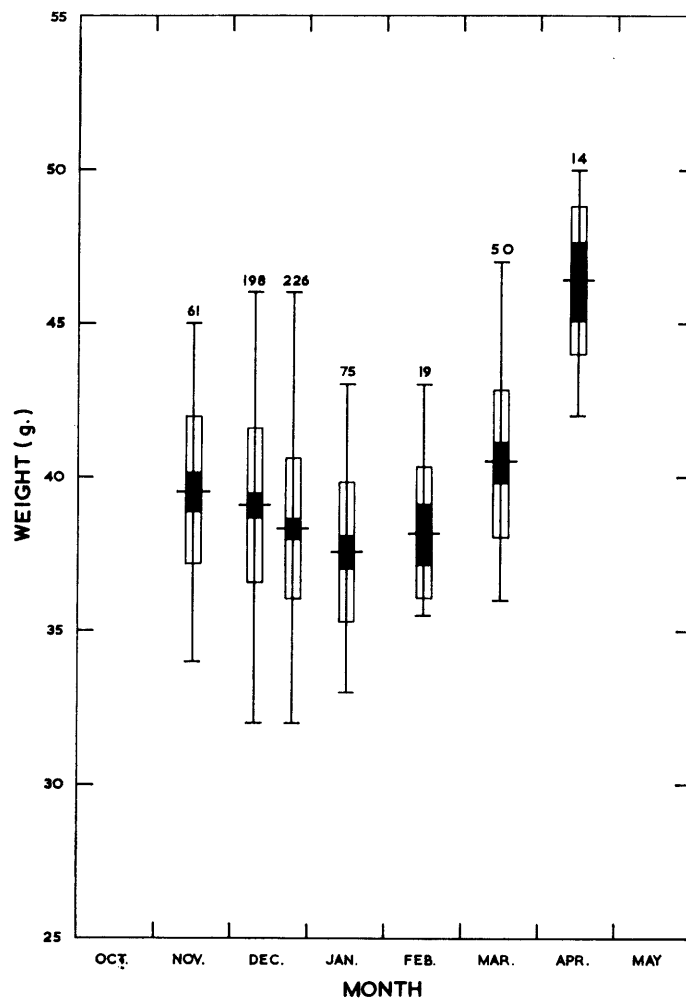


FIGURE 11

Seasonal changes in mean weight in *O. oceanicus* at Signy Island. The numbers above each entry represent the sample sizes. The horizontal central bar represents the sample mean, the open rectangle one standard deviation each side of the mean, the solid rectangle two standard errors each side of the mean, and the vertical line the limits of the range of measurement.

nightly to the colony, while the females visit the nests much less frequently and are able to spend more time feeding at sea. The difference between the sexes disappears during incubation, when weights vary a little more according to the length of time birds have spent incubating. Most weights of incubating birds at Signy Island were taken in the first half of the incubation period. 22 weights from incubating birds at Adelaide Island taken in the period 3–6 February 1969, just before hatching, are also shown in Table XXII.

Weights of 19 birds attending young at Signy Island were considerably higher than those of incubating birds. Four with small chicks weighed in February/March ranged in weight between 36.0 and 41.5 g.; these weights are similar to those of incubating birds and those of 11 birds with small young at Adelaide Island in early February (Table XXII). However, 14 weighed in April and one in May, late in the fledging period, were much heavier (Fig. 11).

The nature of the spectacular and rapid increase in the weight of breeding adults in April is of considerable interest. As all 15 birds weighed after 1 April were feeding large young, it might be thought that birds were heavy simply because they were bringing large amounts of food to the chick. None was killed to check this possibility but several points suggest that it is incorrect. None of the April birds handled had greatly distended bellies, indicating the presence of large quantities of food. Furthermore, if the increases were due solely to stored food, light birds should also have appeared in the sample, for most weights were taken around midnight, several hours after birds arrived in the colony. Presumably by then

TABLE XXII  
WEIGHTS OF BREEDING *O. oceanicus* AT DIFFERENT STAGES OF  
THE REPRODUCTIVE CYCLE

<i>Breeding status</i>	<i>Number</i>	<i>Mean weight (g.)</i>	<i>Range</i>	<i>S.D.</i>
Pre-laying period				
Males	32	39·19	36-43·5	2·11
Females	33	40·03	33-45	2·18
Females carrying an egg	5	48·20	43-51	3·11
Incubation				
Males	7	40·00	36-43	2·30
Females	12	40·54	36-43	2·25
Adelaide Island 1969 (end of incubation period)	22	40·89	36·5-48	3·13
Failed breeders (first half of March)	10	41·30	37-44	2·07
Moulting body feathers (March) (at least two were failed breeders)	6	41·67	39·5-43·5	1·36
Birds with young				
Males	8	45·12	41·5-47·5	2·01
Females	7	43·36	36-50	6·17
Both sexes*	19	44·60	36-50	3·97
Adelaide Island 1969 (start of nestling period)	11	39·41	35·5-49·5	3·71

\* Includes some unsexed birds.

the parent would have already given most of its food to the chick. The minimum weight recorded in April was 42 g., 1 g. less than the maximum weight recorded in January-February. Moreover, two pairs of birds were weighed 3-4 days after the chick had successfully fledged, yet their weights were as high as those recorded for birds attending young. Also, the increase in weight towards the end of the season is not confined to breeding birds, for the March sample in Table XXI and Fig. 11 contained mostly non-breeders and, as shown in Table XXII, failed breeders and moulting birds weighed in March were heavier than birds incubating in January/February. Thus, there are strong indications that the weight increase observed was genuine and not due merely to stored food in the stomach.

Although no April birds were dissected, one non-breeder killed on 18 March 1968 weighed 43·5 g. and contained thick deposits of sub-cutaneous and visceral fat. Probably, therefore, most of the weight increase is due to deposition of fat reserves in preparation for the long migration to the Northern Hemisphere. The fat content of birds at the end of the season has not been determined directly, but it is possible to estimate the probable magnitude of such deposits from carcass analyses of five birds taken on 17 December 1967 (Table XXIII). These were killed by chloroforming and weighed within 2 hr. of death, after the gizzard contents had been removed. The carcasses were stored temporarily in a deep-freeze and later analysed by standard procedures (Odum, 1960) to determine the water, fat and lean dry constituent fractions of the total weight. Petroleum ether (b.p. 60-80° C) was used as the fat solvent. Unlike the bird dissected in March 1968, the five individuals analysed in December 1967 contained no visible fat deposits and, as shown in Table XXIII, the amount of fat present was fairly uniform, ranging from 13·5 to 17·5 per cent of the body weight.

TABLE XXIII  
 PROPORTIONS OF WATER, LEAN DRY MATERIAL AND FAT IN FIVE *O. oceanicus*  
 SPECIMENS COLLECTED ON 17 DECEMBER 1967

Specimen number	Sex	Wet weight* (g.)	Weight of dry bird (g.)	Percentage of water in body	Weight of fat-free dry bird (g.)	Percentage of lean dry material in body	Weight of fat (g.)	Percentage of fat in body
1	Female	35.8	16.7	53.3	11.25	31.4	5.45	15.2
2	Male	34.7	15.1	56.5	10.4	30.0	4.7	13.5
3	Male	36.3	16.3	55.1	10.9	30.0	5.4	14.9
4	Male	39.0	18.8	51.8	12.1	31.0	6.7	17.2
5	Female	34.6	15.8	54.3	11.0	31.8	4.8	13.9
MEANS		36.1	16.5	54.2	11.1	30.8	5.4	15.0

\* Total weight less the contents of the stomach.

In the savannah sparrow, *Passerculus sandwichensis*, and other species, Connell and others (1960) found that the water and lean dry fractions of the body weight remained fairly stable throughout the year, while variations in the total weight were due almost entirely to changes in the amount of fat present. Assuming that the water and lean dry fractions in *O. oceanicus* also remain comparatively stable, then the total weight in April, less the combined mean weights of water and lean dry material, should give the weight of fat present at the end of the season. Weights of birds in April ranged from 42 to 50 g., with a mean of 46.4 g. Using a combined water/lean dry mean weight of 30.7 g. (19.54 + 11.13 g.), the mean proportion of fat in April birds could be 34 per cent (range 27–39 per cent), i.e. approximately double the amount present in December. These are maximum values but they are in accord with fat quantities found in other long-distance migrants (Odum, 1958; Ward, 1963, 1964). Recently, however, Newton (1969) and Ward (1969) have shown in the bullfinch, *Pyrrhula pyrrhula*, and yellow-vented bulbul, *Pycnonotus goiavier*, respectively, that a rise in fat content is accompanied by a corresponding and proportionately greater rise in water content and lean dry weight. Hence, until direct fat determinations have been made on breeding *O. oceanicus* at the end of the season, our figures for the amounts of fat deposited before migration should be considered as generous estimates.

The pattern of weight variation in *O. oceanicus*, with birds leaving in autumn considerably heavier than when they arrived, differs markedly from the situation found in other petrels. In some species there is little seasonal weight variation (*Puffinus puffinus* (Harris, 1966b); *Puffinus lherminieri* (Harris, 1969a)) while in others, e.g. *Hydrobates pelagicus* (personal communication from D. Scott) there is a steady decline in weight through the breeding season. In *Oceanodroma castro*, Harris (1969b) found that weights rose during incubation but declined after the young had hatched. In the Laysan albatross, Fisher (1967) found that the weights of both sexes declined through incubation and early chick development, and then rose slightly as the demands of the young lessened and adults left the breeding grounds 10–15 per cent lighter than when they arrived.

## IX. MEASUREMENTS AND GEOGRAPHICAL VARIATION

FROM his analysis of *O. oceanicus* wing and tail measurements, Roberts (1940) distinguished four populations to which he provisionally gave sub-specific status. These were:

- O. oceanicus oceanicus* South Georgia;
- O. o. exasperatus* Graham Land, South Shetland Islands, Queen Mary Land, Terre Adélie and south Victoria Land;



*O. o. parvus* Iles Kerguelen;  
*O. o. magellanicus* Falkland Islands and Tierra del Fuego.

There were significant differences in mean wing length between all groups except South Georgia and Iles Kerguelen, which were distinguishable by a significant difference in mean tail length. He also showed that wing and tail measurements varied clinally in agreement with Bergmann's Rule, with the largest birds breeding at high latitudes. Roberts admitted, however, that his sub-division into four races was of limited application, for the overlap in measurements meant that only known breeding birds could be assigned to any particular group with confidence. These doubts were shared by Murphy (1960) and Bourne (1964), who considered that geographical variation in this species had been over-emphasized. These authors suggested that it would be preferable to recognize only two forms characterized by size and climatic zone. Bourne (1964) proposed that all small northern populations, together with the intermediate South Georgian form, should be referred to the nominate race *O. o. oceanicus*, and the large Antarctic populations to the form *O. o. exasperatus* designated by G. M. Mathews.

As Roberts (1940) had been unable to include skins from the South Orkney Islands in his analysis, we measured a large series of mist-netted birds at Signy Island in December 1966. Also D.W.B. measured over 40 birds at Adelaide Island during February 1969. In addition to work on live birds, in order to relate our field measurements to a known standard, we have measured a number of skins in the British Museum (Nat. Hist.) collections of birds taken on the breeding grounds. Table XXIV compares measurements

TABLE XXIV  
 COMPARISON OF MEASUREMENTS FROM LIVE BIRDS AND FROM MUSEUM SKINS

Locality		Wing (mm.)	Tail (mm.)	Culmen (mm.)	Tarsus (mm.)	Mid-toe and claw (mm.)	
<i>Signy Island</i>	Live birds	Number	155	69	69	69	69
		Mean	151.4	69.6	12.6	34.2	29.6
		Range	142-160	61-75	11.0-14.5	31.5-36.5	27-32
		S.D.	3.91	2.30	0.68	1.12	0.98
	Museum skins	Number	13	13	13	13	13
		Mean	146.7	66.8	12.6	35.0	28.7
		Range	142-151	63-70.5	12-13.5	32-36.5	26-30
		S.D.	2.61	2.14	0.47	1.34	1.10
<i>South Shetland Islands/ Graham Land</i>	Live birds (Adelaide Island)	Number	42	42			
		Mean	150.1	72.06	Not	Not	Not
		Range	143-160	65-77.5	measured	measured	measured
		S.D.	4.09	3.17			
	Museum skins (various localities)	Number	24	24	23	24	24
		Mean	151.6	68.8	12.6	35.0	28.5
		Range	142-157	63-73	11.5-14	33-37	27-31.5
		S.D.	3.99	2.56	0.63	1.17	1.08

of live birds and skin material for the South Orkney Islands and Graham Land populations. Wings were measured in the flattened position to obtain the maximum reading; tails were measured from the base of the central rectrices to the tip of the outermost feather. Measurements were made by both authors and combined; earlier comparison of duplicated measurements had shown that errors due to differences in technique were very small.

The wings and tails show most geographical variation (Roberts, 1940) and measurements for these characters are graphed separately for statistical comparison in Figs. 12 and 13. The top part of each figure shows data given in or calculated from Table II of Roberts' (1940) paper, while the bottom part presents measurements of both live birds and museum material taken in the present study.

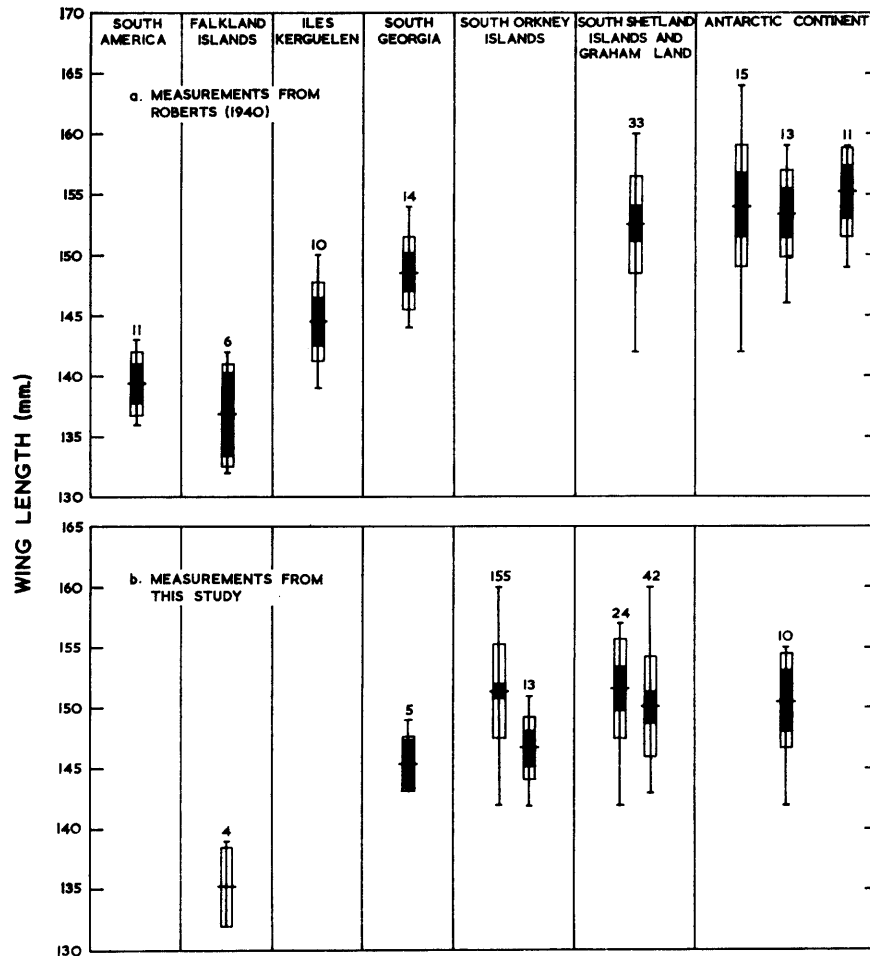


FIGURE 12

Geographical variation in wing length in *O. oceanicus* populations. The horizontal central bar represents the mean, the vertical line the range of measurement, the open rectangle denotes one standard deviation either side of the mean, and the solid rectangle twice the standard error on each side of the mean.

It may be noted in passing that there are two discrepancies in Roberts' measurement data. His measurements of birds from south Victoria Land (Roberts, 1940, table I, p. 146) contain three duplicated entries for birds with British Museum numbers 1905.12.30.267-69 inclusive, and these are included in his table II. Also, although four of the six British Museum skins from the Falkland Islands measured by Roberts are undoubtedly adults, with typically worn coverts and primaries, two are almost certainly juvenile birds nearly ready to leave the nest. Both have prominent whitish edges to the greater coverts, fresher plumage and dark fringes on the white rump feathers, while the tail is very short in one bird. The numbers of these birds are 1932.7.2.24 (Fox Bay) and 1940.12.7.47 (Grand Jason).

Figs. 12 and 13 show that the South Orkney Islands population represents an intermediate link in the north-south cline of wing and tail measurements. Despite the isolated northerly position of the South

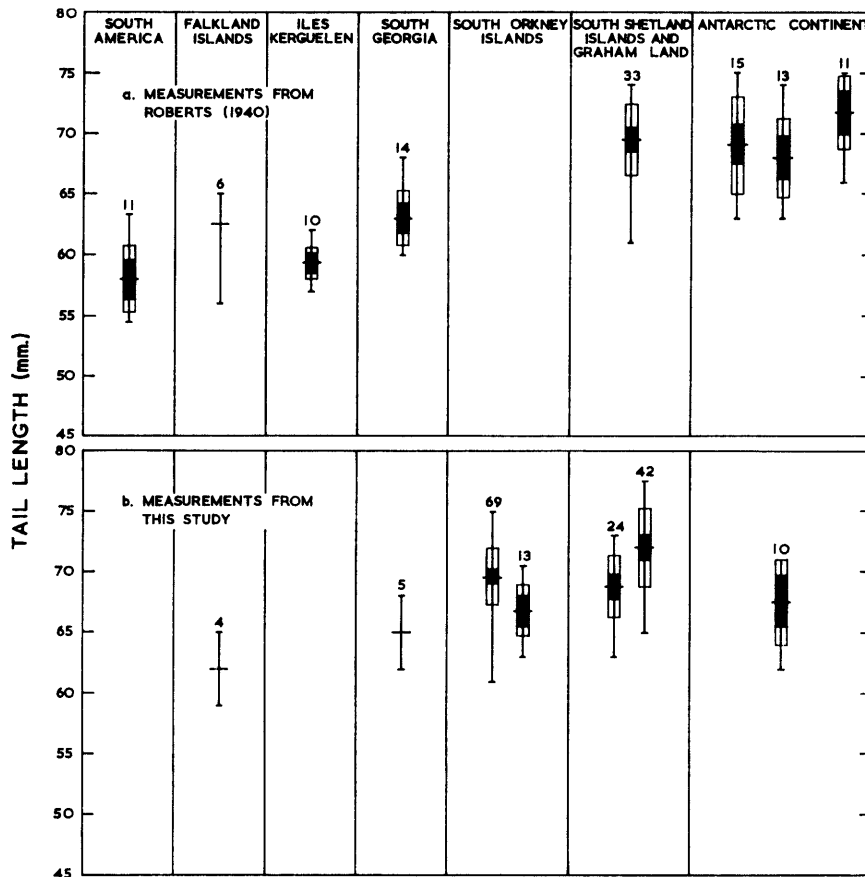


FIGURE 13

Geographical variations in tail length in *O. oceanicus* populations. The horizontal central bar represents the mean, the vertical line the range of measurement, the open rectangle denotes one standard deviation either side of the mean, and the solid rectangle twice the standard error on each side of the mean.

Orkney Islands, measurements from this group are nearest those of the large birds inhabiting Graham Land and the Antarctic continent. The amount of overlap between successive populations in the latitudinal series, however, is large, and we agree with Murphy (1960) and Bourne (1964) that no useful purpose is served by recognizing more than the two zonal races, *O. o. oceanicus* and *O. o. exasperatus*.\* The former would comprise all populations to the north of the Antarctic Convergence and the latter all populations to the south, including the apparently intermediate South Georgia population. Such a sub-division seems biologically more satisfactory, reflecting adaptive differences in breeding and feeding ecology associated with regions of dissimilar climate as well as differences in mensural characteristics.

## X. DISCUSSION AND CONCLUSIONS

THERE are large year-to-year variations in the temperature regime, snow cover and amount and duration of sea-ice cover in the Antarctic. Consequently, it is difficult to assess how typical the results of any short-term study are, or how representative one sub-colony is of an island population. Our results show that the breeding success of Wilson's storm petrel can vary greatly. The variation was due almost entirely to the effects of snowfall.

Nests in the study colony exposed to wind scour were less subject to snow blockage than more sheltered sites. This was demonstrated in 1967-68 and 1968-69, when all eggs and young in the sheltered part of the study area perished, and the only nests where young were reared were those in exposed positions on a rocky crag above the normal height of blowing snow. Thus, the snow conditions on the east coast of the

\* Dr. B. B. Roberts is now in agreement with this view. In 1940 he was trying to draw attention to the fact that isolated breeding populations, as distinct from individual specimens, can be distinguished apart by statistical treatment of their measurements. There is no longer any compelling reason to reflect this conclusion in nomenclature.

island in the lee of prevailing winds may differ markedly from those on the west coast exposed to predominant onshore westerlies. The annual production of young in the colony studied was found to be insufficient to offset the annual mortality of adults and maintain a stable population. If, however, breeding success is higher in other more exposed colonies, the east coast populations may be maintained by the steady recruitment of young birds reared elsewhere on the island.

While visiting Adelaide Island in February 1969, D.W.B. was impressed by the exposed locations of many *O. oceanicus* nests there, some of which were merely placed in the lee of large boulders and the incubating birds were clearly visible. This suggests less risk of mortality from snow blockage and also lack of predation by skuas there. Certainly, breeding success at Adelaide Island in 1969 promised to be relatively high, for 95 per cent of 40 nests examined contained eggs or small young. By contrast, no young were fledged from marked nests at Signy Island in that season. Hence our observations seem to indicate that Wilson's storm petrels at Signy Island breed in conditions at least as severe as those encountered in southern Graham Land and, in some years, the output of young may be considerably less than in the more southerly colonies.

It might be supposed that, because of the shortness of the Antarctic summer and the super-abundance of krill and other macro-plankton from January to April, all the petrels feeding on zooplankton would lay at about the same time and could later feed young simultaneously without competing for food. Variation in laying dates at Signy Island is nevertheless substantial; the difference between the modal dates of laying in one of the largest krill-feeding petrels (*Pagodroma nivea*) and the smallest (*Oceanites oceanicus*) is approximately 7 weeks. A comparable and more puzzling difference is found in the Adélie and chinstrap penguins, *Pygoscelis adeliae* and *P. antarctica*, breeding on the island, which both feed extensively on krill, yet their mean laying dates are 3 weeks apart (personal observations).

The adaptive significance of these differences in breeding season in the five smaller petrels at Signy Island has been discussed elsewhere (Beck, 1970). While the various species appear to begin laying as early as they are able, there is a marked difference in timing between the large fulmarine petrels, *Daption capensis* and *Pagodroma nivea*, on the one hand, and the three smaller species, *Pachyptila desolata*, *Fregatta tropica* and *Oceanites oceanicus*, on the other. This difference is related indirectly to body size. *Daption* and *Pagodroma* are large enough to be almost immune to skua predation; they have strong bills and feet, and defend themselves by forcibly ejecting large quantities of oil over considerable distances. Skuas kill some young of both species but adult *Daption* are hardly ever caught and adult *Pagodroma* only occasionally, probably when surprised asleep on the nest or otherwise taken off-guard. The type of nest site chosen reflects the degree of predation suffered by each species. *Daption*, the largest and least vulnerable, is diurnal and nests on exposed cliff ledges; *Pagodroma*, although also diurnal, is smaller and weaker, and lays its egg in more sheltered places in recesses and large cavities in cliffs, where there is some overhead and side protection. Both species are powerful enough to be able to clear snow and ice from their nests as early as October, helped by the warming effect of incident solar radiation, but egg-laying does not begin until mid-November, possibly because the female cannot find enough food to form the egg earlier.

On the other hand, the prion and two storm petrels are so small as to be almost defenceless against attacks by skuas or gulls. They can eject oil only feebly. Their nocturnal habits confer some protection, although this is ineffective in the 24 hr. continual illumination of mid-summer. Their small size, however, while making them easy prey for skuas, also enables them to survive by retreating underground to nest in crannies and small holes inaccessible to both skuas and marauding sheathbills. But, because of their size and weak build, they are unable to clear hard-packed winter snow and ice from these holes and must depend on the spring melt in late November for access to the nest. Breeding is thus delayed and the first Wilson's storm petrels begin to lay 5 weeks after the first snow petrel eggs appear. The dove prion is an interesting partial exception because, although it is still subject to the restrictions of habit and nest site imposed by its size and by predation, it has a stronger bill and feet than the two storm petrels and can clear its nest and begin laying a little earlier.

By late December, when Wilson's storm petrels begin to lay, plankton is more abundant than in November (Foxton, 1956) when the fulmarine petrels lay and so the female storm petrels presumably have less difficulty in finding the additional food necessary to form the egg. The delay in egg-laying may also explain why *Fregatta tropica* and *Oceanites oceanicus* are able to lay proportionately very large eggs (26–29 per cent of the body weight) compared with their lower-latitude counterparts and compared with the fulmarine petrels, in which the egg forms only 15–21 per cent of the body weight. A large egg and chick might be

advantageous to an Antarctic species, for the young would be better insulated against heat loss and also better able to withstand periodic starvation when nests are snow-blocked.

Apart from the disparity in laying season, the three nocturnal species also differ from the two larger petrels in their degree of synchrony in breeding activity. Whereas egg-laying in *Daption* and *Pagodroma* is closely synchronized (Beck, 1970) with 80 per cent of eggs laid in 3 days either side of the mean date, laying in *Pachyptila* is spread over 28 days (Tickell, 1962), while *Fregetta* (Beck and Brown, 1971) and *Oceanites* pairs are even less in phase, with egg-laying spread fairly evenly over about 36 days. As breeding is already delayed until nests become snow-free, this protracted laying period means that a considerable number of young cannot leave the nest before April/May, when air temperatures drop to  $-5^{\circ}\text{C}$  and chicks run the risk of becoming entombed by increasingly frequent autumn snowfalls. Losses of young from this cause are potentially so great that there must be very strong selection pressure favouring early synchronized laying. As this is not the case, it is probable that there is some opposing pressure which outweighs these disadvantages.

Our observations on the pre-laying exodus suggest that variability in the time taken for individual females to form their egg in different seasons could contribute substantially to the spread in laying dates. This, together with variability in copulation dates and possible delayed laying in birds breeding for the first time, seem to be the main factors influencing the date of laying in individual pairs. Natural selection might favour this spread in egg-laying in the following manner. In some years, birds laying early would lose their egg or chick through heavy snowfalls in the early part of the breeding season, whereas chicks from later eggs would be likely to survive if there were little snow in autumn. Conversely, in other years, with no early snow but severe falls towards the end of the season, the early breeders would rear their young successfully, while the progeny of later breeders would perish. Hence, some pairs would be favoured in some seasons and some in others, while a proportion of young would probably survive each year whatever the conditions. The net result would be a spread in laying dates, the start of which would be determined by the spring melt and/or availability of food, and the end by the time at which weather conditions were regularly so severe that successful breeding would always be impossible. The extent of laying in *O. oceanicus*, although wider than that of any of the larger petrels breeding on Signy Island, is still considerably less than that of storm petrels breeding in lower latitudes, e.g. *Hydrobates pelagicus* (Davis, 1957) and *Oceanodroma castro* (Harris, 1969b), which lay over a period of 2-3 months.

In conclusion, it is of interest to compare the general findings from this study of an Antarctic storm petrel with those of Harris (1969b) for the tropical species, *Oceanodroma castro*, living in the opposite climatic extreme (Table XXV). Apart from those features which are common to both species and are consequences of their pelagic feeding habits, e.g. clutch of one, low adult mortality and population turnover, deferred maturity, protracted development of egg and young, and the deposition of fat reserves in the young (Lack, 1966, 1968), the main differences between the species can be traced to differences in the food supply in the two areas. Both species feed on marine organisms caught at the sea-surface but it seems that the very rich food supplies in the Antarctic permit *O. oceanicus* to form its proportionately larger egg relatively quickly, incubate in shorter spells and allow the young to grow faster (Table XXV). Discussion of the factors affecting timing of breeding in *O. castro* was greatly complicated by the existence of two separate populations of birds breeding with apparently equal success 6 months out of phase with each other. Harris considered, however, that owl predation had an important effect on the degree of synchrony in breeding activity, while less than annual breeding was probably prevented by the need to undergo a prolonged moult between breeding attempts. In *O. oceanicus*, the overall breeding period is considerably shorter than in *O. castro*, the difference being accounted for by the shorter fledging period and greater degree of synchrony in laying. This is because *O. oceanicus* has adapted its lengthy breeding cycle to fit as far as possible into the brief summer period of milder weather. As has been shown, these adaptations have been produced by the complex interaction of such diverse factors as body size, predation, nest site, snowfall and food supplies.

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TABLE XXV

COMPARISON OF BREEDING DATA FOR *Oceanites oceanicus* AND *Oceanodroma castro*

<i>Feature compared</i>	<i>O. oceanicus</i>	<i>O. castro</i>
Breeding area	Antarctic/Sub-Antarctic	Tropics/Sub-tropics
Body weight (g.)	38·2	40·3
Pre-egg period (days)	c. 45	c. 60
Pre-laying exodus (days)	11	? 20
Laying period (days)	35	80–90
Egg as percentage of female's weight	28·5	21·4
Incubation spell (days)	2·5	6·0
Incubation period (days)	40	42
Chick brooding period (days)	2–3	2–3
Fledging period (days)	60	70 (hot season) 78 (cold season)
Overall breeding period (days)	145	172–180

All data for *O. castro* from Harris (1969b).

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PLATE I

Wilson's petrels (*Oceanites oceanicus*) at South Georgia.

(Photograph by I. Everson.)

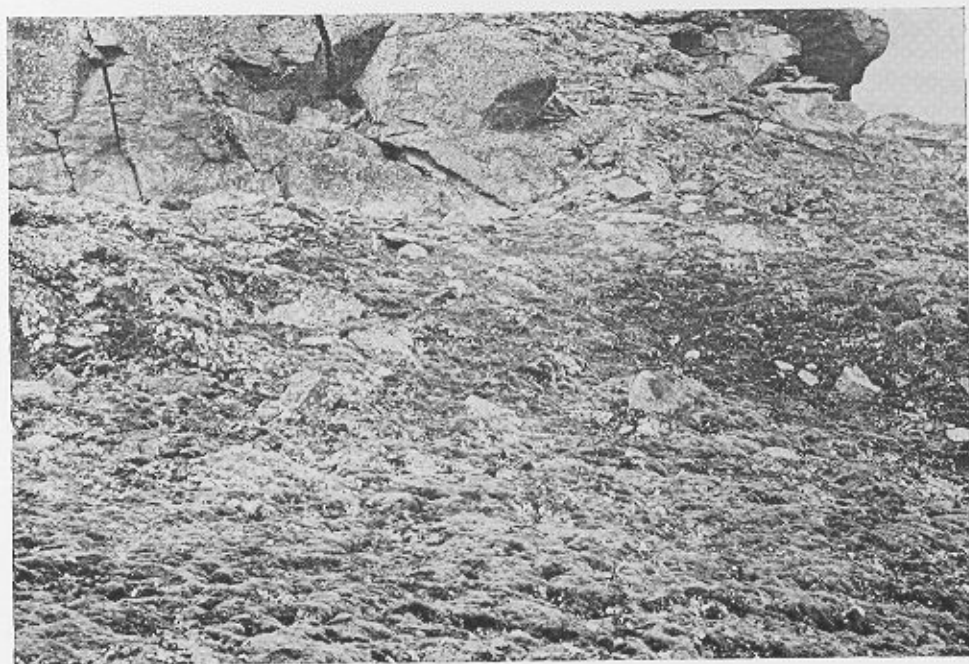


PLATE II

- a. Part of the breeding colony behind the British Antarctic Survey station hut at Factory Cove. Mist-net site 1 was approximately in the centre of this area.
- b. A section of the breeding colony at the foot of Factory Cove bluffs.



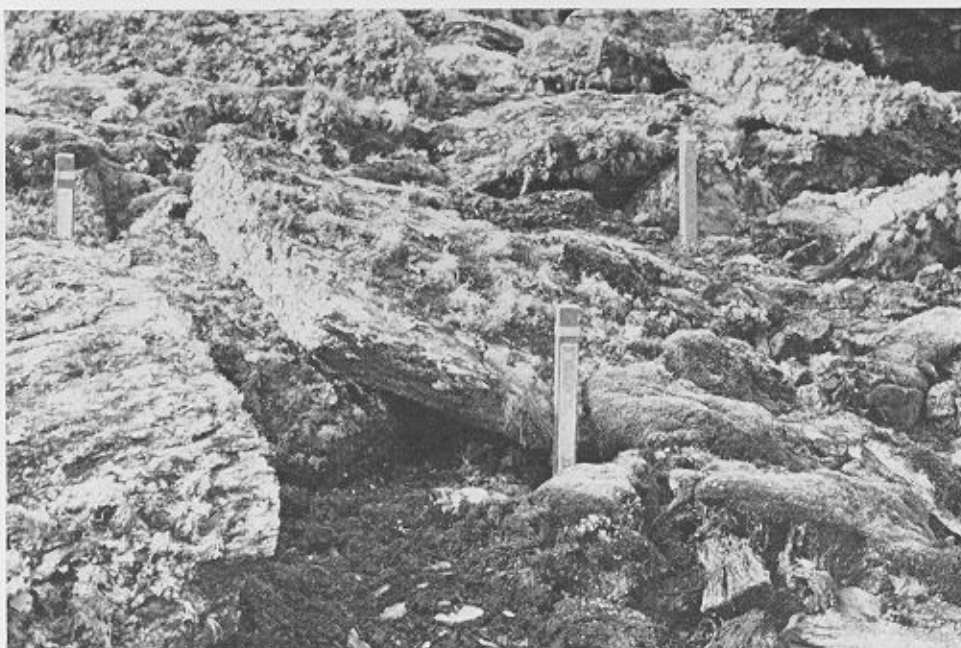
a



b

PLATE III

a. and b. Numbered stakes used to mark nest sites, with gauges for recording snow depth.



a



b

PLATE IV

- a. Adult attempting to dig into nest through hard-packed snow.
- b. Adult resting on snow at night.





a



b



PLATE V

- a. Chick aged 8-10 days.
- b. Chick aged 28 days.
- c. Chick aged 37 days.
- d. Chick aged about 45 days.



a



b



c



d

PLATE VI

a. and b. Adults feeding offshore.

PLATE VI



a



b