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BREEDING BIOLOGY OF THE SNOW PETREL *PAGODROMA NIVEA* (FORSTER)

by
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BREEDING BIOLOGY OF THE SNOW PETREL *PAGODROMA NIVEA* (Forster)

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(Manuscript received December 1965)

ABSTRACT

The breeding cycle of the Snow Petrel *Pagodroma nivea* (Forster) in the vicinity of the Australian National Antarctic Research Expeditions' stations, Mawson and Davis, is described. The account is based on studies made during two seasons and includes a description of the climate and of the geographical features which form the species' nesting habitat.

The Snow Petrel breeds in rock crevices or in cavities under boulders. Colonies are found in ice-free areas all round the coasts of Antarctica and on neighbouring island groups; they are largest at heights over 65 m above the level of the surrounding sea, ice or land where potential nest sites are most numerous and least subject to blockage by drifting snow. Colonies also occur up to 250 km inland.

The feeding range is concentrated in the pack ice, but may extend northwards to the Antarctic Convergence in winter. Banding results indicate that adult breeders return each year to the same nest and the same mate. At both Mawson and Davis, breeding birds arrive in October; courtship and mating take place early in November. Both sexes are absent from the nest for most of the period between mating and egg-laying. One egg is laid (27 November to 9 December) and both sexes incubate alternately, the male participating first. The incubation period is 41-44 days (mean 43 days) and hatching occurs about mid-January. The chick, which is left unguarded 4-8 days after hatching, reaches adult weight at 26-30 days and maximum weight at 30-34 days. It is fed on krill and both parents share in the feeding duties. The nestling period is 48-54 days (mean 51 days).

Chicks fly early in March. Breeding birds re-occupy nests from late April until about mid-May. They are only occasionally seen in winter.

The egg and chick losses at Mawson are greater than at Davis, the difference probably being accounted for by more frequent snow blockage of nests at Mawson. Other causes of mortality are discussed.

The plumage is the same in both sexes but the males are slightly larger than the females. Although breeding birds at Mawson and Davis are generally similar in size, comparative measurements indicate that a much larger form breeds at Dumont d'Urville in Terre Adélie.

I. INTRODUCTION

The object of this report is to provide a preliminary account of the breeding cycle of the Snow Petrel *Pagodroma nivea* (Forster), based on field observations and specimens collected in Antarctica by the author during two years with the Australian National Antarctic Research Expeditions (ANARE).

A. Historical outline

The Snow Petrel was first mentioned in the journal of Captain James Cook (1777). On Friday, 11 December 1772, he reported: "At noon we were in the latitude of 51°50′ South, and longitude 21°3′ E., where we saw some white birds about the size of pigeons, with blackish bills and feet. I never saw any such before; and Mr. (J. R.) Forster had no knowledge of them. I believe them to be of the petrel tribe, and natives of these icy seas." A similar description was published by J. R. Forster's son, J. G. A. Forster (1777), who was also a member of Cook's expedition: ". . . a petrel, about the size of a pigeon, entirely white, with a black bill and blueish feet . . . . Its colour induced us to call it the snowy-petrel." He also gave it the name *Procellaria nivea*. Gmelin (1788) published the first systematic description of the species. J. R. Forster's own systematic description was not published until 1844, under the heading "*Procellaria nivea* F. (Fig. picta G.) *The Snowy Petrel or Snowbird*". "Fig. picta G." referred to paintings made by J. G. A. Forster when the first specimens were collected, on 30 December 1772, in about 60°S, 16°E.

According to Mathews (1912-13), further descriptions of the Snow Petrel were made by Peale (1848) who, after the United States Exploring Expedition of 1838-42, introduced the name *Procellaria candida*, and by Bonaparte (1855) who, setting aside the existing naming, re-named it *Pagodroma nivea*, and proposed two sub-species, *P. nivea major* and *P. nivea minor*, but gave no details. Coues (1866) stated that Bonaparte based the two sub-species on variations in bill size and shape which Coues concluded were independent of differences in body size. Mathews (1912-13) recorded that Schlegel (1863) differentiated two forms for which he used the names *Procellaria nivea* and *Procellaria nivea minor* after Bonaparte's *Pagodroma nivea major* and *Pagodroma nivea minor* respectively.

Sharpe (1902) pointed out that there was an extraordinary variation in size, not due to difference of sex, among the specimens collected during the voyage of the *Southern Cross* to Victoria Land in 1898-1900, and suspected that there might be two species. After examining specimens in the British Museum (Natural History), London, Mathews (1912-13) concluded

that, from the Cape Adare area, large birds were consistently large, and small ones consistently small, and that no intermediate forms existed. In consequence, he proposed that the small form should be referable to *P. nivea* (Forster), *P. candida* (Peale), and *P. nivea minor* (Schlegel), and be known as *Pagodroma nivea candida* (Peale). For the large form he proposed *Pagodroma confusa* (sp.n.), the dimensions all being larger than those of *P. nivea*. Hartert (1926), while viewing Mathews' findings with some reserve, did assert that the name *Pagodroma nivea* must be accepted for the smaller form, but posed the question whether large and small birds nested in the same places. He concluded that, if they had separate nesting places, they would best be treated as sub-species which apparently occurred together when not breeding.

After an extensive examination of specimens in the British Museum (Natural History) and also in Edinburgh, Paris and New York Museums, Lowe and Kinnear (1930) were unable to settle the division of this petrel into sub-species. They concluded that, until further specimens were taken from as many breeding grounds as possible, sub-speciation was not justifiable.

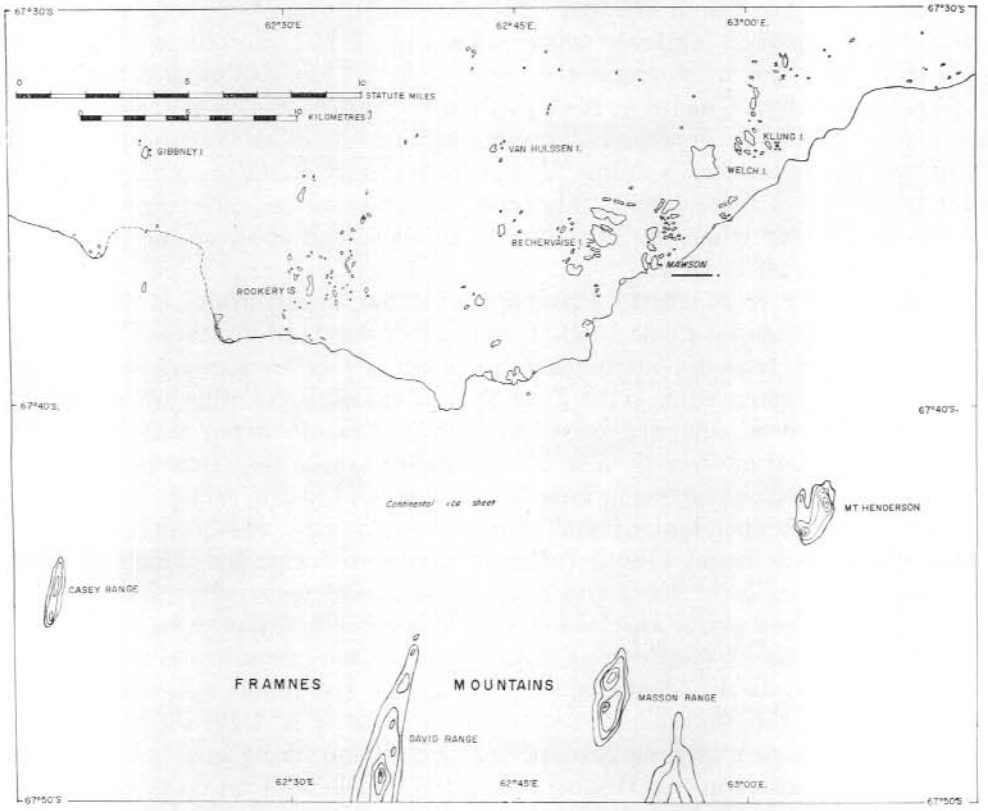
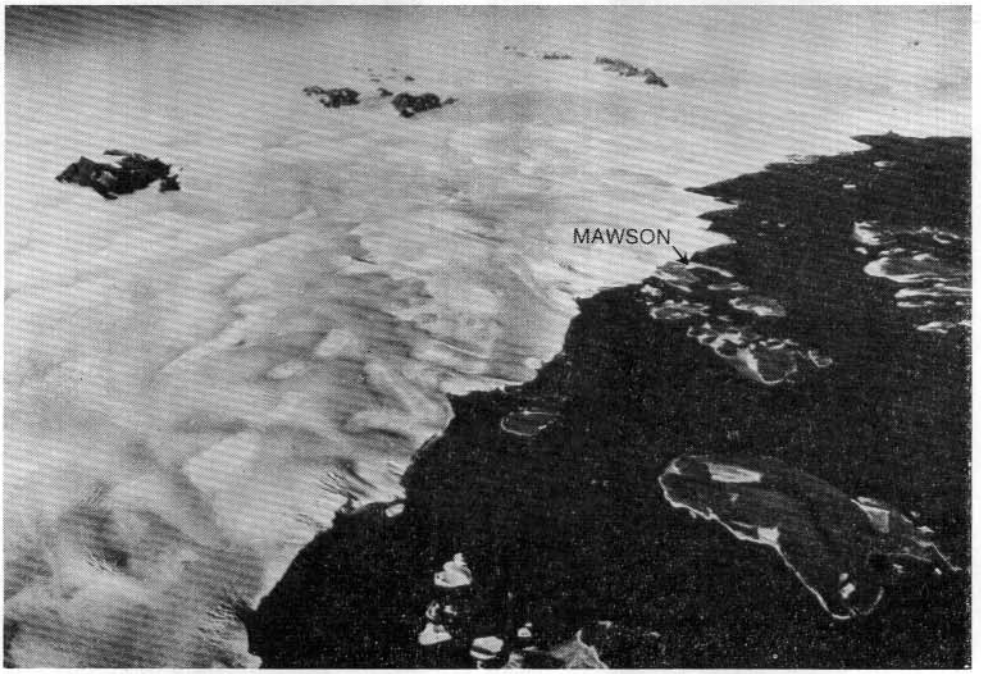


FIG. 1. The general locality of Mawson, Antarctica.

B. ANARE investigations

The author's investigations were made at the ANARE stations at Mawson in February 1958-February 1959, and at Davis in January 1961-January 1962. Further investigations, requested by the author, were carried out by members of successive ANARE parties at Mawson during the period January 1959-January 1962. Some additional information, mainly confined to winter sightings on the mainland and to oceanic and inland distribution, has been obtained from ANARE ship, station and field biological logs.



United States Navy photo

PLATE 1

The general locality of Mawson, Antarctica, looking south-west. Mawson ANARE station and Horseshoe Harbour are right of centre; the inland mountains from the left are Mount Henderson, Masson Range and David Range.

Mawson (67°36′S, 62°53′E) is situated on the south-eastern shore of Horseshoe Harbour in Mac.Robertson Land, Antarctica (Figure 1; Plate 1). In this vicinity, the general trend of the coast is south-west and north-east, and there are numerous off-lying islands. The surface of the inland ice sheet rises steeply behind Horseshoe Harbour and forms ice walls on either side of it. About 15-50 km to the south-west, the Framnes Mountains (Mount Henderson and the Masson, David and Casey Ranges) project 500-650 m above the ice sheet and up to 1000 m above sea level. Snow Petrels nest on most of the off-shore islands, on coastal rock outcrops and in great

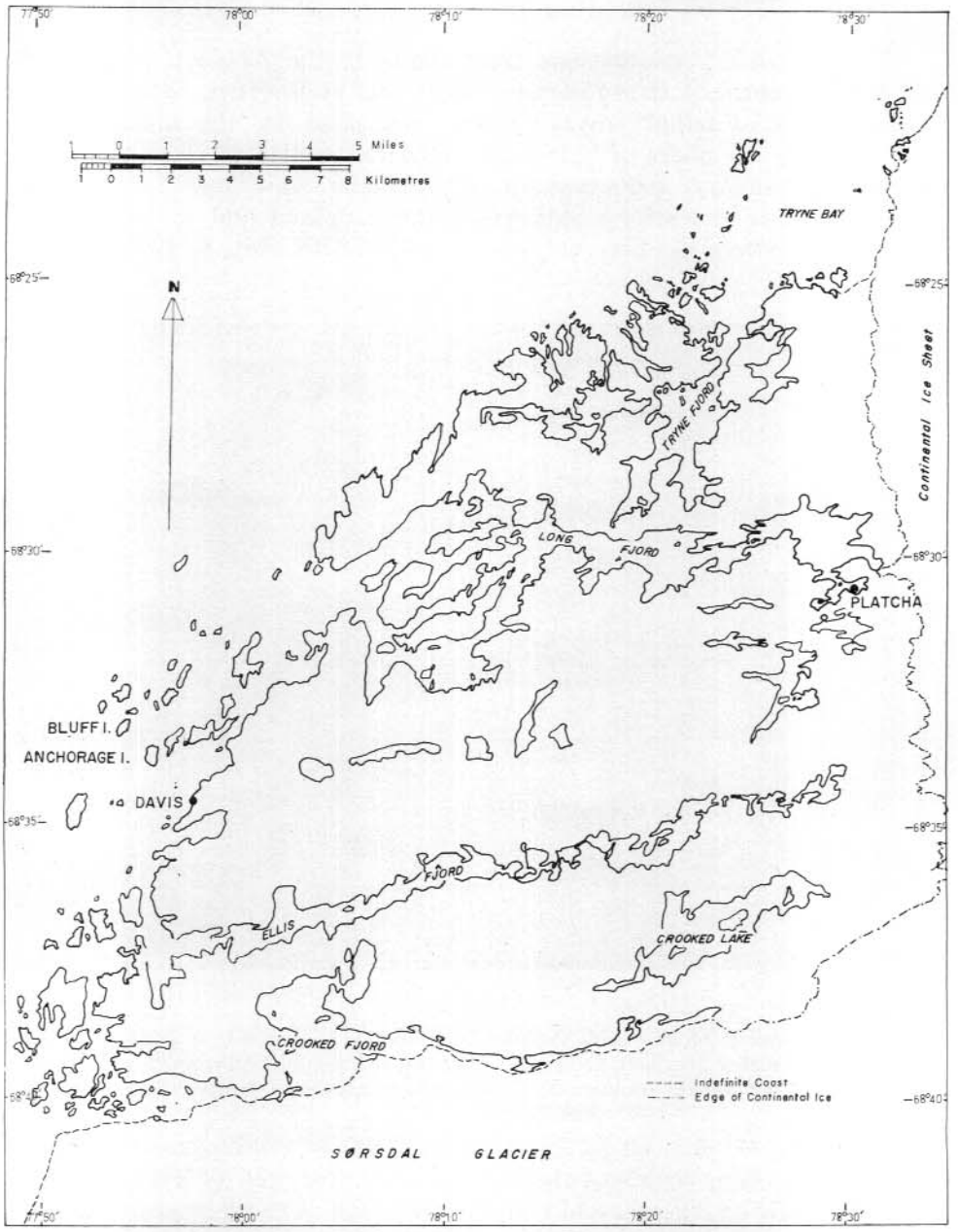
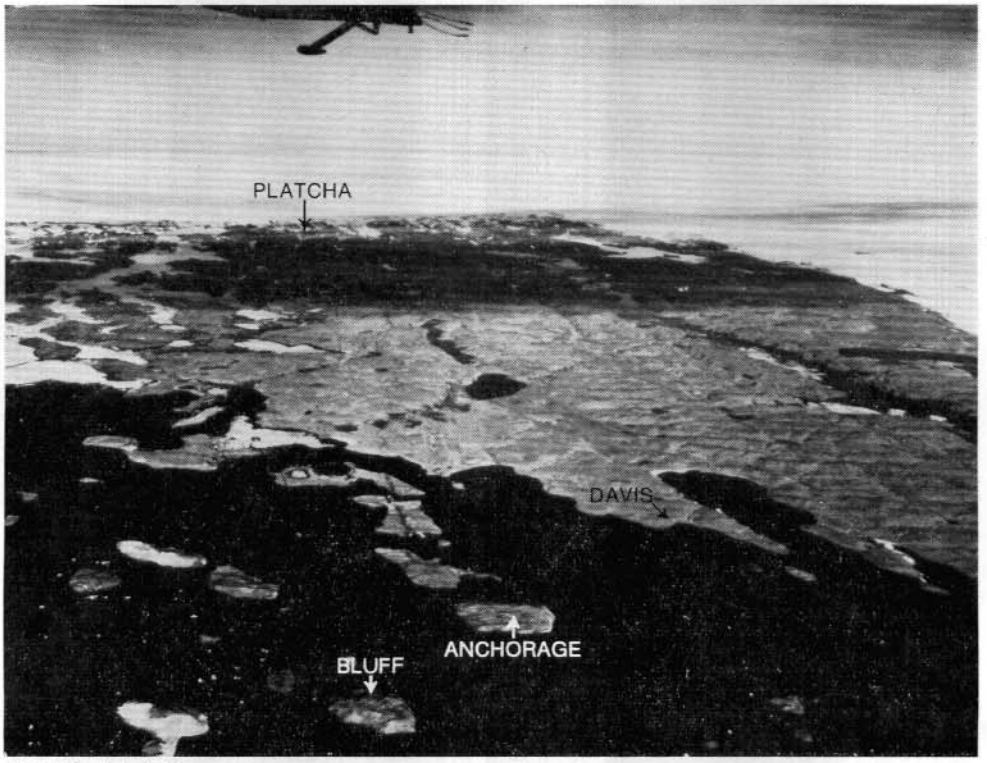


FIG. 2. Vestfold Hills, Antarctica, showing the general locality of Davis, Anchorage Island and Platcha.

numbers on the inland mountains, particularly the Masson Range. Details of the author's study area at Mawson are given in Section IV.

Davis (68°35′S, 77°58′E) is situated on the east side of Prydz Bay in Princess Elizabeth Land, Antarctica (Figure 2; Plates 2, 3). In the



ANARE photo 7177

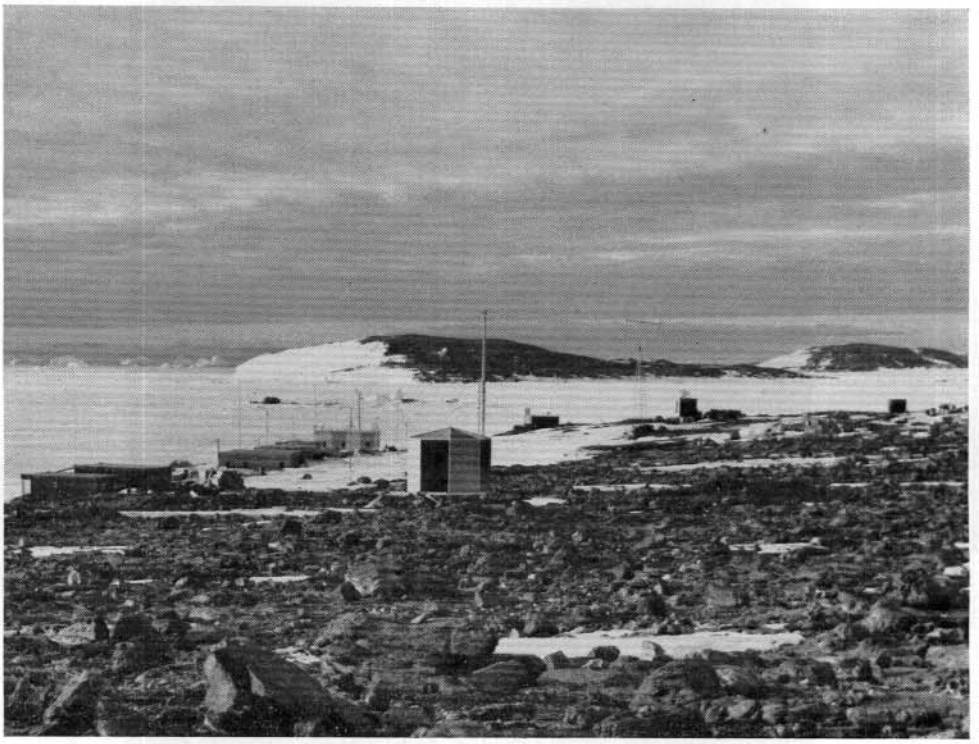
PLATE 2

The general localities of Davis and the Vestfold Hills, Antarctica, looking east-south-east. Long Fjord on the left; Anchorage Island centre foreground.

vicinity of the ANARE station, the general trend of the coast is south-west and north-east, and there are numerous off-lying islands. One of these—Anchorage Island (68°34′S, 77°56′E)—was the author's principal study area in 1961-62. It lies about 2·5 km north-west of the station. Eastwards from the station is a roughly triangular ice-free area, about 500 sq km in extent, known as the Vestfold Hills. These hummocky hills, up to 230 m in height, are broken by moraine-filled valleys, long narrow fjords and numerous lakes, and are bounded to the east by the inland ice sheet and to the south by the Sörsdal Glacier. Platcha (68°31′S, 78°31′E) a satellite weather station, lies near the eastern margin of the Vestfold Hills, at the head of Long Fjord, and was the author's subsidiary study area in 1961-62. It is about 23 km east-north-east of Davis. Snow Petrels nest on the cliffs of

many of the off-lying islands and on the hills and ridges. Details of the study areas on Anchorage Island and in the vicinity of Platcha are described in Section IV.

All specimens collected by the author have been deposited either with the National Museum of Victoria in Melbourne or with the Queensland Museum in Brisbane. ANARE field note books, logs and nest records are in the archives of the Antarctic Division, Department of External Affairs, in Melbourne.



ANARE photo 9986 D. Hobby

PLATE 3

The ANARE station at Davis, Antarctica. Anchorage Island is in the middle background.

II. DISTRIBUTION

The distribution and known breeding localities of Snow Petrels in the Antarctic, are shown on Figure 3.

A. Breeding range

Snow Petrels probably breed wherever exposed rock provides suitable nest sites on the sub-Antarctic islands, on the coasts of Antarctica and off-lying islands, and for many kilometres inland in Antarctica. In some localities they are extremely numerous; for example, on the Masson Range,

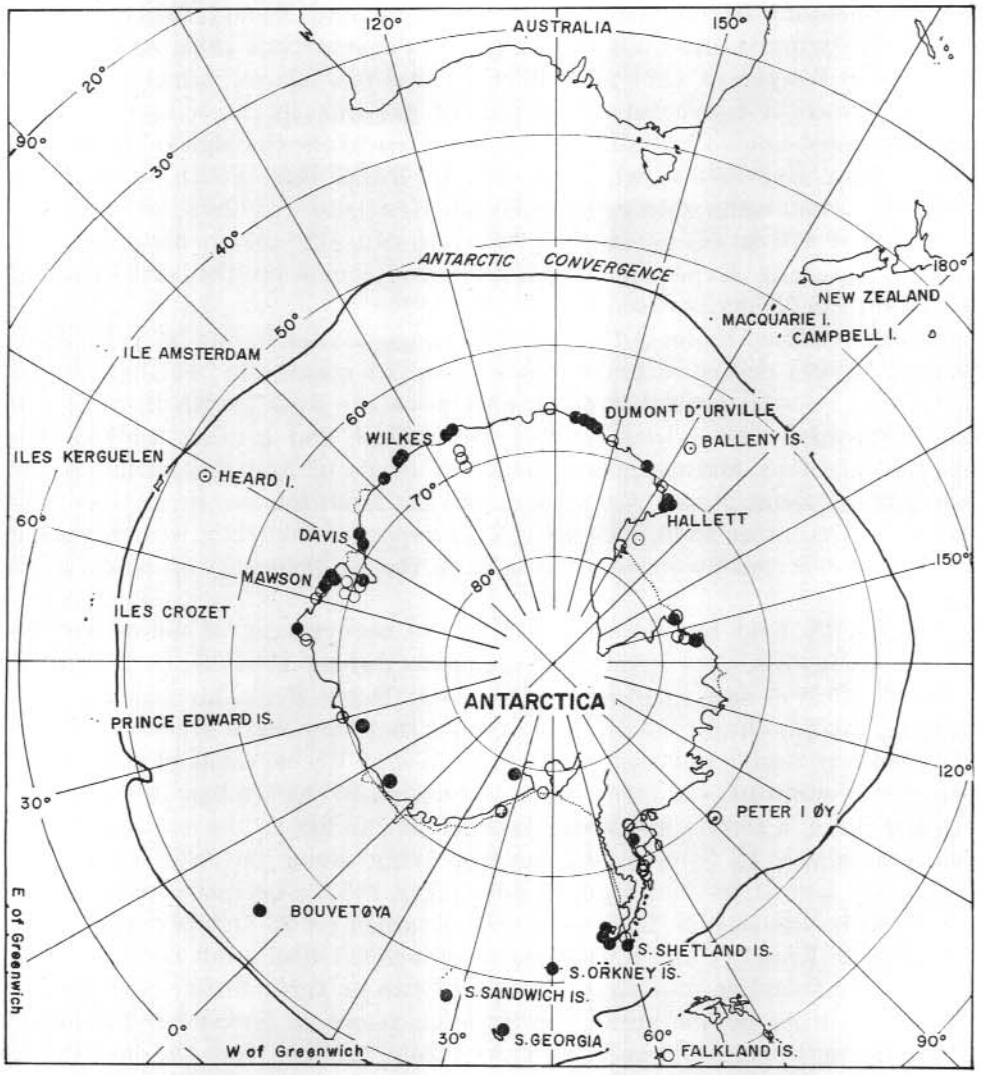


FIG. 3. Distribution and known breeding localities of Snow Petrels in the Antarctic.

Mac.Robertson Land, thousands are known to breed. They are more often found in relatively small colonies of less than a hundred nests.

Snow Petrels might be expected to breed on the Balleny Islands and Peter 1 Öy, but no nests were seen during brief visits to these islands in 1927-28 and 1947-48 respectively (Holgersen 1945, 1957). At the Balleny Islands, in March 1964, Kinsky (Hatherton *et al.* 1965) saw Snow Petrels disappearing into cracks in the rock walls on Sabrina Islet, and "assumed" that they bred there. They breed in the South Sandwich, South Orkney and

South Shetland Islands (Ardley 1936; Kemp and Nelson 1931; Murphy 1936). They breed also on South Georgia (Pagenstecher 1885, *cit.* Murphy 1936) and Bouvetöya (Solyanik 1959). These two islands, which are south of the Antarctic convergence but free of pack ice in the winter, are the northernmost-known breeding places. Members of the German International Polar Year Expedition, who wintered in Royal Bay, South Georgia, in 1882-83, found nests with eggs on Mount Krokisius (54°29′S, 36°06′W) at a height of 470 m (Pagenstecher 1885, *cit.* Murphy 1936). Members of a Soviet Antarctic Expedition reported two colonies on the east coast of Bouvetöya in November 1958 (Solyanik 1959).

The southern limits of the breeding range are far inland in Antarctica. Wilson (1907) described Snow Petrels as great wanderers; during 1901-04 they were seen by several sledging parties on the Ross Ice Shelf, some 110 km from open water. In December 1934, Siple and Lindsey (1937) discovered a colony and described the great flocks of breeding birds on the summit of Mount Helen Washington, 82 km from the sea in Edward VII Land. In December 1940, Eklund (1945) reported that they were breeding in the Fosdick and Swanson Mountains in the western part of Marie Byrd Land.

ANARE field parties recorded inland occurrences of Snow Petrels south of Mawson on a number of occasions during 1954-58. In December 1954, R. Dovers saw them several times at Depot Peak, an isolated peak 160 km inland, but, although he suspected that they were breeding, he did not find any nests. Further south, near Mount Béchervaise in the Prince Charles Mountains, six birds were sighted on 27 November 1955, and at Beaver Lake, a frozen meltwater lake about 135 km to the south-east and 250 km inland, B. Stinear saw several flying along the tide cracks and round the sandstone bluffs on 16 November 1957. Conclusive evidence of breeding in the Beaver Lake area was obtained on 28 October 1958 by I. McLeod, G. Knuckey and R. Oldfield when several dead adult birds and one chick were found at nest sites. Groups of two or three birds were seen at inland localities by the author on three occasions in November-December 1958, the most southerly sighting being about 415 km from the sea and 90 km west of the Prince Charles Mountains. In 1961, N. Smethurst of ANARE recorded similar numbers about 360 km inland from Wilkes (66°16′S, 110°32′E) in Wilkes Land.

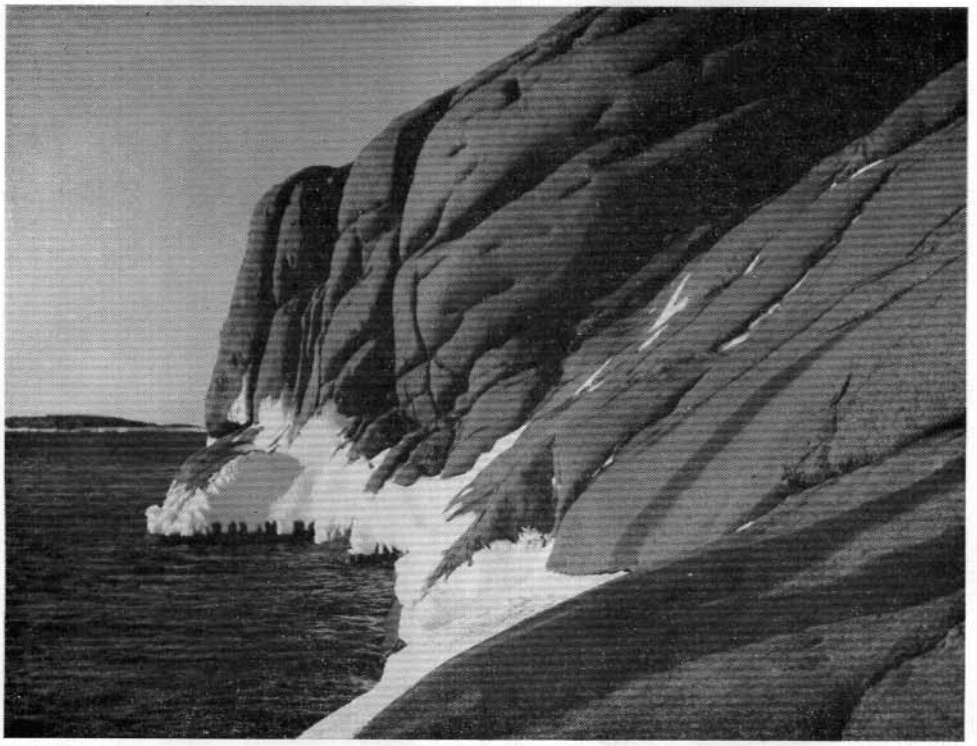
During the British Commonwealth Trans-Antarctic Expedition of 1955-58, Snow Petrels were reported on Mount Faraway in the Theron Mountains of Coats Land, 250 km from the sea and probably the southernmost breeding place. During a flight by the same expedition to the east of Halley Bay on 11 January 1957, a number of birds were seen flying near the summit of a 2130 m peak in mountains estimated to be 415 km from the coast (Fuchs and Hillary 1958).

Lövenskiold (1960) reported Snow Petrels breeding on the mountains known as Fimbulheimen, 160-210 km inland in Dronning Maud Land, and

Van Autenboer (1962) reported colonies in the nearby Sör-Rondane group, about 200 km inland.

B. Non-breeding range

Routh (1949) and Holgersen (1957) found that Snow Petrels followed the receding ice very closely and scarcely ever moved out of sight of it: the maximum distance from the ice edge at which they were observed was 60 km. All biological logs, since annual ANARE expeditions to Antarctica commenced in 1953-54, confirm previous accounts that, at sea, Snow Petrels are rarely seen away from pack ice, none being seen north of 62°S. It appears that they never occur regularly or in numbers north of about 60°S, except in the neighbourhood of ice-covered islands (Saunders 1901, *cit.* Murphy 1936) where they probably breed. They are rare visitors to Heard Island, just south of the Antarctic Convergence (Downes *et al.* 1959), and were formerly winter visitors to the Falkland Islands (Bennett 1926), but have not been recorded there recently (Cawkell and Hamilton 1961). Cook (1777) first saw them among icebergs in 51°50′S, 21°03′E, in December 1772.



ANARE photo 7763B D. A. Brown

PLATE 4

Cliffs on the western side of Horseshoe Harbour, near Mawson. Snow Petrel nests are located in the weathered joints of the bedrock.

The non-breeding distribution can be related to seasonal pack ice distribution and water temperatures as described by Mackintosh and Herdman (1940), and Mackintosh (1946). The non-breeding distribution is also related to food supply enhanced by the cold water melt of the pack ice.

III. ENVIRONMENT AND BREEDING HABITAT

A. Types of breeding habitat

Snow Petrels breed in ice-free areas. They use naturally occurring holes and crevices in rocks which provide overhead cover as a protection against predators. Although their digging is restricted to clearing away snow, they are the Antarctic counterpart of the burrowing petrels of lower latitudes. The densest populations occur on cliffs, hills and mountains, at heights of more than 65 m above the surrounding sea, ice or land.

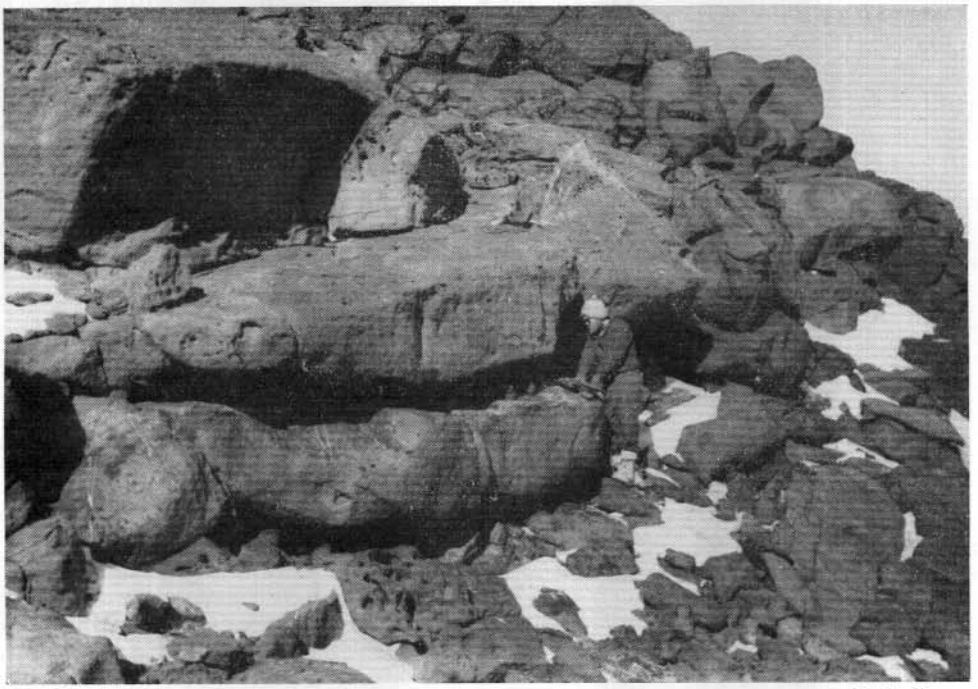
The nest sites are of two main types; the first consists of cracks in the bedrock caused by weathering along vertical and horizontal joints, and the second of spaces under and between boulders in moraines. The former occur in coastal cliffs (Plates 4, 5) as well as on inland peaks and ridges where

ANARE photo D. A. Brown

PLATE 5

Typical cliff-nesting terrain near Platcha in the Vestfold Hills. In the foreground is rafted sea ice.

wind has removed most of the overlying moraine and exposed the bedrock (Plate 6). Moraines cover many islands, and are common on both coastal and inland rock outcrops. In sheltered places the morainic material is of every size, from large boulders to small stones and sand which fill the crevices (Plate 7). With increasing elevation and exposure, wind removes progressively larger material until, on high ridges, only large erratic boulders and bedrock remain, and more and more potential nest sites remain uncovered. In the second type, nest sites are less frequent at lower levels, being more readily blocked by blown sand and by falling or drifting snow.



ANARE photo D. A. Brown

PLATE 6

Nesting terrain at high elevation near Platcha in the Vestfold Hills. Note absence of small morainic material and snow accumulation.

Sand is a problem only in extensive low-lying, ice-free areas such as the Vestfold Hills, but falling snow is important at all locations. In coastal regions drift is widespread, frequent and confined to low levels. When drifting snow, which is dry and powdery, accumulates on the lee sides of rocks, it freezes and blocks the crevices. The height to which it rises is governed by the wind speed, but even in the worst storms this height rarely exceeds 65 m. Probably it is this vulnerability to drift, together with the availability of sites at high levels, which accounts for Snow Petrels breeding on inland mountains.

Frozen spray may permanently block potential sites on the windward sides of coastal cliffs. Near Davis, occupied nests were found on the leeward sides of several islands, just above high tide mark and only a little over one metre from the water's edge.

ANARE photo D. A. Brown

PLATE 7

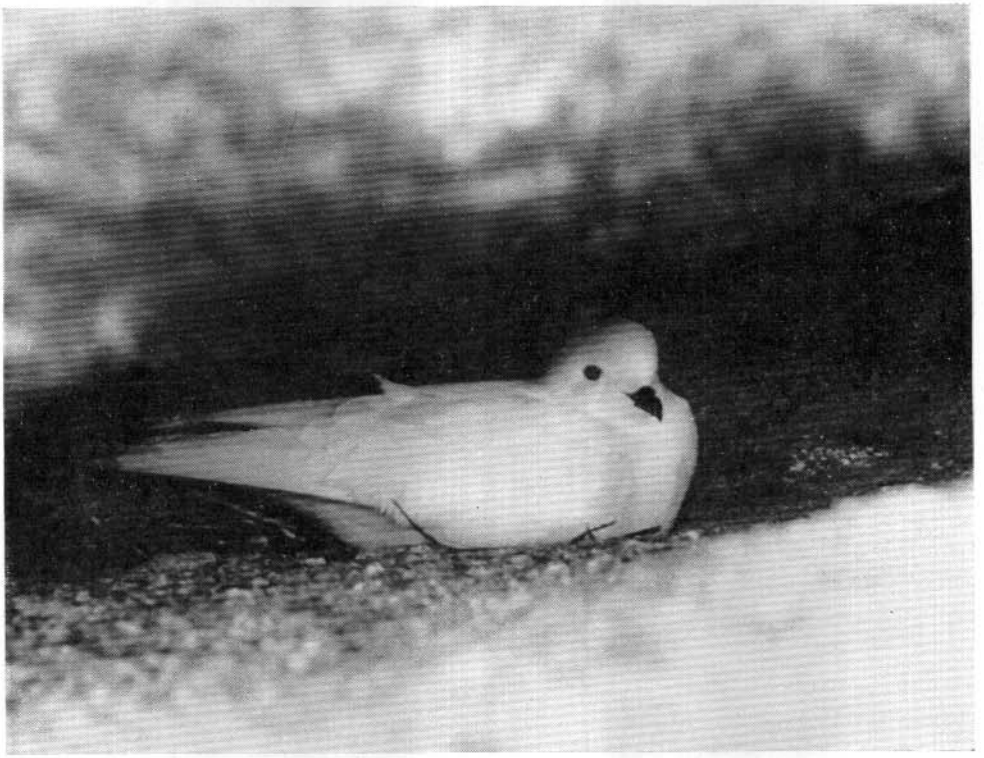
Moraine-covered nesting terrain at intermediate elevation near Platcha in the Vestfold Hills. This type of coastal terrain generally provides the most common nesting facilities for Snow Petrels.

Snow Petrels do not compete with other birds for nest sites, but may be inconvenienced by them. At Bluff Island, near Davis, where Cape Pigeons *Daption capensis* frequently nested on ledges in front of crevices occupied by Snow Petrels, the latter had to make repeated attempts—in one case lasting for several days—before they could enter their holes.

B. The nest

Once the basic requirement is satisfied—a hole or crevice protected against predators and relatively free from blockage—the nest may take many forms. For example, nests under moraine debris tend to be larger than those in rock crevices. The entrance may be more than a metre wide, it may be so small that the bird has great difficulty in squeezing through, or it

may take the form of a natural tunnel more than a metre in length. While many nests have only one entrance, two entrances are more common, and three have been observed in the moraine type of habitat. Multiple nest sites are frequent, especially in moraine associations where as many as eight nests may be grouped together under one rock only a metre or so in diameter; the cave colony on Laurie Island in the South Orkney Islands, described by members of the Scottish National Antarctic Expedition in 1903-04 (Brown *et al.* 1906) is an extreme case. In all habitats the nest entrances were found to face all directions equally, being dependent more on the terrain than the prevailing winds.



ANARE photo R. J. Francis

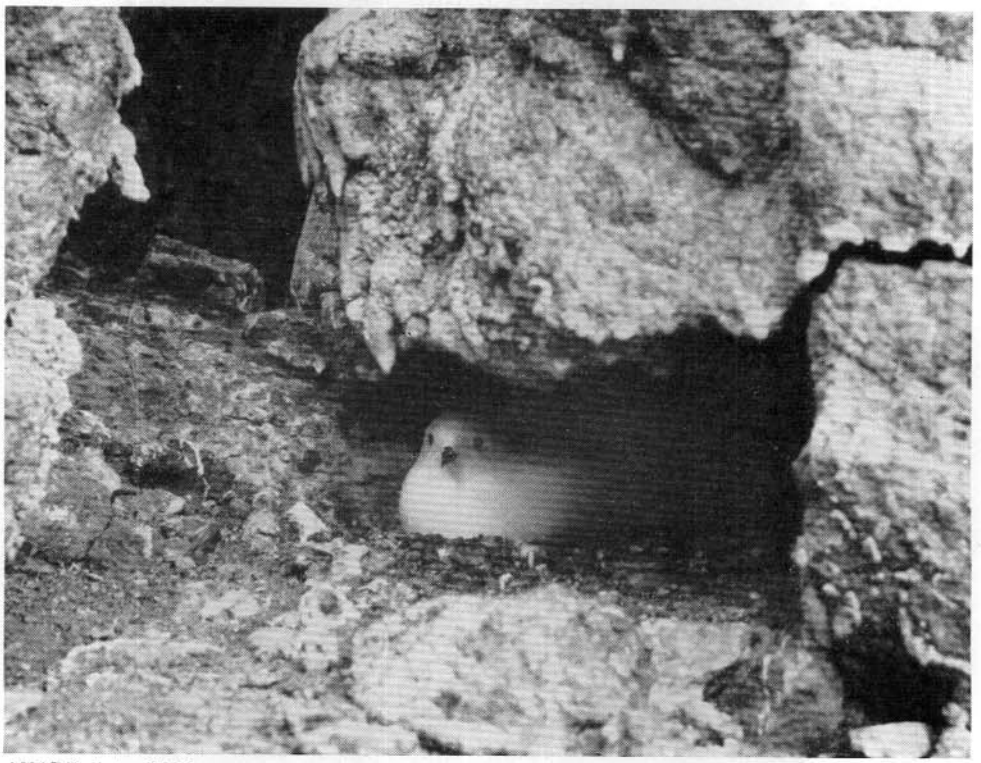
PLATE 8

Snow Petrel on nest with Adélie Penguin feathers as part of the nesting material.

The floor of a nest chamber is usually flat and consists of small rock fragments; on some coastal outcrops and islands it also includes sand and feathers of Snow Petrels and Adélie Penguins *Pygoscelis adeliae* (Plate 8). On rare occasions small quantities of marine algae are also present. Since Snow Petrels do not collect nest material, it is presumed that the penguin

feathers are blown into some nests after the annual moult. Dead chicks and old eggs from previous seasons are pushed to the edges of nests and out of them by the birds' movements; they are neither used as nest material nor deliberately ejected. In some nests which have very restricted openings, as many as 13 dead chicks and several eggs have been noted.

All nests show signs of former habitation and most of them are clearly recognizable by accumulations of a dried, light-coloured oily substance both at the entrances and inside the nest chambers (Plate 9). This is solidified



ANARE photo 6390B J. Béchervaise

PLATE 9

Incubating Snow Petrel in well established nest site with accumulations of solidified stomach oil adhering to the surrounding rock surfaces.

stomach oil, for Snow Petrels, like other petrels, use the oily secretion of the proventriculus in self-defence. When incubating adults and unguarded chicks are disturbed by non-breeding birds, they drive them away by screeching and discharging oil. Much of this oil lands on the surrounding rock and solidifies. In coastal areas, the season's deposit melts and evaporates in summer, leaving only a whitish film; in the colder inland areas, such as the Masson Range, it accumulates from year to year and may be several centimetres thick. Originally orange in colour, the deposits turn opaque after freezing and then bleach in the summer sunlight.

IV. STUDY AREAS

A. Physiography

The study areas at Mawson were close to the ANARE station. Plate 10 gives a general view of the locality and Snow Petrel nests in this locality are shown on Figure 4. The west-facing cliff on the western arm of Horse-

ANARE photo 5591 P. G. Law

PLATE 10

Entrance to Horseshoe Harbour. The ANARE station buildings are in the centre; Mount Henderson in the background.

shoe Harbour (Plate 4) is almost vertical, about 15 m high, and provides nest sites of the first type described in Section IIIA. Geological features at and near Mawson have been described by Crohn (1959). Close to and south of the ANARE station, the bedrock of porphyritic charnockitic granite is dotted with large boulders (Plate 11); an area of 12,000 sq m of the highest ground (which rises to 34 m) is completely covered with moraine (Plate 12). On the exposed slopes, rock fragments of diameter less than 15 cm have been removed by the wind; in sheltered places, fragments of diameter less than 25 mm cover the bedrock to a depth of 8-15 cm. Nest sites of the second type described in Section IIIA are concentrated mainly in the exposed moraine.

Anchorage Island, the principal study area near Davis, is about 55 m high and largely covered with moraine. Snow Petrel nests are predominantly of the second (moraine) type and are concentrated at all levels on the south-eastern slope, which faces across the prevailing wind (Figure 5; Plate 3). Even on exposed slopes the moraine still includes rock fragments

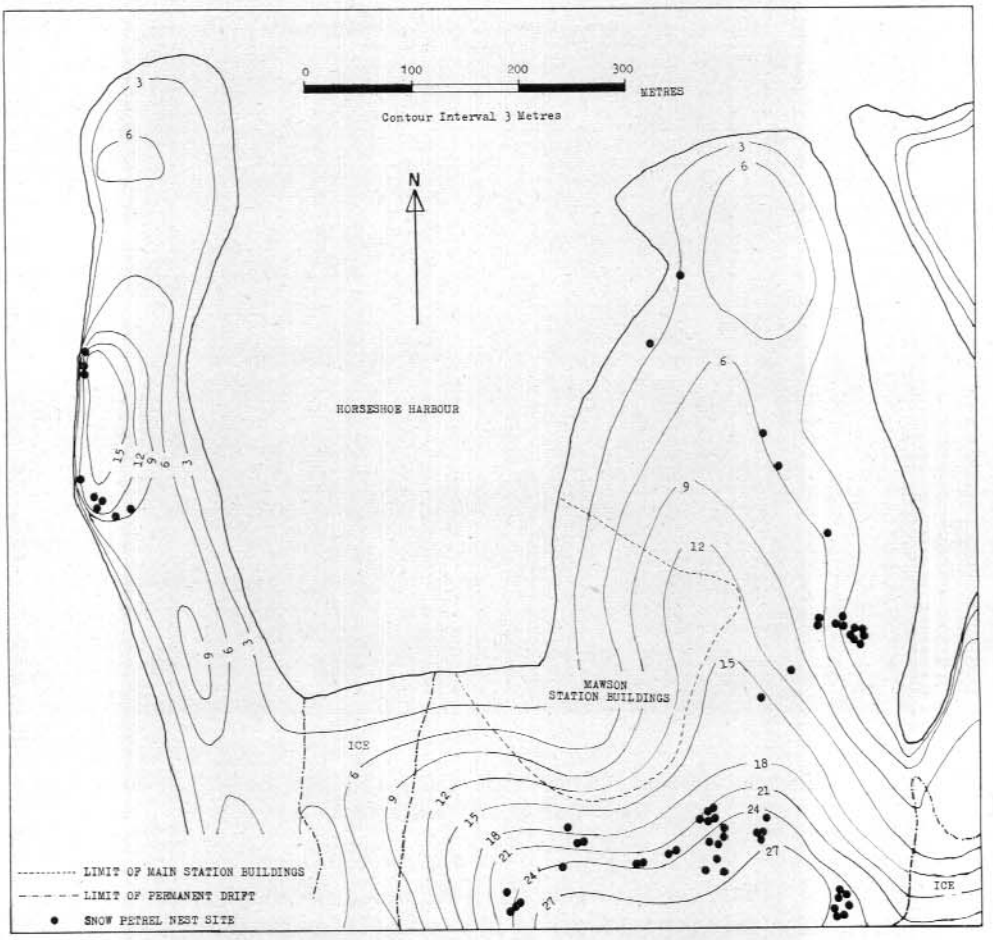


FIG. 4. The location of Snow Petrel nests in the vicinity of the ANARE station at Mawson.

as small as $2\frac{1}{2}$ cm in diameter; in sheltered places, sand has accumulated to a depth of several centimetres. At higher elevations in the Vestfold Hills, only the larger moraine material remains. The bedrock is composed of medium-grained gneiss. Snow Petrel nest sites near Platcha, the subsidiary study area, are located mainly on the highest ridges (Plate 13), and are predominantly of the first type described in Section IIIA.

B. Climate

The climate at both Mawson and Davis is cold, with high winds often accompanied by surface drift. The following figures have been taken from ANARE Reports covering the years 1954-58 at Mawson and 1957-58 at Davis (Bureau of Meteorology 1957, 1958, 1959, 1960, 1961), and from unpublished records from both stations covering 1958-61.

Temperature data for both stations are summarized in Figures 6 and 7 and Tables 1 and 2. The overall mean annual temperature is slightly higher at Davis than at Mawson; also the monthly means. The extremes are

ANARE photo 8518 J. Béchervaise

PLATE 11

The ANARE station at Mawson. There are Snow Petrel nests under the morainic rocks.

TABLE 1

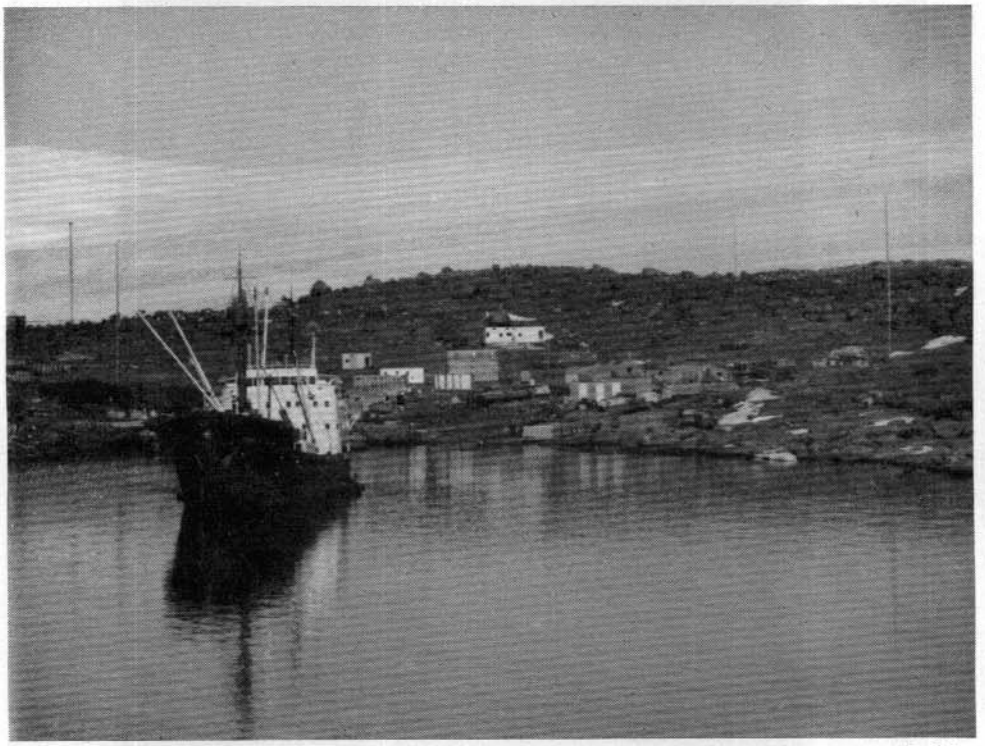
Mean temperatures at Mawson and Davis (°C)

	Daily			Maximum			Minimum		
	January	July	Annual	January	July	Annual	January	July	Annual
Mawson	−0·1	−17·6	−10·9	2·3	−14·9	−8·2	−2·8	−20·1	−13·7
Davis	0·1	−17·0	− 9·9	1·7	−14·3	−7·6	−2·1	−20·0	−12·7

TABLE 2

Extreme temperatures at Mawson and Davis (°C)

	Maximum			Minimum			Extreme
	January	July	Annual	January	July	Annual	Range
Mawson	7·7	−1·3	8·3	−8·0	−32·6	−34·7	43·0
Davis	6·0	−1·3	7·2	−8·6	−37·9	−37·9	45·1



ANARE photo 8858 H. Price

PLATE 12

Extensive moraine coverage at higher elevations at Mawson.

slightly lower. These differences may be due to the lower wind speed and greater cloud cover at Davis. In December and January the higher temperatures are associated with frequent light sea breezes, short calms and much sunshine. Inland temperatures may be as much as 33°C below coastal ones at any time of year. The temperature lapse rate is about 10°C/1000 m of altitude.

At Mawson, the sun is wholly below the horizon between 31 May and 13 July (44 days) and wholly above it between 2 December and 11 January (41 days). At Davis the corresponding periods are 25 May-19 July (56 days) and 26 November-17 January (53 days).

The cloud cover (Table 3) is greater at Davis than at Mawson.

TABLE 3

Illumination at Mawson and Davis

	Mean Daily Sunshine (hours)			Mean Monthly Cloud (eighths)		
	January	July	Annual	January	July	Annual
Mawson	9·4	0·7	5·0	5·0	4·0	4·5
Davis	9·3	0·2	4·0	5·0	5·2	5·2

The most striking climatic difference between Mawson and Davis is the mean wind velocity (Table 4), which at Mawson is more than twice that at Davis. The difference occurs consistently throughout the year. Mawson, which is close to the inland ice sheet, lies in the path of strong

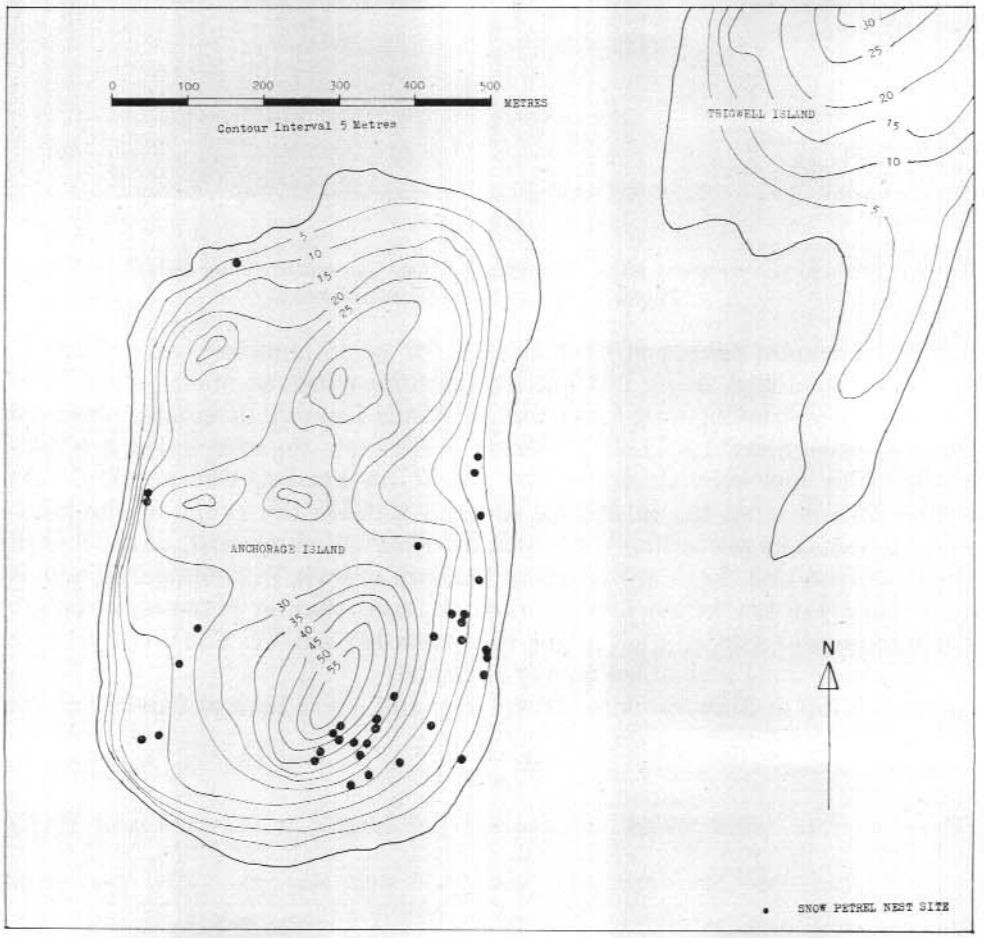


FIG. 5. The location of Snow Petrel nests on Anchorage Island near Davis.

ANARE photo D. A. Brown

PLATE 13

Long Fjord and the Vestfold Hills near Platcha. The densest breeding colonies of Snow Petrels are on the highest ridges.

katabatic winds; speeds of over 100 km/hr being common and the maximum recorded gust being 208 km/hr. Onshore winds at Mawson are light and rare, constituting only 7 per cent of winds from all directions observed during 1955 (Shaw 1957). In summer, at Mawson, the afternoons are relatively calm but evening winds are about 55 km/hr. Davis, which lies nearly 25 km from the inland ice sheet, is outside the range of the katabatic winds. The prevailing wind is approximately north-east, parallel with the coastline, and there are frequent onshore breezes in summer. Winds of more than 110 km/hr are less common at Davis than at Mawson, although the maximum recorded gust at the former is 187 km/hr. The wind pattern at Platcha in 1961 resembled that at Mawson.

Snowfall at Mawson is relatively low, and lower than at Davis, but the

TABLE 4

Mean surface wind speed (kilometres per hour) at Mawson and Davis

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean
Mawson	30·4	37·4	38·7	37·6	43·5	41·7	42·6	41·7	41·7	39·3	35·6	29·8	38·3
Davis	17·4	20·8	20·6	13·0	15·4	16·7	17·4	14·6	15·2	16·3	18·0	20·2	17·1

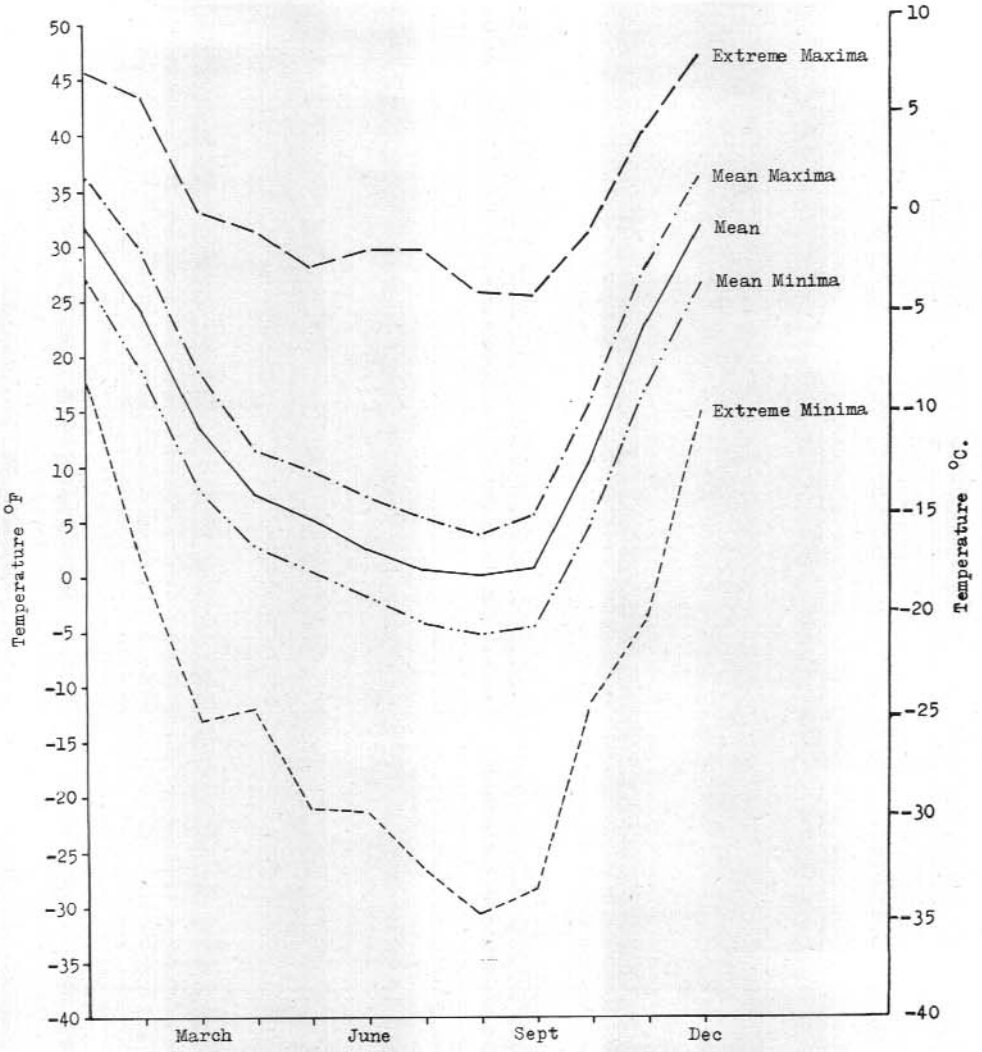


FIG. 6. Temperature variations at Mawson, 1954-62.

combination of snowfall and drift is greater than at Davis in summer. Since drift depends mainly upon wind, it follows that Snow Petrel nests in the vicinity of Davis should be less liable to snow blockage than at Mawson: observations have confirmed that this is so. This is offset, however, by sand blockage of potential nest sites in parts of the Vestfold Hills, a hazard which does not occur at Mawson.

C. Sea ice

The following is based upon a report by Mellor (1960) on sea ice measurements at both Mawson and Davis in 1954-58, and upon the author's observations.

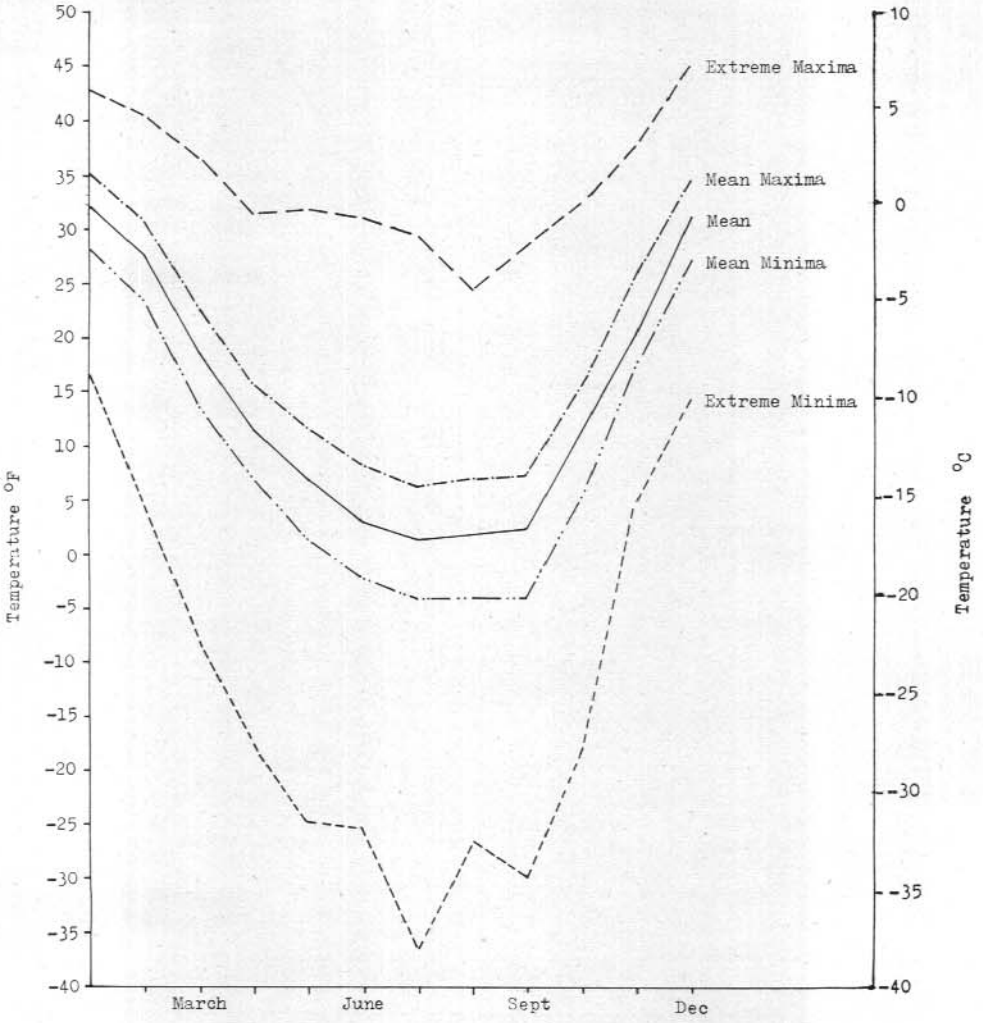


FIG. 7. Temperature variations at Davis, 1957-62.

At both stations pancake ice normally forms in early March and, by late March, the inshore waters are completely frozen. The sea ice reaches its maximum thickness and extent in late September or early October. From mid-October onwards it is progressively eroded and in January the last of it is usually blown out to sea, leaving an ice-free belt between the land and the pack ice.

During the winter, both tidal movements and slow-moving icebergs may, at times, create open leads. On unprotected coasts, ice may break out at almost any season. In summer, the final break-out may be delayed in enclosed bays and by off-shore islands and grounded icebergs. Bunt (1960) has shown that thick sea ice may delay the onset of photosynthesis in the

ocean in spring and the consequent rise in the plankton population beneath the ice. A wide belt of fast ice persisting into the summer is not only a physical barrier which breeding birds must cross in order to feed, but it also depresses food production.

V. METHODS OF STUDY

At Mawson, 68 nests were studied during 1958-59. They were marked with yellow numbers painted on the rocks under which nests were situated. These numbers were used for nest identification until 1962.

Banding was completed during the courtship-mating period in 1958. Seventy-one birds (35 pairs) were banded with approved CSIRO Wildlife Survey metal bands, size 080. Twenty-one pairs could not be banded due to the inaccessibility of their nest crevices. Six of the remaining 11 nests were occupied infrequently by single birds. Five nests were never occupied.

In the summer of 1958-59, observations at Mawson were made every day during the courtship, egg-laying and hatching periods and every second or third day during the intervals between these periods, except when blizzards prevented observations on four days between courtship and egg-laying, and for a similar period halfway through the incubation period. Chicks were checked every day after stormy weather and, when the nests were clear of snow, every second day. Abandoned and unused nests were checked infrequently after the first week in February. In the early part of the season observation times varied but, when hatching commenced, they were consistently at about 1900 hours local time.

During the years 1959-62, work at Mawson was confined mainly to recovering banded birds at nest sites and determining egg-laying, chick-hatching and departure dates.

At Anchorage Island, near Davis, 25 nests were studied during 1961-62. None was marked with paint. Instead, the nest positions were carefully plotted on a contour map of the island and each was allotted a number. This method was adequate for a small colony and was adopted in this case to minimize interference. For the same reason no birds were banded, but a spot of "Waxoline" dye was used to identify individuals during incubation and brooding. The dye was applied to the forehead with a small piece of cotton wool attached to the end of a long, slender rod. Nineteen pairs were marked and two colours were used—blue for one bird of a pair and red for its mate. Although touching-up was necessary from time to time this method of identification was adequate.

Observations at Anchorage Island were made daily from 5 November 1961 to 14 January 1962, with the exception of four separate days when high winds prevented travel from Davis across the sea ice. Two of these days were between courtship and egg-laying, the remaining two halfway through the incubation period. Observation times varied between 2100 hours and midnight local time until 23 December 1961, after which they were at about 0900 hours local time (the safest time to cross the sea ice).

Descriptions of behaviour at both Mawson and Anchorage Island are based on field observations lasting from one to four hours each day of the breeding cycle. Notes were made at the colonies in field note books and were written up later in the permanent logs and on nest record sheets at the stations. Chicks were weighed in sheltered positions close to nest sites with spring balance scales accurate to one gram. Egg and bird specimens collected in the Davis area were weighed with medical scales accurate to one tenth of a gram. All linear dimensions were measured with vernier calipers. Identification of the different sexes is based on the following distinctions:

1. Males had consistently lower-pitched calls than females.
2. Males of mated pairs were larger than females (see Section X and Table 11).
3. The heads, necks and chests of males appeared to be larger, in relation to their overall size, than females (see Plate 15).

The distinctions were determined as follows:

The pitches of the calls of 14 individuals (six mated pairs) in the Davis area were recorded in 1961—two on magnetic tape. Subsequent dissection of the collected birds confirmed that males had lower-pitched calls than females. Similar results were obtained at Anchorage Island in November 1961 by recording the pitch differences of seven mated pairs, then positively identifying the sexes during copulation.

To test the accuracy of the remaining factors, the sexes of 20 birds (10 mated pairs) collected in the Davis area in November 1961 were assessed before dissection: 18 were correct. There was some doubt about the remaining pair since both birds were small and they did not exhibit clearly the physical differences listed above.

It is emphasized that all three distinctions must be considered before an accurate assessment of sex can be made. It is further emphasized that, while this method of sex identification was not completely satisfactory for casual assessments of isolated individuals in the field, it was accurate for mated pairs, especially those at the marked nest sites on Anchorage Island, since both sexes were under close scrutiny from early November 1961 until mid-January 1962.

VI. ARRIVAL, COURTSHIP AND MATING

A. Arrival

Figure 8 depicts a typical Snow Petrel breeding cycle and Table 5 summarizes the known arrival, egg-laying and departure dates at Mawson, in the Davis area (within 5 km radius of the ANARE station) and in the Platcha area (within 2 km radius). At Mawson in 1958-59 and in the Davis and Platcha areas in 1961-62 particular attention was paid to early arrivals and late departures.

In the Platcha area in 1961, fresh Snow Petrel footprints and faeces

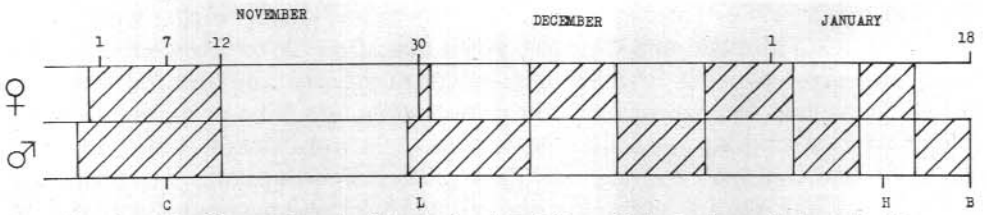


FIG. 8. Attendance at nest of typical pair of Snow Petrels from first arrival to end of brooding period. Hatched sections indicate presence of bird at nest.

C = copulation; L = laying of egg; H = hatching of chick; B = end of brooding period.

were first noted at or near snow-blocked nests on 9 September, and calls were heard at late dusk on 12 September. The first of these birds seen, at dusk on 13 September, were mainly single birds, with only occasional "pairs", which flew back and forth along the cliff faces and over land containing nest sites. Some single birds sat quietly on snow-covered ledges, but none was occupying nests or trying to gain access to them by digging in the snow. Small flocks of up to five (one of 25) birds were present each evening until 18 September; then only a few calls were heard each evening until 22 September, after which the birds were absent until the evening of 1 October. By that date, the snow in many nest crevices had melted and, on 2 October, four birds were seen in nests. Two of these were collected; both males. Their testes were enlarged (9·9 × 7·7 mm and 11·8 × 8·3 mm) compared with those of a specimen collected in late April (7·0 × 4·0), but smaller than those of specimens collected at Cape Hallett, Ross Dependency,

TABLE 5

Summary of arrival, egg-laying, and departure dates of Snow Petrels at Mawson and in the Davis and Platcha areas, 1954-1962

(The most reliable dates are in italics; a dash indicates that no record is available)

Locality	Season	First seen	Main influx	First egg	Last seen
Mawson	1953–54	—	—	—	4 April
,,	1954–55	14 October	4 November	4 December	10 May
,,	1955–56	*22 September*	*18 October*	4 December	*25 May*
,,	1956–57	10 October	1 November	—	27 April
,,	1957–58	3 October	31 October	—	*25 May*
,,	1958–59	*20 September*	*19 October*	*30 November*	*25 May*
,,	1959–60	*1 October*	—	—	24 May
,,	1960–61	—	30 October	—	*25 May*
,,	1961–62	17 October	*27 October*	*27 November*	—
Davis area	1956–57	—	—	—	4 May
,, ,,	1957–58	5 October	—	—	16 May
,, ,,	1959–60	—	—	*1 December*	8 May
,, ,,	1960–61	*15 September*	—	—	*1 June*
,, ,,	1961–62	*15 September*	*20 October*	*29 November*	—
Platcha area	1960–61	—	—	—	*5 June*
,, ,,	1961–62	*13 September*	*20 October*	*28 November*	—
Crooked Fjord*	1961–62	*19 September*	—	—	—

* Observation by author.

in November 1960 (Maher 1962). Three more single birds were seen entering nests at dusk on 3 October. Each flew directly to the vicinity of its nest and, after passing it three or four times, landed and entered immediately. It is not known exactly how long they stayed—probably several hours—but at midday the following day all nests were vacant, and remained so until late October. During this first period of occupation the birds sat quietly, neither digging out snow nor renovating their nests and only rarely calling feebly after dusk.

Apart from two calls heard on the evenings of 7 and 10 October, Snow Petrels were not seen again in the Davis or Platcha areas until 20 October, when the first birds of the main influx arrived. These were single birds of both sexes (identified by size, call and physical features only) which flew in from the sea at dusk and selected and sat on prominent rocks or ledges from which they took frequent short flights. During the next 10 days these activities continued and some single birds, mainly males, investigated or occupied nest sites in which they often remained during daylight.

Snow Petrels are rarely seen in numbers flying round their colonies during the day, unless snow blockage prevents entry to their nests.

B. Constancy of site and mate

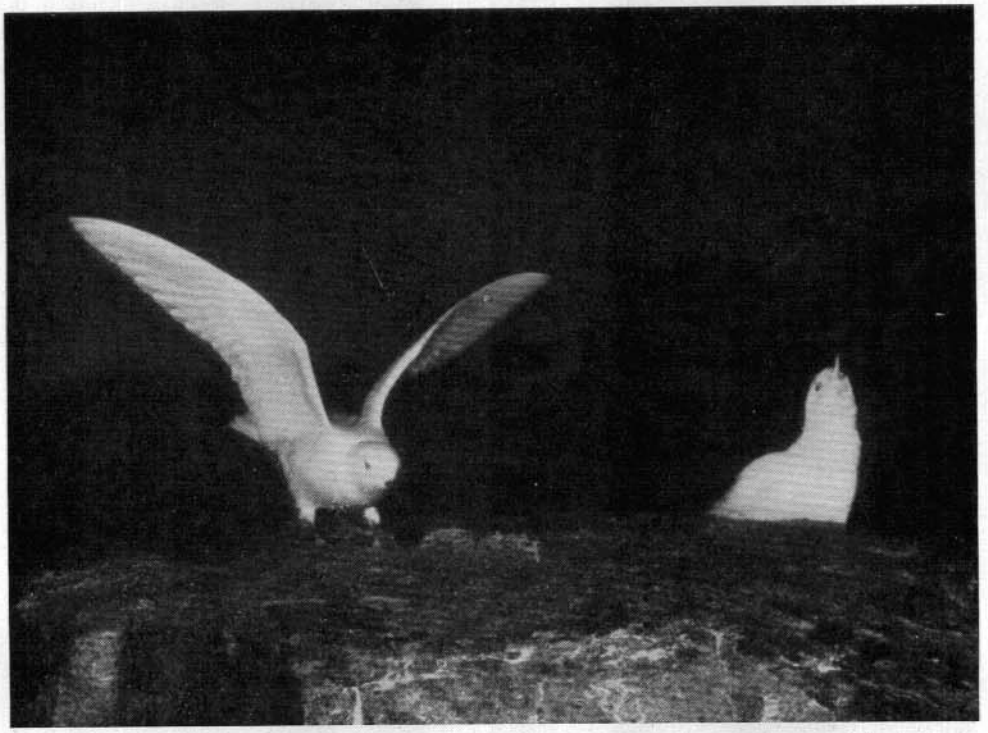
Banding results indicate that adult Snow Petrels return to the same nest each year and breed with the same mate. Of the 71 birds banded at Mawson in 1958, 39 had been re-sighted by December 1961; of these, 34 had re-occupied their old nest sites. This number included 10 pairs; the remaining 14 were either alone or with mates for which the band was not sighted. The five individuals which had not re-occupied their old nest sites were re-sighted during the courtship period, four of them being in nests only a few feet from their own. Each of the five was sitting with a companion, two of which were caught. One of these was not banded, and the other banded and in its correct nest. Two of the former mates of the five displaced birds were found at their correct nests, three were not re-sighted. The displaced birds may have been disturbed by recovery operations and they had shifted temporarily.

When mated pairs were collected from established nest sites at Anchorage Island during the courtship-mating period in 1961, their nests were not used for breeding that season. The holes were frequently occupied by single birds and non-breeding pairs, the latter occasionally staying for days at a time. At this colony there is no shortage of nest sites to limit breeding.

C. Courtship and fighting

At Anchorage Island, the peak influx of birds occurred on 1 November 1961. For the next few days, some birds remained at the colony during daylight; others, mainly un-mated, left again soon after sunrise. The length of the courtship-copulation period was not precisely determined, but was of the order of 10-15 days.

During courtship, differences in the behaviour of males and females at Anchorage Island were quite apparent. While the females remained for much of the time sitting on prominent rocks or in front of nest crevices, the males were constantly on the move, flying back and forth along the cliffs. In due course a male would make close but hesitant aerial approaches to a sitting female, whereupon she would start calling and shuffling about, with her bill wide open and head upturned in the direction of the male's flight movements (Plate 14). This appeared to be an invitation to courtship, and



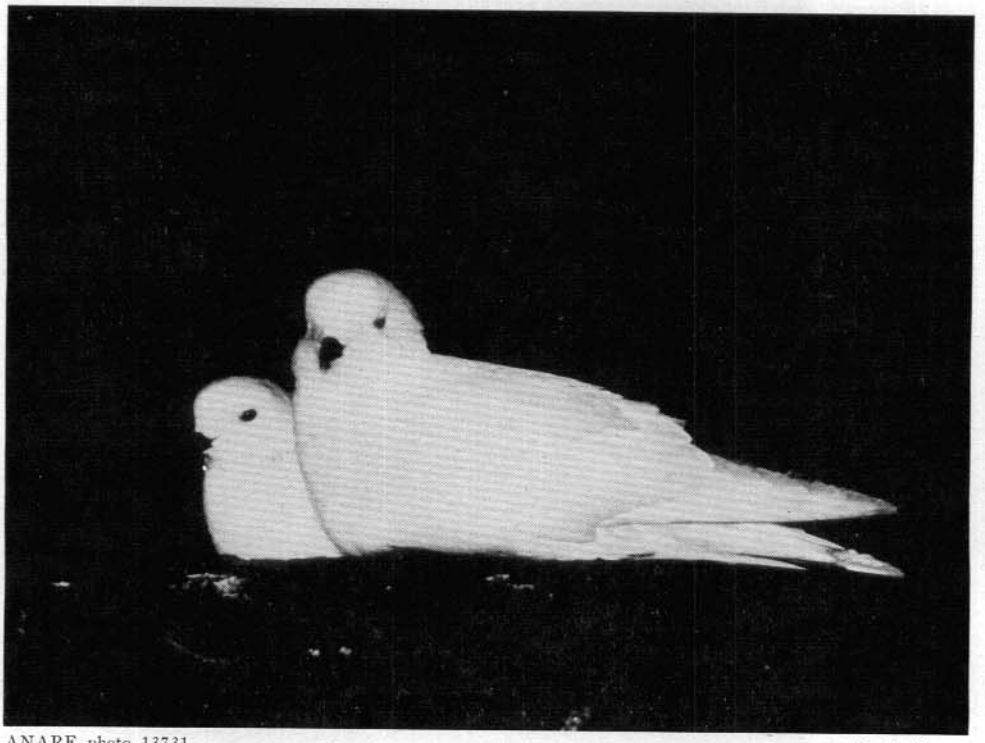
ANARE photo 13730 D. A. Brown

PLATE 14

Landing technique of the male Snow Petrel, and reaction of female during courtship.

mutual acceptance was immediately shown by an aerial courtship display. First, the female flew along the cliff at a height of about 15 m above sea level and at normal speed, the male following about one metre behind her and emulating every movement she made. Then, after about 10 seconds, both birds reduced flying speed and the female began a continuous series of chirring calls which were followed at once by the more normal calls of the male. At the same time both birds assumed a half-gliding, half-fluttering flight, with wings held high and legs extended slightly downwards. Bodies were arched so that the heads (which moved gently from side to side) and the tails were pointing upwards; at this stage the male was only a very

short distance behind the female and generally slightly above her. This display continued for about 10 seconds. Both birds then "chirred" in unison and lost about half of their original height. Finally, they resumed their normal flight and calls, and returned to the resting place or nest site. They remained together (Plate 15) indulging in minor mutual preening, accompanied by spasmodic calling and sometimes by gentle touching and quick retractions of bills. Both birds called loudly at any intruders flying low overhead or landing nearby and the male did not hesitate to fight them.



ANARE photo 13731 D. A. Brown

PLATE 15

Mated pair of Snow Petrels in front of nest site during the mating period. Note the different physical features of the two birds; female on left.

Courtship displays at Anchorage Island reached a peak during the first week of November. They were repeated several times each evening until copulation took place, then gradually fell off in frequency and intensity during the following seven days. After this, displays by mated birds were rarely seen. Non-breeders continued to display until the latter part of November but, if at this stage males displayed behind females, the latter responded either very weakly or not at all. By early December the last displays had changed to aerial chases during which the females usually took refuge in unoccupied nests or under rocks.

During courtship, signs of the intense competition both for partners and for nest sites were demonstrated by the large numbers of birds with plumage stained orange by the stomach oil of opponents. Fights followed either intrusion by unattached males on mated pairs, or attempted entry by mated pairs to occupied nests. They varied from short skirmishes to battles on the ground lasting several minutes. Only the males fought actively. A fight usually began at the nest entrance with the defending male rushing suddenly at the intruder. Both birds then grasped each other with bills interlocked, one bird holding the maxilla of its opponent, the other grasping the lower mandible. This was accompanied by violent levering of heads from side to side, loud screeching, lashing of wings, and forceful regurgitations of stomach oil. The wings appeared to be used for balance and leverage only, not as weapons. The bird holding the lower mandible of his opponent appeared to have a distinct advantage and invariably won. The losing bird made a final break on the ground, but was chased into the air by the victor which often grasped its tail feathers in mid-air, sometimes pulling out one or two. If the victor managed to grasp the loser by the flank or by the base of the tail with its bill, both fell to the ground together and the fight was resumed. The bird already in possession appeared to have a definite advantage over the intruder: of the 20 or more fights seen, the intruder always lost.

Stained birds retired to nearby snow ledges and drifts, where they removed the orange stains from their plumage. The whole process of cleaning might last up to 10 minutes and was achieved by sifting snow through the feathers in a manner similar to the dust baths of sparrows. Stains covering the eyes, forehead and cheeks were removed by pushing the bill its full length into soft snow, then vigorously rotating the head from side to side. Similar behaviour was also observed among Giant Petrels *Macronectes giganteous* at Davis after they had been feeding on the carcasses of seals.

D. Copulation

Observations showing pre-egg-laying activities at marked Snow Petrel nests on Anchorage Island are summarized in Table 6.

Copulation was first observed at this colony on the evening of 5 November and on subsequent days until 8 November 1961. At Bluff Island, about 1·5 km north-west of Anchorage Island (with a much larger Snow Petrel population), the last successful copulation was seen on 12 November 1961. Another, seen there on 14 November, may not have been complete.

Copulation always took place at night outside the nest. Paired birds moved to the entrances at dusk and sat together, calling frequently, rubbing bills and indulging in minor mutual preening. The female often placed her partly open bill between the upper and lower mandibles of the calling male (Plate 16) and the latter responded by gently pressing the underside of his bill on her forehead and nape. The female remained in a sitting position

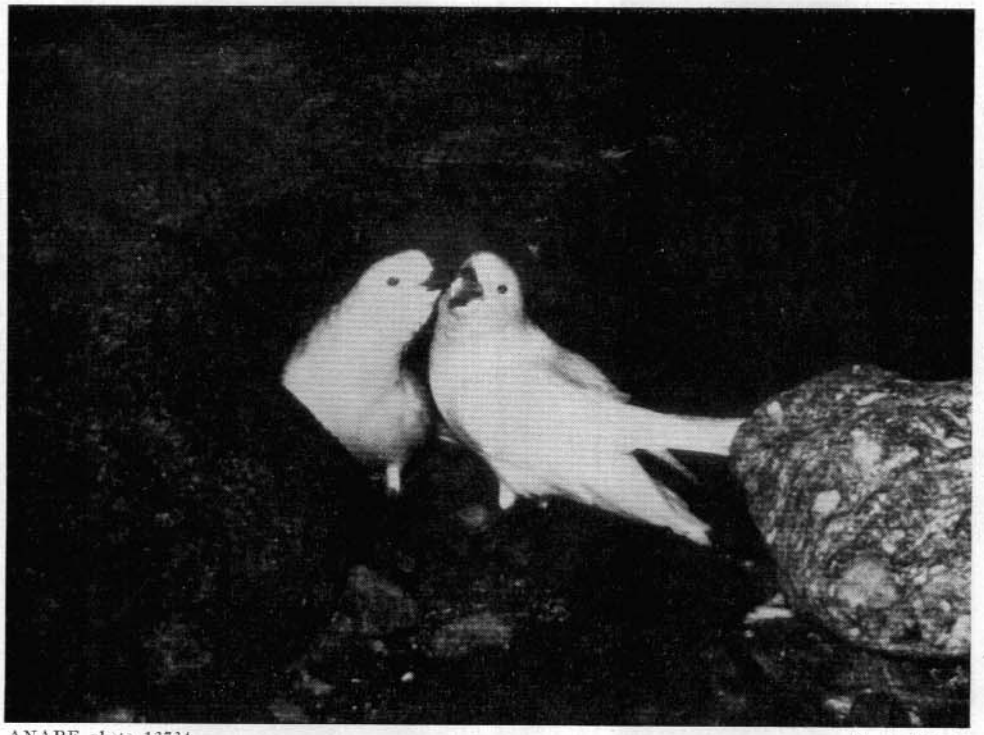
TABLE 6

Pre-egg-laying activities of Snow Petrels at marked nests on Anchorage Island, November-December 1961

Two sets of observations were made on 14, 22 and 30 November and on 1 December; one set only was made on the remaining days.

– = No observation
0 = No birds at time of observation
1 = One bird at time of observation
2 = Two birds at time of observation
C = Copulation occurred at time of observation
‡ = Egg laid
* = Blizzard; nests not affected by snow
† = Non-breeders

Date	November 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	December 1	2	3	4	5	6	7
Local Time	|	1645	|	|	2200	2200	2200	2100	2359	2359	2359	2359	*	1500 2359	2200	2359	2200	2345	2200	2345	2315 1645	2300	*	2330	2345	2315	2330	2330	2345 1500	2245 0300	2245	2300	2330	2300	2359	2359	2359
Nest Number																																					
1	–	–	–	–	2C	1	2	1	2	2	2	2	–	01	0	1	0	0	0	0	0	00	–	1	0	0	0	0	0	00	00	1	0	2	1‡	1	1
2	–	–	–	–	2C	2	2	2	1	1	0	1	–	00	1	0	0	0	0	2	1	00	–	0	0	0	0	0	0	00	21‡	1	1	1	1	1	1
3	–	–	–	–	2	2C	2	0	0	1	1	1	–	00	1	1	0	0	0	0	0	00	–	0	0	0	0	0	0	00	01	1‡	1	1	1	1	1
4	–	0	–	–	2C	2	2	2	1	1	0	0	–	00	1	0	1	1	0	0	0	00	–	0	0	0	0	0	2	‡11	11	1	1	1	1	1	1
5	–	0	–	–	2	2	2C	2	2	2	2	2	–	10	1	0	0	0	1	0	0	01	–	0	0	0	0	0	0	00	00	0	0	0	1	1	1‡
6	–	0	–	–	2	2	2	2	2	2	2	2	–	01	0	0	0	0	0	0	0	11	–	1	1	0	0	1	2‡	11	11	1	1	1	1	1	1
7	–	0	–	–	2	2	2C	2	2	2	2	2	–	00	0	0	0	1	0	0	0	00	–	0	0	0	0	0	0	11	11	1‡	1	1	1	1	1
8	–	–	–	–	–	–	2C	2	2	1	2	2	–	01	2	0	0	0	0	0	0	00	–	0	0	0	0	0	0	01	11‡	1	1	1	1	1	1
9†	–	–	–	–	–	2	2	2	2	2	1	2	–	00	2	2	2	0	0	0	0	00	–	0	0	0	0	0	0	00	00	0	0	0	0	0	1
10	–	–	–	–	2	2	2	2	2	0	1	1	–	00	0	0	0	0	0	0	0	00	–	0	0	0	0	0	0	01‡	11	1	1	1	1	1	1
11†	–	2	–	–	2	2	2	2	2	2	2	2	–	01	1	1	1	1	1	1	1	00	–	0	0	0	0	0	0	00	00	0	2	2	0	0	2



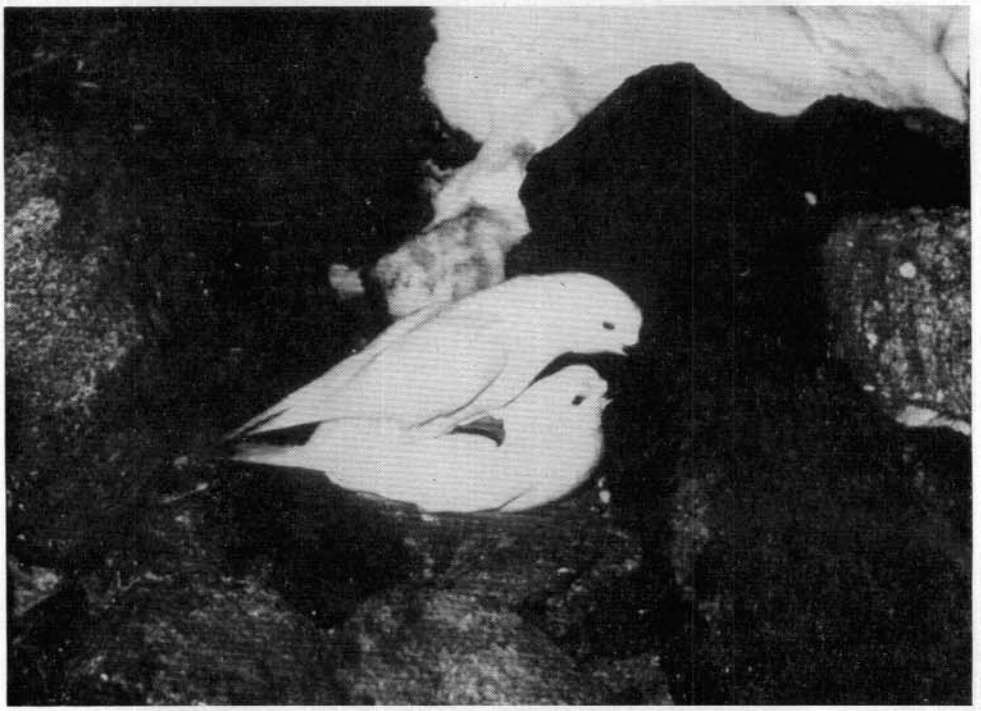
ANARE photo 13734 D. A. Brown

PLATE 16

Prelude to copulation of Snow Petrels; the female placing her bill in that of the male while he is calling.

with her wings slightly spread and the male stood well up on her back with his feet at the junction of her wings and body (Plate 17). While he gently rubbed her bill and forehead, both birds uttered continuous calls, the male a series of soft clucking sounds, the female a high pitched chirring note. All of these actions continued and intensified until coition later took place. For the first two or three minutes the male never stopped moving his weight from one foot to the other. Subsequently, he moved one foot down the female's back until it rested on her upper tail coverts. She immediately moved her tail feathers to one side as the male pointed his downwards. Body and tail feather movements of both birds became increasingly agitated until, after about another two minutes, ecstatic vibrations occurred. The female raised her vent as the male lowered his, both spreading their tail feathers at the same time and, after three or four seconds of complete stillness, coition was completed. The male usually slid to the rear of the female, sitting motionless while she preened her disarranged feathers. As soon as preening was completed, both birds made a short flight before returning to the nest.

Several attempts were usually necessary before successful copulation,



ANARE photo 13732 D. A. Brown

PLATE 17

Copulation of Snow Petrels.

due to interference from other birds, clumsiness of the male, and unpreparedness of the female who invariably interrupted the union by first screeching, then pecking at and dislodging the male.

It cannot yet be definitely stated that, for a given pair, only one successful copulation takes place, but only one occured in all of the numerous observed cases.

E. Pre-laying exodus

After copulation, mated pairs at Anchorage Island remained in their nests for two to seven days (Plate 18), taking frequent short flights at night. They cleared snow out of the nest cavities and moved dead chicks and old eggs either to the perimeters or just outside the entrances. It was not clear whether this removal was intentional; it may have been brought about by the constant movement of the birds in and out of the nests. Both sexes took turns in removing snow, thrusting strongly with the bill to break it up. Leaning forward on their chests, with wings half extended, they pushed themselves forward with their feet, which were also used to toss the loose snow behind them.

After clearing out their nests, nine breeding pairs left the Anchorage Island colony until 28 November-5 December, that is, until from one to four

days (mean 2·2 days) before egg-laying (Table 6). In nine study nests the interval varied from 14 to 23 days (mean 18·4 days), during which time birds of either sex occasionally visited their nests in the evening or at night. In seven nests, the interval between copulation and egg-laying was 24-30 days (mean 26·5 days). During daily checks of the study nests between 14-28 November, single birds were recorded 20 times and a pair twice; in fact, birds were present at only 20 per cent of individual nest checks. During this period some non-breeders also left the colony.

ANARE photo G. R. Cresswell

PLATE 18

Mated pair of Snow Petrels in nest after completion of snow excavations prior to egg-laying; female on left.

This exodus between mating and egg-laying is known in other petrels (for example, the Short-tailed Shearwater *Puffinus tenuirostris* and the Cape Pigeon (Murphy 1936)) and is thought to allow both sexes to feed intensively before the female lays her relatively large egg and the male takes the first spell of incubation.

During the last four days before egg-laying, single birds of mated pairs, predominantly males, occupied their nests almost continuously. When the female arrived, usually at dusk and only a few hours before the egg was laid, she made a small depression in any loose material on the floor of

the nest. Both birds then remained until the egg was laid and incubation had progressed for several hours. The male took over and the female left the nest. Of 18 eggs collected at Bluff Island on 1 December 1961, 14 were laid between 0130 and 0230 hours local time. Laying times for the remainder are not known.

VII. INCUBATION

Only one egg was laid and incubation commenced immediately. If lost, it was not replaced. The egg was pure white, ovoid to elongate in shape, with a shell of medium thickness. The surface had no gloss and was minutely roughened, with occasional irregular nodules. The average weight of 21 fresh eggs collected in the Davis area during 1961 was 47·4 grams (41·0-55·0 grams) ; their average dimensions were 55·5 × 39·4 mm, the extreme dimensions being *59·1* × 38·6; 56·6 × *41·8*; *52·0* × 40·2; and 51·1 × *37·3* mm.

The egg-laying and hatching dates in 19 nests at Anchorage Island in 1961-62 are shown in Table 7.

TABLE 7

Incubation of Snow Petrels in marked nests at Anchorage Island, 1961-62

The hatching date is defined as the day on which the chick was first completely free from the shell.
(A dash indicates incubation still in progress at last observation.)

Nest number	Date of laying (all 1961)	Date of hatching (all 1962)	Incubation period (number of days)
1	5 December	Egg broken	—
2	1 ,,	13 January	43
3	2 ,,	13 ,,	42
4	30 November	13 ,,	44
5	7 December	—	—
6	29 November	10 January	42
7	2 December	15 January*	—
8	1 ,,	13 ,,	43
10	30 November	12 ,,	43
13	29 ,,	12 ,,	44
14	30 ,,	13 ,,	44
15	30 ,,	11 ,,	42
16	1 December	14 ,,	44
17	30 November	12 ,,	43
18	30 ,,	13 ,,	44
20	3 December	Egg frozen	—
21	1 ,,	Egg addled	—
23	3 ,,	Egg broken	—
24	6 ,,	—	—
Peak dates	30-November-1 December	13 January	
Mean incubation period			43·2

* Exact date uncertain; egg chipped 4 days preceding 15 January, chick present 21 January 1962.

In 32 nests observed at Mawson during 1958-59, egg-laying continued from 30 November to 9 December, the peak dates being 4-6 December. The incubation period at eight nests ranged from 41-44 days, mean 42·4 days. In 1961, egg-laying continued from 27 November to 7 December, the peak dates in 15 nests being 1-2 December. The incubation period was not determined.

Similar records were obtained during 1961 from seven nests in the vicinity of Platcha in the Vestfold Hills. Egg-laying continued from 28 November to 5 December, the peak dates being 30 November-1 December. The incubation period was not determined.

Both sexes shared incubation. Table 8 shows the pattern over the whole incubation period at nine nests on Anchorage Island. Usually, each parent

TABLE 8

Role of male and female Snow Petrels during incubation period at marked nests, Anchorage Island, 1961-62

♂ = Male incubating
♀ = Female incubating
* = Both male and female absent
— = No observation
M = Male and female present, male incubating
F = Male and female present, female incubating
H = Chick hatched

Days after egg-laying	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Nest number																								
2	**M**	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂
4	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	*	♂
6	**F**	♀	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂
8		♀	♀	♀	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂
10		♀	♀	♀	♀	♂	♂	♂	♂	♂	**F**	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	**M**	♂	♂
13		♀	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♂	**M**	♂	♂
16		♀	♂	♂	♂	♂	♂	♂	♂	♂	♂	*	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂
17		**M**	♂	♂	♂	♂	♂	♂	♂	**F**	♂	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂
18		♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	♂

Days after egg-laying	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
2	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	H♂	♂	—	—
4	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	♂	H♂	♀	—
6	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	H♀	♂	♀	♀	♀
8	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	H♂	♂	—	—
10	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	H♂	♂	♂	—
13	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	♀	H♀	♀	♀
16	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♀	♀	H♀	—	—
17	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♂	♂	♂	♂	♂	♂	♂	♀	H♀	♀	♀	—
18	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀	♂	♂	♀	♂	♂	♂	♂	♀	♀	♀	H♀	♀	—

had three spells of incubation, the means in the Anchorage Island colony being 10·2, 8·1, 6·2 days for the male, 9·0, 8·2, 1·4 for the female. In four nests the chicks hatched during the males' third spell. Gradual re-adjustments followed any initial irregularities as at Nest 4; the two following spells were short ones.

Visits to incubating birds by their mates between change-overs are apparently extremely rare. There was only one definite record of such behaviour in two seasons' study: at Nest 17, Anchorage Island, on 1 December 1961, the female returned 20 hours after being relieved by the male. Since she had incubated the egg for the first 24 hours, this might have contributed to her unusual behaviour.

Changeovers at both the Mawson and Anchorage Island colonies always took place at night, the relieved bird sometimes departing immediately, sometimes remaining in the nest for a few hours. On two occasions at Anchorage Island birds left the nests a few hours before their mates arrived, but the chicks hatched normally.

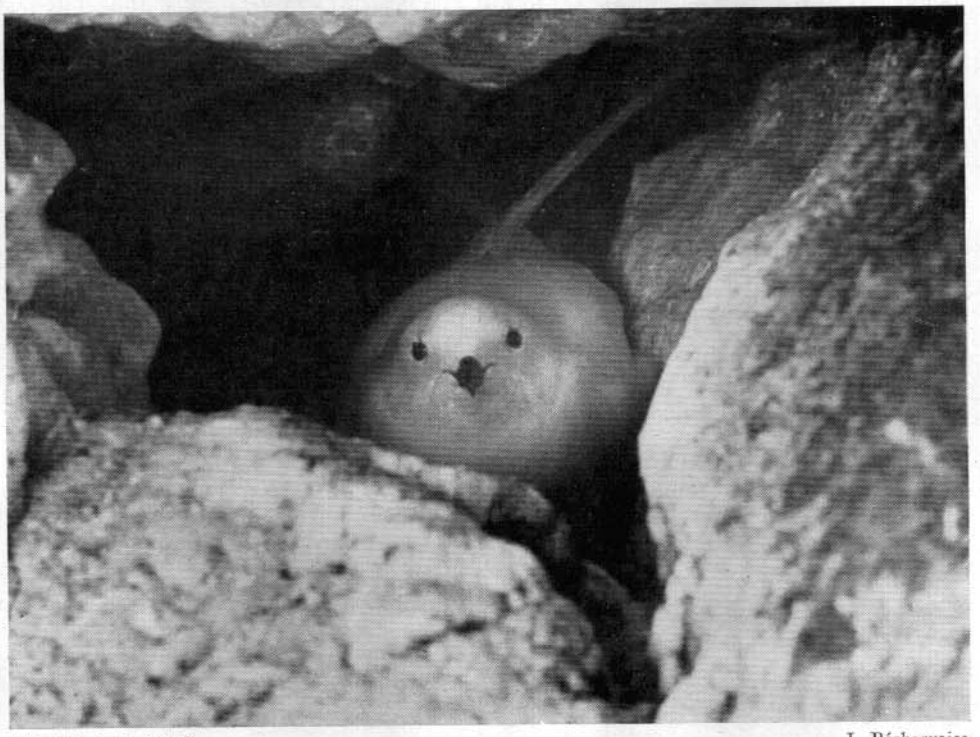
The changeover ceremony was simple. After two or three circuits round the nest site, the incoming bird flew straight in and both birds called simultaneously, facing each other with out-stretched necks. The newcomer sat 10-15 cm from its mate which stood up and quietly moved away from the egg. The newcomer moved to the egg, stood over it, then gently tucked it under with its bill. Both birds clucked softly until the newcomer had settled down, then they called frequently, sometimes preening each other's heads and necks between calls. The outgoing bird always circled the nest site two or three times before departure.

Incubating birds spent much of their time sitting motionless or sleeping, sometimes with their heads placed under their scapular feathers. They normally faced into the wind unless there was movement of sand during storms in which case they faced downwind. When danger threatened, for example, when skuas flew nearby or humans approached closely, they were quickly alert, but often betrayed their position in hidden nests by calling. They were frequently disturbed by non-breeding birds trying to enter their nests. When disturbed they adopted the threat posture; a slight stretching of the neck and lowering of the head (Plate 19). To drive off intruders, incubating birds screeched and discharged stomach oil for distances of more than one metre over the intruders and the surrounding rocks.

During incubation small quantities of down from the brood patch and covert feathers accumulated in the nests, and some birds picked up small pebbles within reach and placed these round the perimeters. Incubating birds and chicks evacuated liquid faeces into remote corners of their nests or out of secondary entrances, where it formed a thin layer which dried rapidly.

Egg losses at Mawson in 1958-59 were 17 out of 35 (48·6 per cent) and, in 1961-62, 16 out of 21 (76·2 per cent), while at Anchorage Island in 1961-62, they were only four out of 19 (21·1 per cent). Prévost (1953)

estimated mean egg losses at three separate colonies in the vicinity of Dumont d'Urville as 18 out of 49 (36·7 per cent). Most losses at Mawson and Anchorage Island were due to fractures caused by clumsy or agitated movements of incubating birds; breeders often completely dislodged eggs from nests during changeovers, or when changing their positions on nests. Other causes were absences exceeding 24 hours (in which cases the eggs froze) and confusion between new and old eggs in one nest (in which cases the birds either tried to incubate both at once or each alternately for several days).



ANARE photo 6369B J. Béchervaise

PLATE 19

Incubating Snow Petrel in threat display; ejection of stomach oil follows almost immediately.

Snow at the Anchorage Island colony never blocked nests during incubation, whereas at Mawson nests were snowed-up every few days and eggs were often either broken or buried in the snow as the birds dug their way in and out. This probably accounts for the difference in egg losses between Mawson in 1958-59 and Anchorage Island in 1961-62. The exceptionally high losses at Mawson in 1961-62 are attributed to marauding husky pups which either killed the parent birds or caused the eggs to be broken.

Behaviour pattern following egg losses varied according to the circum-

stances of the loss. In 15 cases observed at Mawson in 1958-59, the following was noted:

(i) One egg froze five days after incubation had started; the egg remained intact and both birds continued normal incubation, with one break of two days, until the forty-fifth day. Neither bird was recorded at the nest again that season.

(ii) Five eggs were fractured in snow-free nests between the first and eighteenth day of incubation. All five were vacated immediately, then re-occupied by the mates at the normal changeover times. Two of the five eggs remained intact and incubation of these continued, with several short breaks, until the twenty-ninth and fortieth days respectively. At the three remaining nests the eggs disappeared before the mates returned at the normal changeover times, and only infrequent visits, each lasting one or two days, were made until the thirty-sixth, thirty-eighth and forty-second days. No further visits were recorded at these five nests.

(iii) Seven eggs were broken at snow-blocked nests between the thirty-fourth and forty-second days of incubation. Incubation at two of these was resumed and lasted until the forty-fifth and forty-seventh days. The remainder were either visited once or twice for a few hours until the forty-sixth day, or were not visited at all.

(iv) One egg was found to be addled on the forty-fourth day and incubation continued until the fifty-first day before it was abandoned.

(v) One fresh egg was substituted for a broken one but there was no attempt to incubate it.

At Anchorage Island in 1961-62 the behaviour pattern was similar to that at Mawson. Of the four eggs lost, all were in snow-free nests; two were broken, one frozen and one addled. This last followed confusion with an old egg in the same nest, and incubation was still in progress on the fifty-first day when the last observation was made.

VIII. CARE AND GROWTH OF CHICKS

A. Hatching and brooding

Chick hatching dates at Anchorage Island in 1962 are shown in Table 7; those at Mawson in 1959 in Table 9. The nestling period at Mawson in 1959, which varied between 48 and 54 days (mean 51) was longer than at Dumont d'Urville where Prévost (1958) recorded three such periods of 44, 44 and 48 days.

Eggs began to chip two to four days before chicks hatched. Chipping started at the large ends of the eggs, the patterns being round at first, but gradually becoming larger and more elongated. Small shell fragments were left in the nests after the chicks hatched and, while larger pieces including the membranes were pushed out behind the brooding birds, no attempts were made to remove this material completely from the nests (Plate 20).

TABLE 9

Hatching and departure dates of Snow Petrel chicks at marked nests at Mawson, 1959

(A dash indicates that chick died before fledging)

Nest number	Date of hatching (all 1959)	Date of departure (all 1959)	Nestling period (days)
2E	16 January	5–6 March	48–49
2SW	16 ,,	8 ,,	51
6E	14 ,,	9 ,,	54
6SW	16 ,,	10 ,,	53
15	13 ,,	3–6 ,,	49–52
21NW	14 ,,	—	—
22NE	16 ,,	5–6 March	48–49
33SE	17 ,,	—	—
XX	9 ,,	—	—
B	19–20 ,,	10 March	49–50
Peak date	16 January		
Mean nestling period			51

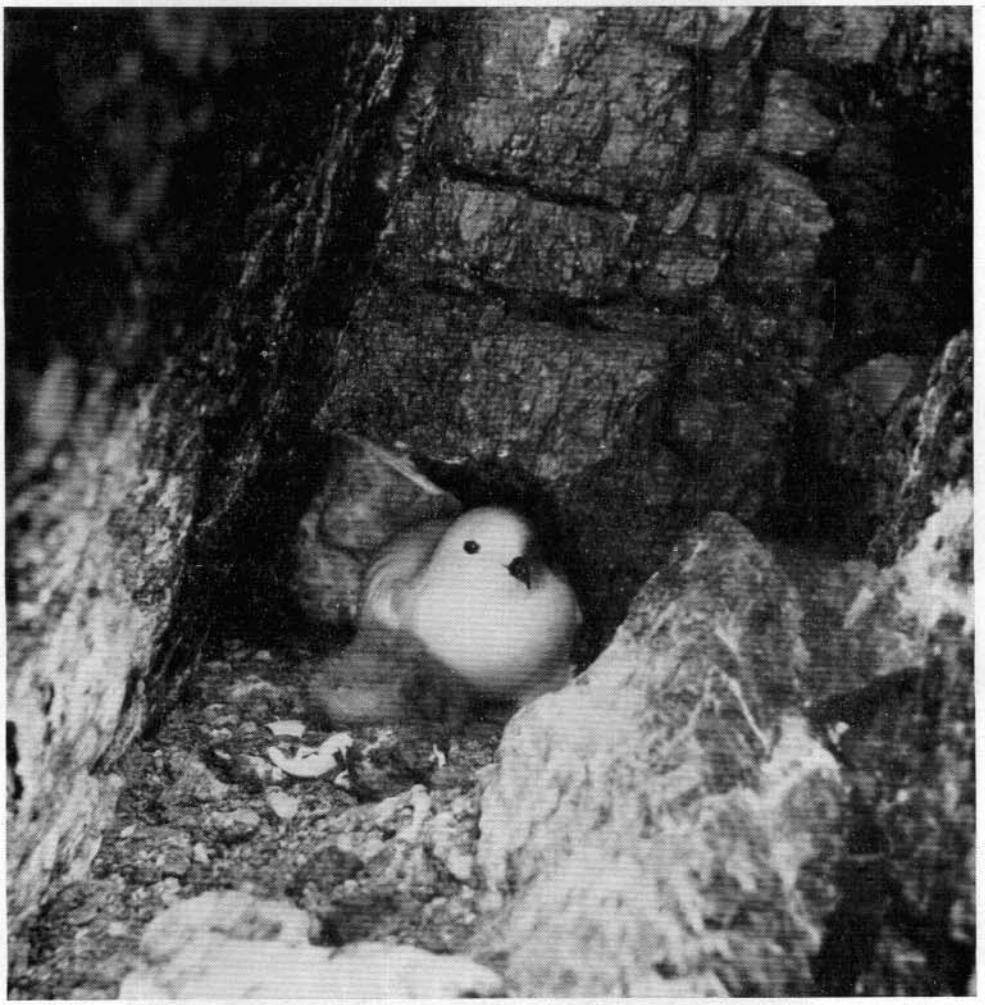
Ten of the 13 chicks at Anchorage Island hatched during daylight hours (between 0900-2130 hours local time) ; hatching times for the 3 remaining chicks were not determined. All of these chicks had their eyes open when first seen. During the first two or three days their movements were feeble and they supported their heads by placing the tip of the bill on the ground. By the fourth day most chicks sat at the sides of their parents. Brooding lasted for from four to eight days, during which the parents changed over once. Subsequently, both parents left the nests, visiting them only to feed the chicks.

B. Feeding

When disturbed or handled, very young chicks vomited minute quantities of clear oil. In older, unguarded chicks the oil was orange, like that of adult birds (see Section IIIB). When handled immediately after feeding, older chicks regurgitated both partly-digested and complete krill *Euphausia superba* which varied in length from one to $2\frac{1}{2}$ cm.

Feeding of 2 to 3-week-old chicks was observed at Mawson on several occasions in 1959 and 1962 between 1630 and 1900 hours local time. It is doubtful, however, whether this is exclusively a daytime function; adults were often seen flying round the colonies at dusk and after dark. As soon as the adult entered the nest, the chick chirrupped continuously, except when taking food, and the adult clucked softly between regurgitations. The adult and chick sat at right angles to each other so that their bills were close together. The chick encouraged regurgitations by calling and rubbing its bill in vibrant movements along the side of the adult's lower mandible, from tip towards gape. The adult swallowed several times and opened its bill, then the chick obtained food by placing its bill crosswise into that of

the adult. Regurgitations averaged about 10 a minute and no food was spilt on the ground. Feeding generally lasted about 15 minutes, but only small quantities of food were passed during the first two and last three minutes. When finished, some adults immediately flew off, while others spent some minutes preening the chick's head and back. When the adults left the nests, the chicks stopped calling, settled down and often went to sleep.



ANARE photo 6382A J. Béchervaise

PLATE 20

Newly-hatched Snow Petrel chick beside parent. Note egg shell fragments in foreground.

C. Growth

Growth curves of five accessible chicks in the Mawson colony are shown in Figure 9. The observations on chicks A, X, Z, and 6SW were made in

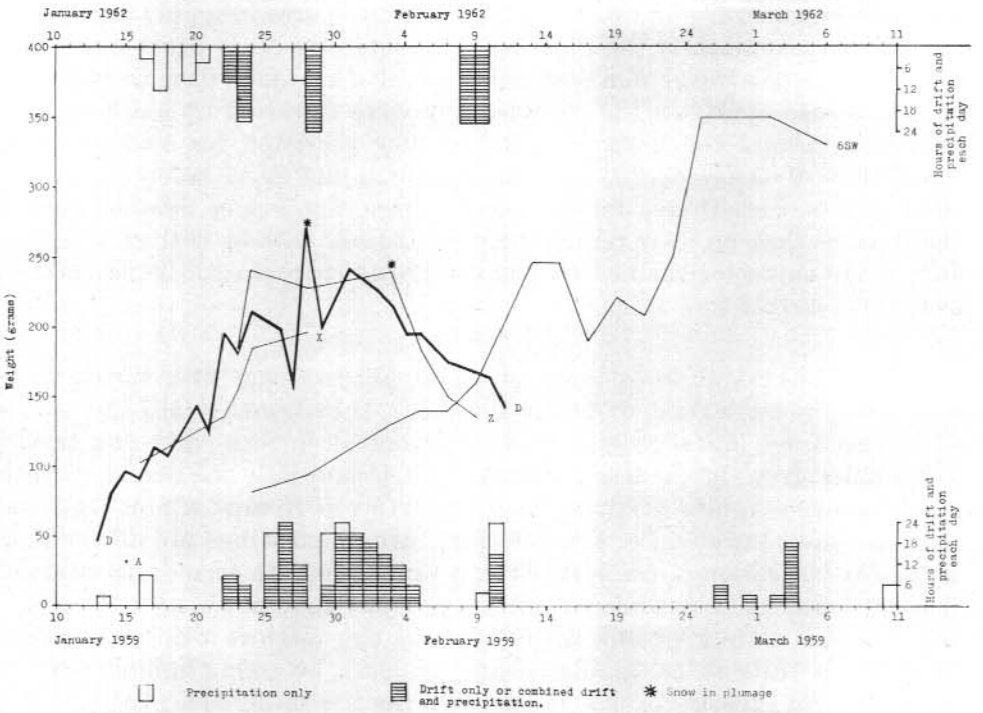


FIG. 9. Growth curves of Snow Petrel chicks at Mawson, 1959 and 1962.

1959; those on chick D in 1962. The dates of hatching of A, X, 6SW and D were known; chick Z was already some days old when found. Chick A died within 24 hours. Weighing of chicks X and 6SW did not begin until they were left unguarded, respectively five and seven days after hatching. Chick D was weighed at about the same hour almost every day from birth. Only chick 6SW fledged successfully at 53 days old.

Prévost (1958) established from the growth curves of three chicks that maximum weight was reached 30-34 days after hatching and adult weight after 26-30 days. At Mawson, chick 6SW took 40 days and 38 days respectively but, if due allowance is made for starvation between the thirty-first and thirty-sixth days, its growth would be approximately the same. The growth curves show a steady weight increase during the first two weeks, with small fluctuations which suggest that feeding takes place on alternate days. The large fluctuations which follow are due to starvation caused by snow blockage of the nest or by shortage of food at sea. Figure 9 illustrates the weight loss of chicks Z and D after blizzards. In the case of chick X, snow blockage of the nest was so severe that the chick died from suffocation before losing weight. Chick 6SW did not lose weight after blizzards, for its nest was in an exposed position, and was never blocked by snow; shortage of food at sea was probably the cause of its weight loss during a period of fine weather.

After a blizzard the parents immediately started digging into their snow-filled nest sites. If the snow was still soft they could burrow through it at the rate of a metre in a few hours but, if wind and a drop in temperature hardened and froze the surface, they were thwarted by much smaller blockages. Under the latter conditions, they persisted for two or three days; then, if unsuccessful, they retired for a day or so before renewing their efforts. Sometimes, during their absence, fine sunny weather melted the snow so that, on their return, they could enter with or without digging. But, if the surface remained frozen and the chick could not be reached, it eventually died of starvation.

D. Plumage

The thick natal down has two colour phases, each with minor variations. In the more common form (Plate 21), the dorsal surface and crown of the head are uniform light grey; the ventral surface, chin and throat are a paler grey. In the less common form (Plate 22), the dorsal surface and head are a lighter grey; the ventral surface is creamy white; the forehead is almost pure white; and the chin, throat and wings are a very pale grey. The coloration of the soft parts is similar in both forms: the maxilla is black from tip to nostril, becoming gradually lighter towards the gape; the nostril is slate grey and quite soft; the egg tooth is white, the lower mandible is white at the tip, then black, gradually becoming lighter towards the gape; the eyes are brown/black, with the iris milky-blue; the legs are dark grey; the webs are light pinkish-grey and the claws are black with white tips.

Measurements of chicks of various ages are set out in Table 10.

TABLE 10

Measurements and weights of Snow Petrel chicks of known age

* = figure approximate
— = accurate measurement not possible

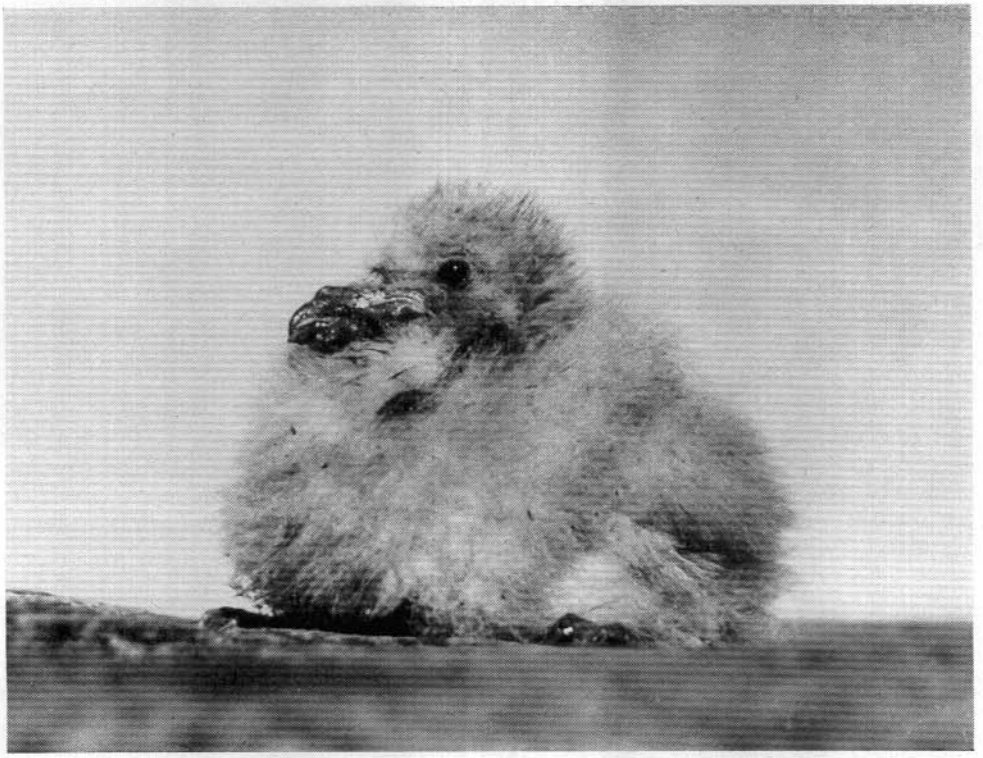
Age (days)	ANARE catalogue number	Wing (mm)	Length (mm)	Culmen (mm)	Tarsus (mm)	Toe (mm)	Claw (mm)	Weight (gm)
1	A61/B/85	—	—	11·7	—	—	5·0	40
17	A62/B/16	109	—	15·7	27·0	27·0	7·0	250
18	A62/B/17	101	—	16·2	27·0	27·5	8·0	280
29	A62/B/18	146	—	16·4	29·0	29·0	8·0	150
31	A61/B/93	134	—	17·5	26·5	28·0	8·5	180
*35	A62/B/19	181	275	18·4	33·0	33·5	8·0	280
39	A61/B/92	191	264	18·4	32·0	32·0	9·0	170
*45	W62/B/2	212	302	21·0	33·0	34·0	10·0	240
*51	W62/B/1	215	—	17·1	32·0	32·5	9·0	315

The following notes were made at Mawson in 1959 during the nestling period.

2-8 days Gape, not so transparent in appearance, now fleshy white. Wing feathers not visible through down, tips unsheathed; the

longest measured 2·5 mm including sheath. Tail feathers not present.

9-11 days (Plate 21, 11-day-old). Bill noticeably darker, particularly on chicks with white forehead; gape pinkish-grey. Longest wing feathers 10·2 mm, tail feathers not visible.



ANARE photo D. A. Brown

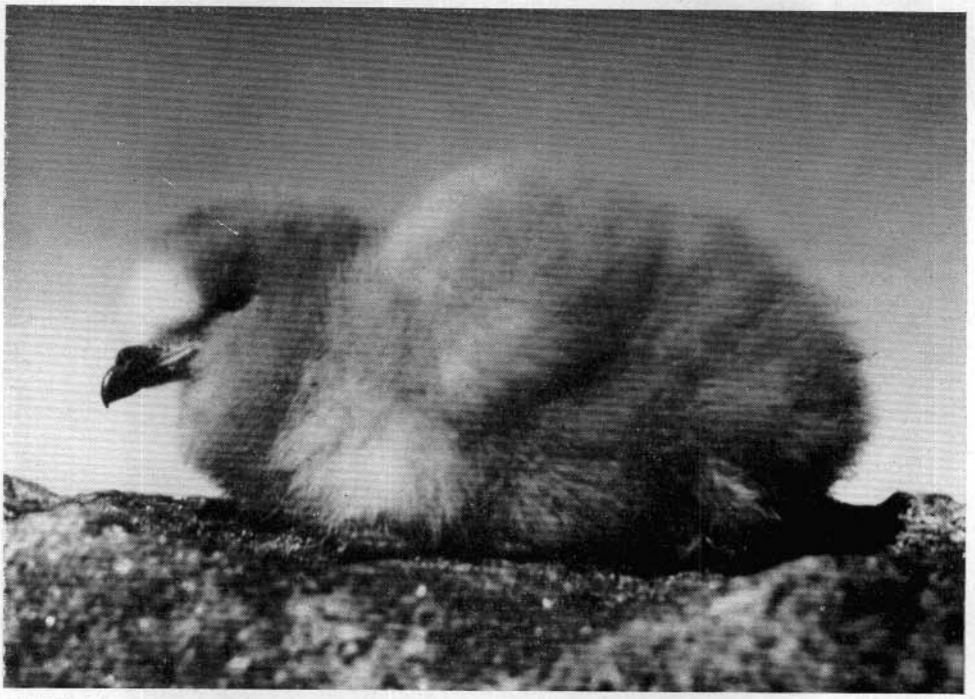
PLATE 21

Eleven-day-old Snow Petrel chick showing the more common uniform grey plumage. Note the small amount of food adhering to the bill after regurgitation, and the feet set wide apart.

12-19 days (Plate 22, 12-day-old). Wing feathers 28 mm, tail feathers 7·5 mm; neither yet visible through down. Eyes darkening but iris still milky-blue in colour.

20-23 days Wing feathers 40·5 mm, tail feathers 15·0 mm; both visible through down. Slight loss of down at base of bill and feathers visible; scapulars also visible. Chicks display more aggressiveness when disturbed; call noticeably similar to adult.

24-33 days (Plate 23, 28-day-old.) Wing feathers 45·5 mm, tail feathers 35·5 mm. Moult commencing. Very faint grey vermiculations on dorsal feathers; grey wash on leading edge of first two or three flight quills.



ANARE photo D. A. Brown

PLATE 22

Twelve-day-old Snow Petrel chick showing less common form of plumage with white coloration on the forehead down.

34-39 days Accurate feather measurements not possible. Head and neck free of down. Iris still milky-blue but darker. Chick more vocal, constantly clucking and uttering whistling chirrups.

40-45 days Moult in final stage. Iris bluish-brown. Grey vermiculations plainly visible on dorsal contour plumage.

45-54 days Only very small wisps of down on nape, upper and lower tail coverts and flanks. Iris brown.

When chicks were starved for more than a few days feather growth was retarded and down remained intact for longer than usual, but the reserves of body fat were apparently sufficient to ensure normal departure.

Chicks always remained in the nests right up to the time of departure, and moved very little unless forced to do so by an infiltration of snow. It is not clear whether they continued to be fed until the time when they left, or whether there was a starvation period, but Maher (1962) recorded a fully-fledged chick which had recently been fed.

E. Losses

At Mawson in 1959, eight out of 18 chicks survived to leave the nest, a chick mortality rate of 55 per cent. This figure is consistent with the 65

per cent estimated by Roberts (1940) for Wilson's Storm Petrels *Oceanites oceanicus* which appear to have similar nesting habits and snow blockage problems at Galindez Island (65°15′S, 64°15′W) in the British Antarctic Territory.

Of the 10 casualties, six died from starvation due to snow blockage, one from suffocation, two from exposure when the parents deserted within 24 hours of hatching, and one was eaten by skuas *Catharacta skua maccormicki*. The ages of these chicks ranged from 1-30 days.

ANARE photo D. A. Brown

PLATE 23

Twenty-eight-day-old Snow Petrel chick, showing wing and tail feathers through down, and moult commencing on forehead and lores.

At Anchorage Island in 1962, the chick mortality, 30-35 days after hatching, was only 20 per cent of 15 chicks. The three casualties were killed and eaten by skuas. This marked contrast with the Mawson losses was entirely due to the complete freedom from snow blockage of the Anchorage Island nests.

Widespread skua predation was noted in the vicinity of Platcha, where hundreds of Snow Petrel carcasses were found in valleys and on low ridges. They were mainly fledglings. The carcasses consisted of the body bone-structure which had been picked clean, with both wings still attached and sometimes, the head and tail still intact. On almost every peak where skuas

habitually rested, large quantities of their pellets contained complete bones and skulls bound with feathers; some pellets were quite fresh, others were bleached by weathering over many years. The stomach of a dead skua found in the area contained nothing but Snow Petrel remains.

Death from other causes were rare; one chick was killed near Platcha by a fall of rock from the roof of its nest.

F. Fledglings

In flight, the general appearance of fully-fledged chicks is similar to that of adults except that the flight quills and retrices are shorter. Other distinguishing features, not discernible in flight, are the more intense grey vermiculations on the dorsal plumage and sometimes a more extensive grey wash on the leading edge of the primary flight feathers.

The movements of fledglings are not well known since there is insufficient evidence to determine whether or not they return to their nests once they have left them. It is suspected that they move out to the pack ice to feed, travelling steadily northwards as the sea ice forms during autumn and winter.

Evidence of the northward range of a juvenile Snow Petrel was obtained by John Gould, who collected a specimen during his voyage from England to Tasmania in 1838. Hindwood (1938), describing Gould's voyage, stated that the route was via the Cape of Good Hope, Ile St Paul and Ile Amsterdam and that he arrived in Hobart on 18 September. The specimen, which is housed in the National Museum of Victoria in Melbourne (Catalogue number B2425), and was described by Gould as being collected from the "southern seas off Australia", is a juvenile. The measurements from the skin are: wing 219 mm, length 311 mm, culmen 17·8 mm, tarsus 32·0 mm, toe 32·0 mm and claw 11 mm. Gould did not include this species in the Australian checklist, since the collecting area was probably in the vicinity of 50°S, between 110°E and 130°E, that being part of the preferred route of sailing ships when they "ran the easting down" on voyages between the Cape of Good Hope and Tasmania.

IX. GENERAL OBSERVATIONS

A. Winter activities

Following an almost complete absence of Snow Petrels at Mawson and in the Davis area during March and early April, large numbers returned in mid-April and remained in their breeding areas until late May (Table 5).

During the April-May period at Mawson in 1958, single birds and small flocks were seen regularly throughout the day flying about the islands and icebergs, and single birds occasionally occupied nest sites for a few hours. The flights were largest at dusk when greater numbers of single birds and small flocks flew above the promontories, while others sat on rocks and ledges or in nests, calling and spitting at each other until several hours

after dark. There are no records to show whether banded birds re-occupied their own nests, but such post-breeding re-occupation is known in the case of several sub-antarctic petrels, for example the Soft-plumaged Petrel *Pterodroma mollis* (Murphy 1936) and, very probably, in Cape Pigeons (Prévost 1953).

In the more densely populated area near Platcha during April-May 1961 the general pattern was the same except that, on several occasions, flocks of 100 to 1000 birds were observed sitting on snow-covered sea ice during daylight, then dispersing at dusk. While on the sea ice, these birds sat one third to one metre apart, facing into the wind, and not calling. Since individuals in such flocks were constantly moving to the windward sides, these flocks moved gradually upwind. Suddenly a whole flock would move as one (each bird ascending, perhaps 100 m or more, in an independent spiral) then disperse quickly and reform nearby a few minutes later. The last and largest of such flocks was seen on 17 May 1961, after which the population fell sharply. Activities at nest sites became more nocturnal as single birds sat in them, calling for hours after dark. During the very short days of late May, birds were almost completely absent and, by 5 June, 12 days after continuous winter darkness had set in, they had all departed.

Occasional single birds and pairs were seen in winter. Three single birds were recorded between 4 and 9 July in the vicinity of Platcha, three at Davis between 11 and 29 July, and two pairs, also at Davis, between 5 and 9 August. At Mawson in 1958, a single bird was seen on 10 July.

Little is known of the habits and distribution of Snow Petrels during the Antarctic winter; it is assumed that they move northwards with the pack ice. They are regular, but infrequent, visitors to such points on the Antarctic coast as Pointe Géologie in Terre Adélie (Prévost 1953), Cape Denison in George V Land (Falla 1937) and ANARE stations at Mawson, Davis and Wilkes. South of the Antarctic circle the lack of daylight for phytoplankton production would depress zooplankton levels, and consequently krill, so that there would be relatively little food for Snow Petrels, as well as little daylight to search for it.

At the northern limit of their range, Snow Petrels are regular winter visitors to the South Orkney Islands and South Georgia (Murphy 1936), the latter being free of pack ice. There is a sight record at Heard Island, on one occasion in August 1948 (Gilchrist 1952). Breeding adults probably go no further from their breeding grounds than is necessary in the search for food.

B. Flight and locomotion

The normal flight of the Snow Petrel is level to undulating, wing beats and gliding alternating almost equally. The feet are held together and concealed in the tail coverts so that only the dark bills and eyes contrast with the white plumage. This graceful and silent flight, which was seen on calm sunny days, is very different from the extraordinary agility shown during flights in stormy weather. While executing turns at high speed along cliff

faces and round mountain peaks, the wings are held close to the body like those of hawks diving on their prey. The noise of flight can then be heard 100 metres away as small groups swoop low over colonies and climb to 100 metres or more in seconds. When cruising along cliff faces in high winds, individual birds follow the irregular contours of the rocks very closely, manoeuvring by constant checking with the tail feathers and dipping from side to side with the wings, the tips of which frequently touch the rocks.

Snow Petrels fly at heights up to 150 metres in the vicinity of their colonies. At the study areas, on calm sunny days during the breeding season, they soared at greater heights for long periods. They were able to follow meteorological balloons upwards at the rate of 150 metres per minute, continually circling and making passes at them as they ascended, sometimes to heights of 900 metres. When confronted with strong surface winds, they flew high. In the Mawson area during strong off-shore winds, large numbers flew inland towards the Masson Range, at heights up to 1800 metres.

Snow Petrels do not travel in compact flocks like Antarctic Petrels *Thalassoica antarctica* but singly, in pairs or, less often, in groups of up to four or five birds. Large flocks congregate in the vicinity of dense breeding areas during the courtship and mating period and just before winter departure, and their movements appear to be restricted to the immediate localities. Large but widely dispersed flocks are sometimes seen heading out to sea during the breeding period, especially after long spells of stormy weather. They fly in loose open groups with no permanent leader, individuals in a flock overtaking those in front from time to time. When foraging for food they fly low, either alone or in widely dispersed flocks over the sea and pack ice. They glide for long periods, alternately skimming the surface and rising again to dip this way and that in their search for food. Wilson's sketches published by Lowe and Kinnear (1930) are excellent examples of such behaviour. In calm weather among open pack ice or on the sea, they either alight on the water and feed in a sitting position, rotating their bodies and frequently thrusting their heads under the surface, or they alight on the floes where they feed on the marine animals exposed there. In windy weather they head into the wind, treading water with wings momentarily raised high while taking the food, then moving forward again. Routh (1949) noted that they rest on icebergs (a practice common among all Antarctic bird species), using them for a time as bases. From these, individuals and small flocks set off to feed within a radius of a few kilometres. During stormy weather, icebergs and pack ice provide refuge. When more than one species take refuge on one iceberg—a not uncommon occurrence—there is very little overlap between them; each keeps to its own area.

Snow Petrels take off from rock or snow surfaces merely by springing off, but on smooth ice even in windy conditions they have to run a few paces before becoming airborne. Plate 14 illustrates the landing technique:

as soon as contact is made with the ground, the birds sit down with their feet set apart.

Movements on the ground are ungainly and awkward; the birds waddle along in a half raised position for short distances, then sit down again. In windy conditions their wings are also extended so that the birds are partly airborne and move more quickly and easily. The tarsi are rarely in contact with the ground, except during movement down an incline. When moving up snow slopes, the birds lift themselves much further off the ground, stepping quickly with only the claws and about half of the foot touching the surface.

C. Calls

Snow Petrels are silent birds except at their breeding colonies, from which their harsh guttural calls can be heard more than a kilometre away in calm weather.

The normal call consists of a series of five or six rough, guttural caws lasting up to 10 seconds and sounding like K-K-K-KAA-KAA-KAA-KAA-KAA-KAA. It starts off softly at a low pitch and quickly reaches greatest volume and highest pitch at the first or second KAA. The remaining notes are longer and in a descending scale. In times of alarm or danger, the notes are longer, louder and more numerous. The guttural quality is equally evident in both sexes, but tape recordings show that the female call is consistently higher than that of the male, the difference being more apparent where the pairs are larger birds. The principal variations from the normal call during courtship and mating have already been described in Section VI C and VI D.

D. Food

The stomachs of 20 specimens collected in the Davis area in November 1961 contained strong-smelling orange oil combined with partly digested food, some of which was identified as *Euphausia superba*. Two of the stomachs contained minute quantities of an unrecognizable green substance, suggestive of well-digested herbage, together with a small amount of a clear oily liquid. The green dye of this substance left a stain similar to plant chlorophyll.

While all previous writers agree that *Euphausia superba* is the staple diet of Snow Petrels, food from other sources is not uncommon. Falla (1937) described recognizable material from 17 BANZARE specimens as follows: *Euphausia* (12); pelagic prawns (2); isopods (1); cephalopods (6); pteropods (2); and ship refuse (1). Murphy (1936) stated that fish have occasionally been found in their stomachs and Maher (1962) found fish flesh and vertebrae regurgitated by a chick. Like most petrels, they are not averse to carrion and have been observed eating from the carcasses of teal *Nettion georgicum*, whales and seals (Murphy 1936, Prévost 1953, Dr M. N. Orton—personal communication). At Platcha in May 1961, two Snow Petrels were seen breaking up and flying off with sledge dog faeces; a

third picking at a discarded food tin. This behaviour is perhaps not surprising as the formation of sea ice must have caused a local food shortage.

E. Moult

At Anchorage Island in 1962, moulting was first observed on 3 January. Secondary flight feathers and coverts were seen in a nest occupied intermittently by a non-breeding pair since mid-December 1961. Several more non-breeders (including one marked pair) were seen in moult at nest sites between 6 and 12 January, but remained for only 1-4 days before leaving the colony and did not return. Loss of primary flight feathers was first observed on 11 January 1962.

At Mawson in 1959 and 1962, non-breeders were seen to leave about the same date as at Anchorage Island. A close watch on all breeding birds at the study colonies failed to reveal any significant moult occurring up to the time the chicks left. Two birds collected in late April 1961 from the Platcha area were apparently in the final stages of moult; although the new feather growth appeared complete, large quantities of feather sheath particles fell from the plumage when the birds were handled. Routh (1949) recorded the first Snow Petrels in moult at sea on 19 January 1947, and observed advanced stages of moult four days later. Wilson (1907) stated that, during the northward voyage of *Discovery* from McMurdo Sound in 1904, most of the Snow Petrels seen after mid-February were in moult while, in 1902, moulting birds had been obtained on 11 January.

Mr. McEvey, Curator of Birds at the National Museum of Victoria, has examined 21 specimens consisting of 10 mated pairs collected in the Davis area between 8 and 12 November 1961 and one breeding adult collected at Mawson on 2 February 1959; also three specimens of unknown status, two of them collected at Platcha on 2 October 1961 and one at Mawson on 6 November 1954 (Table 11). There was no significant sign of moult in any of them.

The evidence suggests that moulting of non-breeders is gradual and that it lasts from January (possibly earlier) until late April. No conclusive evidence was obtained at Mawson or Anchorage Island to show whether or not breeding birds moult during the breeding cycle. Maher (1962) recorded that seven out of 13 adults collected at the Cape Hallett breeding colony in November 1960 were shedding contour feathers, three of them quite heavily. The breeding status of these seven birds was not known, but their gonads were the same size as those of non-moulters collected at the same time. Maher (1962) concluded that moult and breeding were concurrent. Warham (1962) found that moult and breeding were concurrent in the Giant Petrel.

F. Parasites

From a total of 24 adult Snow Petrels collected in the Davis and Platcha areas in 1961, 3 were infested with lice, *Pseudonirmus charcoti*

TABLE 11

Measurements and weights of Snow Petrel adults and chicks of unknown age

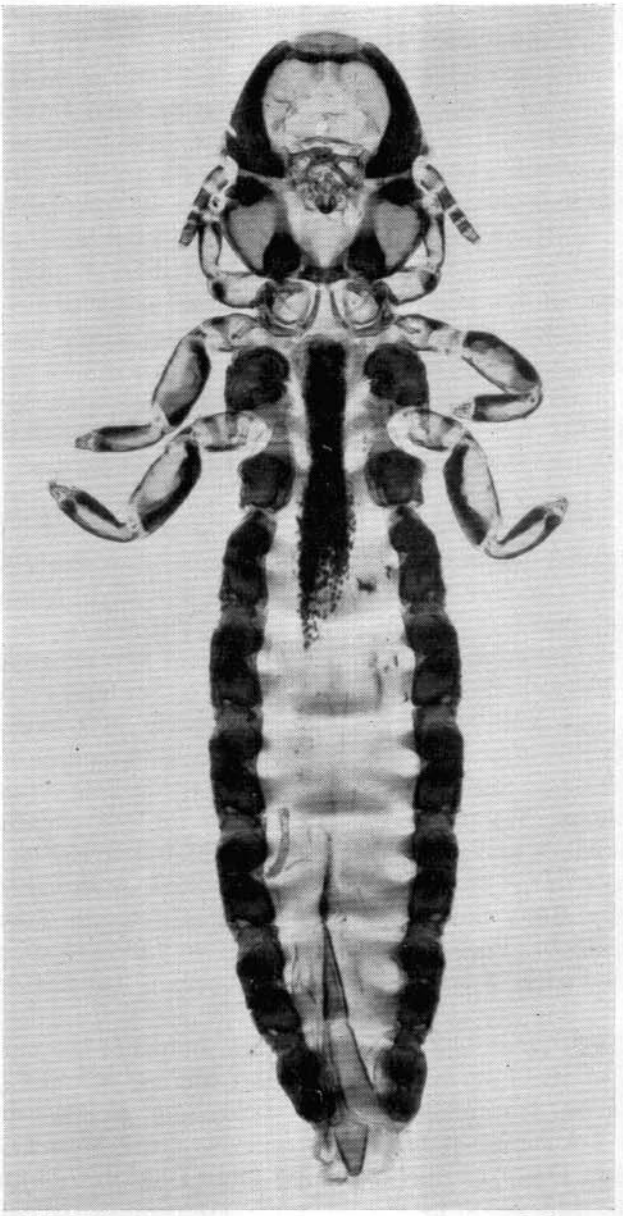
All specimens were collected by the author except B6862 (by Dr. R. O. Summers) and B7701 (by Mr. H. Geysen)
Museum numbers prefixed by "W" are preliminary.
* = Measured from skin † = Measured from feathers on forehead to tip of bill. ‡ = Date of death not known.
– = Accurate measurement not possible.

Location of specimen	Museum number	ANARE number	Date collected	Sex	Locality	*Wing (mm)	Length (mm)	†Culmen (mm)	Tarsus (mm)	Toe (mm)	Claw (mm)	Weight (gm)	Remarks
National Museum, Melbourne	B6862	—	6.11.54	♀	Mawson	275	360	22·0	34·0	36·0	12·0	—*	
Q'land Museum, Brisbane	O.6452	S/58/B18	21. 1.58	♀	Pointe Géologie	272	363	22·4	35·0	36·0	11·5	—*	
do.	O.6453	S/58/B19	,,	Chick	,, ,,	—	—	13·7	—	—	—	—*	Chick of S/58/B18
do.	O.6454	S/58/B29	7.2.58	Chick	Larseman Hills	72	—	13·8	—	—	—	—*	
National Museum, Melbourne	W4697	A/58/B5	2.2.59	Chick	Mawson	—	—	—	—	—	—	169	
do.	W4696	A/58/B6	,,	Chick	,,	—	—	—	—	—	—	245	
do.	B7499	A/58/B8	,,	♀	,,	265	333	19·8	32·0	35·5	11·0	247*	
do.	W4698	A/58/B17	,,	Chick	,,	—	—	—	—	—	—	177	Chick of A/58/B8
do.	W4699	A/58/B10	13.2.59	Chick	,,	—	—	—	—	—	—	130	
do.	B7701	—	— .60	♀	,,	255	333	19·5	31·0	34·5	10·0	—*	
do.	W6024	A61/B/1	29. 4.61	♀	Platcha area	265	333	20·7	32·0	34·0	11·0	201·9	
do.	W6025	A61/B/2	30. 4.61	♂	,, ,,	265	329	20·0	31·0	34·0	9·0	206·7	
do.	W6026	A61/B/15	2.10.61	♂	,, ,,	257	335	19·9	31·0	34·0	11·5	310·0	
do.	W6027	A61/B/16	,,	♂	,, ,,	264	333	22·3	34·0	34·0	11·0	312·1	
do.	W6028	A61/B/17	8.11.61	♂	Anchorage Is.	261	318	20·2	34·0	35·0	11·0	306·3	Matedpair; male infested with lice
do.	W6029	A61/B/18	,,	♀	,, ,,	256	317	18·8	31·0	33·0	11·0	241·0	
do.	W6030	A61/B/19	,,	♀	,, ,,	252	307	19·4	32·0	33·0	11·0	219·0	Mated pair; male infested with lice
do.	W6031	A61/B/20	,,	♂	,, ,,	264	327	21·3	31·5	33·0	11·0	266·8	

TABLE 11—(*Continued*)

All specimens were collected by the author except B6862 (by Dr. R. O. Summers) and B7701 (by Mr. H. Geysen)
Museum numbers prefixed by "W" are preliminary.
* = Measured from skin † = Measured from feathers on forehead to tip of bill. ‡ = Date of death not known.
– = Accurate measurement not possible.

Location of specimen	Museum number	ANARE number	Date collected	Sex	Locality	* Wing (mm)	Length (mm)	† Culmen (mm)	Tarsus (mm)	Toe (mm)	Claw (mm)	Weight (gm)	Remarks
National Museum, Melbourne	W6032	A61/B/21	8.11.61	♀	Anchorage Is.	257	317	18·0	33·0	33·0	10·0	262·7	Mated pair
do.	W6033	A61/B/22	,,	♂	,, ,,	269	328	20·0	35·0	35·0	11·0	300·3	
do.	W6034	A61/B/23	,,	♀	,, ,,	258	308	18·9	33·0	34·0	11·0	262·1	Mated pair
do.	W6035	A61/B/24	,,	♂	,, ,,	261	316	20·4	33·0	34·0	10·5	297·3	
do.	W6036	A61/B/25	12.11.61	♀	Bluff Island	260	329	19·5	33·0	35·0	10·0	249·8	Mated pair
do.	W6037	A61/B/26	,,	♂	,, ,,	266	320	20·7	32·5	33·0	11·0	255·3	
do.	W6038	A61/B/27	,,	♀	,, ,,	256	318	19·6	32·0	33·0	10·5	247·2	Mated pair
do.	W6039	A61/B/28	,,	♂	,, ,,	262	323	20·8	32·0	33·0	10·5	248·3	
do.	W6040	A61/B/29	,,	♂	,, ,,	262	326	21·8	31·0	33·0	10·5	251·9	Mated pair
do.	W6041	A61/B/30	,,	♀	,, ,,	272	327	20·4	33·0	34·0	11·0	239·9	
do.	W6042	A61/B/31	,,	♂	,, ,,	261	315	20·5	33·0	35·0	10·0	295·5	Mated pair
do.	W6043	A61/B/32	,,	♀	,, ,,	254	310	18·8	32·0	34·0	9·5	230·1	
do.	W6044	A61/B/33	,,	♂	,, ,,	263	327	21·0	33·0	33·0	10·5	280·6	Mated pair; female infested with lice
do.	W6045	A61/B/34	,,	♀	,, ,,	261	312	20·5	31·0	33·0	11·0	235·0	
do.	W6046	A61/B/35	,,	♂	,, ,,	268	326	20·8	33·0	34·0	12·0	279·1	Mated pair
do.	W6047	A61/B/36	,,	♀	,, ,,	253	327	19·8	32·5	34·5	11·5	274·9	
do.	W6007	A62/B/3	29. 1.62	♂	Mawson	262	324	23·1	32·0	33·5	12·0	250·0*‡	
do.	W6008	A62/B/4	,,	—	,,	268	331	20·5	32·5	34·5	11·5	260·0*‡	
do.	W6013	A62/B/9	,,	♀	,,	256	310	19·5	32·0	33·5	11·0	255·0*‡	
do.	W6015	A62/B/11	,,	—	,,	262	332	20·0	32·0	34·0	12·5	255·0*‡	
do.	W6016	A62/B/12	,,	—	,,	257	330	21·4	33·5	35·0	12·0	300·0*‡	
do.	W6018	A62/B/14	,,	—	,,	258	323	20·1	34·0	34·5	11·0	300·0*‡	
do.	W6019	A62/B/15	,,	—	,,	255	311	20·7	33·5	34·5	10·5	275·0*‡	



CSIRO photo I. Roper

PLATE 24

The louse *Pseudonirmus charcoti* (Neumann). Magnification approximately × 50.

(Neumann), (Plate 24). One louse was found on the feathers of each of two males and seven on one female.

One male and three female paratypes, and one pupa of a new genus and species of flea *Glaciopsyllus antarcticus* (Smit and Dunnet 1962) were obtained from accumulated nest material on Anchorage Island on 28 December 1961. Similar fleas were also found in nests of the Silver-grey Petrel *Fulmarus glacialoides* on Ardery Island near Wilkes in 1961. Little is known as yet of their local environment, but Smit and Dunnet (1962) observed that the nesting places of the hosts, that is, the biotope where the immature stages of the flea develop, are buried under a metre or more of snow for most of the year. The nest on Anchorage Island was free of snow from mid-November until the date of collection, but was occupied during that period on only four occasions, each time for less than 24 hours. It may be significant that for most of that time the nest material was slightly damp and was kept relatively warm by long days of sunshine.

X. ADULT PLUMAGE AND MEASUREMENTS

The adult plumage of both male and female Snow Petrels is completely white except for the ivory-coloured shafts of the flight quills and a small margin of black feathers in front of, and over, the eye. There is also a grey wash on the leading edge near the tip of the first two flight feathers which varies in intensity without correlation with either age or sex. The grey vermiculations on the dorsal plumage, formerly attributed by Murphy (1936) only to juveniles, are also present on most breeding adults, but are very faint. The bases and aftershafts of the contour feathers are similar in colour to the dense grey down concealed under the contour plumage.

The bill is black and greyish-white to pinkish-grey-white at the base of the latericorn towards the gape. The eye is black with a brown iris. The legs vary from light blueish-grey to dark slate-grey (sometimes with brownish toe joints). The webs are light grey to pinkish-grey and the claws black. The outer edge of the fourth toe is generally the darkest part of the leg and foot.

Coues (1866) described the Snow Petrel as one of the most remarkable generic types of the Family Procellariidae, having a facial aspect that is peculiarly its own. He attributed this to the long, depressed sloping forehead which is not found in any other species of this Family, and that the effect is brought about by the flattening and elongation of the bones composing the forehead, aided by the forward extension of the frontal feathers on the bill. Coues' statement that the wings are rather short when folded and do not reach the end of the tail is incorrect; they extend well beyond the tail both in adults (Plate 15) and fledglings.

Males are predominantly larger than females. The measurements of 13 males and 11 females from the Davis and Platcha areas are compared below, the figures being minimum, maximum and mean length or weight respectively:

	Males	Females
Wing	257-269 mm (263·3 mm)	252-272 mm (258·5 mm)
Length	315-335 mm (324·8 mm)	307-333 mm (318·6 mm)
Culmen	19·9-22·3 mm (20·8 mm)	18·0-20·7 mm (19·5 mm)
Tarsus	31·0-35·0 mm (32·6 mm)	31·0-33·0 mm (32·2 mm)
Toe	33·0-35·0 mm (33·8 mm)	33·0-35·0 mm (33·7 mm)
Claw	9·0-12·0 mm (10·7 mm)	9·5-11·5 mm (10·7 mm)
Weight	206·7-312·1 gm (277·7 gm)	201·9-274·9 gm (242·1 gm)

The male of a pair may be distinguished from the female by his larger size, thicker neck and head, and by the lower pitch of his call. The female is rather dove-like in appearance. In flight, the chest of the male is generally much thicker than that of the female. It is sometimes difficult, however, to distinguish the sexes when both birds are small.

Table 11 shows that the specimens from the Mawson and Davis areas are, in general, similar in size. One notable exception is the female (B6862) collected at Mawson in November 1954; it is larger than are others and very similar to a breeding specimen collected by the author from Pointe Géologie, Terre Adélie, in 1958. Subspeciation based on size was originally proposed by Bonaparte (1855) and has been advocated by some later writers. It was not supported by Lowe and Kinnear (1930) on the grounds that there were insufficient specimens of known breeding status available at the time to justify it. The existence of a larger form at Pointe Géologie has been indicated by the weights of two males (521 and 484 grams) and of one female (425 grams) recorded by Prévost (1958). Prévost's chick weights were also consistent with a larger form, the maximum weights of three being 530, 534, and 560 grams. The maximum weight of the chicks examined in the Mawson and Davis areas did not exceed 350 grams and that of adults 312·1 grams. The presence of the larger form at Mawson during the courtship period cannot be disputed, but its status is unknown and, until it is found breeding there, it may be assumed that only the small form breeds in both the Mawson and Davis areas.

XI. DISCUSSION

Climate (especially wind and drift), length of day and the extent of sea ice all affect the breeding of Snow Petrels.

Near sea level the amount of wind and, therefore, of drift, with consequent blocking of nests, materially affects breeding success. At Mawson the mean wind velocity is twice that at Davis. At Mawson in 1958-59 the losses during the period from egg-laying to fledging were 78 per cent, while at Anchorage Island in 1961-62 they were estimated to be approximately 50 per cent, the difference being observed as due to blockage of nests by drifting snow. If the colonies above drift level, for example high on the Framnes Mountains, are as successful as those in the Davis area, it seems likely that the high level colonies owe their large populations not only to the larger

numbers of available nest sites but also to very limited snow blockage of nests during the breeding season. For colonies far inland, however, a decisive factor must be an abundant and reliable food supply. At Beaver Lake, for example, parent birds must fly at least 500 km each time they feed their chick, in addition to finding the necessary food. The fledged chick must travel at least half of that distance before it can feed at all. A late breakout or early formation of sea ice or a decrease in the amount of krill could have disastrous results.

Maher (1962) has shown that the breeding cycle of the Snow Petrel, like that of other Antarctic-breeding birds, is timed to take advantage of the annual cycle of plankton abundance, the chicks fledging in mid-March at the time of maximum zooplankton availability. Both duration of daylight and the extent of sea ice, particularly the fast ice of winter and spring, may affect this timing.

Over much of its range (at least between 65°S and 72°S) the Snow Petrel's breeding calendar appears to be the same in the Mawson and Davis areas, as for example at Cape Denison in George V Land and in Enderby Land (Falla 1937), in Dronning Maud Land (Lövenskiold 1960) and probably at Cape Hallett in the Ross Dependency (Maher 1962). Pointe Géologie in Terre Adélie (Prévost 1953, 1958) is apparently an exception, with slightly later egg-laying and hatching dates. This may be a genetic effect, for the birds at Pointe Géologie are larger than those at the other localities mentioned, and they may be genetically isolated. However, the colonies are very small and scattered and in other species such as the Kittiwake *Rissa tridactyla* (Coulson and White 1960), at such low-density colonies, birds were found to breed later than at more crowded colonies.

The main recorded variations between one colony and another and between one year and another consist of the occurrence of winter visits and the date of first arrival in spring. Snow Petrels have been seen occasionally in all the winter months at, for example, Cape Denison (Falla 1937), at Pointe Géologie (Prévost 1953), and at Wilkes (unpublished American and ANARE records), Mawson and Davis (ANARE records and author's observations), but not at Cape Hallett (Maher 1962). At Pointe Géologie, Prévost (1953) gave the mean arrival date of breeding birds as 1 October. In both the Mawson and Davis areas, the author observed the first birds in mid-September, although the main influx of breeding birds did not begin until 19-20 October and reached a peak on 1 November. Other reliable dates at Mawson are 22 September 1955 and 1 October 1959 for first arrivals, and 18 October 1955 and 27 October 1959 for the main body. At Cape Denison breeding birds were first seen on 6 October 1930 (Falla 1937) and, at Cape Hallett, not until 31 October 1960 (Maher 1962). The copulation date is no earlier at Pointe Géologie than it is in the Mawson and Davis areas, in spite of the earlier arrival.

Both north and south of the above range, breeding dates appear to be rather different. At the South Orkney Islands (between 60°S and 61°S),

Snow Petrels are regular winter visitors and the breeding birds arrive in large numbers in September. Clarke (1906) found eggs on 25 November 1904 and Ardley (1936) saw chicks several days old on 4 January and a late chick hatching on 8 January 1933; laying must have been completed in November. At Bouvetöya, Solyanik (1959) found eggs on 27-29 November 1958. In the Rockefeller Mountains (about 78°S) Siple and Lindsey (1937) found eggs in the early stages of incubation as late as 19 December 1934. It appears that the dates of egg-laying may vary by three weeks or more between the northern and southern limits of the breeding range.

These variations may be controlled by a combination of several factors: the direct effect of daylight on the birds, stimulating gonad development; the differing effects of daylight at different latitudes on plankton production; the effect of sea ice as a physical barrier between breeding and feeding grounds; and the effect of sea ice in depressing plankton production in spring.

During winter, Snow Petrels are presumed to feed in the pack ice and may reach land as far south as the Antarctic circle (for example, at Pointe Géologie) if the belt of fast ice separating it from the feeding area is relatively narrow. South of the Antarctic circle, the midwinter darkness inhibits photosynthesis and consequently plankton production. The numbers of the larger zooplankton (for example, Euphausiids) may be low, especially in surface waters (Foxton 1956), and there is no evidence to indicate that Snow Petrels feed in darkness. Thus, even though open water or pack ice may be within flying distance of land in the latitudes south of the Antarctic circle, Snow Petrels rarely reach it (as, for example, in the Vestfold Hills).

In early spring, gonad development is stimulated by increasing daylight. The most northerly breeding Snow Petrels (at South Georgia and Bouvetöya) are the first to respond, either because they are the first to reach the stimulatory day length (before the spring equinox), or they are the first to receive the necessary amount of light, or perhaps because of such subsidiary factors as temperature and food supply (Marshall 1961). They are not cut off from their breeding grounds by wide belts of fast ice, and food supplies within easy reach of land are good enough to allow the return of large numbers in September. Courtship probably occurs in late October and egg-laying in November. Birds breeding further south are not ready to lay until the very end of November, perhaps because they do not receive the necessary amount of daylight until later in the spring. Although the strongest or most responsive are able to visit some breeding grounds by mid-September, the sea ice is then at its maximum extent and thickness. Bunt (1960) has shown that, at the latitude of Mawson (67°36′S), photosynthesis beneath the ice is impossible before mid-September because the oblique rays of the low sun cannot penetrate the ice. In open water, photosynthesis begins earlier, and in September zooplankton is beginning to rise to surface waters (Foxton 1956), although this process begins progress-

ively later with increasing latitude. The numbers of Snow Petrels visiting any colony during late September and October would be governed by the amount of open water and of food at its surface within easy flying distance. Not until late October and November are all breeding birds assured of enough available food to allow them to visit the more southerly colonies nightly, sometimes staying for several days at a time. Probably, also, rising temperatures facilitate the clearing of snow-blocked nests at this time. The southernmost breeding birds may not winter any further south than the main body and need not be slower in reacting to light in spring. However, the spring rise of plankton would be later in the Ross and Weddell Seas than further north, because of the longer winter darkness and the poorer illumination of the sea by the lower sun. Snow Petrels breeding in the Rockefeller and Theron Mountains would not be assured of enough food for courtship activities until the middle of November.

At Mawson, in the Davis area and at Pointe Géologie, Snow Petrel chicks fly at the end of February and early March. The date is the same as that for other Antarctic breeding petrels, such as the Cape Pigeons and Silver-grey Petrels (Prévost 1958). Chicks are fed during the months of least ice cover, that is January and February, when surface plankton is increasing. They become independent when it is maximal. Mid-March is the time when sea ice is beginning to form in earnest and days are shortening towards the equinox. It is doubtful whether the parent birds could continue to feed the chicks in the second half of March; the hours of daylight might not be long enough for them to find the necessary food and then to re-cross the ever-widening belt of sea ice in order to feed them. Presumably the newly-fledged chicks would not be incommoded by this belt of sea ice, since those which are reared at inland colonies are known to fly long distances (250 km) as soon as they leave the nest and before they feed.

It thus appears that the breeding season of Snow Petrels is timed to fit very closely into the period when conditions are most favourable. In their re-occupation of breeding colonies in late April and May, Snow Petrels resemble Cape Pigeons and some sub-Antarctic petrels, such as the Soft-plumaged Petrels of Tristan da Cunha.

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