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THE DOVE PRION, *Pachyptila desolata* Gmelin

By

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*Falkland Islands Dependencies Survey*



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## ABSTRACT

THE DOVE PRION is nocturnal on land. It appears that adults return each season to the same nest hole and mate, and show strong territorial behaviour in the breeding colonies. During the pre-laying period the pair spend the daytime at sea, returning to the nest each night; but about ten days before the egg is laid the female departs on the so-called "honeymoon" flight, rarely returning until the night of laying. In the meantime, the male returns to the nest alone each night and eventually takes over the initial incubation. A single egg is laid during December and hatched at the end of February. Incubation is shared by both sexes in shifts of 3-4 days. Neglect is shown to be irregular and more frequent in the early stages of incubation, and it is held to account for the wide range of apparent incubation, the true period being about 45 days. Chicks are brooded for the first 5 days and fledge in about 50 days. There is an indication that parents feed their young less frequently in the final stages of fledging.

Analysis of recent data has provided a means of revising nomenclature and distribution. Three subspecies with the following distribution are proposed:

*P. d. desolata* (Gmelin). Îles de Kerguelen.

*P. d. banksi* A. Smith. South Georgia, South Orkney Islands and Heard Island.

*P. d. alter* Mathews. Auckland Islands and Macquarie Island.

## CONTENTS

	PAGE		PAGE
I. Introduction ... ..	2	12. The Chick ... ..	26
II. Methods of Study ... ..	2	a. The Chick Period ... ..	26
III. General Distribution ... ..	3	b. Growth of the Chick ... ..	29
1. Breeding Distribution ... ..	3	c. Final Days in the Nest ... ..	30
2. Distribution at Sea ... ..	3	13. Departure ... ..	33
IV. Distribution in the South Orkney Islands	5	14. Behaviour of Unsuccessful Breeders	34
1. Habitat ... ..	5	15. Seasonal Changes in the Gonads ...	35
2. Breeding Species ... ..	5	a. The Testes ... ..	35
3. Status of the Dove Prion ... ..	6	b. The Ovary ... ..	36
a. General ... ..	6	16. Body Temperature ... ..	38
b. The Borge Bay Colony ... ..	6	a. Adults ... ..	38
4. Association with Other Species ...	8	b. Chicks ... ..	39
V. Life Cycle ... ..	8	17. Predators ... ..	40
1. Return of the Dove Prion to the South		a. The Brown Skua ... ..	40
Orkney Islands ... ..	8	b. Other Species ... ..	41
2. Occupation of the Colony ... ..	9	18. Parasites ... ..	41
3. Nocturnal Habit and Feeding ... ..	9	19. Food and Feeding ... ..	42
4. Occupation of the Nest Site ... ..	11	20. Flight ... ..	42
5. The Nest ... ..	11	21. Voice ... ..	42
6. Age Groups ... ..	14	22. Homing ... ..	43
7. Pre-laying Activities at the Nest ...	14	23. Moulting ... ..	44
a. Visits to the Nest by Breeding Adults	14	VI. Taxonomy ... ..	44
b. Copulation ... ..	16	1. General ... ..	44
c. Territory and Fighting ... ..	18	2. Methods and Technique ... ..	45
8. The Egg and Egg-laying ... ..	19	3. Differences between the Sexes ...	45
a. The Egg ... ..	19	4. Conclusions ... ..	46
b. Egg-laying ... ..	20	5. Nomenclature ... ..	51
9. Incubation ... ..	21	VII. Acknowledgements ... ..	53
10. Share of the Sexes in Incubation ...	24	VIII. References ... ..	53
11. Hatching ... ..	25		

## I. INTRODUCTION

THE genus *Pachyptila* has been the subject of considerable taxonomic confusion, but its division by Murphy (1936), Falla (1940) and Fleming (1941) into three sub-genera and six species, with *P. desolata* the prion of the Antarctic zone, has been accepted for the purposes of this work. *P. desolata*, the Dove Prion, was selected for the present study on the recommendation of Murphy (1936) concerning work on the Procellarii: "We need still more, however, an exhaustive study of the life history of any single species by an observer or group of observers prepared to camp at the nesting ground [from] before the date of arrival of the first birds . . . [to] the exodus of the whole population."

Most of the field work was carried out at Signy Island in the South Orkney Islands (lat. 60°43'S., long. 45°36'W. between November 1954 and March 1957, whilst the author was serving as a meteorological observer at one of the Antarctic bases of the Falkland Islands Dependencies Survey (Tickell, unpublished F.I.D.S. Base Reports). As there were large colonies in the vicinity of the station (Plate Ia, b), it was possible to carry out a detailed observation of nest routine, despite the many conflicting duties of base life. Further observations were made at Bird Island, South Georgia (lat. 54°00'S., long. 38°02'W.) between November 1958 and March 1959 (Tickell and Cordall, 1960).

## II. METHODS OF STUDY

*Pachyptila desolata* and related species generally nest in burrows excavated in soil and moss, where they are invisible from the outside, but in the South Orkneys and on the Antarctic continent at Cape Denison, *P. desolata* nests in rock fissures. Opportunities for observations on Signy Island were, therefore, especially favourable.

During the course of three summer seasons the more easily accessible nests were located, numbered and plotted on a large-scale map. For marking birds the first rings used were of aluminium, either the normal B.T.O.\* size 2 pattern (8 × 20 mm.) or size 3 cut down to the same length (9 × 20 mm.). Both types were found to wear very quickly; after two summer seasons they were seriously abraded, whilst after three they were often completely unreadable and some had probably been lost. In the year 1955-56, therefore, an overlapped pattern of size 2 with double inscription was used. Adults were always ringed on the left tarsus and nestlings on the right (Plate Vb). All rings were supplied by the F.I.D.S. Bird Ringing Scheme (Sladen and Tickell, 1958).

To avoid the necessity of handling at each observation, some additional method of individual recognition was required. The typical petrel habit of walking on the tarsi, coupled with the difficulty of observing in a burrow (Serventy, 1956b), precluded the use of coloured rings but a successful method of marking with paint was devised. Using quick-drying cellulose aircraft-paint, coloured spots were painted on the forehead and lores in various patterns and combinations (Plate Vb). Up to four spots could be employed in nine easily distinguishable patterns. In the first year, 1954-55, only one colour (yellow) was available and a terra cotta cellulose ski-lacquer was employed as a second. Later, combinations of black, white, red, blue, green and yellow gave a possible number of combinations far in excess of requirements. This method of colour-marking was also used on larger open-nesting species such as the Cape Pigeon (*Daption capensis*) as well as on the smaller Wilson's Petrel (*Oceanites oceanicus*).

The spots, painted on with a matchstick, varied between 3 mm. and 6 mm. in diameter according to the pattern in use. Such spots were quite prominent and were quickly recognisable at night by a brief flash of the torch into the nest. It was necessary to ensure that the paint penetrated well behind the feathers as well as covering the surface but, even so, the marks had to be renewed once during the breeding season. To avoid disturbance at a critical period, repainting was not carried out until the parents had finished brooding the chick. Nestlings were ringed during their last ten days in the nest and it was never necessary to colour-mark them.

Fledglings and random birds caught outside the nest during the course of night observations were ringed on the spot, but adult birds collected from the nest holes were usually kept in boxes and carried back to the hut for routine examination. For extracting the prions from their holes, a short "puffin hook" (see Lockley and Russell, 1953) about three feet in length was indispensable.

\* British Trust for Ornithology

Any specimens killed were weighed, measured and examined for parasites before sexing. The gonads were removed and fixed in Bouin's fluid for later histological examination. The proventriculus was examined for food and the viscera preserved in 70 per cent alcohol. Skins were preserved in paradichlorobenzene soap and whole carcasses in 70 per cent alcohol. A number of specimens were returned to the British Museum (Natural History) in deep freeze.

Once the occupants had been marked, nightly visits to the nest were as brief as possible in order to minimize disturbance; it was often possible to assess the situation at a particular nest in a matter of seconds. Attempts at systematic observations of behaviour proved unprofitable and it was necessary to rely on chance observations for such aspects of behaviour as copulation and feeding the young.

During the first two summer seasons systematic observations were carried out during part of the breeding cycle only, the remainder being covered by intermittent observations which gave a general picture of the breeding routine. Further detail was provided by daily and nightly observations during the final season, 1956-57, from 18 November to 1 April. The daytime inspections were made at any time between 0900 and 1700 hr. L.M.T. (Local Mean Time), and those at night were made at the estimated peak of return to the nest, i.e. between 2200 and 2300 hr. L.M.T.

The only method of sexing the birds in the field was by observation of copulation or by handling females just before laying, when the eggs could be easily felt in the distended abdomen. At the conclusion of the field work 25 individuals were killed and sexed by dissection and all have confirmed the method of sexing by pre-laying behaviour. Unfortunately, not having access to the literature while in the field, the author was unaware of the method of sexing by cloacal inspection devised by Richdale (1951) for penguins and later adapted by Serventy (1956a) for petrels.

### III. GENERAL DISTRIBUTION

#### 1. BREEDING DISTRIBUTION

*Pachyptila desolata* is known to breed on a number of Antarctic and sub-Antarctic islands (Fig. 1)—the South Orkney Islands, South Georgia (Matthews, 1929; Murphy, 1936), the Îles de Kerguelen, Heard Island (Coues, 1875; Milon and Jouanin, 1953; Paulian, 1953; Downes *et al.*, 1959), Macquarie Island and the Auckland Islands (Wilson, 1907; Falla, 1937). It is probable, though not verified by observation, that it also breeds on the South Shetland Islands, South Sandwich Islands and Bouvetøya. There is, however, only one record of the species breeding on the mainland of Antarctica (at Cape Denison, King George V Land, where the colony is apparently very small), and although this may be because little of the Antarctic coastline is known in detail it is more likely due to the presence of pack ice throughout the summer.

The young are fed at first by both parents almost every night; fairly rich plankton supplies must therefore be obtainable within six hours flying and searching time from the nest, and this species does not feed within the pack ice. Although winters in the South Orkney Islands are severe, the pack ice does not persist there throughout the summer as it does along much of the mainland coast, and suitable feeding grounds are therefore accessible. All other known breeding stations are distinctly less polar in climate: South Georgia and Heard Island are just to the south of the Antarctic convergence (Mackintosh, 1946), the Îles de Kerguelen are on it, and Macquarie Island and the Auckland Islands are just to the north of it.

It seems reasonable to assume that the numbers of this species breeding on the Antarctic mainland and on islands close inshore, are very small in comparison with those breeding on islands farther north.

#### 2. DISTRIBUTION AT SEA

As early naturalists and mariners did not differentiate between the two genera, *Pachyptila* and *Halobaena*, no detailed review of the sight records from the literature has been undertaken.

*Pachyptila* species are extremely common in the southern oceans and sometimes occur in large concentrations in areas rich in plankton. Within the Antarctic zone, *P. desolata* occurs as far south as the edge of the pack ice although it does not usually feed within it (Falla, 1937; Routh, 1949). Its distribution is not limited northwards by the Antarctic convergence, as it breeds at the Auckland Islands and Macquarie Island and has been identified at Marion Island (Rand, 1954). The upwelling of the cold Antarctic waters

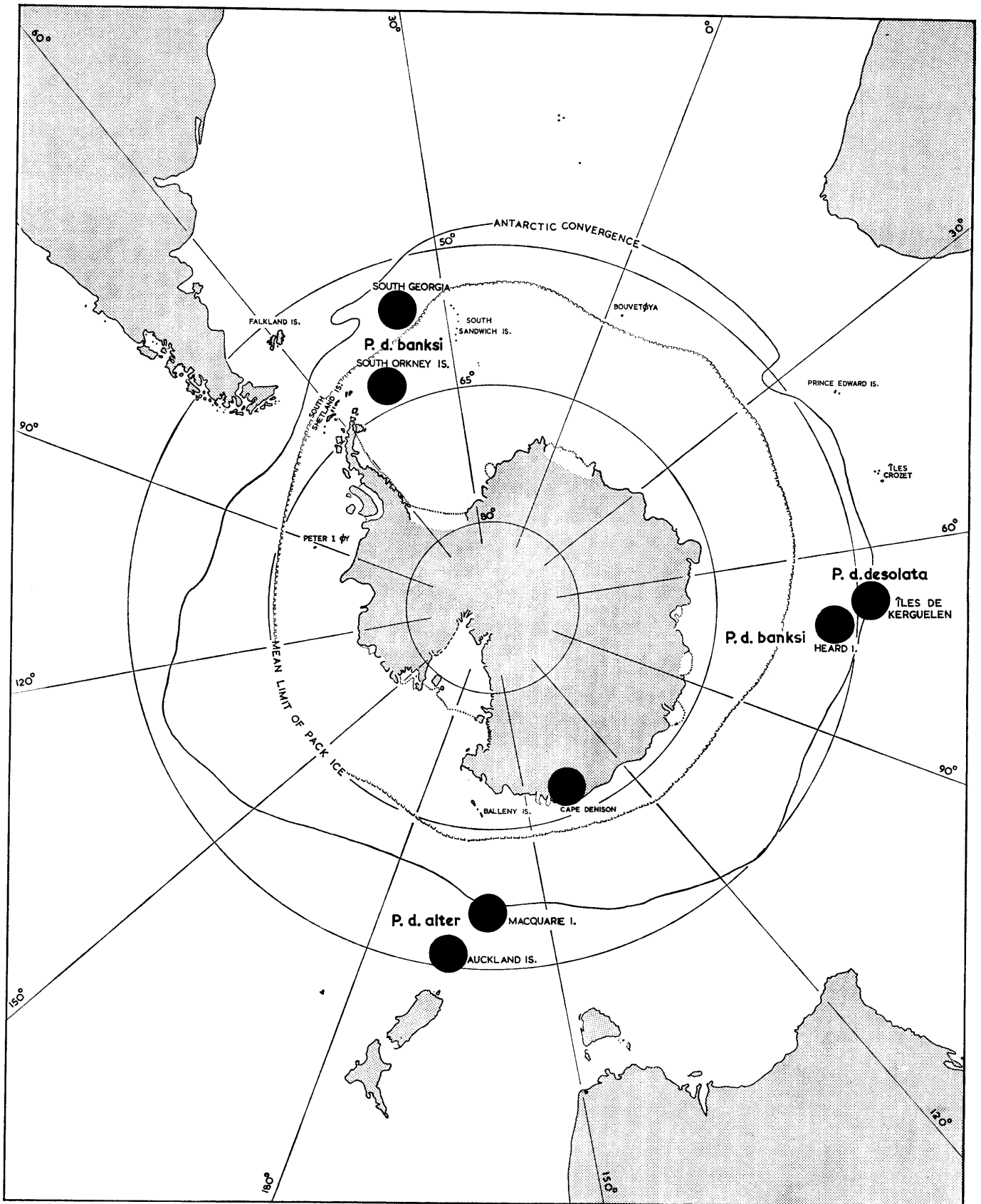


FIGURE 1  
The distribution of breeding colonies in Antarctica and the Southern Ocean.

from below the warmer sub-Antarctic surface layer at the Îles Crozet and Prince Edward Islands, might account for the presence of *P. desolata* in those regions.

Although *P. desolata* is so commonly seen in the Antarctic zone it is evidently not evenly distributed. Holgersen (1957), recorded the presence of *Pachyptila* between 90° and 150°W., but mentioned a scarcity in the Bellingshausen Sea off the south-west coast of Graham Land from long. 60° to 90°W., and in the Ross Sea west of long. 155°W.; van Oordt and Kruijt (1954) noticed a similar lack of prions in the Ross Sea and also from long. 100° to 140°E. during January and February. Within the sub-Antarctic zone any large concentrations of small food organisms would attract them, unless the birds are very selective in their food species. Nevertheless, the large numbers of storm-blown wrecks of prions on the coasts of Australia and New Zealand include very few *P. desolata*, and even young birds which probably disperse to a greater degree than adults are comparatively rare.

Van Oordt and Kruijt (1953), referring to another species of *Pachyptila*, suggest that the large concentrations, which are sometimes found at sea during the breeding season, may be largely composed of non-breeding birds spending the summer away from their breeding stations. It has long been suspected that some species of petrel, at least, do not breed until they are several years old. Recent work by Serventy (1957) has shown that the young of the *Puffinus tenuirostris* do not return to the colony where they were reared until they are three years old and then spend only a short time ashore. This may well apply to most of the Procellarii.

## IV. DISTRIBUTION IN THE SOUTH ORKNEY ISLANDS

### 1. HABITAT

Coronation Island is the largest island in the South Orkney Islands group. It is heavily glaciated over almost the whole of its area, a large proportion consisting of highland ice over 3,000 ft. above sea level. Numerous small promontories, coves and low off-lying islands are free of snow and ice during the summer. These, together with the exposed rock faces of cliffs, provide the only areas suitable for nesting.

The other main islands of the group, Laurie Island, Powell Island and Signy Island are all smaller and comparatively low-lying. Associated with them are numerous smaller islands which provide important breeding grounds for the various species.

Signy Island is just under eight square miles in area and rises to a maximum height of 907 ft. The permanent ice cap covers only about one-third of the total area, and most of the coastal region is free of snow at some time during the summer. This coastal region consists of four types of terrain:

- i. Exposed crags, both inland and along the coast.
- ii. Rocky headlands and promontories, often with flat tops and gently sloping platforms.
- iii. Large expanses of moraine and small rocks; glacier debris and moraine ridges in initial stages of consolidation.
- iv. Open moss and boulder-strewn slopes. The moss banks are sometimes as much as 5 ft. thick.

### 2. BREEDING SPECIES

The following sixteen breeding species are recorded from the South Orkney Islands and of these all except the Silver-grey Fulmar are found on Signy Island.

Adélie Penguin, *Pygoscelis adeliae*  
 Chinstrap Penguin, *Pygoscelis antarctica*  
 Gentoo Penguin, *Pygoscelis papua*  
 Macaroni Penguin, *Eudyptes chrysolophus*

Giant Petrel, *Macronectes giganteus*  
 Silver-grey Fulmar, *Fulmarus glacialisoides*  
 Cape Pigeon, *Daption capensis*  
 Snow Petrel, *Pagodroma nivea*

Dove Prion, *Pachyptila desolata*  
 Black-bellied Storm Petrel, *Fregetta tropica*  
 Wilson's Petrel, *Oceanites oceanicus*

Brown Skua, *Catharacta skua lönnerbergi*  
 Dominican Gull, *Larus dominicanus*  
 Antarctic Tern, *Sterna vittata*

Sheathbill, *Chionis alba*

Antarctic Blue-eyed Shag, *Phalacrocorax atriceps*

### 3. STATUS OF THE DOVE PRION

#### a. General

Members of the Scottish National Antarctic Expedition, 1902–04, (Clarke *et al.*, 1913) recorded large numbers of prions at sea within the vicinity of the South Orkneys, and the species was said by Clarke (1906) to “. . . deserve a place in the avifauna of the group.” They did not, however, find any Dove Prions breeding on Laurie Island nor on any of the smaller islands which they visited at the eastern end of the group.

The first nests were discovered in 1914–15 by A. G. Bennett (1926) who was then serving as whaling magistrate on the floating factory *Falkland* at the South Orkneys. He gave no indication of their location, but it is probable that they were part of the colony found in January 1931, on the slopes above Borge Bay, Signy Island, during a voyage of the R.R.S. *Discovery II* (Ardley, 1936).

The Falkland Islands Dependencies Survey manned a base at Cape Geddes, Laurie Island from 29 January 1946 to 17 March 1947, but saw no evidence of breeding (F.I.D.S. Base Reports; unpublished). When the station was moved to Borge Bay on the east coast of Signy Island, the colony first located by R.R.S. *Discovery II* was found to be of considerable size. Subsequent exploration of the island revealed several other colonies, the largest of which are at Paal Harbour, Moe Island\* (Hall, 1957a) and North Point (Fig. 2).

On Coronation Island, Dove Prions nest in large numbers at Shingle Cove on the south coast (Fig. 3); there is also some evidence of them at Sandefjord Bay in the extreme north-west (Cordall, 1956), but it is doubtful if there is any suitable terrain on the north coast. A diligent search at the eastern end of Coronation Island failed to locate any nests or other indication of the birds (Hall, 1957b). On Powell Island they have been heard calling from holes.

Nests also occur elsewhere and there are many areas that are suitable for colonization, but Signy Island is, without a doubt, the main breeding centre in the South Orkney Islands.

In the vicinity of the station at Borge Bay, the Dove Prion is the commonest breeding species, and in all probability it is one of the most numerous breeding species on the island as a whole. Although it is difficult to estimate their numbers, the total for Signy Island is probably about 50,000 pairs.

#### b. The Borge Bay Colony

This colony (Fig. 2; Plates Ia, b) is scattered over an area of open slope, scree and crag, conveniently close to the F.I.D.S. base. Ringing and nest-marking were begun in the 1951–52 season when A. W. Mansfield marked some 60 accessible nests and ringed 258 of their occupants. Some of these original birds were recovered when the present study began in 1954–55. An additional 35 nests were marked and 279 birds ringed, but only a small proportion of the 95 marked nests were suitable for close observation.

The early rings, recovered from 1955 onwards, were unfortunately so badly abraded that some were completely illegible, and many more must have been lost. For this reason records of pairs together in the same nest extend over the last three seasons only, although there is ample evidence of single birds breeding in the same nest over a period of six seasons. The only evidence of change of nest site by a pair of mature adults was from site 49 to 49a in 1956–57 but this is not conclusive for the reasons given later.

Ringed adults have been found “visiting” or “keeping company” at other nests, but there is so far no direct evidence of any “divorce” or re-pairing.

\* For the purpose of this work, Moe Island is considered as part of Signy Island.

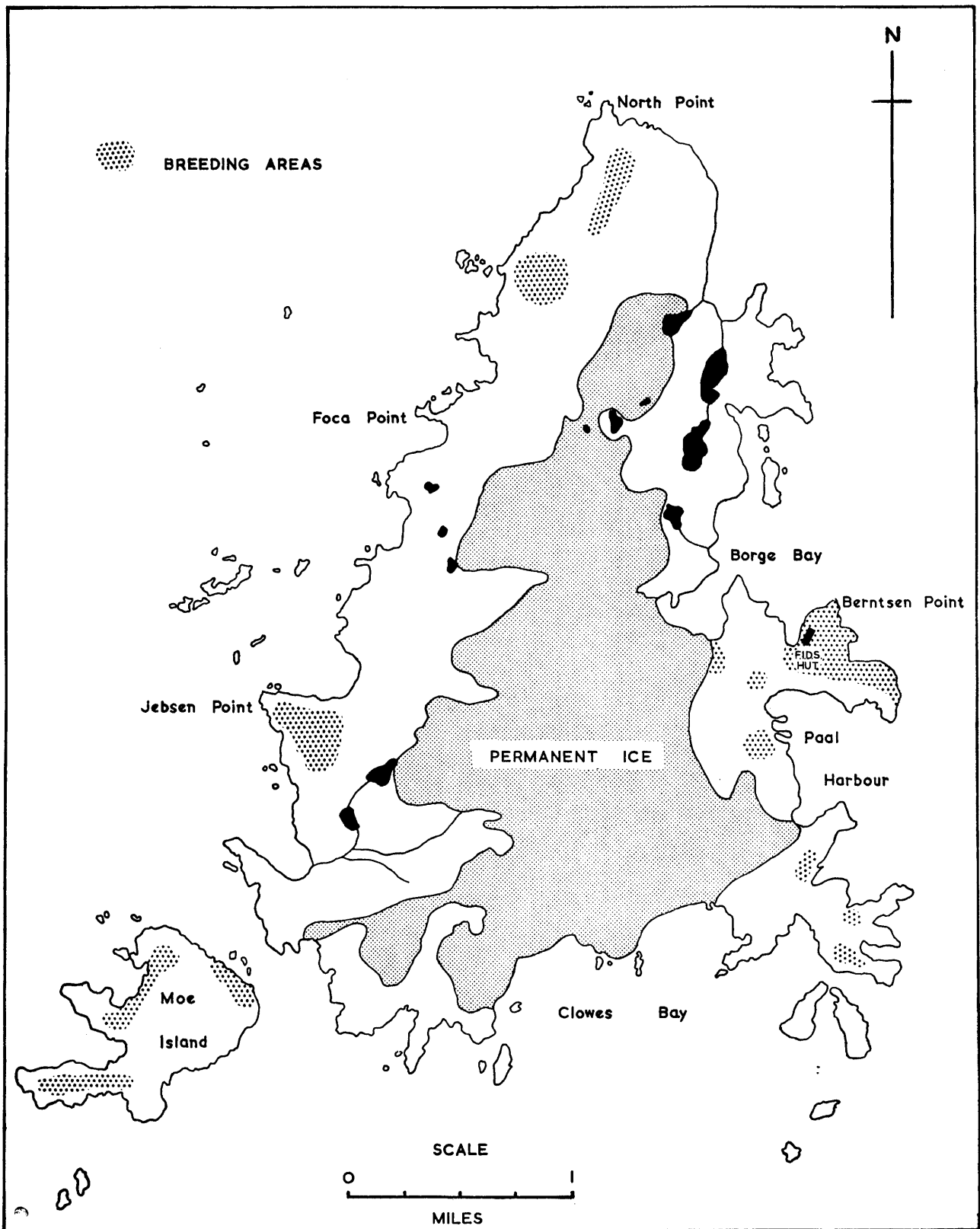


FIGURE 2  
The known breeding colonies of the Dove Prion on Signy Island.



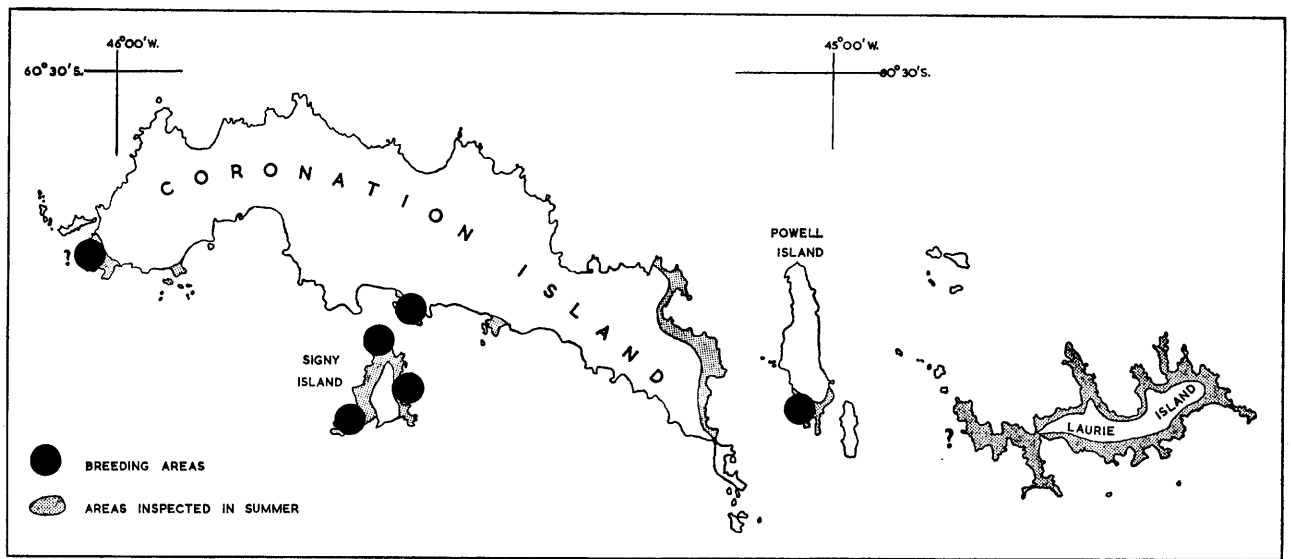


FIGURE 3  
The known breeding colonies of the Dove Prion on the South Orkney Islands.

#### 4. ASSOCIATION WITH OTHER SPECIES

According to the early naturalists at South Georgia (Will, 1884; Steinen, 1890; Lönnerberg, 1906), the Dove Prions nested in different areas from the Diving Petrel, *Pelecanoides georgicus*, preferring the tussac-covered hills to the sand and gravel moraine. However Murphy (1936) states that the Dove Prion colonies found in Possession Bay "... were not only on the high slopes intermingled with those of the diving petrels but also on the soft sand banks just above the level of the bay." More recently on Bird Island, South Georgia (Tickell and Cordall, 1960), it was found that both *P. desolata* and *Pelecanoides sp.* occupy the same burrow systems in the tussac grass, *Poa flabellata*. However, burrows in the fine silt-like scree above the tussac slopes are occupied by Diving Petrels only.

At Kerguelen, Hall (1900) reported that Dove Prions sometimes utilised the abandoned burrows of the introduced European rabbits, whereas Falla (1937) says that "... to some extent the spread of rabbits on the mainland restricted the areas of their [the Dove Prions] breeding grounds, but all steep places unsuitable for rabbits and hundreds of small islets are extensively burrowed." Also at Kerguelen, Paulian (1953) mentions mixed colonies of *Halobaena* and *Pelecanoides* containing small numbers of Dove Prions, and at Macquarie Island Dove Prion colonies are said to be associated with those of *Pterodroma lessoni*.

At the South Orkney Islands, in the absence of any other hole-nesting species, Dove Prions nest on all three main types of terrain—scree, open slope and cliff. Very occasionally the Snow Petrel is found nesting in the entrance of prion nest holes.

## V. LIFE CYCLE

### 1. RETURN OF THE DOVE PRION TO THE SOUTH ORKNEY ISLANDS

Dove Prions are absent from the breeding grounds during the winter months. The available records show that the date of return varies slightly from year to year according to the severity of the winter. In hard winters such as 1948 and 1957, the birds' return appears to be delayed by a few days.

Their first return, however, is not as closely correlated with ice conditions as is that of the Cape Pigeons, *Daption capensis*. The Cape Pigeons are normally absent for the winter but are observed at the time of any major break up of the sea ice, even if it is during the winter and only temporary. This suggests that

the adult Dove Prions are more dispersed from the islands during the non-breeding season than are the Cape Pigeons.

Since the station on Signy Island is situated in the middle of the Dove Prion colony, the birds are likely to be seen or heard very soon after they arrive. The dates given in Table I, therefore, can be taken as being fairly accurate.

In an average year it is clear that, although some individuals are present during the second and third weeks of October, most Dove Prions arrive during the fourth week of the month and are present in full force early in November. Of the breeding Procellarii in the South Orkney Islands, only the two storm petrels (Wilson's Petrel and the Black-bellied Storm Petrel) return to the islands later than the Dove Prions.

TABLE I  
ARRIVALS AT SIGNY ISLAND, 1947-57

<i>First Report</i>	<i>Observations</i>	<i>F.I.D.S. Observer</i>
20 October 1947	First seen 27 October 1947 Heard earlier	G. de Q. Robin
20 October 1948	Present in force on 25 October 1948	R. M. Laws
16 October 1949	Present in burrows on 21 October 1949	R. M. Laws
22 October 1952	Had evidently been back several days	A. W. Mansfield
12 October 1955	Very few. Present in force on 21 October 1955	W. L. N. Tickell
18 October 1956	None present on previous nights	W. L. N. Tickell
23 October 1957	Heard and seen. None present on 15, 16 and 20 October 1957	C. D. Scotland

## 2. OCCUPATION OF THE COLONY

The Borge Bay colony was under observation during the first weeks when the birds returned for the 1955-56 season. Inspections of the marked nests were not sufficiently frequent to give a complete picture of the activities at each nest, but an analysis of the observations covering the period 12 October to 24 November 1955 is interesting. A sample of 48 marked nests from the colony has been used; these were nests in which breeding or some definite activity had been observed during the preceding season.

Visits by the birds to the colony at this time of year were spasmodic. On some nights, chiefly those which were bright and calm, only one or two individuals were present, while in stormy weather they were not only more numerous at night but sometimes also flew in over the land by day. From the time of the first arrivals the number of birds taking up territories by night steadily increased (Fig. 4), but few as yet were spending their days in the burrows. However, even when none were recorded during the daytime in the marked nests, one could often hear them in other nests hidden within the cliffs. Nevertheless, it appears that these daytime visits are far less important and frequent than was suggested by previous naturalists who were not studying marked individuals or marked nests. Therefore, as discussed more fully below, it may be assumed that from mid-October to mid-November most of the population are spending their days feeding at sea.

## 3. NOCTURNAL HABIT AND FEEDING

As already stated, Dove Prions are generally not seen about the colony during the day. Those which are not occupied underground within the burrows go to sea before dawn and return one or more nights later. This habit is shared in the South Orkney Islands only by the Black-bellied Storm Petrel, *Fregetta tropica*; other species such as the Wilson's Petrel, although predominantly nocturnal, do visit their nests during the hours of daylight which at midsummer number between 21 and 22 out of the 24.

On the rough stormy days which are of such common occurrence in these regions, one frequently finds numbers of prions flying in and even entering their nests well before dusk. The 1954–57 notes for Signy Island contain numerous references to early arrivals at about 1830 hr. L.M.T. or even (in October and November) as early as 1500 hr. L.M.T.; these were always on days that had been notably stormy. Mansfield (unpublished) who made similar observations at Signy Island in 1952–53, once saw a prion flying as early as 1015 hr. L.M.T. Murphy (1936) noted the preponderance of prions on stormy days in the bays of South Georgia, and Paulian (1953) at the Îles de Kerguelen similarly mentioned increased numbers of prions in the Baie du Morbihan.

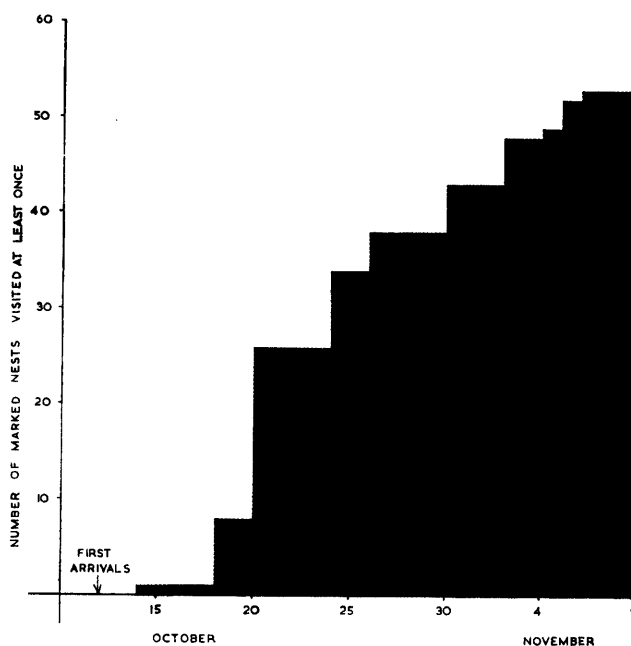


FIGURE 4

Histogram showing the rate of re-occupation of the marked colony in Borge Bay in 1955.

In the South Orkney Islands prions never swim or feed in the bays and inshore waters, though they have twice been reported as doing so at Heard Island, and the impression is that they do not feed within the immediate vicinity of the group. During the summer, boat journeys were frequently made between Signy Island and the adjacent coast of Coronation Island. Prions were observed on only three occasions and these were in the early evening before dark when they appeared in large numbers, assembling prior to coming in to land (Plate IIa, b). On the first occasion, in February at about 1700 hr. L.M.T., we came upon flocks of prions flitting about over the sea, some singly, others in varying groups of between fifty and seventy individuals. This was about a mile offshore and they were not seen within that limit or on land when we arrived back in Borge Bay. In the following season on 19 December 1956, we found this "zone of prions" about two miles offshore, and two days later we went out in our boat and watched them arrive. At 1900 hr. L.M.T., when we reached the area about two and a half miles offshore, there were no birds to be seen other than a few Wilson's Petrels. We waited, drifting for about half an hour, until a dense mass of birds suddenly appeared on the horizon. We approached them, and estimated that the first wave consisted of about 1,500 birds. Frequently they all settled on the calm water, but on our arrival they rose and circled in a dense flock. This was at midsummer when the days were at their longest; birds assembling at that time of year come into land under cover of darkness at between 2200 and 2300 hr. L.M.T.

Falla (1937) says "... such [Dove] prions as were feeding at sea off Heard Island were obtaining their food within a few yards of the cliffs in Atlas Cove and the glacier face in Corinthian Bay." Similarly, an Australian National Antarctic Research Expedition report (Downes *et al.*, 1959) states that "From

December to March prions often feed close inshore a little further out than the Cape Pigeons", which must mean just a few hundred yards from the shore. It is not known whether this occurs at any of the other breeding stations, but there is an indication that there is some difference in feeding habits between the two island races. The diet of the Heard Island birds appears to consist mainly of amphipods which possibly occur close inshore, but the euphausians which are important in the diet of the prions of South Georgia occur in their heaviest concentrations outside a belt some 15 miles wide which is notably poor in plankton (Hardy, 1928; Hardy and Gunther, 1935). It may be that the prions of Kerguelen have the same feeding habits as the Heard Island birds but there is no indication of their feeding so close inshore. Certainly such behaviour is completely alien to the Signy prions. During January 1933 when the R.R.S. *Discovery II* was in the vicinity of the islands, it was reported that "Although Prions were never seen near the islands in daytime, in the surrounding seas they are usually very numerous . . ." Mentioning previous visits to the area, Ardley (1936) says: "In February 1931 forty were seen thirty miles south of Coronation Island, and twenty at a position forty miles north of the island. In November at least a thousand were observed between ten and sixty miles south of Scotia Bay, and in January about 1,500 between twenty and a hundred miles north of Laurie Island. Almost certainly these were all *P. d. banksi* [see p. 51]. The islands were several times approached when they were surrounded by pack-ice, and on these occasions no birds at all were seen within ten miles of the ice."

#### 4. OCCUPATION OF THE NEST SITE

Dove Prions are gregarious at sea, sometimes congregating in huge numbers, but it is not known whether the members of a pair of any of the Procellarii associate at sea away from the breeding grounds, although Richdale (1949) believes that Royal Albatrosses are already paired when they arrive at the breeding grounds.

Breeding adults are amongst the first to be seen at the beginning of the season. They usually fly around the colony or cliff a few times before alighting, but apparently there are few such preliminaries and if their nests are free of snow they generally enter them without delay. The author has no evidence of nuptial flights, such as those observed by Roberts (1940) in the Wilson's Petrel, or those observed by the author in the Snow Petrel (p. 15). Circumstantial evidence indicates that almost all the time breeding Dove Prions are ashore they are in the nest or its immediate vicinity, especially when the pair are present together.

There must be a considerable number of other birds present in addition to breeding adults, but evidence again is very slight as the large size and complexity of the colony prohibited the marking and following of the whole population. It is not yet known at what age the young Dove Prion first returns to its nesting grounds. By comparison with other species (see p. 15), it is not unreasonable to postulate that the population must contain a considerable proportion of non-breeding birds of several age groups, together with breeders that have been unsuccessful for one reason or another. Marshall and Serventy (1956) show that immature Short-tailed Shearwaters, *Puffinus tenuirostris*, arrive after the breeding adults and depart before them. Richdale (1942) on the other "Mutton Bird", *Puffinus griseus*, indicates that about half the population on Whero Island consists of immature birds. If there is a similar proportion of non-breeding Dove Prions on Signy Island, they probably comprise the majority of those birds flying around and roosting in the open.

Breeding Dove Prions are known to use the same nest site in successive seasons. Ringed pairs which bred successfully in marked nests during the 1954-55 season, occupied the same nests in the following three seasons. In addition, a few individual breeding birds which had been ringed in 1951-52 were using the same nests in 1956-57, but information about these birds is scanty as most of the rings were very badly worn and were consequently illegible; many more rings must have been lost.

There is evidence from marked birds, therefore, of pair-bonds maintained over four seasons and nest sites held for over six years.

For an account of territorial behaviour, see p. 18.

#### 5. THE NEST

In the South Orkney Islands there is generally insufficient soil for burrowing, but where their nest holes have soil floors, e.g. as in the cavities underneath boulders, the Dove Prions of Signy Island do a great deal of digging.

At all the other known breeding stations (with the exception of Cape Denison on the mainland of Antarctica) the nests are typically in burrows excavated in the soil. These may not necessarily be entirely the work of the prions, for they often live in the same localities as other burrowing petrels and introduced mammals. At Heard Island, however, Downes *et al.* (1959) remark that whilst the majority of the Dove Prions make "... their burrows under the *Azorella* hummocks in the steep grass-covered slopes wherever there is sufficient depth of soil ... other nests have been found in crevices amongst the mounds of broken lava ... [where] the sitting birds can occasionally be seen from outside without disturbing the site [and may even be within reach of the sun's rays]".\* This latter habitat is characteristic of the South Orkney Islands and is presumably resorted to at Heard Island because of competition for burrows in the *Azorella*.

As described by Lönnberg (1906) and Pagenstecher (1885) the burrows below the tussac grass, *Poa flabellata*, in South Georgia are 9 in. to 3½ ft. in length, rarely more though they are sometimes very crooked. The nest chamber is 8–12 in. below the surface and has no lining. The burrow leading to it is likely to be wider than it is high but the greatest diameter is only about 5 in. Falla (1937) describes the nests in the *Azorella* at Heard Island as being deep and tortuous, with walls frozen hard, and states that those at Macquarie Island may be as much as 6 ft. long with a roomy nesting chamber and a nest of tussac built up, often from a wet floor. Downes *et al.* (1959) mention complex branching burrows at Heard Island with nest chambers as much as 5 or 6 ft. from the entrance, some of which shared a common entrance. One nest chamber was found to be 9 in. long, 8 in. wide and 5 in. deep. The eggs were laid in a shallow depression with little or no lining.

Very little actual nest construction is found in the South Orkneys, but where the nest has a soil floor a hollow is excavated, and the egg sometimes becomes half-buried and is consequently lost.

Loose material, such as small sticks, mosses and lichens, which was used as palisades to indicate whether the nest had been visited the previous night, was frequently taken into the nest. Such material, especially the local lichen, *Usnea*, was sometimes used as lining in nests where no palisades had been erected. In two instances, *Usnea* was taken in after the egg had been laid but, unlike the Dove Prions at Macquarie Island and other burrowing petrels, the Signy prions made no attempt to raise the egg from its damp surroundings. Water was therefore fatal. Some nests were especially liable to flooding, and eggs in these were found immersed in water and also embedded in solid ice.

Roberts (1940) and Paulian (1953) have recorded temperatures within the burrows of Wilson's Petrels, *Oceanites oceanicus*, and the Blue Petrel, *Halobaena caerulea*. These burrows are found in banks of moss, *Acaena* and *Azorella*, which ensure a fairly steady temperature above the shade temperature. In the absence of an incubating bird, however, it is uncertain whether this insulation is sufficient for the survival of neglected and chilled eggs. No instruments were available for the measurement of nest temperatures at Signy Island, but it is worth pointing out the essential difference between such burrows in the *Azorella* etc. and the nesting holes characteristic of the South Orkney Islands. At Signy Island the deeper holes below the rocks and in the depths of the cliffs may be comparable to the moss burrows found elsewhere, but many others are exposed to strong draughts; some are scarcely below the surface and are almost open to the winds. In the latter, as there is much less shelter or insulation, conditions inside the nest may not be any milder than those of other species in the open. Consequently, with the exception of the Wilson's Petrel and the Black-bellied Storm Petrel, Dove Prions are probably more affected than all the other South Orkney Islands' birds by the bad weather prevailing at the end of the winter (Fig. 5).

Fine drift-snow can fill nesting holes in a very short time, and this may thaw to give pools of ice-cold water which will later re-freeze and take longer to disperse. Nevertheless, although it is a great danger to most nests, drift-snow might considerably improve some by sheltering them from the wind and acting as an insulator, provided that it does so without filling up the cavity or completely blocking the entrance.

As described below, the prions are quite well equipped to dig through the snow to their nests, and this they do with great accuracy even when the topography of the whole area has been obliterated by drift. Even so, there are limitations to their capabilities, for whilst fresh dry powder snow presents little difficulty, wind slab and consolidated older snow are more difficult to excavate. Worst of all is the crust of ice which forms on the surface of drifts as a result of alternate thawing and freezing. This is very difficult for the birds to get through, and being relatively common in the Antarctic summer may cause exclusion of the adults from the nest and entombment of the chick.

\* Personal communication

On Heard Island where the two prion species, *P. desolata* and *P. crassirostris* (Downes *et al.*, 1959) occur together, the former nest almost exclusively on the open soil-covered slopes whilst the latter, the Fulmar Prions, are limited to the crags. In the South Orkney Islands, however, nests are found below the surface both on steep crags and on open slopes. Most of them are situated in cracks and crevices which have been enlarged wherever possible by digging, and it is almost impossible to distinguish between occupied and unoccupied holes. On the crags, nests may be many feet from the surface and it is known that a number of individuals use common entrances and utilize the same caverns. On the open, boulder-strewn slopes which are covered with mosses and lichens, it is possible to find an occasional burrow excavated solely in the moss—a habitat typical of *P. desolata* breeding on islands in lower latitudes. Consolidated scree is also used by large numbers of birds.

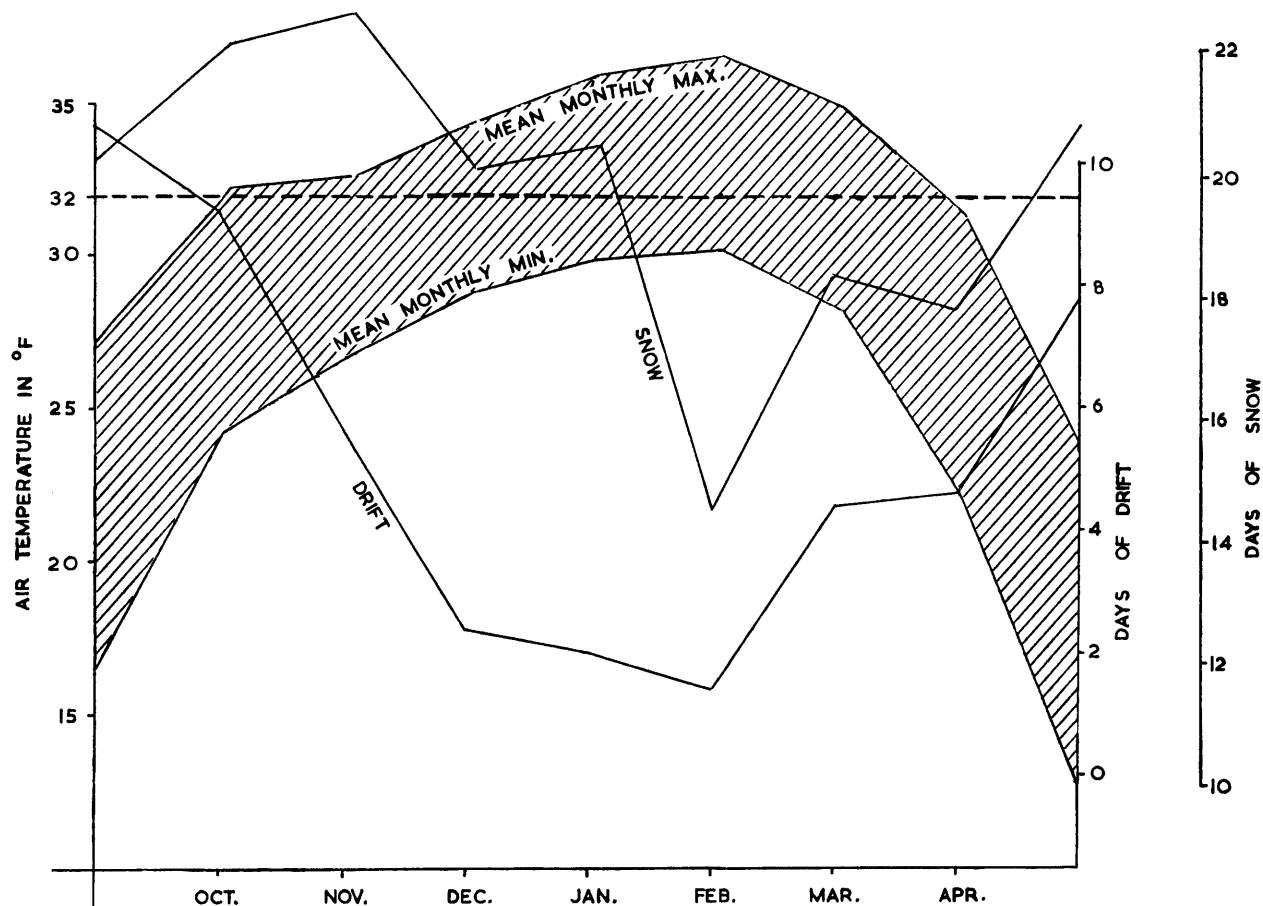


FIGURE 5

Weather factors affecting burrow-nesting petrels. Means are calculated from data covering the seasons 1947 to 1956.

The position of the nest within the nest hole may be moved at any time during the season, by burrowing in the soil or by shifting to an adjacent crevice or chamber. The extent, distance and frequency of the move vary with the nature of the individual hole, since some nests are on rock within the confines of a narrow crack whilst in others soil and rock are combined in varying proportions. Although some pairs moved nest sites, others with nests in extremely poor and exposed positions showed no signs of shifting, despite repeated failure to rear young. Nest 41, for instance, was in a large open cavern which for three consecutive seasons filled up with snow, water or ice and was therefore deserted each time after the egg was laid.

It was not possible to observe the actual process of digging at Signy Island, but birds which must have been digging at the time of capture were frequently handled. The soiled state of their bills indicated that they are used in conjunction with the feet and this agrees with Rankin's (1951) observation in South Georgia where the prions "... showed their resentment at my excavations by digging vigorously farther

into the bank with beak and claws." He goes on to say: "I was amazed to see the speed at which they progressed, beak loosening the soil and feet sending showers of it behind." On 18 October 1955, very early in the season, a bird was discovered with its claws worn right down to the webs; this must have been caused by abnormally heavy abrasion, possibly due to it digging in the frozen gravel. When the floors of the burrows become filled with ice one often notices a tendency to dig in the soft soil under the edge of the ice, but burrowing is much more noticeable and probably more frequent later in the season when the soil has thawed. It is not unusual for eggs to become partially buried or displaced and consequently deserted; in any case they become very soiled during such excavations. If ice blockage persists late into the season, and the egg is deserted, adults are often found at night in an adjacent chamber. The position of nest 86 was moved by excavation in the middle of incubation and the egg was lost, but in this instance desertion was almost certainly brought about by disturbing activities of a nearby pair in the same cavity.

The two nests, 49 and 49a, are interesting in a different way, for although they were very close together the connecting holes through the rock were not big enough to allow passage between them. In 1954-55 an established pair reared a chick in nest 49, but were thwarted by snow the following season although another pair appeared in 49a and successfully reared a chick. Then during the third season, the old pair from 49 occupied 49a in lieu of their original hole, and successfully reared their young. The original nest was visited occasionally during the chick-feeding period; the other pair from 49a was not seen again although it is suspected that they moved into one of the other holes nearby.

## 6. AGE GROUPS

It is impossible to distinguish any age groups, other than nestlings, by plumage alone, but the study of a marked population over a number of years would provide much useful information.

At present, it is not known at what age Dove Prions reach maturity nor whether they return to breed in the colonies in which they themselves were reared. Moreover, until recently, very little was known about the age groups of any petrel species. Serventy (1957) however, ringed large numbers of Short-tailed Shearwaters, *Puffinus tenuirostris*, over many years and has established that the chicks first return to the islands on which they were reared when three years old, but spend a comparatively short time ashore. In their fifth year they arrive earlier and stay longer. The females start breeding at between 5 and 7 years of age and the males at 7 to 8 years. Many of the non-breeding birds present were found to range from 5 to 7 years in age, and it may be that if a bird cannot find a mate or territory after 7 years it goes on to another island (*op. cit.*).

In attempting to distinguish the various age groups of Dove Prions according to particular aspects of behaviour the data for the Short-tailed Shearwaters provide the best standard for comparison.

## 7. PRE-LAYING ACTIVITIES AT THE NEST

### a. Visits to the nest by breeding adults

It can be seen from the analysis of the 1955 results (Table IIa), that by about the middle of November most of the adult birds are coming into their holes at night, but Table IIb shows that the number of pairs spending the daytime in their nests is negligible at this time. It is likely, therefore, that most well-established pairs first come together again at night. The pairs which stay ashore in the daytime draw attention to themselves by fighting (p. 18) and other activities, and this has led observers to overemphasize the importance of these daytime visits. Ardley (1936) speaking of the Borge Bay colony says that in most nests where no eggs were found both parents were present during the daytime. L. H. Matthews (1929) in South Georgia also stated that before the egg was laid most birds were usually in the burrows during the daytime, and Pagenstecher had made the same observation in 1885. These observations, however, do not generally apply to the South Orkney Islands' birds, moreover, it appears likely that the physiology of egg-production would prohibit these vigils ashore immediately prior to laying (p. 37).

Events more typical of the South Orkney Islands are summarized in Table III. Out of a total of twenty night inspections of nest 68 between 19 November and 11 December, the pair were found to be present together on sixteen, the male was present alone on three, and only once was the nest found to be empty. Corresponding day inspections showed that the pair were together only once and that the male again stayed alone on three occasions. It is worth noting that on the occasions when there was only one bird

present it was always the male and never the female. Between 11 and 22 December, the female was not once seen in the nest, although the male was present every night and also on one day. The female then re-appeared and both birds were present on the nights of the 22 and 23 December; the egg was laid on the 23 December.

TABLE II  
ANALYSIS OF NEST OBSERVATIONS, OCTOBER TO NOVEMBER, 1955

a. Night Inspections

Date	Total Number of Nest Holes Inspected	Both Parents Present	One Parent Present	Empty Nests Showing Evidence of Visits	Percentage of Inspected Nests Occupied
<i>October</i>					
12-15	48	0	1	2	6
16-19	96	2	4	13	20
20-23	96	3	23	2	29
24-27	96	13	30	3	48
28-31	68	15	21	10	68
<i>November</i>					
1- 4	105	9	31	23	60
5- 8	74	21	26	6	72
9-12	114	40	19	1	53
13-16	96	58	20	2	83
17-20	76	36	17	1	71
21-24	81	46	14	4	79

b. Day Inspections

<i>October</i>					
12-31	196	1	6	*	4
<i>November</i>					
1- 4	48	1	0	*	2
5- 8	96	3	2	*	5
9-12	60	4	5	*	15
13-16	48	3	3	*	13
17-20	48	2	0	*	4
21-24	18	3	2	*	28

\* — No observation.

Nest 68 seems typical of successful pairs. Although there are some individual variations, observations at other nests confirm that the female exhibits a distinct lack of interest in the nest for a period varying from seven to fourteen days prior to laying. During that time she may not visit the nest at all or, as often happens, may make only one or two returns by night. The behaviour of the male during this period is equally remarkable, for whilst the female is absent, his interest in the nest is as strong as ever. The importance of this will be discussed when laying and incubation are considered (p. 20).

It has been known since the beginning of the century (Valette, 1906) that Cape Pigeons depart on a "honeymoon" flight for about ten days prior to laying. Murphy (1936) mentions vague reports of similar behaviour in some other petrels and shearwaters. This phenomenon was observed by the author on Signy Island amongst the Snow Petrels (see p. 11) and the Cape Pigeons which occupy the cliffs behind the base hut. All these observations indicate a more general exodus of the breeding birds than occurs in the Dove Prion. Marshall and Serventy (1956) mention a similar pre-laying exodus in the Short-tailed Shearwaters. These birds almost entirely forsake the nesting island early in November and remain at sea until 19-21 November when they return and lay, the eggs being deposited over a period of about twelve days. The temporary desertion of this colony of Short-tailed Shearwaters is fairly complete and is quite conspicuous.

In the Dove Prions, and perhaps in other species of *Procellariidae*, parallel behaviour is not apparent unless nest routine is followed very closely. The only nights on which my notes record a general drop in



numbers are 8 – 12 November, at the time when the females were absent. The departure is not so obvious in Dove Prions, firstly because the breeding males, together with a good following of non-breeders, still return each night, and secondly because laying is extended over three to four weeks and pairs are consequently not so closely in phase with each other as in *P. tenuirostris*.

Venables (1952, 1955) has shown that a similarly obscured exodus occurs in the Fulmar, *Fulmarus glacialis*, and there is evidence (Richdale, 1949) that the females of the Royal Albatross, *Diomedea epomophora*, appear ashore only periodically during the month preceding laying. Finally, in the Storm Petrel, *Hydrobates pelagicus*, Davis (1957) has demonstrated an almost complete cessation of daytime occupation during the week preceding laying, and remarks that prior to that the males tend to remain in the nest by day more often than do the females. However, he gives no account of night activity during this period.

This pre-laying departure in the *Procellariidae* may be connected in some way with the physiology of egg production. The eggs of petrels are large, those of *Pachyptila desolata* weighing 30 to 35 g. which is approximately one-fifth to one-quarter of the bird's body weight. It is assumed that oocytes mature and grow in the normal manner during the early part of the breeding season whilst the pairs are visiting the nest together each night. There probably then comes a time when the final deposition of yolk is such a drain upon her resources, that the female is forced to spend almost all her available time feeding, or at least close to the richest feeding grounds. Further evidence of the strain to which the female petrel is subjected can be seen in the fact that as soon as the egg is laid she departs, presumably to the feeding grounds to recover, leaving the initial incubation to the male.

TABLE IV  
OBSERVATIONS OF COPULATION

Dates	Comments
<b>1955-56</b> 3 November 5 November – 6 December 11 December	First heard. Heard and seen frequently. Last heard.
<b>1956-57</b> 7 November 9 November 11 November – 22 December 29 December  5-14 January	None observed or heard yet. Mounted pair seen for first time. Heard and seen frequently. A distinct absence of the "copulation call" about the colony but twice attempted in nest 32 following loss of egg. Heard twice.

In 1949 Laws first observed copulation on 28 November and in 1952 Mansfield reported it on 12 November.

#### b. Copulation

This has been observed on numerous occasions (Table IV), both in the nest hole and in the open, and all observations except one on 5 December were at night.

It is preceded by remarkably few preliminaries. After landing and calling, pairs were usually observed either to face each other or to sit head to tail. Then after more calling and moving about, one bird following the other, each tried to initiate "billing" and "nibbling". This was resisted, and the result was a clashing of bills and continual parrying with incipient pecking of the head.

It is often possible to get a sufficiently long glimpse of copulation to determine the sex of the individuals in marked nests, but if one surprises a pair in the act they cease immediately. On one or two occasions the author saw a pair performing in the open close by. The first time this was observed the pair alighted after flying over the nearby rocks and then gave the normal calls. One bird (presumably the male) then excitedly mounted the other which uttered a high-pitched piping whistle, and stayed in position for about half a minute though it could not be confirmed that actual coition occurred. Shortly afterwards the male attempted unsuccessfully to re-mount. At night, the Signy Island prions roost on the open snow-covered slopes in large numbers which no doubt include many immature birds. Mounted birds have been observed among them on several occasions.



The high-pitched whistle already mentioned was heard only from copulating pairs and appeared to be uttered only by the female. It was, however, heard on one other occasion—during an examination of a live bird in the laboratory, when attempting to insert a cloacal thermometer (p. 38). The call could have been mistaken for only one other prion call, that of the young chick begging for food, but as this occurs at a completely different stage in the life cycle (the young do not appear until February) confusion is unlikely.

In the 1954–55 season, work did not start on the colony until after laying, but observations of copulation covered the whole of the following two breeding seasons. In both of these, although copulation was first recorded at the end of the first week in November, it was generally observed later but had ceased almost completely by the end of December. The estimated peak period was between 27 November and 7 December. There is evidence that under certain circumstances copulation is attempted after the egg is laid. In one instance, the egg had rolled away from the nest and thus upset the sequence of behaviour, possibly causing a return to the copulatory phase.

The detailed nest records (Table III), show that copulations were observed in the selected nests just prior to the departure of the females on their “pre-laying” flight.

### c. Territory and fighting

The Dove Prion shows strong territorial behaviour and, before laying, the colony is the scene of noisy squabbling and fighting which is typified by one particularly raucous call.

Most of the fights occur in the nest holes and most of them are at night when large numbers of non-breeders probably enter the colony. Surface fights, however, were observed by Mansfield (1952) in the fully occupied colony at night.

The Dove Prion is probably the only petrel of the South Orkney Islands which does not eject stomach oil as a method of protection, although it will occasionally vomit and excrete when being handled. Its lack of such a defence mechanism might account for its aggressive behaviour, so different from that of the Cape Pigeons and Snow Petrels which rarely fight on their breeding grounds. The author frequently watched prions fighting in their holes by the light of his torch, the belligerents taking no notice of the sudden illumination, and when ringing, often came across prions showing signs of battle—ruffled plumage, wounds and blood—mostly about the head. Once, a prion was discovered with the horn of the mandible completely torn away from the bone at the base of the bill, and on another occasion a bird was found with an amputated leg, although the latter may not have been due to fighting.

Three dead birds were also found in nests, two of them in circumstances indicating that they had been killed in fights. One of the two was a male with well developed testes. The other, a female, was found alongside a nest with fresh blood on the wing and one of its legs broken, and as it had not been present the previous day it must have been killed during the night. The nest was occupied by a pair which had bred for three consecutive seasons, and the female was then (10 December) incubating a five-day-old egg.

As already stated (p. 11) there are several different types of nest holes:

- i. Single, small culs-de-sac, with one or two entrances, containing a single pair.
- ii. Larger “caverns”, below rocks on open slopes or in the depths of cliffs, containing two or more nests.
- iii. Cracks, burrows and fissures in a complex network of tunnels and chambers amongst boulders or in consolidated screes or cliffs.

The first type is the easiest to defend, and the whole of the nest chamber and tunnel appears to be defended territory. The shallow nest holes, being easier to watch, comprised the majority of the marked nests, and in some of these the egg was laid and incubated within a foot of the entrance and fully illuminated during the daytime. Time and again the author stopped by these nests, where the owners were loudly advertising their presence, and watched the entrance of strange birds. It was typical of such visits that the intruder was rapidly evicted, but fights were also frequent.

In the second type of nest hole, in which several pairs may have to enter by the same crack, territory is of necessity limited to the nest areas within the “cavern”. One would expect such territories to be less stable than those of the first type, where there is only one entrance to defend and no chance of encroachments and border feuds. Nests 86 and 87, for example, were in the same chamber within twelve inches of each other. Both pairs were established and raised young in the 1954–55 season. The following summer an egg was laid in nest 86 on 14 December and incubated until 20 December, when it vanished. On the same day

one appeared in 87 and, although neglected at the time of observation, it was incubated in 87 the following day but then disappeared. Both nests were empty and deserted during the day up to 30 December when another egg appeared in 87. At first, it was thought that the pair in 87 had laid a second egg, but it is more likely that there had been a scuffle between the two pairs and that the first egg had rolled down from 86 into 87 and had been lost (perhaps in another scuffle or movement of the pair), while the egg of 87 was laid later.

More troubles dogged these two pairs in the following season, for after the egg had been laid in 86, there was a remarkable amount of digging and the nest was eventually moved some 6 in. further back. In the process the egg became half buried and the parents ceased to incubate. Later, the chick that had been reared in 87 was found in 86 (by then deserted during the daytime) and was observed to sit for several days in a position midway between the two nests.

Owing to the cramped quarters, fighting must almost invariably take the form of pecking, biting and tearing with the bill at the opponent's head, neck or bill, and once one bird has secured a hold they grapple back and forth. When attacked, the intruder appears to be at a disadvantage and tries to escape, but such is the swiftness of the first encounter that this is sometimes impossible. If the intruder is then cornered in a cul-de-sac, it is forced to fight it out, whereas in a less confined space it might be able to retreat. The forcible eviction of intruders was frequently observed.

One fight which was observed is worth special mention. On the night of 17 March, the author heard a commotion in a particular hole and went to investigate. Two of the three occupants were locked together by their bills, very ruffled and bleeding. They took no notice of the torchlight and continued squeaking and struggling for some time. Eventually they separated and the author extracted the outermost and placed it on a rock nearby, but it made no attempt to fly off. The combatant in the hole then started feeding the third bird which must have been a fully fledged young. This fight was apparently between a parent at the nest and a fully fledged young intruder that had just left its own nest that night and had either lost its way or trespassed deliberately. The intruder's behaviour was distinctly indicative of a young bird. It was, moreover, observed on one of the peak nights for the departure of the young (p. 33).

In addition to "border feuds" between neighbours and intrusions by the young, fights are also caused through the intrusions by non-breeding adults already mentioned on page 18. There must be a considerable number of non-breeding birds present at the colony (p. 15), and they probably comprise the majority of birds flying around and roosting in the open. These non-breeders seem to be attracted to, rather than repelled by, burrows where calling pairs are present. Nest 52 always had two or three of these birds outside its entrance. Strangely enough, although the author frequently watched such birds enter nest 52 (and be subsequently evicted) he never caught one inside, whereas in other nests he ringed up to three additional birds besides the owners. Most of these strangers were never caught again except in nests where new pairs took up territories after the original owners had been unsuccessful and had departed.

## 8. THE EGG AND EGG-LAYING

### a. *The egg*

The single egg is white, matt and without any markings. It varies in shape between sub-elliptical and short sub-elliptical sometimes being wholly elliptical (to use the terminology of R. S. Palmer, 1956).

The shell is thin and the average weight of eight empty shells was 3.8 g., the extremes being 5.0 and 2.5 g.

Data from small samples of eggs from South Georgia, the Îles de Kerguelen, Macquarie Island, the Auckland Islands and the Antarctic mainland at Cape Denison have been examined. With a single exception they all fall within the range of the Signy Island eggs (Table V). The one specimen from Cape Denison, measuring 43.4 × 32.2 mm., was shorter than any of the Signy Island eggs.

TABLE V  
MEASUREMENTS OF DOVE PRION EGGS FROM SIGNY ISLAND

	<i>Number</i>	<i>Mean</i>	<i>σ</i>	<i>Standard Error</i>	<i>Range</i>
Length (mm.)	42	47.1	1.77	± 0.27	44.0-52.0
Width (mm.)	42	34.6	1.28	± 0.18	31.0-36.5
Weight (g.)	23	32.8	2.19	± 0.46	29.0-36.0

TABLE VI  
DATES OF LAYING

	December 1955	December 1956
<i>Nest Number</i>		
68	20	24
68a	18	23
81	14	19
70	15	15
29	12	5
27a	19	18
27b	20	17
49a	16	16
41	23	12
86	15	10
87	30	19
52	30-31	16
69	25-26	27
91	7-11	27
32	7-11	8
50b	25-26	18
Other pairs	(11)* 11-31	(13)* 5-25
<i>Mean Date</i>	20	19
$\sigma$	6.34	6.34
<i>Standard Error of Difference</i>	1.73	
<i>Range</i>	7-31	5-27

The difference between the means for 1955 and 1956 is less than twice the standard error and is therefore not significant.

Mansfield for the 1952-53 season gave observed egg dates as 14, 15-16, 16-19, 20, 22 and 25-27 December.

\* — Number of pairs.

#### b. *Egg-laying*

Eggs are laid throughout December, the earliest record being 5 December 1956 (Table VI and Fig. 6). The date of laying depends on the date of return to the colony which is, in turn, slightly affected by the accessibility of feeding grounds and nesting sites (p. 3). It is unlikely that laying could ever be much earlier than 5 December, as the winter preceding the 1956-57 summer was particularly mild and short, and there is an indication that it was slightly later in the summer of 1955-56. It is possible that a few eggs are laid as late as the first week of January but freshly laid eggs were never found in marked and regularly inspected nests after December.\* All records are of well-established breeding adults.

Mansfield's (1952) data taken from marked nests which were under constant observation two seasons before my arrival, are in complete agreement with my own. The dates (17-21 January) given by Ardley (1936), which are to some extent supported by Robin (1947) and Laws (1949) in the early F.I.D.S. records, appear to be altogether too late.

\* In 1956, a number of nests on the ridge south-east of Borge Bay were still without eggs on 21 December, but many of these had been closed by drifting snow.

As the dates of arrival and observed copulation given by Robin and Laws are comparable with Mansfield's and the present author's, it is surprising that their dates of egg-laying are substantially later. It is true that the winters in those years were harder, but it is possible that the dates recorded are the result of isolated observations and are not representative of the colony as a whole. It is unlikely that there could have been such a marked change in the timing of the breeding cycle. Moreover, calculating from the known incubation period of about 45 days, Laws's date for the appearance of the first chicks, 16 February 1949, indicates that laying occurred on 1 January 1949, some 13 days earlier than his first egg dates.

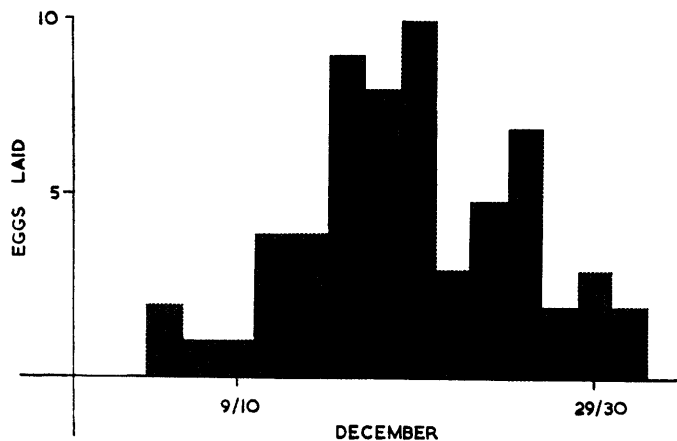


FIGURE 6

The distribution of 61 laying dates from three seasons. Class intervals—two days.

Ardley (1936) states that "Between January 17 and 21 about 120 nests were examined and of these forty contained eggs most of which were freshly laid. The most advanced egg was not more than a week incubated." As he himself points out later, this is extraordinarily late when compared with the South Georgia Dove Prions which lay in the period from the end of November to the middle of December (L. H. Matthews, 1929). Even in the comparatively mild winters of recent years Dove Prions would have found it difficult to keep their nests open throughout April, and it is unlikely that eggs were not laid earlier than 10 January in 1933. It is worth remembering that eggs which have been deserted and chilled may not be viable but in a cold climate will remain fresh and give the appearance of being freshly laid.

As the laying period of the Dove Prions lasts approximately four weeks, the successive phases of pre-laying behaviour overlap throughout the colony and are not obvious unless individual nests are observed closely.

Only one egg is laid each season; it is unlikely that a second is laid, even if the first is removed, and this conclusion applies to all other *Procellariidae* although two eggs have been found in some nests. Two eggs are frequently seen in Dove Prion nests but the additional eggs are invariably old and addled ones from previous years. They are mostly soiled and are often half buried, but they sometimes lie in the nest itself alongside the fresh egg. Fresh eggs may also become very dirty and caked with mud, and in such circumstances, the two may easily be confused by the parent so that the fresh one is neglected while the old one is incubated. As regards time of laying, it appears that females generally lay their eggs on the night of their return, although sometimes not until the following night.

## 9. INCUBATION

As the females arrive back virtually at the point of laying, it is important that there is no delay in getting into the nest. The nightly visits of the male to the nest immediately before the egg is laid serve to keep the nest hole open while the female is away at sea. In periods of snowfall, such frequent visits are most valuable as they prevent the snow from accumulating and consolidating; the bird is, therefore, more likely to be able to clear the hole in a single night. This may explain why the Dove Prions do not depart together, as do the Short-tailed Shearwaters, *Puffinus tenuirostris* (Marshall and Serventy, 1956) and other petrels previously

mentioned. Even so, some eggs are laid in the open, presumably by birds which cannot get into their nests, indicating an inability to "hold back" the egg for long if the nest is not ready. This has been observed in other species, particularly the Great Shearwater, *Puffinus gravis*, (Rowan, 1952) on Nightingale Island where there is severe competition for burrows. There is no such shortage of nest sites on Signy Island.

The beginning of incubation is the time when failure most often occurs in burrow-nesting petrels, the marked pairs associating only for a short period each night. In Dove Prions and many other petrel species (e.g. the Fairy Prion), naturalists have observed that the egg is neglected for one or more days soon after laying, but rarely in the final stages of incubation. Desertion in the early stages is mostly due to the failure of the male to take over immediately the egg is laid, either through his absence or the lack of an incubation impulse. Although the females are capable of long sittings (p. 25), it seems that they rarely take over incubation immediately the egg is laid; possibly the urge to sit is subordinated to some feeding impulse. Any inefficiency in the male will, therefore, increase the possibility of failure.

Because of the low temperatures, neglect of eggs in the Antarctic is always risky and often disastrous. The author has no quantitative data on the resistance to chilling and survival of neglected eggs, but eggs of *P. desolata* have hatched after being neglected for one or two days and sometimes for a total of six days throughout the incubation period. In such cases, the time of incubation was apparently increased to compensate for the interruption in development (p. 23). Similarly, Roberts (1940) found that the egg of the Wilson's Petrel remained viable after two days' chilling. However, the difference between the body temperature of the incubating bird and the mean shade temperature is considerably greater in the polar regions than elsewhere (the body temperature being about 105°F and the shade temperature ranging from about 20°F to 50°F during the summer), and in the sudden cold spells which are quite frequent neglected eggs do not survive long. The number of eggs from previous seasons to be found in the nests is evidence of such losses. G. V. T. Matthews (1954) has shown that in the Manx Shearwater, *Procellaria puffinus*, only about one per cent. of the undisturbed nests examined contained neglected eggs. Such eggs survived chilling in the burrow for up to 7 days and others remained viable in the laboratory for up to 13 days, but in this species, however, the chilling did not approach freezing.

The author rarely saw the eggs of the Cape Pigeon, *Daption capensis*, neglected, and those of the Snow Petrel, *Pagodroma nivea*, only occasionally. Fisher (1952) mentions that "Man is probably the only animal in Britain that can put the Fulmar, *Fulmarus glacialis*, off its egg", this probably being because of the danger of egg predation by gulls. Richdale (1952) indicates that the Royal Albatross, *Diomedea epomophora*, similarly "sits tight" from the time the egg is laid. It is apparently only in the burrow-nesting petrels of nocturnal habit that such lapses occur.

Although temperature in the South Orkney Islands generally remain just above freezing point, drifting snow constitutes a danger even during the Antarctic summer. Drift can block or completely fill a nest within an hour or so, and a deserted egg thus buried has no chance of survival. This happened in nest 32 during the 1956-57 season, and resulted in the loss of an egg which had been left for only one day.

Shifting of the egg within the nest hole, already referred to (p. 19), may also cause desertions. The boundaries of the nest itself are often very ill-defined and in the disturbance caused by the second parent taking over incubation, the egg may roll a short way out. After this, it appears to be completely ignored and no effort is made to retrieve it and recommence incubation. In experiments with the eggs of the Cape Pigeon, I found that those placed on the rim of the nest are retrieved whilst those placed just outside are ignored. Some Dove Prion nests are so badly placed that if the egg is moved even slightly it will roll away, sometimes completely out of the nest and burrow; this happened in nest 28 in two consecutive seasons. Mansfield mentions also that melting ice may tilt the nest floor and cause the egg to roll away.

Imitation eggs made from Plaster of Paris were never accepted and were immediately deserted although they were identical in shape and size with the real eggs. This was probably because of their rougher and more porous surface. Eggs of other species, such as the Snow Petrel and the domestic fowl ( $\times 1\frac{1}{2}$  and  $\times 2$  the volume of Dove Prion eggs), however, were readily incubated when substituted. Similarly, the egg of the Antarctic Tern, *Sterna vittata*, which is approximately the same size as the prion's, was accepted and incubated normally in spite of its colour.

Table VII<sup>7</sup> gives the dates\* of laying and hatching at marked nests by marked birds during three seasons. Observations on unmarked nests and birds are not included in this particular analysis. It will be seen that the periods between laying and hatching vary from 42 to 50 days but, as already stated, this exceeds the true incubation period by the total time (if any) during which the egg was deserted. It was possible to follow

the daily routine at ten nests sufficiently closely to determine how many days and nights each parent spent incubating, and also whether and for how long, the egg was temporarily deserted. (Tables VIII and IX.) The true incubation period is therefore known and gives a mean of 44.8 days. The apparent incubation period can exceed this by at least 6 days.

TABLE VII  
THE APPARENT INCUBATION PERIOD

<i>Nest Number</i>	<i>Laying Date</i>	<i>Hatching Date</i>	<i>Apparent Incubation Period (days)</i>
55	20 December 1952	31 January 1953	42
8a	16-19 December 1952	3 February 1953	46-49
60	15-16 December 1952	27 January 1953	43
68	20 December 1955	4 February 1956	46
69	25-26 December 1955	7 February 1956	44-45
85	30 December 1955	13 February 1956	45
29	12 December 1955	26 January 1956	45
74	17 December 1955	1 February 1956	46
49a	16 December 1955	30 January 1956	45
50b	25-26 December 1955	9 February 1956	46
68a	23 December 1956	5 February 1957	44
69	27 December 1956	9 February 1957	44
29	5 December 1956	22 January 1957	48
52	16 December 1956	30 January 1957	45
67	14 December 1956	30 January 1957	47
87	19 December 1956	4 February 1957	47
94	18 December 1956	2 February 1957	47
82	23 December 1956	c. 10 February 1957	c. 49
83	25 December 1956	c. 10 February 1957	c. 47
68	24 December 1956	12-13 February 1957	49-50
49a	16 December 1956	30 January 1957	44
62	11 December 1956	29-30 January 1957	48-49

TABLE VIII  
THE TRUE INCUBATION PERIOD

<i>Nest Number</i>	<i>Apparent Incubation Time (days)</i>	<i>Number of Days Egg Deserted</i>	<i>True Incubation Period (days)</i>
68a	44	Nil	44
69	44	Nil	44
29	48	1 day and 2 nights	? 46
52	45	Nil	45
67	47	2 days	45
87	47	2 days	45
94	47	1 day	46
68	49-50	6 days and 3 nights	44-45
49a	44	Nil	44
83	c. 47	2 days	45



Of all the apparent incubation periods recorded, only one is less than 43 days, i.e. Mansfield's for 1952-53 in nest 55 which is 42 days. This exception may perhaps be due to the retention of the egg in the oviduct, as observed by Nice (1953) in the Cow-Bird, *Molothrus ater*. She states that the egg is very occasionally retained in the oviduct for 12-24 hours (the period of one day's incubation) and in such cases true incubation would begin before the egg is actually laid. This phenomenon might also occur in the *Procellariidae*. The females spend quite a lot of time at sea during the growth of the egg, returning to the colony with it fully formed and ready to lay. It is quite possible that a petrel with a fully-formed egg, might take 24 hours to return to the nest. It is also possible that in certain circumstances a female might be obliged to drop the egg at sea before reaching the breeding grounds.

TABLE IX  
MEAN LENGTH AND RANGE OF INCUBATION PERIOD

<i>Number of Nests</i>	<i>Mean Incubation Time (days)</i>	$\sigma$	<i>Standard Error</i>	<i>Range (days)</i>
10	44.8	0.56	0.18	44-46

#### 10. SHARE OF THE SEXES IN INCUBATION

The most experienced successful pairs share the incubation of the egg equally, although there is a tendency for the females to sit for only single days more often than males. This is most frequent during the early stages of incubation when, as discussed later, females normally have a low incubation urge. The change-over from one parent to the other should be so ordered that there is no period when the egg is neglected. Each partner spends an average of 3-4 days on the egg before being relieved, and it is not visited by its mate in the interval. By direct observation at four nests it was established that each bird spent a total of 22-23 days incubating, but most other nests were not as well ordered. The few other nests for which records are complete provide examples of both male and female taking the greater share of incubation. (Table X.) If the male Dove Prion takes the larger share of incubation, it may be because of its strong incubation urge, but if the female incubates longest it may be because of a lack of this urge in the male rather than a dominance on the part of the female. The record at nest 52 however, does seem to show a stronger incubation urge in the female.

The importance of the male being strongly attracted to the nest in the absence of the female, both prior to laying (in keeping the nest open) and immediately afterwards (in taking the initial incubation shift) has already been shown. Richdale (1952) observed that there is a tendency at this stage for the male Royal Albatross to take charge of the egg even if it necessitates forcibly moving the female. The male Short-tailed Shearwater (Marshall and Serventy, 1956) and the male Storm Petrel (Davis, 1957) also take the first incubation shift.

The length of the incubation shift is controlled by the interaction of two factors: the urge to incubate or brood and the necessity of feeding. Presumably the brooding urge is dependent upon an endocrinal mechanism, sometimes strong enough to cause the bird to stay in the nest during the day but not as a rule until the egg is present. In this pre-laying stage starvation or hunger is unlikely as the bird is able to feed each day.

However, once an incubation shift commences, the urge to feed must gradually become stronger until it finally exceeds the urge to incubate, and the bird is forced by hunger to leave the egg whether relieved at the nest or not. The correct time for a bird to return and relieve its mate is when the effects of starvation are just beginning to be felt. This time will probably vary from one individual to the next and thus account for the range of incubation shifts.

In a well-ordered cycle, the incubating bird leaves the egg as soon as, but not before, its mate arrives to relieve it. The ensuing changeover generally takes place very quickly and in most nests, which were generally inspected two hours or less after sunset, it had already occurred.

Should a bird return to the nest before its incubating mate really requires relieving, say after one or two days, the brooding urge of the sitting bird will not have been overcome by hunger and the egg may therefore not be given up. Consequently, the returning bird may go to sea again (or, more rarely, will stay in the nest with its mate throughout the day) coming back to take over on another night. On other occasions, changeover may take place even after one day, but observations show that such short intervals are more frequent in the earlier than the later part of incubation. Richdale (1952) noted almost identical behaviour in the Royal Albatross, yet in his work on the Fairy Prion, *Pachyptila turtur*, (1944c) he had assumed that a changeover occurred whenever a parent returned to the nest.

TABLE X  
SHARE OF THE SEXES IN INCUBATION

<i>Number of Days for which Incubating Bird Sits before Relief</i>		<i>Number of Instances</i>		
		<i>Male</i>	<i>Female</i>	<i>Total</i>
1		3	9	12
2		10	13	23
3		13	13	26
4		19	18	37
5		3	2	5
		48	55	103

<i>Number of Shifts</i>	<i>Mean Duration of Shift (days)</i>	$\sigma$	<i>Standard Error</i>	<i>Range (days)</i>
103	3.0	1.12	0.11	1-5

Analysis of 103 individual incubation shifts, each terminated by a successful relief.

If the mate fails to return, the sitting bird will sometimes remain longer than the normal three to four days, waiting for relief. For example, in nest 70 the female returning to a deserted egg incubated for six days and nights without relief. She then spent two days at sea and returned for one day on the egg before finally going off for four days. This pair had the same difficulty the previous season when the male, having behaved in a normal way up to the time of laying, then suddenly departed leaving the female to incubate alone. The egg was thereafter incubated and deserted at intervals of four days, until finally the female ceased incubation and only visited the nest hole spasmodically at night. Such behaviour might be due to a mature and experienced adult having lost its mate and re-paired with an inexperienced bird. It shows a remarkable, inherent rhythm, that although periodically going to sea, each time the female came to the nest she stayed for the full four days despite the absence of her mate.

## 11. HATCHING

All known hatching in four seasons took place between 22 January and 13 February, the peak occurring about 30 to 31 January. (Table XI, Fig. 7.) The range is, therefore, just over three weeks and the records for individual seasons do not show any marked difference. Laws's dates, as mentioned earlier for eggs, lie outside these limits but are open to some doubt.

TABLE XI

## ANALYSIS OF HATCHING DATA COMPOUNDED FROM FOUR SEASONS

<i>Number</i>	<i>Year</i>	<i>Range</i>
5	1952-53	27 January- 3 February
21	1954-55	24 January- 9 February
9	1955-56	26 January-13 February
13	1956-57	22 January-23 February

<i>Total Number</i>	<i>Mean Date</i>	$\sigma$	<i>Standard Error</i>	<i>Range</i>
48	2 February	2.04	0.29	22 January-23 February

It is often possible to hear the young chick calling whilst still in the egg even before it shows signs of "starring" or "pipping"; in one nest, a chick was heard two days before hatching. Once pipping has started, the chick is generally out of the shell within 24 hours (Plate IIIa). The empty shell is often moved by the parent from the nest into the entrance or some other part of the hole, but whether this is intentional or accidental it is hard to say and it may be more usual for the shell to be trampled into the nest.

After the egg has hatched the parents sometimes dig, i.e. if the soil floor of the nest has thawed, and sometimes take in bits of debris from outside. Small amounts of the local lichen, *Usnea*, were taken into the bare rocky cleft of nest 69, five days after hatching (see p. 12).

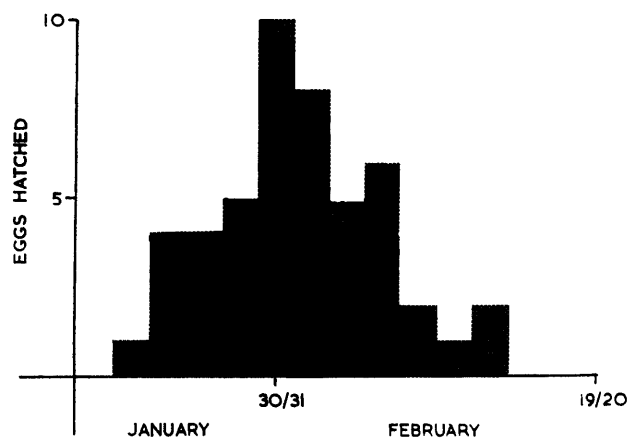


FIGURE 7

The distribution of 48 hatching dates from four seasons. Class intervals—two days.

## 12. THE CHICK

a. *The chick period*

From hatching to departure the chick spends between 43 and 54 days in the nest (Table XII).

It is brooded for a short while following hatching, the length of this period varying from three to five days (Table XIII). Both male and female brood the chick but the well-established, routine shifts of the previous six weeks tend to become disrupted.

In nest 68, the chick was left alone on its first day but this is atypical and may be wholly attributed to the poor incubation routine prevailing in this nest. The same had happened at this nest in the previous season, 1955-56; the male incubated longer than the female, routine reliefs were seldom in phase and the egg was consequently neglected from time to time. The 1956-57 egg hatched on 4 February, and the male was still brooding the chick on the following day but had deserted it by the 6 February. When the author visited the nest at 2000 hr. L.M.T., the chick was apparently dead so it was collected as a specimen. Back in the hut, whilst weighing and measuring it it began to revive, first gasping for breath then after a few minutes breathing normally and calling. Evidently the warmth of the bench lamp was responsible for this. The chick was returned to the nest where one parent was present but was again deserted and died two days later.

TABLE XII  
THE FLEDGING PERIOD

<i>Number</i>	<i>Mean Number of Days</i>	$\sigma$	<i>Standard Error</i>	<i>Range in Days</i>
22	50.5	2.85	0.61	42.5 - 54.0

Time spent in the nest by 22 chicks between hatching and departure.  
Records from four seasons.

This chick weighed only 15 g. which is below normal for newly hatched young. When found it was completely torpid with no visible signs of breathing, presumably as a result of chilling, but like the embryo in the egg, the chick at this time is probably able to survive a limited amount of chilling in a torpid condition.

During about 180 daytime inspections of six nests throughout the chick period, not one adult was seen. After the initial brooding period, both parents spend their days at sea and return only at night when the young are fed. At this time they spend more of the night together than in the incubation period when the parent generally returns only on changeover nights. During the first part of the chick period, it is more usual to see both parents together in the nest at night than one parent on its own. In the latter half of the period, however, they usually visit the nest singly. Over the whole of the nestling period, males appear to visit the nest slightly more often than females. Table XIV is an analysis of these observations in six nests throughout the nestling period, including the brooding of the chick; the latter is also shown separately (Table XIII). In the first half of the nestling period, at least one of the parents returned to the nest each night (there was only one exception out of a total of 153 nest inspections), whilst in the latter half of the nestling period there were 28 occasions when the chick was observed alone in the nest at night. It is possible that towards the end of the chick's time in the nest the author's very brief visits did not coincide with the visits of some parents, so that the results may indicate that the visits are much shorter rather than that they are less frequent. However, fine palisades of stocks or lichen set up at the nest entrances (see p. 12) definitely showed that parents come ashore to feed the chicks less frequently at this time.

The author observed the chick being fed on two occasions, but the torchlight disturbed the birds and caused them to stop, so no attempt was made to repeat these observations. The chick sits facing its two parents or parent, and attracts their attention by nibbling at their breast plumage or calling with a high-pitched "cheeping". Eventually one of the parents is seen to gobble in the throat in an effort to regurgitate; it opens its bill and the chick inserts its head right down into the throat, picks out a morsel, withdraws its head and swallows. Nothing was seen adhering to the outside of the chick's bill or down, and one gets the impression that the chick picks its food out and does not have a large amount forced down its throat. After one mouthful the chick remains quiet for a little while before the sequence is repeated. The above description, however, probably applies only to young chicks. The feeding process might later be modified to facilitate the passage of larger meals.

TABLE XIV

OBSERVATIONS OF PARENTAL ATTENDANCE DURING FLEDGING PERIOD

Nest Number	Number of Nights Adults Present						Number of Nights between Last Visit of Parents and Departure of Young				
	First Half of Period			Second Half of Period							
	Pair ♂ & ♀	Single ♂ ♀ ?		Nil	Pair ♂ & ♀	Single ♂ ♀ ?		Nil			
68A	17	5	4	0	0	4	10	6	0	6	2
68	18	5	2	0	0	15	2	4	0	4	1
52	18	4	2	0	1	14	2	2	3	4	3
69	14	8	4	0	0	5	8	3	2	8	5
49A	13	9	4	0	0	11	8	6	0	2	0
71	20	1	1	3	0	11	0	0	9	3	2

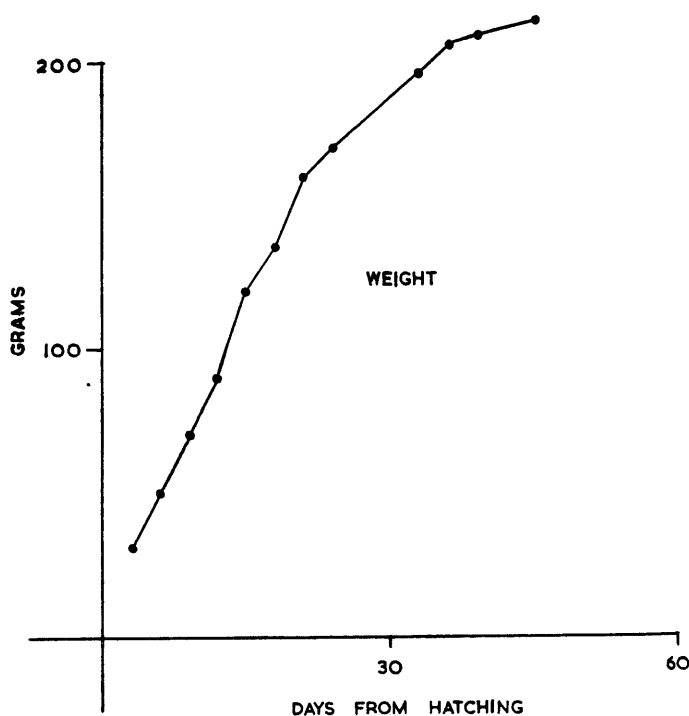


FIGURE 8  
Mean rate of growth. Class intervals—three days.

b. Growth of the chick

At hatching the chick weighs between 21 and 25 g.; on the second day it is usually about 35 g. but may be as much as 40 g., and on the following two days its weight may go up to 55 or 60 g. (Fig. 8). When first hatched, the eyes are closed and the head is supported by the bill on the ground but the chick can call strongly (Plate IIIa, b). There is a dense covering of smoky blue-grey down (protoptyle) which is lighter in colour on the belly. The egg tooth is still present on the sixth day by which time the brooding has

ceased. The protoptyle is 20–25 mm. long on the eighth day and mesoptyle is just beginning to appear below. Remnants of the egg tooth are generally gone by the tenth day, and on the twelfth the mesoptyle has reached a length of some 3–5 mm. with the protoptyle still attached; the mesoptyle may be slightly lighter in colour than the protoptyle. The legs become a brighter blue whilst the bill darkens. As yet there is no development of rectrices or primaries, but the chick at this time has a lot of scale scattered about it from the secondary down shafts. The sheaths of the primaries are 3–5 mm. long and tipped by tufts of down.

By the sixteenth day the primaries have begun to sprout, the webs of the exposed feathers being from 2–7 mm. long and fringed with down (Plate IIIc). The sheaths of these primaries are 15 mm. long and the mesoptyle of the same length. Up to the twentieth day there is an apparent increase in the length of the sheaths of the primary quills but no further sprouting of the feathers themselves. The sheaths of the rectrices are as long as 9 mm. and not sprouting although there are tufts of down. The sheaths of the primary quills are 20 mm. long and the sheaths of the back feathers about 2 mm. long. At twenty-two days, the rectrices are just beginning to sprout from their sheaths; the exposed primaries are black and blue-grey and still fringed with down (Plate IIIId). At this time the pink fleshy webs of the feet have darkened slightly; the edge of the lower mandible is smooth and rounded although the lamellae in the maxilla are only slightly developed and the space in the gape is not yet visible. A thick mat of whitish down covers the belly.

By the twenty-fourth day, about 10 mm. of feather webs are exposed from the sheaths of the primary quills. The coverts are just beginning to sprout and the exposed webs of the back feathers are 30 mm. long in places, though still hidden by secondary down. On the twenty-eighth day there is still a lot of down; the mantle and back feathers are 43 mm. long and still fringed with down, whilst sheaths of the white breast feathers are beginning to appear. The head is still covered with mesoptyle. By the thirtieth day (Plate IVa), the primaries have reached 60 mm. and are losing their fringes, as are the rectrices. Feathering of the throat, neck and sides of the face is beginning, and the weight at this time may be as much as 200 g. The primaries reach 75 mm. by the thirty-second day and are visible, though the rectrices, 35 mm. long, are still obscured by down. At thirty-four days, further development of the white face and blue-grey crown feathers is apparent. The tips of the rectrices as well as of the primaries are now visible.

On the fortieth day (Plate IVb) the face is free of down and the white eye streak is prominent. The white throat feathers are free of down as are the primaries and rectrices although the secondaries and coverts are still fringed. Mesoptyle is gradually being lost from the nape but is still present on the mantle and back (Plate IVc).

Wings and tail reach their full length by the forty-fifth day and together with the head are free of down. Much down still persists about the body but it is disappearing rapidly. Young birds at this time are still generally heavier than their flight weight. By the fiftieth day, only traces of down persist and the birds are losing weight and departing (Plates IVd, Va).

This is a generalized description and variations are to be expected. In particular, partially starved birds may be late in developing. Growth curves for bill, wing and tail are given in Figs. 9 and 10.

### c. Final days in the nest

During the 1957–58 season, members of the F.I.D.S. base on Signy Island\* carried out routine chick weighings in the latter half of the chick period and five chicks were weighed morning and evening up to the time of departure (see Fig. 11). All these young missed some meals during their final days in the nest, but four were fed either on the night of departure or on the preceding night, whilst the fifth (G) was not fed for the last two nights. All the chicks lost weight during this time, and their final weights before departure were 175, 224, 168, 150 and 186 g., in contrast to their heaviest of 211, 247, 231, 209 and 244 g. respectively. These results are comparable to those obtained by Richdale (1944a, c) for the other two *Pachyptila* species and it therefore seems likely that the feeding routines are very similar.

At six of the nests studied one chick was visited by an adult on the night it departed, whilst at other nests the young were alone for one, two, three and five nights prior to their departure. In the Fairy Prion, *P. turtur*, Richdale (1944c) has shown that “. . . while 15·6 per cent of the chicks are fed on the last night, the majority, or 81·2 per cent, miss from one to four meals before they depart.” He goes on to say that “. . . it would appear that normally there is a short starvation period before the chicks leave but in the main

\* B. Beck, P. A. Richards, C. D. Scotland, the late A. Sharman, D. Skilling and J. W. Stammers.

the drop in weight occurs gradually whilst the chick is still being fed." He found similar behaviour in the Broad-billed Prion, *P. vittata* (1944a), the proportions being 23 per cent of chicks fed on the last night and 77 per cent missing from one to five meals before departing.

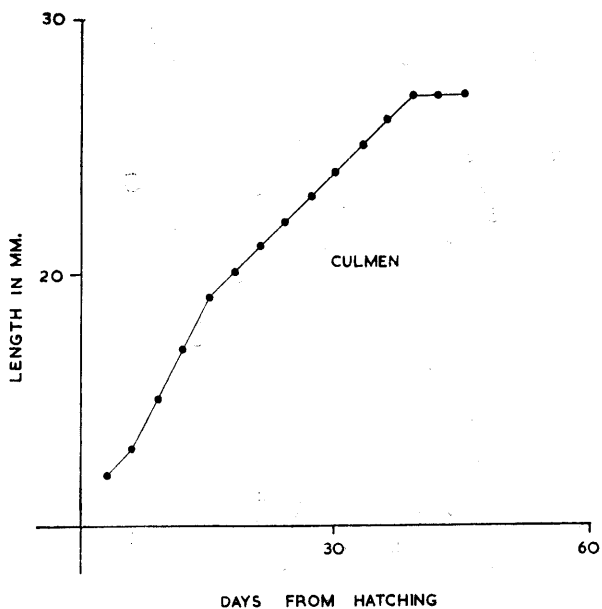


FIGURE 9a

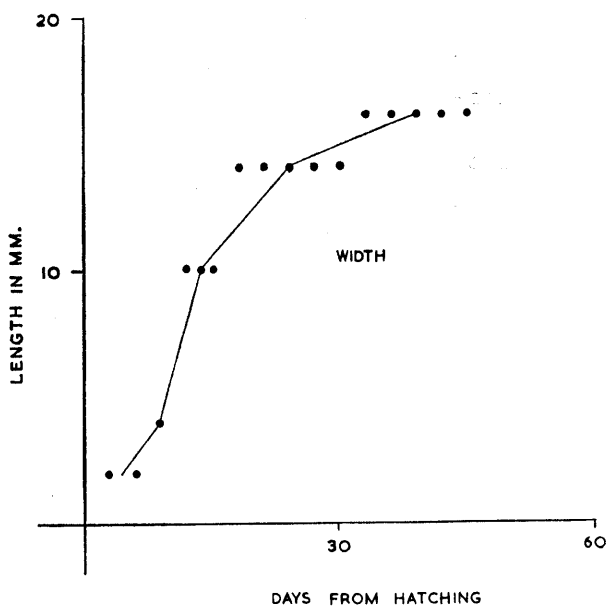


FIGURE 9b

Mean rate of growth of bill. Class intervals—three days.

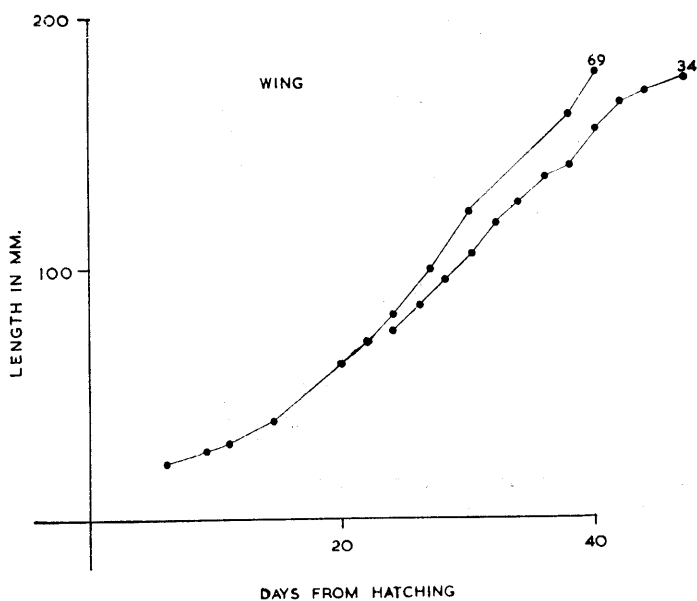


FIGURE 10a

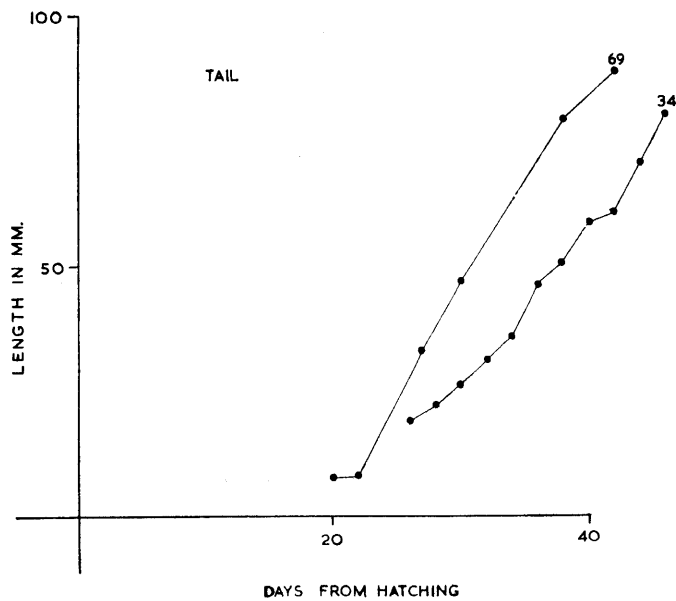


FIGURE 10b

Rate of growth of wing and tail.

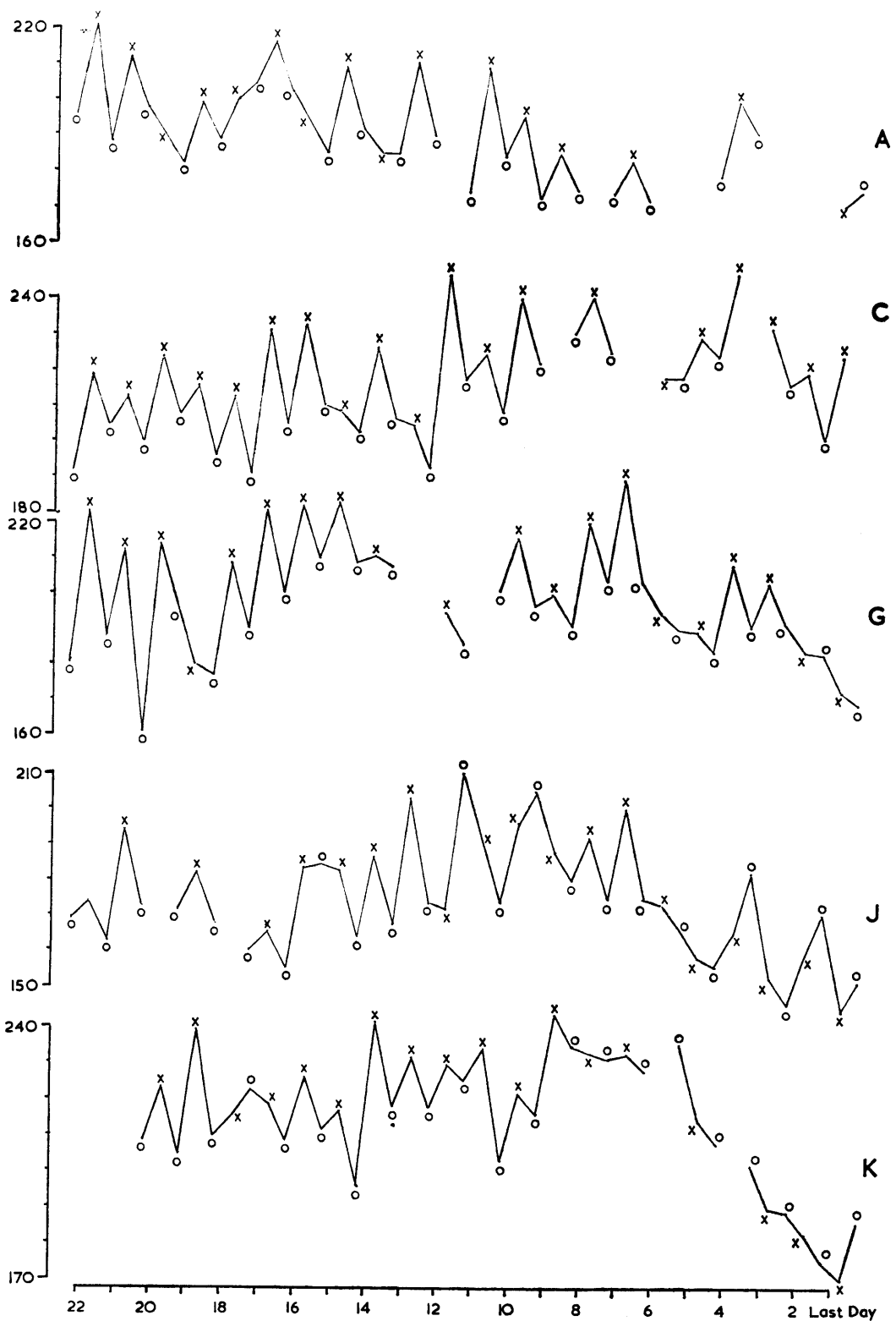


FIGURE 11

Weights of five prion chicks during their last days in the nest, measured at 7 a.m. (x) and 7 p.m. (o). The variations indicate the frequency of feeding; this normally occurred at night but in some instances, when the parents returned early, the chick was fed prior to the evening weighing.



## 13. THE DEPARTURE

This phase was not studied in detail. The earliest date on which a chick was observed leaving the nest was 12 March (Table XV), and the latest on which one was found alive in a nest hole was 7 April but there is an indication in Mansfield's notes (unpublished) of young being snowed up in their nests at an even later date. Probably most of the fledged young leave their holes on the nights between 20 and 30 March.

TABLE XV

## DEPARTURE OF THE YOUNG

Analysis of Records from Four Seasons

<i>Number</i>	<i>Mean Date</i>	$\sigma$	<i>Standard Error</i>	<i>Range Dates</i>
54	25 March	6.19	0.84	12 March-7 April

Chicks in holes after this date are more likely to be exposed to the hazards of the climate, for during April temperatures begin to fall and drifting snow increases with the frequency of gale-force winds. Moreover, since the adults tend to visit and feed the chicks less frequently in the final stages, the dangers of becoming snowed up and of starving are substantially increased. The proportion which fails to survive under such circumstances is unknown but the number of survivals will certainly depend upon how early the winter sets in.

The adults probably begin to depart in the middle of March, at the same time as the young, and the last birds are gone by mid-April. On 17 April 1952, Mansfield (unpublished) observed three birds in flight but found only one adult in a nest hole; all the other nests were blocked by hard-packed drift. Six nests showed tracks and signs of fresh digging which must have occurred after the last heavy snowfall, i.e. during the preceding five nights. A single bird was seen on 21 April, and thereafter none. Laws's (unpublished) last record for 1948 was 6 April, and in the following season 17 April. In 1956, a few prions were seen about the colony on 19 April. There are no later records, and the birds are away from the islands for the following six months (Table XVI).

Occasionally, one finds fledglings that have moved out of the nest into the mouth of the hole or an adjoining cavern, perhaps to exercise their wings prior to flight and it is probable that few return once they have left the confines of the nest. The young Dove Prions are able to fly immediately they emerge from the hole, and this has been demonstrated on numerous occasions by extracting them from their nest and releasing them. There is no indication that young birds are involved in an overland scramble to the sea such as that described by Lockley (1942) for the Manx Shearwater, *Puffinus puffinus*. On the contrary, during the morning of 21 March, to give only one instance, we tried to photograph a fully-fledged chick which had been extracted from nest 52. It scurried around a little, and before we had a chance to obtain a picture it took to the wing and flew away over the sea—quite easily although the flight was not as erratic or twisting as that of an adult. This perhaps explains why it was unable to escape a pursuing Brown Skua *Catharacta skua lönnbergi* (see p. 41).

For their departure, the young prefer dark nights with moderate winds of about 15 knots.; they do not usually leave on brighter moonlit nights, nor during gales or calms. On nights that were particularly windy young birds sometimes appeared to be reluctant to take off, merely rising into the air a few feet and descending a little way off. It may be that on such unfavourable nights young birds that have left the nest try to find shelter, if not in their own hole then in any other that is available (see p. 19). Adults also appear reluctant to fly in such conditions.

TABLE XVI

## SUMMARY OF THE BREEDING CYCLE AT ALL KNOWN LOCALITIES

	<i>Arrivals</i>		<i>Eggs</i>	<i>Hatching</i>	<i>Young Leave</i>	<i>Last Adults Seen</i>
	<i>First</i>	<i>Peak</i>				
Auckland Islands	?	?	?	?	?	?
Macquarie Island	?	?	13-14 December. Fresh eggs plentiful	?	?	?
Îles de Kerguelen	?	?	Early December	Late January	?	?
Heard Island	21 October	15 November	31 December	12 February	End of March	7 May
South Georgia	?	?	14 November-end of December	28 February	Early May	?
South Orkney Islands	15 October	10 November	5-26 December	22 January-14 February	12 March-7 April	15 April
Cape Denison, Antarctica	?	?	11 and 16 December	?	?	?

## 14. BEHAVIOUR OF UNSUCCESSFUL BREEDERS

Breeding failure may be due to chilling or loss of the eggs or to the death of young after hatching. The subsequent behaviour of the adults varies with the stage at which the failure occurs, but it often resembles that of successful breeders.

In nest 29, where a chick was lost at an early stage, the adults visited the nest together each night for the first three weeks just as if the young had been present; the female's visits then fell off, but those of the male continued normally. It was noticeable that visiting Dove Prions were then tolerated in the nest. Male and female appeared to keep company with strange birds, both in their own territory and in other nests nearby, and sometimes showed a marked preference for particular nests. In addition to unmarked birds which may not have bred before, the visitors also included marked breeding birds from adjacent nests.

Interruption of breeding during the egg period has more complex effect on behaviour. Where chilling is the cause of failure to hatch, the incubation period may not be appreciably altered and the parent birds may continue routine incubation shifts until some time after the egg would have hatched. Addled eggs substituted for live ones have been incubated for as much as 55 days compared with the mean incubation period of 44.8 days. In nest 34 where similar substitution occurred, the egg was incubated for 45 days after which the parents appeared at night for a further 8 days; neither was seen during the following 53 days until the male suddenly re-appeared in the nest on 19 March, which was about the normal time of departure. Thus, although the pair apparently left the colony after the failure of the egg to hatch, one of them returned at least once at the end of the season prior to departure.

Incubation may also fail because of neglect or desertion by one of the parents. In such cases, it has been observed that the other parent (e.g. the female from nest 70; see p. 25) maintains its routine shifts of three to five days, and sometimes longer, alternated by periods of desertion. This may continue until the time of hatching has expired, but the single incubating bird may desert earlier. Incubation shifts may also be maintained when eggs have been lost. If desertion occurs early during incubation there is a possibility that a new pair may take over territory in an abandoned hole.

As mentioned earlier (p. 22), desertion exposes eggs to constant danger from drifting snow. In nest 32, where this happened the day after laying, the parents visited the nest only intermittently for the next three weeks and they were twice discovered mounted and apparently trying to copulate. No interest was taken in the egg which had thawed out of the snow. Birds which lose their egg at such an early stage tend to visit the nest intermittently at night for the following six weeks, but the visits become less frequent towards the end of the period.

It is notable that visits by strange birds become more numerous at the time when failed breeders are beginning to lose interest in their territories, and it is evident that this visiting is not solely the prerogative of young non-breeding birds but also includes mature adults (as in the case of nest 29; p. 34). It is not yet known whether the "visiting urge" is greater in the failed breeders at this time or whether they are merely ceasing to defend their own territories, but it is obvious that some breeding adults are attracted to certain adjacent nests when affairs in their own become disrupted. Such birds may have had some previous connection with these favoured nests. Pairs have been observed to return season after season to the same hole to mate, but visiting and "keeping company" (Richdale, 1945; Sladen, 1958) may be the means by which nest sites change from one pair to another and also by which a mature bird will re-pair following the death of its mate.

Visits are also numerous at the beginning of the season and are possibly closely connected with those occurring at the end of the previous season. Some birds might pair up initially at the end of a season, either in fresh burrows or in holes vacated by failed breeders. Whether or not these pairs are able to establish themselves and breed in the following season will depend upon whether they return to the nest sufficiently early to compete with the original owners of the nest. In such instances, the original pairs may have the advantage in that they are experienced breeders and therefore return at the very beginning of the season. However, other birds which have reached sexual maturity and have gained several seasons' experience in homing to the breeding station, will eventually return early enough to compete seriously for the nest sites.

That some nests have few or no visitors at all is probably due to the fact that they occupy unsuitable sites. Nests 34 and 69, in particular, both contained successful pairs but were in very exposed positions most uncharacteristic of prion nests, and perhaps for that reason were little investigated by other birds.

## 15. SEASONAL CHANGES IN THE GONADS

### a. *The testes*

Data on eight testes examined are given in Table XVII. It will be seen that when the males first arrive at the beginning of the breeding season the testes are in an advanced state of development (Plate IVa, b). They have probably reached their maximum size of 8.0–10.0 cm.<sup>3</sup> each, although spermatogenesis is not quite at its height and free spermatozoa do not appear until mid-November. As mentioned on page 17 birds are attempting to copulate early in November, but it is probable that successful coition does not occur until the latter part of the month or even early December—just before the female leaves on her pre-laying flight. After this the testes regress rapidly. The seminiferous tubules shrink, their membranous walls increasing in thickness and the epithelial lining being reduced to resting spermatogonia and spermatocytes; a few of the latter show some activity. A new interstitial tissue arises, many cells containing minute lipoid droplets; these however were present in lesser numbers at the height of spermatogenesis.

By 31 December, when most birds are incubating, a testis usually has a volume of less than 1.0 cm.<sup>3</sup> The *tunica albuginea* is greatly thickened, probably by the development of a new layer (Marshall and Serventy, 1956). At this time birds which have lost eggs have been seen attempting to copulate, and although examination has revealed traces of free spermatozoa in the seminiferous tubules these were in a state of retrogression and quite inactive (Plate IVc, d).

Towards the end of March before the birds leave the colony, final contraction of the tubules occurs eliminating the lumen. The epithelial lining consists of spermatogonia with few inactive spermatocytes; at this stage the volume of the individual testis is usually less than 0.5 cm.<sup>3</sup>

## SEASONAL CH

Serial Number	Date	Remarks	Volume of Right Testis (cm. <sup>3</sup> )	Thi of 1
H.1061	1 November	Killed in flight by wireless aerials. Age unknown.	8.0	2
H.1064	9 November	Taken in open at night. Age unknown.	7.0	2
H.1203	13 November	Found in open at night. Calling.	9.5	2
H.1211	29 November	Found in a hole at night, copulating with H.1212.	4.5	2
H.1227	18 December	Found alone in hole. An adult at least five years old and probably breeding.	1.0	10
H.1234	20 December	Found in hole, copulating with H.1233 after the egg had been laid. Colour of testes, blue-grey.	0.5	6
H.1259	25 March	Mature adult breeding.	0.5	4
H.1262	27 March	Breeding adult. Moulting of body feathers beginning. Brood patch covered with down.	0.5	1

b. *The ovary*

Evidence from marked birds shows that mature breeding adults are the first to return to the breeding colonies. The ovaries of females arriving in mid-October show very little development, the total volume being as little as 1.0 ml. with the largest follicle only 1.5 mm. in diameter. These are very much the same as those of females taken at the end of the breeding season prior to departure. Specimens taken during November and December up to the time of the pre-laying "honeymoon" flight, show a gradual increase in the volume of the ovary up to 2.5 cm.<sup>3</sup> The largest follicle, which measured 5.5 mm. in diameter, was collected from a female found in copulation on 20 December; the second largest follicle in this ovary was 2.5 mm. Some weeks earlier in development one ovary contained several follicles up to 3.0 mm. in diameter, and on 20 November one female had follicles measuring 4.5 and 4.0 mm.

For the Starling, *Sternus vulgaris*, Bissonette and Zujko (1936) show that from 7 December to 25 March the average growth of the largest follicle is 0.009 mm. per day, and by the end of this time it reaches a

I  
THE TESTES

<i>State of Interstitium</i>	<i>Seminiferous Tubules</i>
Interstitial spaces up to 40 $\mu$ but very few cells.	120–240 $\mu$ diameter with tubule membrane less than 2 $\mu$ . No apparent lumen. Many active spermatocytes and spermatids in all stages of development but earlier stages more numerous. No free spermatozoa.
Interstitial spaces greatly reduced with few cells.	180–240 $\mu$ tubules with all stages. Spermatocytes freely undergoing division. All types of spermatids but no free spermatozoa. Spermatids often bunched but not as dense as in H.1203 and arranged around the periphery of the lumen.
Interstitial spaces greatly reduced with few cells.	140–200 $\mu$ very thin membrane. All stages of spermatocytes and spermatids together with free spermatozoa; these with advanced spermatids. The centres of the tubules reveal no distinct lumen but are packed with advanced spermatids and spermatozoa.
Interstitial spaces almost completely absent.	150–250 $\mu$ Spermatocytes dividing and many advanced spermatids with bunched spermatozoa but no apparent lumen to tubules, this being occupied by anucleate tissue (artifacts?).
Interstitial spaces highly developed and packed with cells. Spaces up to 60 $\mu$ between tubules.	Considerable retrogression with tubules 70–80 $\mu$ diameter and membranes up to 8 $\mu$ thick. Conspicuous lumen containing cell debris and some whole cells with nuclei containing chromatin material. No spermatozoa. Few spermatocytes, some active.
Interstitial spaces highly developed and packed with cells. Spaces up to 60 $\mu$ between tubules.	Tubules shrunken, 60–120 $\mu$ diameter with distinct membrane 2–4 $\mu$ thick. Marked tubule lumen frequently with loose cells within. Very occasionally a few free spermatozoa. No activity amongst spermatocytes or spermatogonia.
Interstitial spaces greatly enlarged but packed with cells. Spaces up to 40 $\mu$ between tubules.	About 60 $\mu$ diameter; tubules completely retrogressed with membranes about 4 $\mu$ thick and a strong well-defined lumen. No activity of spermatogonia or spermatocytes.
Interstitial spaces greatly enlarged but packed with cells. Spaces up to 40 $\mu$ between tubules.	Tubules 40–60 $\mu$ diameter; almost completely collapsed, with very narrow lumen.

diameter of 1.65 mm. During the final growth period the average growth of the largest follicle is 0.285 mm. per day, i.e. 31.6 times greater than that of the preceding period. Similarly accelerated growth occurs in the domestic fowl after the oöcyte has reached a diameter of 6.0 mm., the yolk increasing from 6.00 mm. to 35 mm. in a period of six days (Romanoff and Romanoff, 1949). It has also been demonstrated that formation and deposition of the principal components of the yolk, the phospho-lipids and the protein ovovitellin, are accelerated. From this evidence it is reasonable to suppose that a similar mechanism might apply to the Dove Prion and, indeed, to all petrels. The departure of the females on their "honeymoon" flight may be closely correlated with this accelerated growth of the oöcyte.

A female spending the whole of this period feeding at sea is able to utilize much of its food resources for egg production; these would otherwise be largely dissipated as the energy required for flying to and from the breeding grounds. Alternatively, it may be that the total energy level is not important, as long as it is possible to utilize a greater proportion of protein or other specific substances in the diet.

## 16. BODY TEMPERATURE

A limited investigation into the body temperature of both adults and chicks was carried out during the first two seasons.

a. *Adults*

Ninety-three temperatures were taken between the time of arrival in the middle of October and just before egg-laying in December. This period was chosen to avoid any distortion which might be caused by incubation-starvation, which was observed by Folk (1949, 1951) to cause depression of body temperatures in Leach's Petrel, *Oceanodroma leucorhoa*. The Dove Prions were collected in boxes and taken indoors where measurements of temperature were accompanied by weighing and ringing.

This method is open to some criticism as the body temperature may have altered in the interval between extracting the excited bird from its nest hole and reading its temperature—perhaps as much as an hour later (Farner and Serventy, 1956). The temperature investigation was, however, incidental to other work on the captured birds but, even so, the results show interesting variations which are comparable with other investigations employing slightly more refined techniques.

Most of the birds chosen were mature breeding adults from marked nests. The instrument used was a thermometer of the type used in the standard Air Ministry pattern portable whirling psychrometer. This has a very fine mercurial bulb which was easily inserted into the cloaca and covered the range required. Once inserted the thermometer was kept in position for about one minute until the maximum reading was obtained.

Farner (1956) working on the Fairy Prion, *P. turtur*, demonstrated a difference in body temperature according to three classes of activity. He showed that there was no statistical basis for assuming that the temperature of birds held in the hand are either depressed or elevated.

For *P. desolata*, the present author has separated those temperatures taken at night when the colony was active, from those taken in the daytime when the birds occupying the nests were apparently resting (see Table XVIII and Fig. 12). This is not such a fine separation as that of Farner (1956) as no birds were caught on the wing, and those which were taken from the holes might either have just flown in or have been there all day. This complication, however, does not affect the daytime records because the earliest temperatures were measured on birds which had been in the nest ten hours. The standard deviations are relatively high, and the difference between the means are not great although they are statistically significant. From the data it is evident that the mean body temperature of *P. desolata* (41.8°C) is slightly higher than that of *P. turtur* (39.9°C); the temperatures quoted are for active birds taken on the ground at night. Fairy Prions, taken on the wing give a slightly higher mean and smaller range.

TABLE XVIII

BODY TEMPERATURES OF *PACHYPTILA DESOLATA* AND *P. TURTUR*

Temperature in °C

	Notes	Number	Mean	$\sigma$	Standard Error	Range
<i>P. desolata</i>	1. Chick 34: 10th–47th day	37	39.9	0.13	0.02	38.9 – 40.6
	2. Chicks at random	18	39.7	0.05	0.01	38.6 – 40.5
	3. Active adults in holes at night	47	41.8	0.26	0.04	40.4 – 43.8
	4. Resting adults in holes during daytime	46	40.3	0.29	0.04	38.8 – 42.5
<i>P. turtur</i> (Farner, 1956)	5. Taken within one minute of capture during flight	72	41.5	0.21	0.25	40.6 – 42.7
	6. Active adults in burrows and on ground at night	28	39.9	0.54	0.10	38.2 – 41.2
	7. Incubating adults from burrows in daytime	43	38.6	0.46	0.07	37.1 – 39.9

The difference between (3) and (4) is  $1.5000 \pm 0.0002$  and is therefore significant.

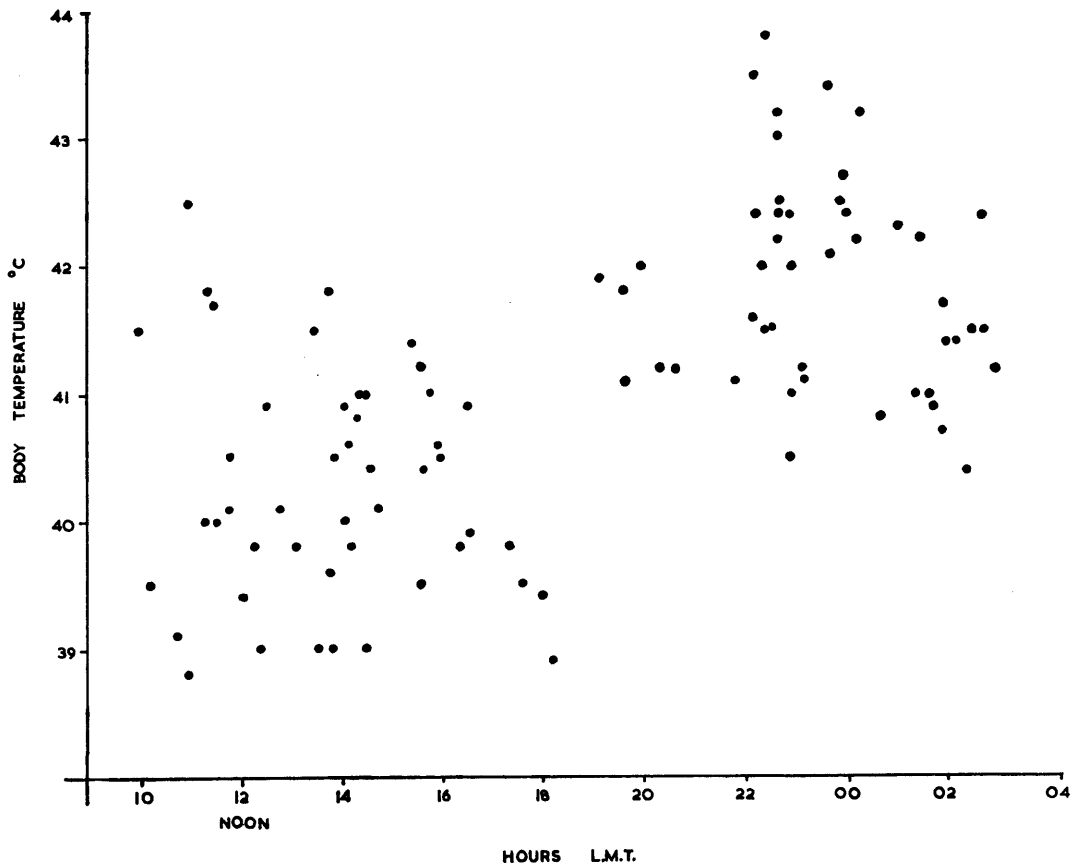


FIGURE 12

Diurnal fluctuations in body (cloacal) temperature of adults.

b. Chicks

During 1954-55, a series of chick temperatures was taken but, because of the danger of desertion in the early chick stage, this was not started until after brooding had ceased. There is, therefore, no direct evidence on the initial chick period, but Roberts (1940) has shown that the temperature of first day chicks may be as much as ten degrees centigrade below the adult mean, and Farner and Serventy (1956) have examined the body temperature of young chicks more precisely. Dove Prion chicks are brooded for an average of four days (see p. 28), and it may be assumed that the mechanism which regulates temperature comes into play fully at the third to fourth day.

The technique used was different from that for adults: a self-registering clinical thermometer was inserted in the axilla but this needed up to four minutes to obtain a maximum reading. A single chick from nest 34 was examined each night between 1915 and 2030 hr. L.M.T., and the temperature taken five to ten minutes

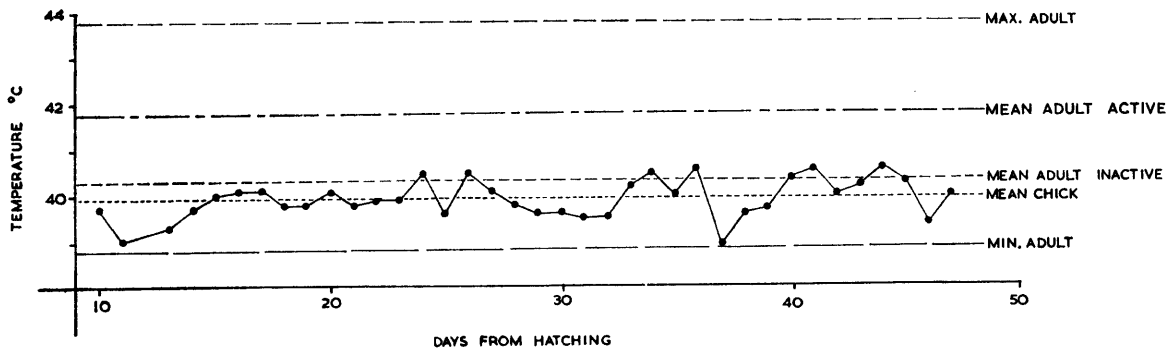


FIGURE 13

Body (axilla) temperature of chick 34 measured daily throughout the fledging period.

after extraction from the nest (see Fig. 13). Between 10 and 47 days after hatching, daily readings were taken as well as eighteen random ones from other chicks (Table XVIII).

Over the age of 37 days, the mean temperature of the chick was very similar to that of other chicks, and differed slightly but noticeably from that of the inactive adult. It appears therefore, that even after the young bird has developed its own temperature-regulating mechanism, its average temperature does not reach that of the adult until after it has left the nest.

There is no evidence that the body temperatures of chicks older than 3–4 days are affected by changes in air temperature.

## 17. PREDATORS

### a. *The Brown Skua (Catharacta skua lönnerbergi)*

At the breeding grounds this is the only natural predator of most prion species. It has been observed at all the known breeding stations of the Dove Prion, except Cape Denison on the mainland of Antarctica where it is replaced by McCormick's Skua, *Catharacta skua maccormicki*.

At Signy Island, Dove Prions nest in scattered colonies over an area of about two square miles which is free of permanent ice (p. 5). There were about 80 breeding pairs of skuas, the nests and territories of which were always strewn with picked remains of Dove Prions. Pairs of wings joined by the pectoral girdle were found, sometimes with the sternum still attached, and scattered, plucked feathers indicating a kill, were frequently found in the colonies. Dove Prions were not their sole prey; the skuas also hunted in the rookeries of the three pygoscelid penguins and the Giant Petrels, *Macronectes giganteus*, in addition to scavenging about the seal pile and dog spans at the F.I.D.S. base hut.

At Bird Island, South Georgia, the Dove Prions were present in enormous numbers and probably were the main reason for the remarkable density of skuas. The Dove Prions and Diving Petrels burrowed in the tussock grass which covered about one and a half square miles, i.e. the greater part of the island. In this small area there were about two hundred skua nests, all of which were littered with numerous remains of Dove Prions and Diving Petrels. It was possible to count the remains of 60 or 70 corpses, and one pair of breeding skuas might easily account for over 50 Dove Prions in a season together with perhaps half as many Diving Petrels. Predation by the breeding population of skuas would therefore account for an annual mortality of about 10,000 Dove Prions on the Island. Other species and their eggs are also taken by the skuas on Bird Island, but the Dove Prions are by far the most important prey.

Observers at other breeding stations all note that *P. desolata* is included in the skua's diet, although its importance in comparison with other prey appears to depend upon the position of the skua nests and the relative abundance of the prions and other species of prey.

At Heard Island, Falla (1937) found skuas' nests amongst prion colonies, but there the supply of food was so plentiful that the skuas were merely disembowelling their victims (mostly *P. desolata*) and leaving the rest of the carcasses untouched. This habit was observed in South Georgia. At Heard Island they were feeding almost entirely on prions, and some pairs were confining their attention to *P. crassirostris*, although there were nests of the Rockhopper Penguin, *Eudyptes crestatus*, within a few feet.

At Macquarie Island, the clean-picked bones of *P. desolata* have been found amongst those of the other petrel species scattered around the skua nests. However, the prions are not common enough in the area visited to form the chief food supply and the skuas were also carrying eggs of the Rockhopper Penguin some distance.

At the Îles de Kerguelen, prions are taken by the skuas but introduced rabbits are apparently more important as food.

Recent workers have all remarked that prions are immune to attack when in flight, but earlier observers give the reverse impression. Lönnerberg (1906), quoting Sorling, mentions that the skuas hunt the prions as soon as they appear in the fjords at South Georgia. Matthews (1929) also mentions them being pursued and devoured in the air. It appears, however, that prions flying in over the coast just before dusk are only rarely attacked by skuas. Sometimes at Signy Island on days of gales, hundreds of prions would come in before dark, often flying in close proximity to skuas which made no attempt to pursue them. Paulian (1953) and Downes *et al.* (1959) have noticed similar behaviour at the Îles de Kerguelen and Heard Island. At the latter, moreover, flocks of prions feeding on the sea just offshore are unmolested even on calm days.



Nevertheless, it is true that when a burrow or nesting hole is disturbed during the day (for example, when it is being dug out by man) skuas will give chase to escaping prions, but although they follow the twisting and turning prion skilfully, it is not often that a kill is made. I have only seen one bird killed by a pursuing skua, and that was a young bird flying for the first time (p. 33). Murphy (1936) at South Georgia watched three prions which he had dug out of their burrows out-manoeuvre skuas in flight, and he inferred that the skuas rarely capture their victims in full flight.

At Heard Island during times of re-occupation prions expose themselves over the breeding grounds by day and rarely attract the skuas' attention, but Downes *et al.* (1959) have seen skuas catch free-flying prions on the wing by day, on two or three occasions. They mention that "Skuas will also attempt to dig prions out of their burrows, but their success must depend on finding a burrow which is very short or otherwise inadequate." Such opportunities rarely occur in the South Orkney Islands, but prions will occasionally burrow in the few available moss banks and a skua was once seen opening such a burrow. At another time at the Signy Island colony, a skua was found eviscerating a chick which had been dragged from a shallow nesting hole. Waite (1909) at the Auckland Islands considers the probability of skuas actually entering the burrows to drag petrels out.

Like other small petrels the Dove Prions are most vulnerable when on the ground, and the skuas wait about the colony at night standing silently and still until the prions come within striking distance. Undoubtedly most prions are caught when entering or leaving their burrows and nesting holes, i.e. at dusk and dawn, but it is probable that the skuas hunt all night. A favourite place of attack is the entrance of burrows and holes where the large numbers of prions present would be loudly drawing attention to themselves. Downes *et al.* (1959) mentions the possibility that many of the prions which fall victim to the skuas may be breeding for the first time, and that they are caught without adequate shelter while attempting to find or excavate new burrows.

#### b. *Other species*

According to Falla (1937) the Weka or Stewart Island Woodhen, *Gallirallus australis scotti*, which was introduced to Macquarie Island, has been a factor in reducing the numbers of burrowing petrels including the prions.

At South Georgia, introduced rats have been resident for more than a century. In areas accessible to these rodents, prion and other burrowing petrel colonies have suffered heavily from their predations.

## 18. PARASITES

All birds examined carried mallophaga, some being infested more than others. Amongst the collections made, only females have been recognised and these do not allow specific identification. The commonest type was *Austromenopon* species, but lesser numbers of *Longimenopon* species were also found. These were identified by Dr. Theresa Clay of the British Museum who states that *Austromenopon* is widely distributed in both the Procellariiformes and Charadriiformes (Clay and Timmermann, 1957). *Longimenopon* is known from comparatively few petrels but is recorded from *P. desolata* at the Auckland Islands. The only other species known from the *Pachyptila* is *Neubates prioni* (Enderlein, 1909), which was found on *P. desolata* at Kerguelen and is also known from *P. forsteri*.

No other ectoparasites were found on prions in the South Orkney Islands but fleas and ticks are important at breeding stations in lower latitudes.

The two fleas, *Parapsyllus magellanicus heardi* (de Meillon) and *Notiopsylla kerguelensis* (Tasch.), are both found in the burrows of *P. desolata* as well as of other petrels, albatrosses, gulls and skuas. The former is confined to Heard and Macquarie Islands whilst the latter has a more extended distribution, being found at South Georgia, Kerguelen, the Antipodes and Heard Island.

Ticks are known from *Pachyptila* only at Heard Island where *Geratixodes uriae* (White), *Ixodes kerguelensis* (André and Colas-Belcour) and *Ixodes auritulus* (Neumann) are all found on *P. desolata* and other species of petrels, albatrosses, penguins and gulls (de Meillon, 1952; Zumpt, 1952).

## 19. FOOD AND FEEDING

Most adult stomach contents examined consisted merely of green slime, but one or two contained euphausians and amphipods together with some crystalline lenses. I have also known a prion in the hand to vomit up a whole cephalopod. Bierman and Voous (1950) found euphausians and cephalopod beaks in a specimen taken at sea in lat. 65°50'S., long. 11°11'W.

More information is available from Heard Island although birds taken from nests there also appeared to contain nothing but green slime. Ealey (1954*a, b*) found that amphipods, especially *Euthemisto antarctica*, were an important factor in the diet of most pelagic birds and that, in contrast to their importance in higher latitudes, the Euphausia were relatively unimportant. It is interesting to note that at Heard Island two species of amphipod, *Hyperiella antarctica* and *Hyperia spinigeria*, and the pteropod *Clio sulcata* are included in the diet of both prion species. The importance of the amphipods in lower latitudes is also shown by the report of Paulian (1953) who found one bird with a stomach full of *Euthemisto*. Falla (1937) also mentions pteropod and cephalopod remains in both adults and chicks. As pointed out earlier (p. 10), Dove Prions at Heard Island are unusual in that they feed inshore, both on the surface and diving with wings half-spread, and have been seen bringing up long, white or pale pink, worm-like creatures to the surface. Rankin (1951) and Matthews (1951) at South Georgia both observed Dove Prions feeding, their descriptions agreeing closely with Murphy's (1936): "The birds worked along with an odd creeping motion resting their bodies lightly upon the surface but holding their wings just above it, the feet apparently furnishing all motive power. Then, as they scurried forward quite rapidly, their heads would be thrust under water and the laminated bills would scoop for food . . . Frequently, however, each one would dive out of sight, to emerge quickly a metre or so ahead. They stayed below the surface not more than a fraction of a second except, perhaps, when they shot through the crest of a wave, but in a definite field on the water the birds disappeared and reappeared with such rapidity that the area fairly twinkled. About as many were below as above most of the time . . . There was a very rugged sea running at the time with wide troughs between the waves, and whenever a great roller with a white and broken crest hurtled along, the birds would not attempt to dive through it but lift themselves daintily from the water at the last moment, fly through the spume of the comber, and settle immediately on the downward slope beyond."

## 20. FLIGHT

The flight is characteristic of the species and, apart from that of *Halobaena* and related species of *Pachyptila* is unlike that of any other petrels. It is extremely fast and apparently erratic, especially in high winds when the birds appear to be tossed about relentlessly in a manner which exaggerates their normally erratic path. Closer inspection, however, reveals a high degree of manoeuvrability.

The most typical feature of their flight is the manner in which they are continually twisting from side to side alternately revealing the white underparts and the blue-grey upper. Nichols (1946), in his analysis of sea bird flight, gives the *Pachyptila* the highest score for twisting flight.

The blue-grey colouring\* gives the individual prions a unique way of periodically vanishing from sight, whilst their white underparts flash conspicuously in the sunlight so that the birds seem to go ". . . fluttering up and down like the silver tree when its leaves are shaken by the wind" (Green, 1887). Bierman and Voous (1950) describe them as "whirling through the air like snips of paper . . . the resemblance being so striking that the Norwegian sailors call them *Papirfugl*." In a large flock, as implied above, this twisting is not generally in unison, but Rankin (1951) mentions concerted movements that give the birds the appearance of a swarm of waders.

## 21. VOICE

At night in the vicinity of the base hut in Borge Bay, the cries of the Dove Prions contributed by far the most noticeable single component to the chorus of the five species which nested nearby.

\* This blue-grey of the prions has been shown by Murphy (1936) to resemble very closely in physical properties (wavelength, etc.) a colour ("Omega Grey") devised by the United States Naval authorities during the 1914-18 war as providing the ideal camouflage for ships at sea.

The birds call when they are within the nesting holes, on the open ground and also when in flight. Eaton (in Sharpe, 1879) also mentions prions calling on the wing at Kerguelen, and although such calls are not frequent they appear to be of fairly general occurrence.

There are several calls. The most general and widespread is a cooing which Murphy (1936) has likened to the calling of Turtle Doves and which other naturalists have described similarly. It is a throaty call. ". . . uc coo uc coo u-u-u-u-uc cuc coo o-o-o-o." A Dove Prion landing near its nest will call and the mate, if inside, will reply; there will then be much interchange of calls before the returning bird finally enters, and once inside the calls are renewed with fresh vigour. Such calling will stimulate birds in the surrounding area, in holes and above ground, to join in. It is possible with only a crude imitation to elicit an answering call.

This call is uttered by thousands of individuals and constitutes an uninterrupted whispering chorus that continues throughout the hours of darkness. Eaton (in Sharpe, 1879) aptly described it as ". . . a low continuous murmuring like the sound of distant traffic in a large town."

Nesting birds appear to contribute less to this nightly chorus once they have started incubation, so it is possible that the young non-breeding birds account for a major part of the chorus after the end of December. For reasons unknown, there was an almost complete lack of calling on some nights and, conversely, some individuals were heard occasionally in the daytime when normally they are silent.

When indulging in fights and squabbles, prions utter loud shrill "squarks" and squeals (p. 18) which are easily distinguishable from normal calls.

The third distinctive call is a characteristic swift trilling or piping whistle and is the most musical note heard from these birds. Almost certainly it was uttered when copulation was actually in progress, though probably only by the female, and may therefore be termed the "copulation call" (p. 17). This whistle was also heard in the laboratory on several occasions when inserting a thermometer into the cloaca of a prion (p. 18). The only call which approaches it at all is that of the chick, but this occurs later in the cycle and confusion between the two is unlikely.

## 22. HOMING

Two homing experiments were carried out. In the first, two nests were selected at a time when the occupants were returning each night to feed chicks. One of each pair was removed from the nest on the night of 7 February 1955 and dispatched on board R.R.S. *John Biscoe* which was bound for South Georgia. Both birds were released on 11 February, one at 1520 hr. L.M.T. and the other at 2000 hr. L.M.T., about fifty miles apart. The first was back in its nest two nights later having travelled 500 miles in about 50 hr. The second, released within ten miles of South Georgia arrived the following night having flown 550 miles. Both birds had been confined for four days whilst in transit and had probably stopped to feed during the homeward flight. The wind during this experiment was westerly, more or less abeam of the birds' course which was south-south-west; at the time of the first release it was about Force 3 but by the time the second bird was dispatched it had increased to Force 5.

The second experiment was carried out the following season before laying had started. Two pairs from adjacent nests were caught on 26 November and dispatched to the Falkland Islands. One bird died *en route*, but the other three were released within 15 miles of the Falkland Islands. One appeared on its nest five days later, having flown 770 miles. Its mate did not appear until 29 December, almost four weeks later, but laid an egg shortly after arrival. The third bird was not seen again.

These experiments, limited as they were, cannot be expected to shed much light upon general problems of navigation in marine species, but they demonstrate the distance that a Dove Prion can fly in a given time. From this, it is possible to draw some conclusions concerning the maximum distance from the feeding grounds at which the species can breed. Inability to fly to open water and back during one night may account for its absence as a breeding species in higher latitudes (see p. 3).

From the experiments we know that a distance of 200 miles per day is well within the bird's capabilities. Therefore, during the pre-laying and chick-feeding periods, when the birds are coming into the colony every night, they are probably feeding within a radius of about 100 miles of the island. Throughout incubation, however, when each member of a pair is spending three or four days alternately at sea and at the nest, the feeding range is extended and it would be possible for them to fly as far as three or four hundred miles from the breeding grounds.

## 23. MOULT

During the latter part of March, feathers of the body and head are being replaced. The brood patch again becomes covered with dark-grey down but there are no new feathers except along the edges.

Moult of wing or tail feathers was not observed in any of the birds handled, and it is evident that it occurs after the birds have left the islands. This may be true of all the *Procellariidae*. Citing *P. gravis*, *P. griseus* and *P. tenuirostris*, Marshall and Serventy (1956) have suggested that "Moult in all adult shearwaters begins during the nesting period: but in trans-equatorial migrants there is a hiatus that allows the retention of the wing and tail feathers until after the completion of their post-nuptial journey. Once the flocks reach their contra nuptial quarters the moult is completed in a short sharp burst."

None of the *Pachyptila* are trans-equatorial migrants, and according to Fleming (1941) some species are restricted to narrow latitudinal belts.

## VI. TAXONOMY

## 1. GENERAL

The *Procellariidae* are the subject of large synonymies and perhaps the most notorious in this respect is the genus *Pachyptila*, in which the number of unsatisfactory sub-species has been particularly large. The work of Murphy (1936) and Falla (1940) disposed of much of the early confusion in this genus and reduced the number of species and sub-species to a manageable few.

In common with the other five accepted species of *Pachyptila*, and indeed of the *Procellariidae* in general, *P. desolata* breeds on widely separated oceanic islands. The non-breeding season is probably spent scattered throughout the Antarctic zone of surface water—a relatively uniform habitat common to all races. Speaking of these island colonies and their taxonomy, Murphy (1936) says "That one or more of the [four] recognizable species may break up into geographic races, I have not the slightest doubt. My complaint is merely that the characters which may actually differentiate such races have never been properly pointed out, and that synonyms have been dumped into the ornithological record in advance of any systematic study even approaching accuracy or thoroughness. . . . The difficulty is complicated by the fact that although such isolated breeding races may exist it is often impossible to separate them on morphological grounds." He previously pointed out that in many instances island breeding grounds a long distance apart but lying on the same parallels of latitude, proved to be the homes of indistinguishable races of petrels (Murphy and Harper, 1921).

The sub-division of species according to generalized characters of appearance and slight differences in plumage must be considered suspect, for opinions vary even amongst the most competent and conservative systematists. Whilst Murphy (1936) describes the Heard Island prions as indistinguishable from the South Georgia birds, both in measurement and appearance of the bill, Falla (1940) says that the South Georgia birds ". . . lack the depth and strong tumescence of the Heard Island birds."

Small differences in mensurable characters do exist but the range possible in each race, and the overlap with the next, are such that it is mostly impossible to ascribe an isolated specimen to a particular race on these characters alone. Statistical analysis applied to large samples must be considered the best method of testing whether there are any characters which might provide a key to the races. Austin (1952) working on a similar problem, holds that a sub-specific name designating a geographical population is of no practical use unless at least three-quarters or more of the individuals of that population can be identified by their morphological characters alone. He adopted the statistical method of Simpson and Roe (1939) as the best practical standard. He also pointed out that "average" differences are of no significance unless it can be demonstrated that the two standard errors on either side of the respective means do not overlap; he considers that, even then, it is impossible to identify individual specimens with any degree of confidence. These criteria have been adopted for the purposes of this work.

## 2. METHODS AND TECHNIQUE

Certain characters were measured as follows:

*Weight.* A small balance, calibrated in 5 g. divisions, was used to estimate weights to the nearest gram. At Signy Island, only live or fresh material was weighed, live birds being rolled in a tube of paper to stop movement.

*Length.\** The birds were laid breast downwards on a sheet of paper and the extremities of bill and tail marked. Measurements given are the flat distance between those points (Plate VIIa).

*Wing span.\** The birds were again placed breast downwards, the wings were stretched to their fullest extent and the flat distance between the two extremities measured (Plate VIIa).

*Culmen.* From the base of the bill to the tip. The base was taken as the line where feathering begins. Measurement was to the nearest 0.5 mm. (Plates VIIb; VIIIc, d).

*Width of bill.* The greatest width, to the nearest 0.5 mm., of the upper mandible taken near the base of the bill. For the examination of specimens from the British Museum (Natural History) and the American Museum of Natural History vernier calipers were used, but to conform with the earlier method the limits of accuracy were kept as 0.5 mm. (Plate VIIIa, b).

*Tarsus.* Length was measured to the nearest millimetre on the upper side.

*Middle toe and claw.* (This method is adapted for use on freshly dead specimens or live birds and probably differs from that of most workers.) The whole foot is flattened on a board or rule, and the claw extended in line with the rest of the toe. Measurement is made from the angle between the middle and outer toe to the tip of the claw. With dried museum skins the foot usually dries in a contracted or bowed position with the claw out of line, and this character was therefore not used for comparison.

*Wing.* Length, measured to the nearest millimetre, from the carpal flexure to the tip of the longest (second) primary.

*Tail.* Length measured with dividers to the nearest millimetre on the dorsal surface from the base of the tail (pygostyle) to the tip of the longest rectrices.

Measurements at Signy Island and Bird Island were made by the author as were those from specimens in the British Museum (Natural History) and the American Museum of Natural History. The data on all other specimens has been used as published or supplied by Dr. D. L. Serventy and Dr. R. A. Falla.

The series of measurements from the different breeding localities are not strictly comparable as some were made on fresh material and others on dried skins which are prone to slight shrinkage, the degree of shrinkage varying with different characters. That amount can, however, be estimated from the parallel sets of measurements which are available for fresh and dried material from Heard Island and South Georgia (see Table XX). Due allowance was made for this when comparing Signy Island data (all from fresh material) with those from elsewhere, with the exception of the bill-width measurements, this correction merely reduces the difference between means which are not statistically significant.

All specimens measured at Signy Island were adults, most of which were known to be breeding, and wherever possible juvenile measurements have been eliminated from the museum series examined.

## 3. DIFFERENCES BETWEEN THE SEXES

Of 31 sexed birds from Signy Island, 12 were female and 19 male. Statistical comparison revealed that there was no significant difference between the means of any of the linear characters compared, but it was found that the mean weight of the males was significantly greater than that of the females (see Table XIX).

As no sex differences were discovered in the characters used for comparison, it was possible to combine all the Signy Island measurements, sexed and unsexed. Similarly, in assembling data from other breeding localities I have not segregated males and females.

\* Available only for freshly killed specimens from Signy Island.

TABLE XIX  
DIFFERENCES BETWEEN THE SEXES

	Males			Females		
	Number	Mean	Range	Number	Mean	Range
Culmen	19	28.0	26.5-31.0	12	27.7	26.0-30.0
Width of Bill	19	14.9	14.5-15.5	12	14.5	14.0-15.5
Tarsus	19	32.5	29.5-35.5	12	32.1	29.0-34.0
Middle Toe	19	36.4	34.5-38.0	12	36.3	34.5-38.5
Tail	19	102	97-111	12	101	95-107
Wing	19	193	182-209	12	192	185-200
Length	13	291	275-304	6	290	283-297
Wingspan	13	632	618-654	6	634	624-648
*Weight (g.)	18	160	138-182	12	153	118-176

Body weight is given in grams; all other measurements are in millimetres. For testing the means of small samples the values of *t* have been calculated and compared with the *t* distribution given by Fisher and Yates (1938).

\*With the exception of body weight there is no significant difference between the sexes in any of the measured characters.

The body weight of adult males is significantly greater than that of females; the odds against such differences occurring by chance being at least 19:1.

#### 4. CONCLUSIONS

In all the series of characters measured there have been overlaps in excess of 50 per cent, but a few means vary enough to allow an 84 : 84 per cent separation.

The means of tarsi and culmen are inseparable throughout the whole series, but the width of bill, and wing- and tail-length measurements, can be used to segregate three races as follows:

<i>Race</i>	<i>Locality</i>	<i>Features</i>
<i>P. d. desolata</i>	Îles de Kerguelen	Narrowest bill
<i>P. d. banksi</i>	South Georgia South Orkney Islands Heard Island	Wide bill Normal wings and tail
<i>P. d. alter</i>	Macquarie Island Auckland Islands	Wide bill Short wings and tail

For the width of bill, the dispersion of variates is so narrow that differences of means as small as 0.5 mm. are held to be significant.

Fig. 14 and Table XX show that there is a significant separation between the means of the two series of measurements (dried and fresh) of bill widths from both Heard Island and South Georgia. The differences in the means are 0.8 and 1.0 mm. respectively. On the basis of these figures I have assumed a shrinkage factor of 0.9 mm. and applied it to the South Orkney Islands data for the purposes of comparison.

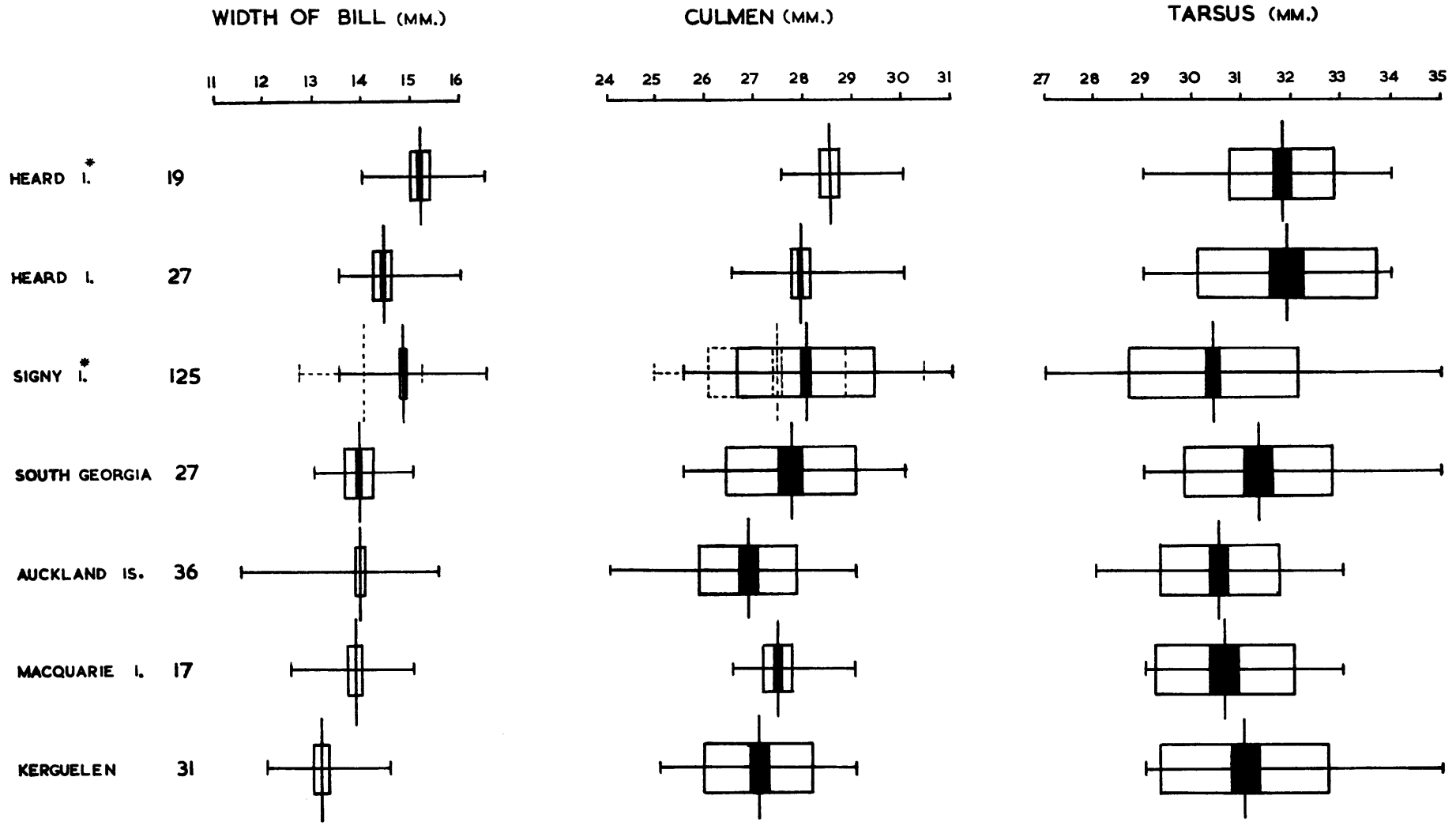
The smaller bill widths of the Îles de Kerguelen birds distinguishes them from all the rest, but it is not possible to differentiate between the mean widths of birds from South Georgia, the South Orkney Islands, Heard Island, Macquarie Island and the Auckland Islands. Thus, on bill width alone it is possible to separate only two main groups. It would be impossible to distinguish the South Atlantic birds from those of the New Zealand sector were it not for the fact that forms from the Auckland Islands, and to a lesser degree Macquarie Island, have noticeably shorter tails and wings. The most diagnostic of these two characters is the tail, which is much shorter in the Auckland Islands than in any other locality although not significantly smaller than the Macquarie Island form.

For wing lengths, although the birds of the Auckland Islands would be separable from three of the other races, the Macquarie Island form is exactly intermediate and cannot be held to be significantly different from either group. There is, in fact, a cline from a long-winged condition at South Georgia to short-winged

TABLE XIII  
CHICK BROODING ROUTINE

Nest Number	Number of Days after Hatching																			
	1		2		3		4		5		6		7		8		9			
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night		
68A	♂	♂	—	♂	♂	♂	♂	☾	♂	☾	—	☾	♂							
	—	♀	♀	—	—	—	—	—	♀	♀	♀	♀	♀							
52		♂	—	♂	♂	♂	♂	♂	♂	♂	—	—	☾	♂	☾	♂	☾	♂		
		♀	♀	♀	—	—	—	—	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	
49A	♂	♂	☾	♂	♂	♂	—	—	♂	♂	—	♂	☾	♂	☾	♂	☾	♂		
	—	—	—	♀	—	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	
69	♂	♂	♂	♂	♂	♂	♂	—	♂	♂	☾	—	☾	—	♂	♂	☾	♂	☾	
	—	—	—	—	—	—	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	
67		♂	♂	♂	—	♂	☾	♂	♂	♂	☾									
	—	—	—	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	
68	☾	♂	♂	—	♂	♂	♂	♂	♂	—	☾	♂								
	—	♀	—	♀	—	♀	♀	—	—	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	
94	♂	—	—	—	♂	—	—	—	—	—	☾		☾		☾				Day inspections only	
	—	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀		
87	●	●	●	●	●	●	●	●	●	☾	☾									

- ♂♀ Male or female brooding.
- Bird brooding but sex unknown.
- ♂♀ Male or female not brooding.
- Second parent absent.
- ☾ Chick alone.



THE DOVE PRION

FIGURE 14a

Comparative measurements of *Pachyptila desolata* from the six breeding localities, grouped and represented by Hubbs-Perlmutter (1942) diagrams from data given in Table XX.

The horizontal lines represent the range of variates, and the vertical indicate the mean. The open oblong denotes one standard deviation on either side of the mean, and the filled block corresponds to twice the standard error of the mean.

\* — Fresh birds.



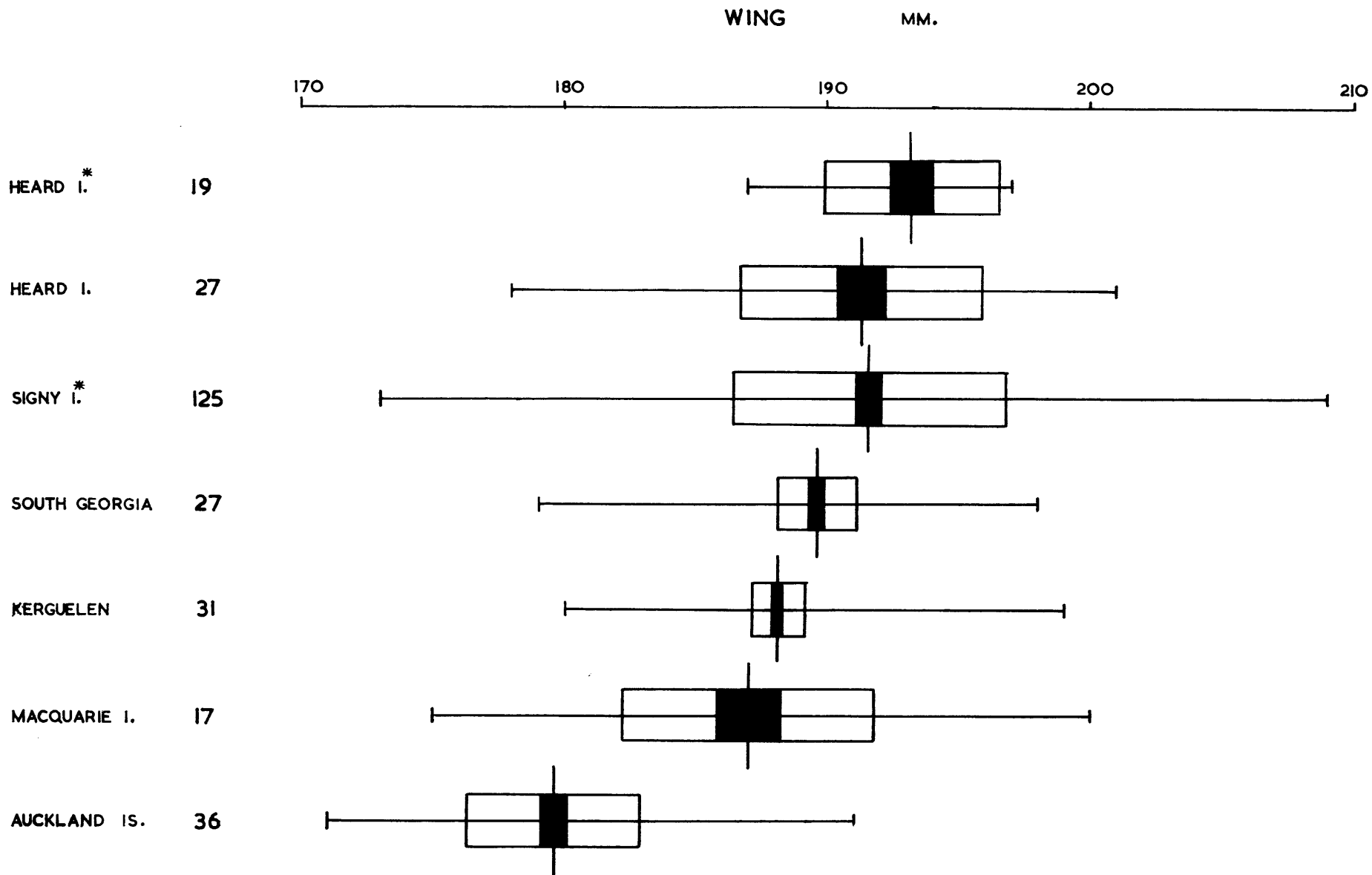
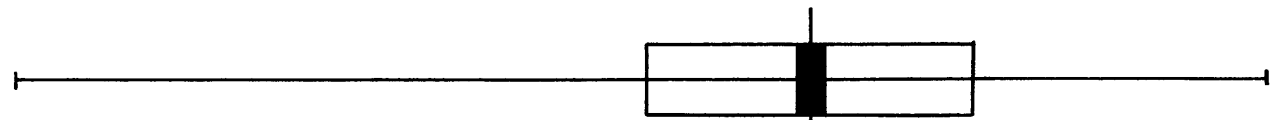


FIGURE 14b

TAIL MM.

70 80 90 100 110

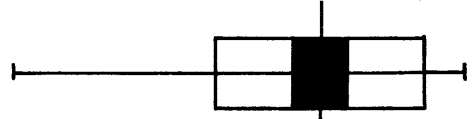
SIGNY I. \* 125



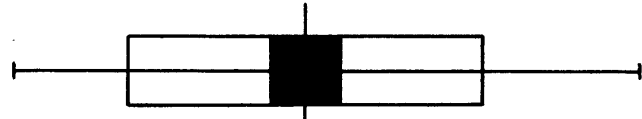
SOUTH GEORGIA 25



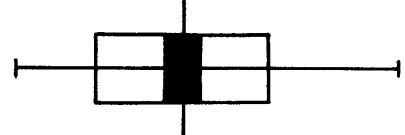
HEARD I. \* 19



HEARD I. 27



KERGUELEN 31



MACQUARIE I. 17



AUCKLAND IS. 34

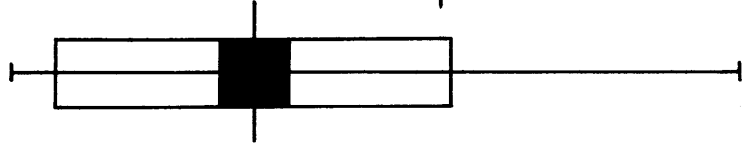


FIGURE 14c

THE DOVE PRION

TABLE XX  
GEOGRAPHICAL VARIATION IN *PACHYPTILA DESOLATA*

Sub-species		<i>P. d. desolata</i>	<i>P. d. alter</i>		<i>P. d. banksi</i>				
Locality		Îles de Kerguelen	Auckland Islands	Macquarie Island	Heard Island		South Orkney Islands	South Georgia	
Number of Specimens (N)		Dried Skins	Dried Skins	Dried Skins	Dried Skins	Fresh Birds	Fresh Birds	Dried Skins	Fresh Birds
		31	34	17	27	19	125	27	69
Width of Bill	Range	12.0–14.5	11.5–15.5	12.5–15.0	13.5–16.0	14.0–16.5	13.5–16.5	13.0–15.0	13.5–16.0
	Mean and Standard Error	13.10 ± 0.03	13.90 ± 0.01	13.80 ± 0.04	14.40 ± 0.05	15.20 ± 0.005	14.80 ± 0.005	13.90 ± 0.05	14.90 ± 0.08
	σ	0.15	0.08	0.15	0.24	0.24	0.06	0.27	0.63
Wing	Range	180–199	171–191	177–199	178–201	187–197	173–209	179–198	184–208
	Mean and Standard Error	188.10 ± 0.19	179.60 ± 0.54	187.00 ± 1.15	191.30 ± 0.90	193.20 ± 0.77	191.60 ± 0.47	189.60 ± 0.28	194.00 ± 0.58
	σ	1.03	3.25	4.75	4.64	3.34	5.22	1.47	4.8
Tail	Range	89–100	72–93	73–96	86–104	86–99	77–113	89–102	(N=24) 91–107
	Mean and Standard Error	93.8 ± 0.45	79.00 ± 0.98	84.40 ± 1.70	94.40 ± 0.98	94.80 ± 0.77	99.90 ± 0.42	97.70 ± 1.23	97.50 ± 0.80
	σ	2.53	5.74	6.96	5.08	3.34	4.68	6.15	3.94

at the Auckland Islands, the two extremes being significantly different but with every grade of intermediate between them. A similar cline in tail lengths exists from the South Orkney Islands to the Auckland Islands.

In the Wilson's Petrel, *Oceanites oceanicus*, Roberts (1940) found that the wing and tail lengths became longer in progressively higher latitudes. This demonstration of Bergman's Rule is also apparent in the Dove Prion, *P. desolata*, the most noticeable change occurring where the breeding localities lie on or progressively north of the Antarctic convergence.

#### 5. NOMENCLATURE

##### *Pachyptila desolata desolata* (Gmelin)

*Procellaria desolata* Gmelin, *Peters Check-list of Birds of the World*, 1, 49, 1931, by subsequent designation. *Syst. Nat.*, 1, 562, 20 April 1789.

*Procellaria fasciata* Bonnaterre, *Tableau Encyclopédique et Méthodique. Ornithologie*, 1, 79, 1791 (for same bird as Gmelin's).

*Prion rossi* Bonaparte, *Consp. Gen. Avium*, 2, 193, 1 October 1857. Antarctic Ocean. (Ex *Prion rossi* Grey, *List of the Specimens of Birds of the Collection of the British Museum*, Pt. 3, 165, 1844; nomen nudum.)

*Prion dispar* Vanhoffen, *J. Orn., Lpz.*, 53, 505, July 1905; nomen nudum.

*Attapriion desolata desolata* (Gmelin), Mathews, *Bull. Brit. Orn. Cl.*, 54, 25, 31 October 1933.

*Heteroprion desolata mattingleyi* Mathews\*, *The Birds of Australia*, 2, 226–31, 30 May 1912.

*Heteroprion desolata alexanderi* Mathews and Iredale\*, *A Manual of the Birds of Australia*, 1, 41–42, 9 March 1921.

##### *Distribution*: Îles de Kerguelen

Murphy (1936) recognized that "the whale-birds of Kerguelen . . . may possibly have slightly smaller bills than those of South Georgia and Heard Island and may prove to be a distinct subspecies". This statement was re-inforced by a good series of specimens which was taken during the B.A.N.Z.A.R. Expedition†, and included some with very narrow bills. These led Falla (1940) to suggest the possibility of two sympatric races differing only by small differences of bill width and breeding times, but having analysed the measurements of 31 Kerguelen specimens the present author considers the existence of two such races highly unlikely. The different bill dimensions all fall within the limits of a single race and are fairly normally distributed, the mean width ( $13.100 \pm 0.026$  mm.) being separated by at least 0.7 mm. from those of other localities. The standard deviations are clearly not overlapping, in fact this race appears to be more reliably differentiated than any of the others.

It is also doubtful whether there is a significant variation in breeding times. The Signy Island records show that although there is a wide range in laying dates, the presence of one or two parents in the nest during the daytime is no indication that one pair will produce an egg earlier than another.

##### *Pachyptila desolata banksi* A. Smith,

*Ills. Zool. Zu. Afr. Aves*, 1840. Cape of Good Hope. By subsequent designation, *Peters Check-list of Birds of the World*, 1, 50, 1931.

*Heteroprion desolata georgia* Mathews, *Bull. Brit. Orn. Cl.*, 52, 147, 28 June 1932. South Georgia.

*Pachyptila vittata georgicus* Mathews, *Bull. Brit. Orn. Cl.*, 52, 214, 27 May 1933. South Georgia.

*Pachyptila dispar* Reichenow, see Vanhoffen, *J. Orn., Lpz.*, 53, 505, July 1905; nomen nudum. Heard Island.

*Pachyptila desolata heardi* Mathews, *Emu*, 41, 264, 10 April 1942. Heard Island.

##### *Distribution*: South Georgia, South Orkney Islands and Heard Island.

Mean bill-widths of fresh material from the three localities are  $14.90 \pm 0.08$  mm.,  $14.800 \pm 0.005$  mm. and  $15.20 \pm 0.05$  mm. There is no significant difference but, also on this character, *P. d. banksi* is in-

\* By subsequent designation Falla, *Emu*, 40, 233, October 1940, and Mathews and Hallstrom, *Notes on the Order Procellariiformes*, p. 24, 1943.

† British-Australian-New Zealand Antarctic Research Expedition, 1929–1931.

separable from *P. d. alter*. Specimens from South Georgia and the South Orkney Islands show a tendency to radiating corrugations on the epidermis of the bill, and their lateral lamellae are exposed at the gape more than in specimens from any other locality. Falla\* is of the opinion that in this character at least, *P. d. banksi* bears some resemblance to *Pachyptila salvini* from the Prince Edward Islands and Îles Crozet (Table XXI). On mean wing and tail lengths the *P. d. banksi* is inseparable from *P. d. desolata*.

There is no significant separation between the mean measurement of fresh material from South Georgia and Heard Island, although samples of dried skins from these two localities show a slight difference. Unlike Murphy (1936), Falla (1940) considers that the two groups of birds could be distinguished. Heard Island may perhaps be the home of a distinct race, but it cannot be readily separated from the South Atlantic Dove Prions on the morphological data available.

TABLE XXI  
OTHER MEASUREMENTS OF *PACHYPTILA DESOLATA BANKSI*

	<i>Number of Specimens</i>	<i>Range</i>	<i>Mean and Standard Error</i>	$\sigma$
<i>Weight (g.)</i>	124	116-199	158.60 $\pm$ 1.17	11.50
<i>Tarsus (mm.)</i>	125	27-35	30.40 $\pm$ 0.15	1.66
<i>Middle Toe and Claw (mm.)</i>	124	29-39	36.50 $\pm$ 0.74	6.71
<i>Length (mm.)</i>	19	275-304	290.50 $\pm$ 1.53	6.67
<i>Wing span (mm.)</i>	19	618-654	632.60 $\pm$ 3.42	14.92

All taken from freshly killed Dove Prions in the South Orkney Islands.

*Pachyptila desolata alter* Mathews,

*The Birds of Australia*, 2, 226-31, 30 May 1912.

*Heteropron desolata macquariensis* Mathews, *The Birds of Australia*, 2, 226-31, 30 May 1912.

By subsequent designation, Mathews, *Novit. zool.*, 39, 173, December 1934.

*Distribution*: The Auckland Islands and Macquarie Island.

This sub-species is tenable solely on the grounds of its short tail, but otherwise it is indistinguishable from *P. d. banksi*. The birds of the Auckland Islands would also be separable on short wing measurements, but in this character Macquarie Island prions form a link with the other races.

The above distribution is based entirely on the analysis of the specimen data available. The six island breeding localities are conveniently grouped into three areas, the Scotia Sea or South Atlantic, the South Indian Ocean and the New Zealand sector. Of the South Atlantic group, South Georgia and the South Orkney Islands are about 500 miles apart but are both well within the Antarctic convergence. In the South Indian Ocean, the Îles de Kerguelen and Heard Island are separated by about 300 miles but whilst Heard Island is south of the Antarctic convergence, the Kerguelen group lies approximately on it. Fluctuations in the position of the convergence in that region are not accurately known but it is probable that Kerguelen is subject more to sub-Antarctic than Antarctic influence, the reverse applying to Heard Island which is climatically very similar to South Georgia.

Such factors may explain why the two races which occupy these islands are very dissimilar although they almost certainly intermingle at sea and visit each others' breeding localities (Falla, 1937); the two islands are much closer together than South Georgia and the South Orkney Islands where the races are indistinguishable. The specimens from Heard Island are very difficult to place, and their grouping within *P. d. banksi* is to some extent one of convenience.

\* Personal communication.

In the New Zealand sector, Macquarie Island lies just north of the mean position of the Antarctic convergence and may be expected to be more subject to Antarctic influence than the Auckland Islands which are 400 miles to the north and well within the sub-Antarctic zone. Here, there is another grade of differentiation within *P. d. alter*, and also between *P. d. alter* and the other sub-species.

Only three specimens are available from the breeding colony at Cape Denison, King George V Land, on the mainland of Antarctica, and the data from these are insufficient to justify placing them within a sub-species. At present, therefore, these specimens must be considered referable to two of the races here proposed.

## VII. ACKNOWLEDGEMENTS

IT is a pleasure to thank Sir Raymond Priestley (Acting Director of F.I.D.S. Office, London, 1955–58) for his encouragement and help, and Dr. D. Lack (Director of the Edward Grey Institute of Field Ornithology, Oxford) for supervising the written work.

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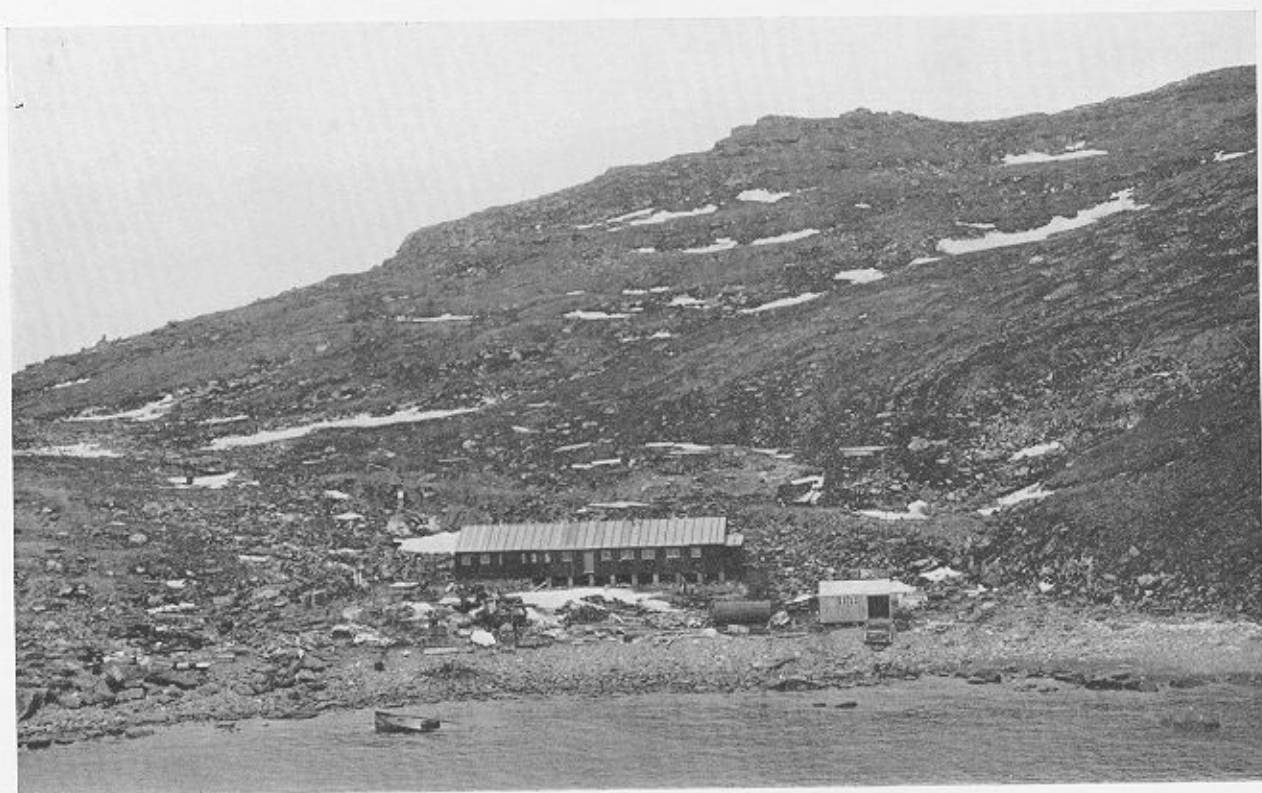


PLATE I

- a. The breeding area at Bernsten Point, Signy Island, showing the F.I.D.S. base hut and the winter snow-cover on the open slopes and crags. (Photograph taken from sea ice in Borge Bay.)
- b. The same area in summer at the height of breeding activity.



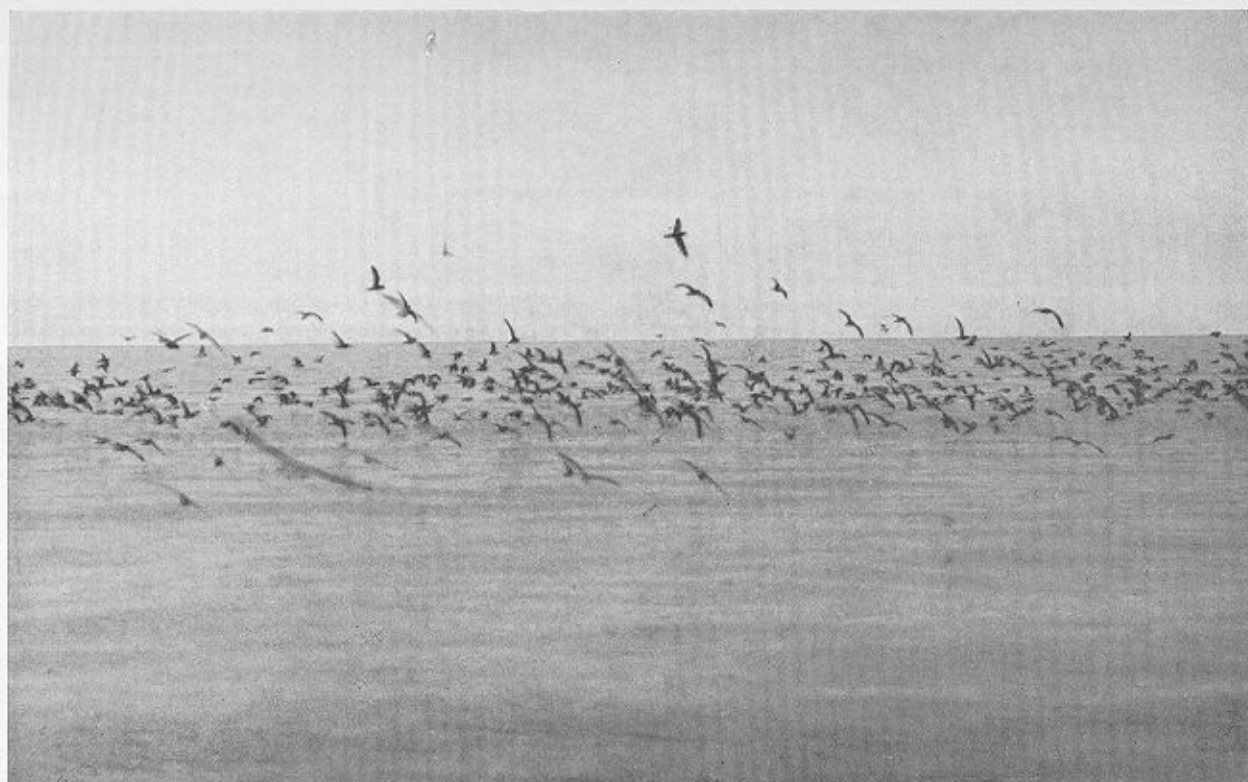
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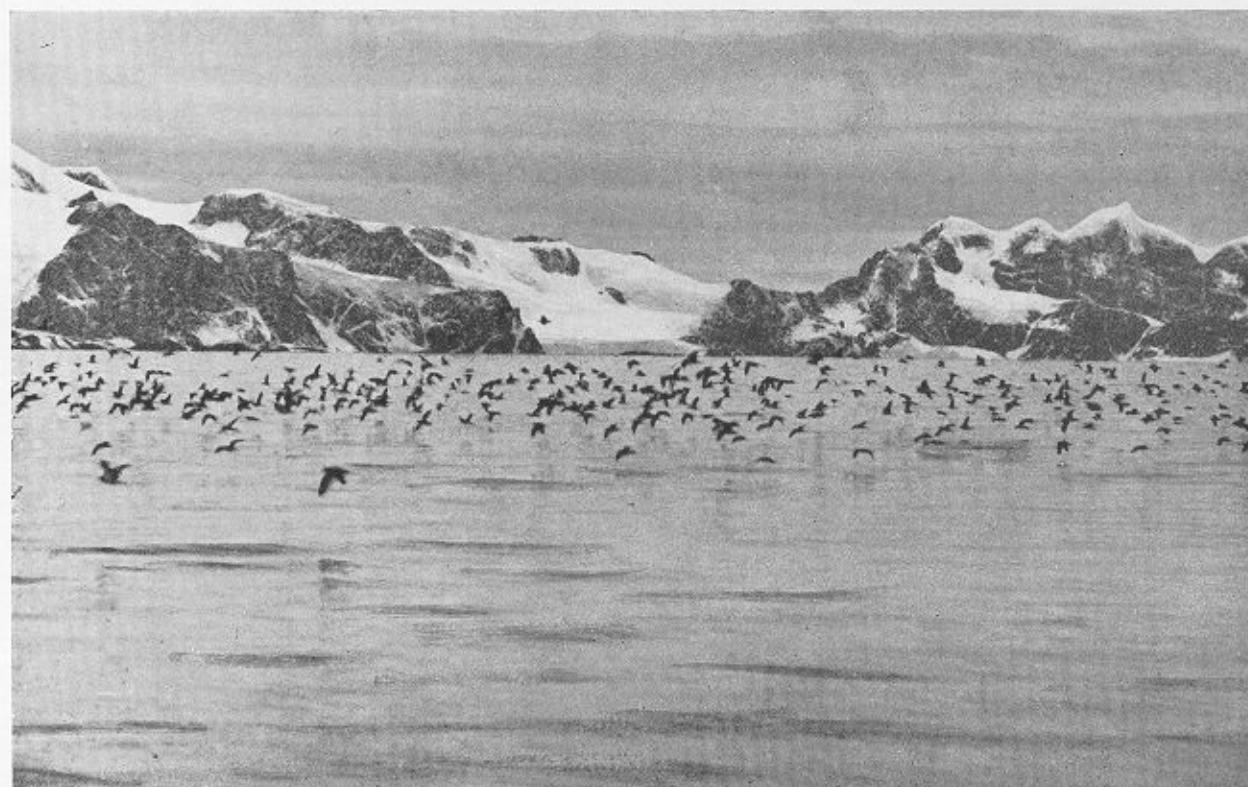
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PLATE II

a and b. Dove Prions assembling before dusk in the "zone of prions" two or three miles offshore.



a



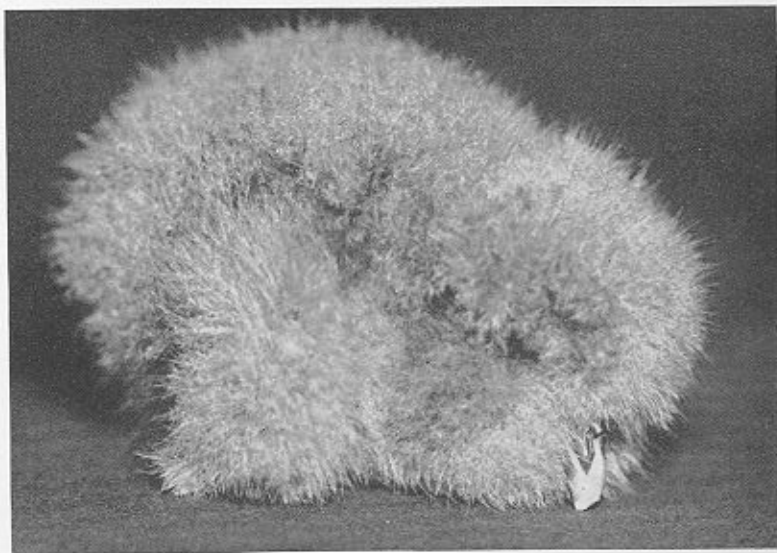
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PLATE III

- a. Dove Prion chick freshly hatched.
- b. Chick one day old.
- c. Chick about 16 days old.
- d. Chick about 21 days old.



a



b



c



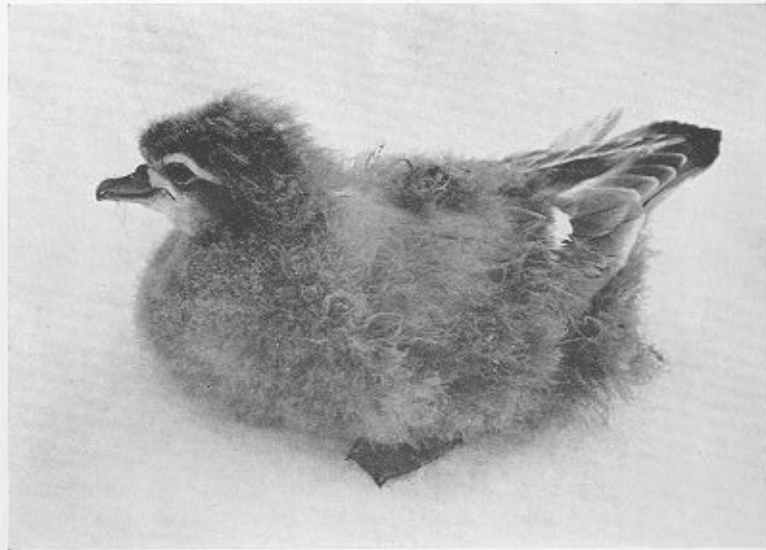
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PLATE IV

- a. Dove Prion chick about 30 days old.
- b. Chick about 38 days old.
- c. Chick about 42 days old.
- d. Young prion, fully fledged, 48 to 50 days old.



a



b



c

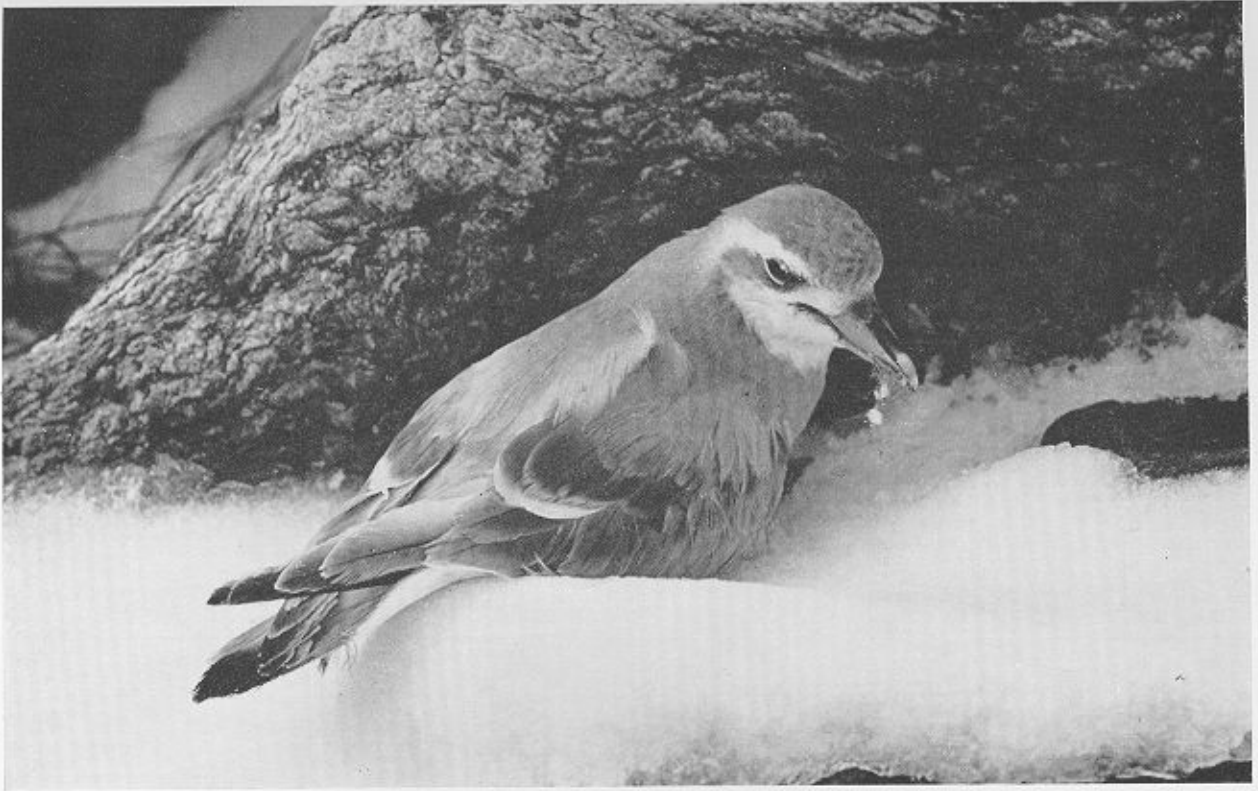


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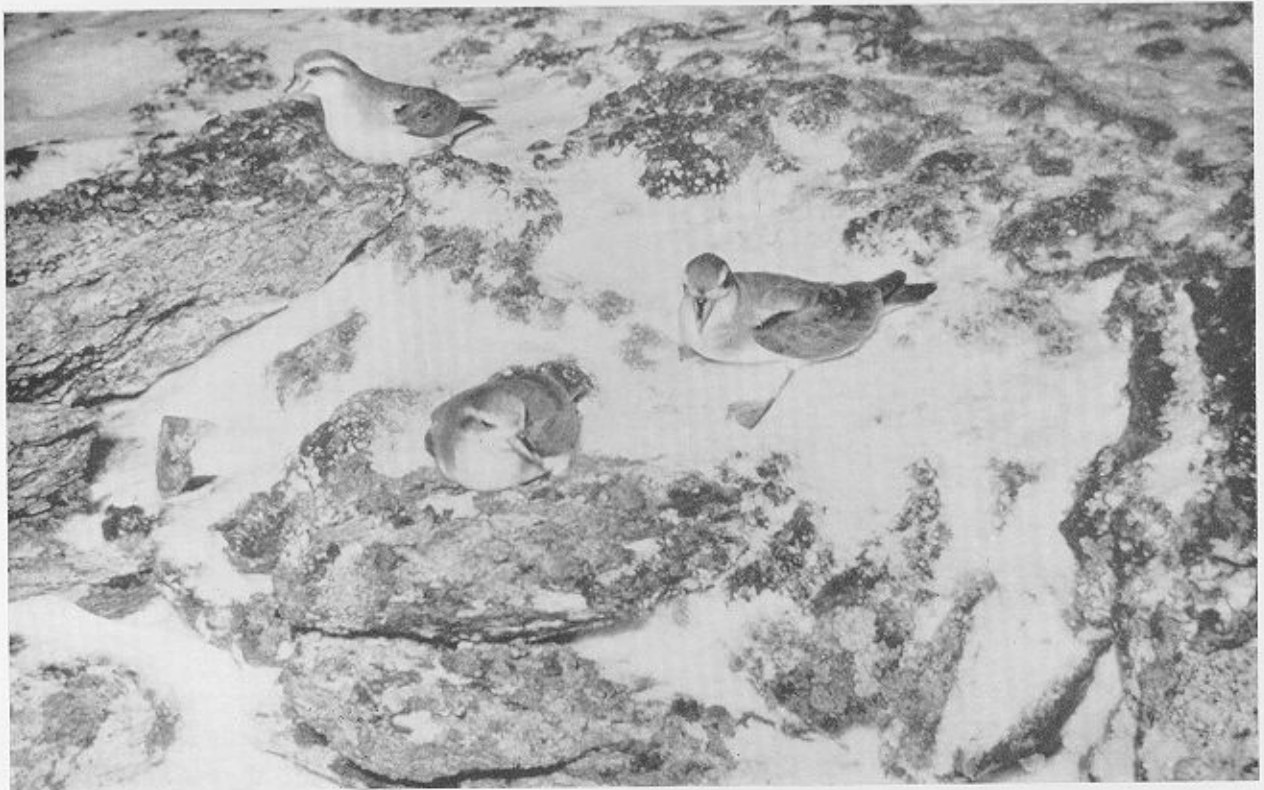


PLATE V

- a. Young Dove Prion, fully fledged.
- b. Adult prions outside their nest at night. Note the ring on the tarsus and the black paint-spot on the forehead of the bird on the right.



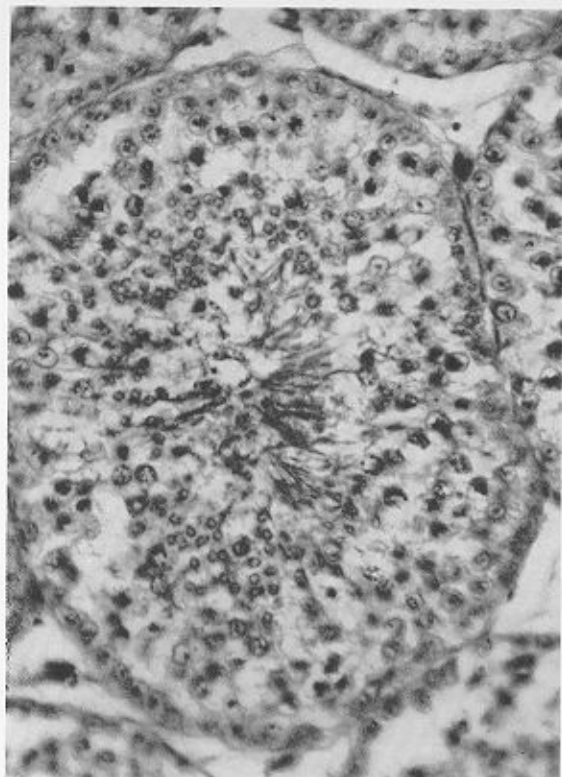
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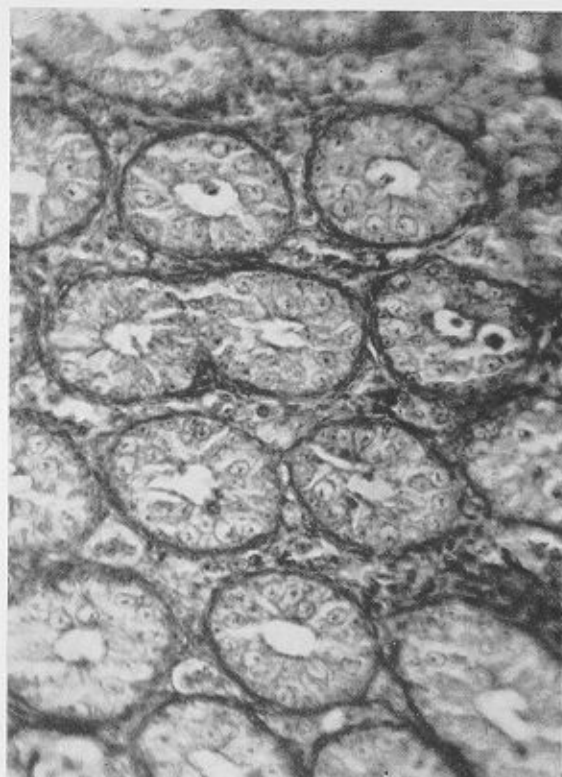
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PLATE VI

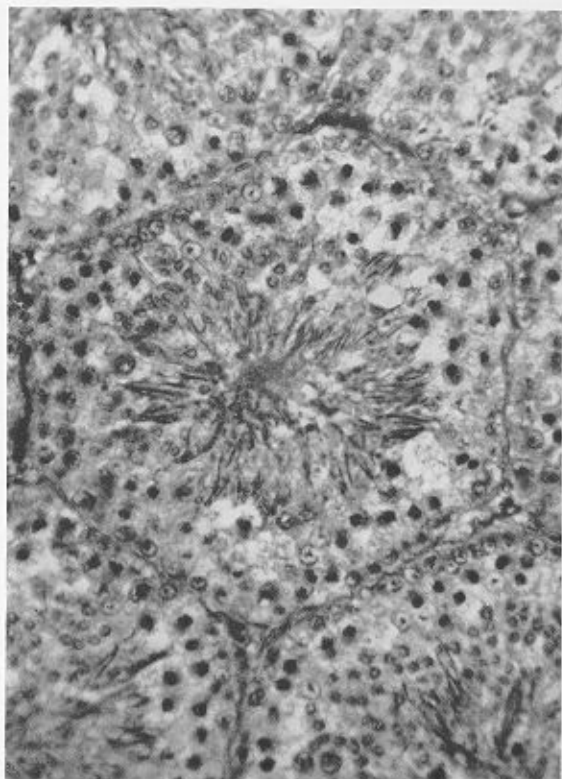
- a. Transverse section of adult testis (H.1061;  $\times$  330) collected at the time of the first return to the colony. Spermatocytes and spermatids are seen in all stages of development.
- b. Transverse section of adult testis (H.1211;  $\times$  330) showing seminiferous tubules at the height of spermatogenesis.
- c. Transverse section of adult testis (H.1234;  $\times$  330) showing retrogression of the seminiferous tubules and development of the interstitial tissue. Free spermatozoa are still present in the lumina of some tubules.
- d. Transverse section of adult testis (H.1259;  $\times$  330) showing the final retrogression of the tubules and the state of the interstitium at the time when the birds are leaving the breeding grounds.



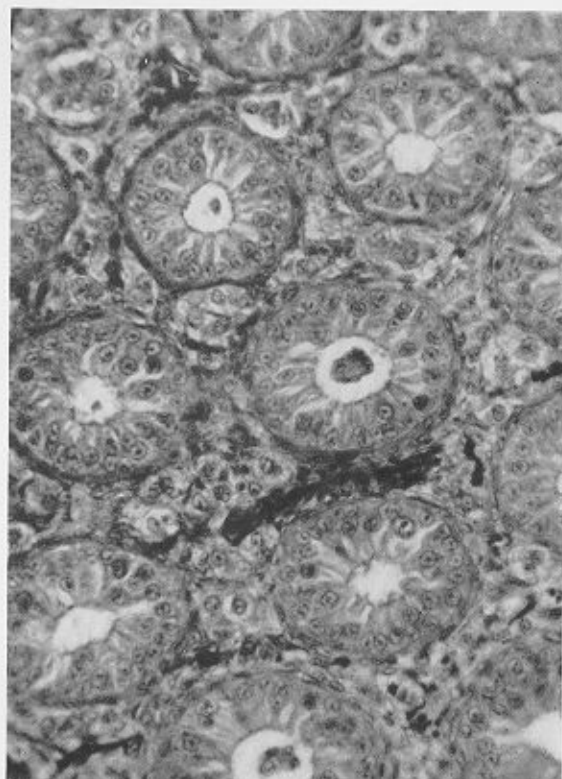
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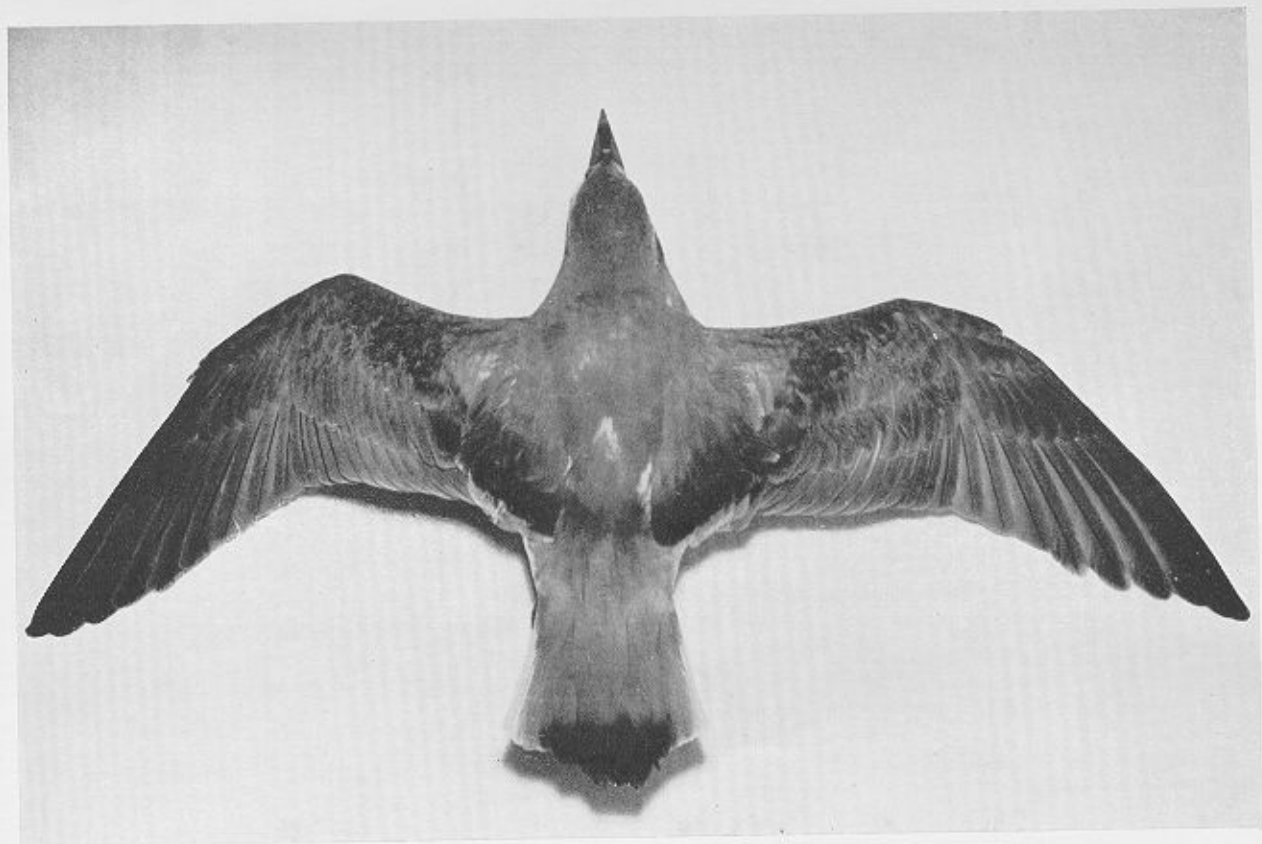
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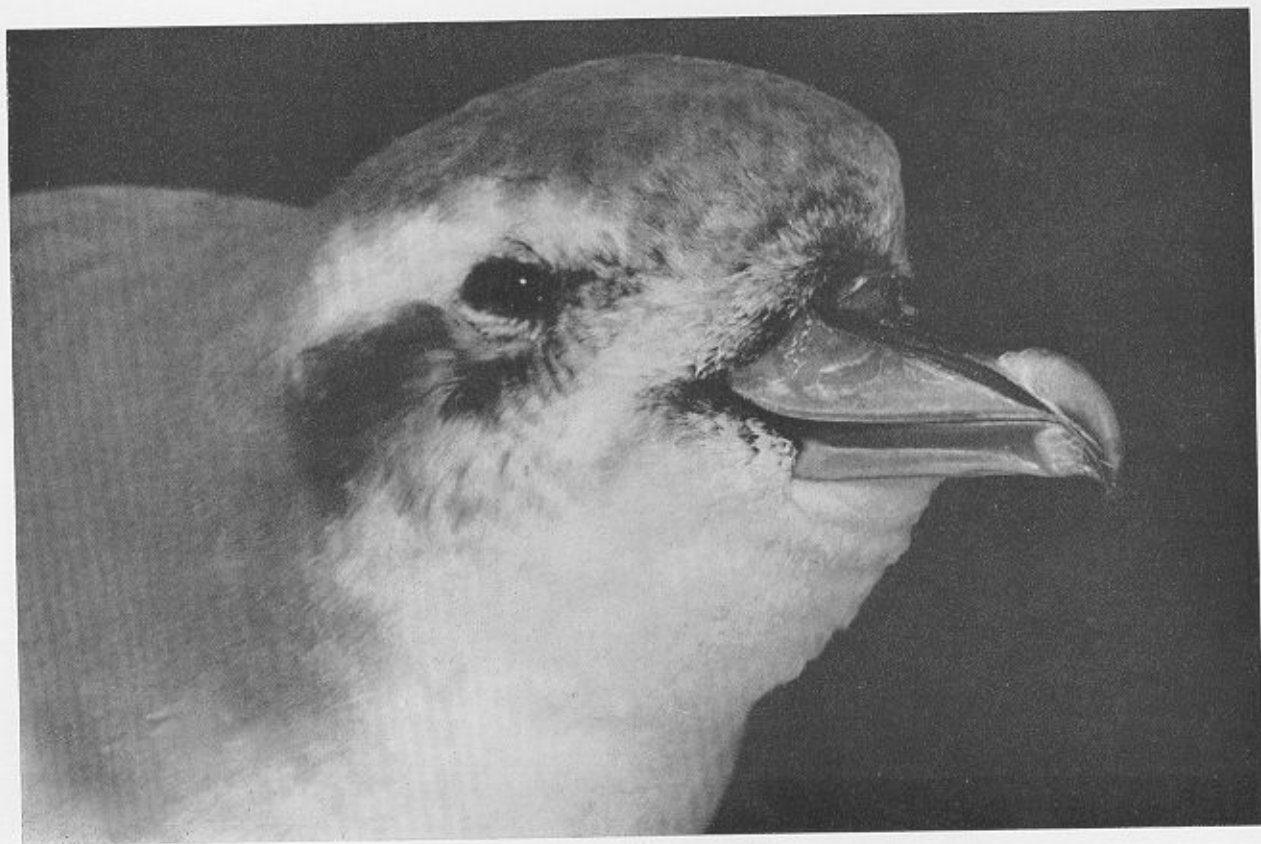
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PLATE VII

- a. Dorsal view of an adult Dove Prion, one-third life size. Note the characteristic black-tipped cunate tail.
- b. The head of an adult Dove Prion.



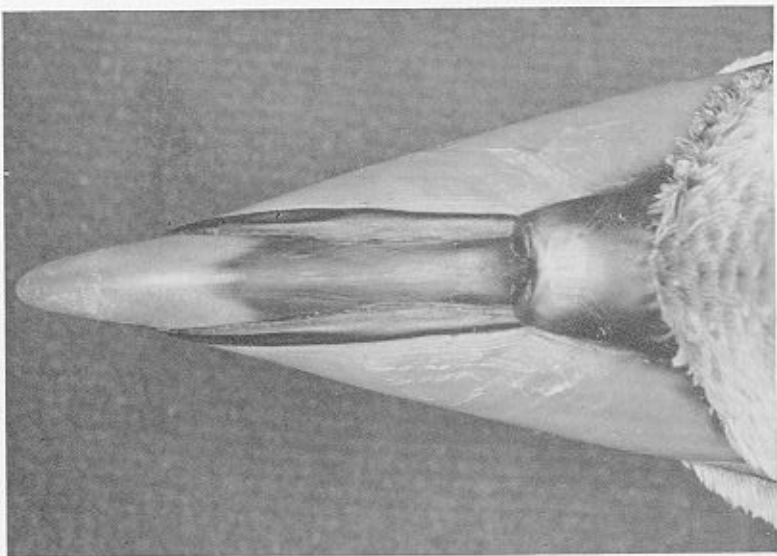
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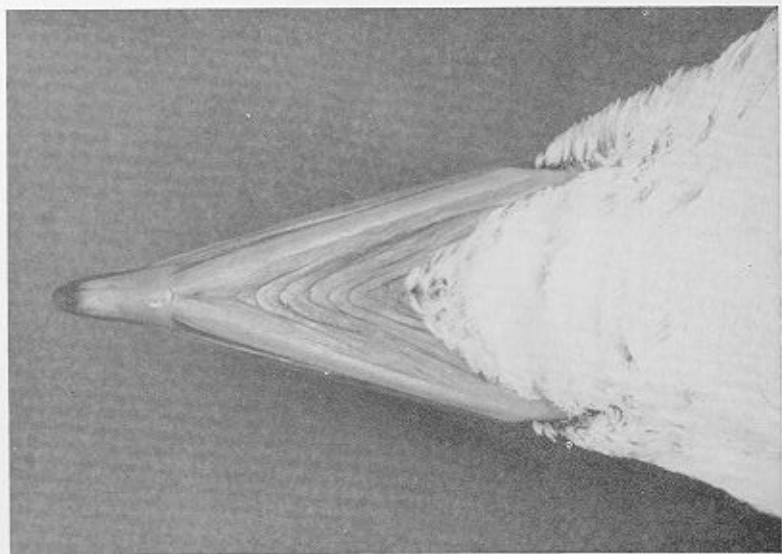
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PLATE VIII

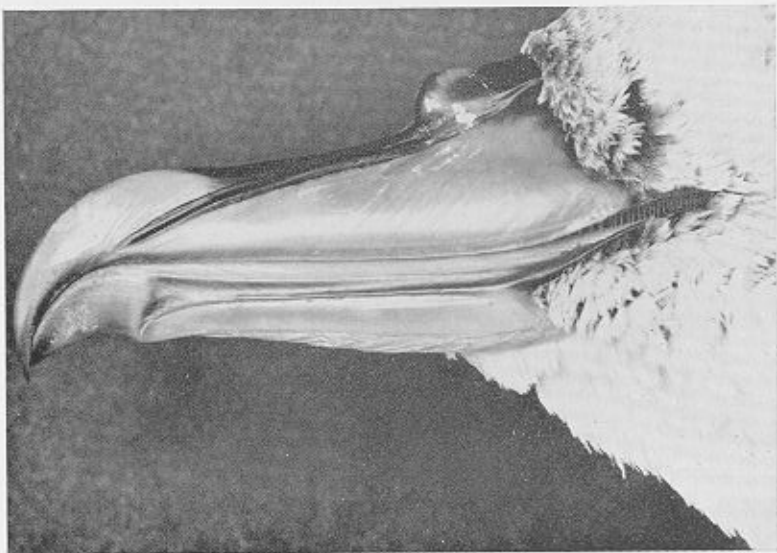
- a. Dorsal view of the bill ( $\times 3$ ); the transverse radiations on the epidermis are faintly visible.
- b. Ventral view of bill ( $\times 3$ ), showing gular pouch between the two rami of the lower mandible.
- c. Lateral view of the bill of a Dove Prion, showing exposed lamellae at the gape and slight transverse corrugations on the epidermis.
- d. Bill open showing lateral lamellae in the upper mandible and the fleshy gular pouch slightly expanded.



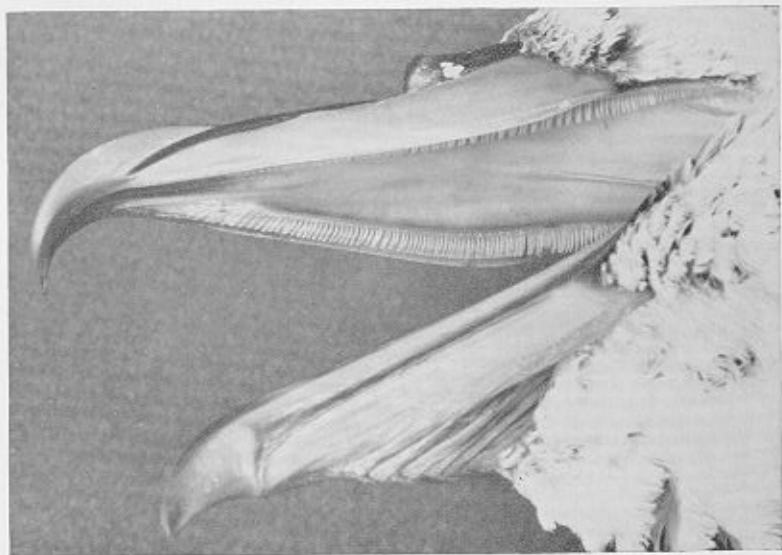
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b



c



d