SIZE VARIATION IN THE SNOW PETREL (Pagodroma nivea)

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ABSTRACT

During a year spent at Casey, Antarctica, in 1977-1978, I made a study of the local population of the Snow Petrel (*Pagodroma nivea*). The breeding distribution of the species in the area is outlined, together with some of the problems encountered.

The Snow Petrel varies widely in size. The literature on the species is reviewed. Large birds (wing over 280 mm) are known chiefly from Dumont d'Urville, Adelie Land. Other published occurrences of large birds have often gone unnoticed or have been disregarded.

Large birds breed at the Windmill Islands, making up 35% of 178 birds measured. Most of these large birds are concentrated in one area and some show the same atypical choice of "open" nests as at Dumont d'Urville. Some large and small birds interbreed. These findings are discussed, and the hypothesis of separate "large" and "small" subspecies is critically examined.

It is concluded that the species has great individual variation in size, and that large birds form a varying proportion of the populations breeding at many localities.

INTRODUCTION

A circumpolar species, the Snow Petrel is not normally found north of the zone of pack ice. It breeds at many places on the coasts of the Antarctic Continent and in some mountain ranges up to 300 km inland (Lovenskiold 1960, Loy 1962, Ardus 1964, Bowra *et al.* 1966, Brown 1966, Brook & Beck 1972). It also breeds on many antarctic islands.

Most specimens are from those areas where exploration has been concentrated, e.g. Victoria Land, the Ross Sea and adjacent areas (see Fig. 1), whereas vast stretches of coast and expanses of ocean are almost unrepresented. Many specimens have been collected at sea, or on land in winter, and so their breeding places are unknown. Several authors have properly emphasised the need to measure birds at their colonies in the breeding season in order to clarify the taxonomy of the species.

It has long been known that Snow Petrels vary greatly in size. Prevost (1969) reviewed the literature from 1777 onwards and traced the development of the hypothesis of large and small forms. The



FIGURE 1 — Antarctica. Places of origin of major collections and records (marked +) of the Snow Petrel (schematic only).

best-known breeding areas of large birds, those with a wing measurement of 280 mm or more, are in the vicinity of Dumont d'Urville, in Adelie Land ("Dumont") and at the Balleny Islands.

There are no measurements of Snow Petrels in the sector 80° E to 140° E, some 3000 km of coastline, except for some eggs (Pryor 1968). Therefore it seemed that a project to measure breeding birds at Casey would be valuable, and it was included in the 1977 programme.

I served as medical officer to the Casey 1977 wintering party during the year February 1977 to February 1978, and the study was made in the summer of 1977-1978. A previous paper (Cowan 1979) described the area, its history, geography and climate, and previous ornithological work.

Casey is Australia's newest antarctic station and lies on the Budd Coast just north of the Antarctic Circle at 66°17'S, 110°32'E. The main geographical feature of this area is the Windmill Islands, a chain of islands varying in size from a few square metres to 10 square kilometres some of which, permanently connected by ice to the mainland, have been renamed peninsulas. In summer, extensive areas of rock are exposed, offering to several species of birds the only nesting place of any size in a stretch of coastline of some 800 km (see Fig. 2).



FIGURE 2— The Windmill Islands, Antarctica. Labelling is restricted to places mentioned in the text.

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Inflatable boats were used to make 15 trips during the 1977-1978 breeding season. Ardery and Odbert Islands were the areas chiefly studied, but visits were also made to the Holl group and Peterson Island. One further trip was made by ship's boat in January 1978. Advantage was also taken of the helicopters carried by the relief ship to visit the Fraziers in February 1977 and January 1978, during the annual changeover operations.

The Snow Petrel breeds on most of the larger islands, some 20 in all, including the Fraziers but excluding the Swains and Donovans, as well as at several mainland localities. Nests are made in any rocky area with suitable crevices under or between the rocks. Because most nests are hidden and many places inaccessible, breeding numbers can only be roughly estimated. Two of the most populous areas are on Ardery and Odbert Islands. A previous estimate (Orton 1963) of 20 nests on Ardery contrasts with my own of 200-300 nests, with 105 birds caught and measured. On Odbert, I estimated 150 nests and measured 39 birds. See Fig. 3.

In general, the birds nested on cliffs and slopes facing north and east. Thus, the nests on Ardery Island were mostly scattered along the north cliffs and at the eastern end; those on Odbert Island were also along the north cliffs and at the eastern end, but a few were in the flat saddle area; those on O'Connor Island were mostly at the north-eastern end. Although some of these cliffs are inaccessible, birds can be seen flying about the nests, which can thus be mapped from a distance.

The orientation of most of the nests is towards the prevailing winds, which are off the land and easterly. A similar situation obtains at Dumont (66°40'S, 140°01'E), where the winds are mainly southeasterly (Mougin 1968) and at Haswell Island (66°33'S, 93°01'E), where they are easterly (Pryor 1968). Slopes exposed to the wind remain relatively drift-free and the scouring of snow that would otherwise fill nest entrances is clearly advantageous to the petrels. On the leeward side of the islands, snow remains accumulated in the summer, sometimes permanently. However, Brown (1966) found no such consistency in the orientation of nests at Davis (68°35'S, 77°58'E).

The breeding cycle is characterised by complex comings and goings at the colonies in early spring, followed, as in the other fulmarine petrels, by a pre-laying exodus which occupies the second half of November. Laying takes place in early December with hatching 6 to 7 weeks later. Detailed accounts of the breeding cycle have been given by Brown (1966) and Mougin (1968) and I have recorded some observations on the behaviour of the birds studied at the Windmill Islands (Cowan 1979).

MATERIALS AND METHODS

Two Hutchinson "Mapa 401" inflatable boats with Volvo "200" outboard motors were used for transport. The usual party consisted of



FIGURE 3 --- Plan of Ardery Island; Snow Petrel breeding areas.

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three men. Conditions were always potentially hazardous as the prevailing wind is off the land and high winds develop suddenly. The sea is very cold and is largely uncharted, abounding with shallow reefs. An enforced stay on an island was always possible, and much gear had to be carried, including tent, radio, food and fuel. The two boats never separated.

Measurements were taken of live birds captured at the nest site and then released, except for one severely injured bird which was measured immediately after being killed. Wing, culmen length and tarsus were measured as in the CSIRO Bander's Manual 1971. The wing was measured with a steel tape and to the nearest 5 mm. Where one wing was obviously shortened by wear, the other was measured, but this was rarely noted. The culmen (feathers to tip) and tarsus were measured with calipers to the nearest mm. All measurements were made by myself as sole observer. Birds were not weighed, and eggs were not weighed or measured.

The birds were not banded as this would have reduced the available time for making observations. However, there was little risk of duplicating measurements, since the nesting areas were extensive and dispersed. As no specimens were collected, the birds could not be sexed.

To measure the birds, most of which sat within one metre of an exit, I had to lie down, introduce an arm into the nest cavity, provoke the bird into setting the sharp hooked tip of its bill into the (gloved) finger, and extract the bird by gripping its bill with the free fingers. Birds not on an egg were more elusive and often an assistant had to block a second exit to prevent escape. The birds always regurgitated during capture and measurement. When released, they returned at once to the nest site.

RESULTS

Measurements

Altogether 178 birds were measured, located as follows.

Ardery Island (northern side)	39	
" (eastern end)	66	
Odbert Island	39	
Budnick cliffs near station	11	
O'Connor Island		
Peterson Island	10	
Field store near station		
Nelly Island		
-		
Total	178	

Figure 4 shows the distribution of each of the three measurements. All show a roughly similar pattern. The wing length has historically



FIGURE 4 --- Dimensions of 178 Snow Petrels

been the chief standard used and is probably subject to the least percentage error in the living bird.

Figure 5 shows the distribution of pairs of dimensions.

I use the terms "large" and "small" here simply for brevity of discussion, and the 280 mm wing length recognised by previous authors (Falla 1937, Prevost 1969) makes a convenient arbitrary division. Certainly, it distinguishes collections like those of Friedmann (1945), Maher (1962) and Brown (1966), none of whose specimens exceeds 269 mm, from the Dumont birds of Prevost, 82% of which exceed 280 mm. Applying this criterion to the Windmill Islands series, some interesting facts emerge. There are 63 large birds, that is, 35%. Of these 63, 54 are from Ardery Island, and 46 from around its eastern end. The rest are from Odbert (4), Peterson (3), O'Connor (1) and Nelly (1) Islands. Note that studies were made chiefly on Ardery and Odbert, and that many other known breeding islands were visited only once or not at all. Large birds probably breed at other places in the area.

The sizes of paired birds

Of particular interest are the nesting pairs, which are shown in Table 1. Although we made special efforts to capture such pairs for measurement, sometimes one or both escaped. However, 28 pairs were measured, only two of which were incubating. (The presence of old eggs from previous seasons is common and can easily lead to errors in recording "incubating pairs"). One other incubating pair was seen, but one of this pair escaped. Presumably the pairs found with an egg are changing over and the changeover periods are brief since, of the 98 eggs being incubated, 95 were attended by a single bird. This brief changeover period applies also to the Antarctic Fulmar (Fulmarus glacialoides), the Antarctic Petrel (Thalassoica antarctica), and the Cape Pigeon (Daption capense). Pairs which have failed to breed or which have lost the egg may be found at the nest together late in the season; such pairs show little site tenacity and readily leave the nest if approached. Some of these may be young birds which are establishing territories but have not yet bred. Of 146 nests examined, no (new) egg was found in 46.

Note that of the nesting pairs measured, four were pairs of a large bird with a small bird.

Nest site in relation to size of birds

The literature had led me to expect that birds in the Casey area would be of the "small" size. The discovery of the concentration of large birds at the eastern end of Ardery caused some excitement, therefore, as did the apparent difference in many of the nest sites. Isenmann (1970) had discussed this difference in nest sites and incorporated it into his hypothesis of two subspecies. Not all but many of the large birds on Ardery had chosen exposed sites, some



FIGURE 5 --- Paired distribution of dimensions

Size of paired birds	Number of pairs	With egg	Without egg	Location	
Both small	16	1	15	Ardery north	5
				Ardery east	3
				Odbert	7
				Field store	1
Both large	8	о	8	Ardery east	7
				Odbert	1
Large with	4	1	3	Ardery north	1
small				Ardery east	1
				O'Connor	1
				Peterson	1

TABLE 1 — Measured nesting pairs of Snow Petrels

of them more appropriate to a Cape Pigeon, with an overhanging rock behind but nothing to provide any difficulty in extracting the bird. In one place towards the south-eastern face, long ledges with overhanging rock behind had rows of nests placed only one or two metres apart, where the birds sat in view of one another. Other large birds chose vertical clefts which were also rather different from the horizontal clefts typically chosen by the small birds. The terrain of the eastern end of Ardery showed no obvious differences from that along the northern cliffs such as might have attracted birds with particular nesting preferences.

The more exposed nests might seem vulnerable to predation by Antarctic Skuas (*Stercorarius skua maccormicki*), but, like Isenmann (1970), we saw no evidence of this. The Skuas' behaviour in the colonies is rather skulking, and although they were seen to snatch deserted eggs, they were not seen to behave aggressively towards petrels of any species, adult or chick, in the mixed colonies of Snow Petrels, Antarctic Petrels, Antarctic Fulmars and Cape Pigeons. Only once was a Skua seen to bring down a Snow Petrel in flight.

Study is needed to show whether the use of exposed sites is

associated with any modification in guarding behaviour. The length of the guard stage reported by Brown (1966) in uniformly small birds is rather shorter than that reported by Mougin (1968) for the predominantly large birds at Dumont. This may be associated with the more open nests chosen by some large birds. However, even the larger Snow Petrels, like the Wilson's Storm Petrel (Oceanites oceanicus), a concealed nester, have a shorter guard stage than species which always make open nests (Brown 1966, Mougin 1968).

The concealed site protects the chick from predation and perhaps to some extent also from cold. In the Antarctic Petrel, which is an open nester, we found that the chicks had acquired the vomiting habit by the time they were left unguarded. However, we found several Snow Petrel chicks in concealed nests which although already left alone, did not appear capable of vomiting at us. The concealed nest may permit the parents to leave the chick unguarded before it has acquired this protective habit.

The large birds seemed to be less difficult to capture and less pugnacious in the hand. Their eggs were visibly larger.

REVIEW OF THE LITERATURE

(All measurements are in millimetres and are of wing length unless otherwise stated.)

Ross (1847) visited a Snow Petrel breeding colony at Cockburn Island (64°12'S, 56°49'W) on the Antarctic Peninsula on 6 January 1843. He wrote: "The eggs of this bird, which have never before been seen, are 2.2 inches [56 mm] long, 1.6 inches [41 mm] broad . . ." These dimensions correspond with those of eggs of typical small Snow Petrels. (See Isenmann 1970.)

Sharpe (1902) studied specimens collected by the Southern Cross expedition. These fall into two groups. Firstly, there are seven birds collected during the first fortnight of January, corresponding with the late incubation period. All but one are exceptionally large with a mean wing of 292 (262-300). (I have converted Sharpe's figures from inches.) These birds were shot in the pack ice about 400-500 km north of the Balleny Islands (67°S, 164°E), not then known to be a breeding place and about as far again from the coast. Secondly, there are six birds shot at Cape Adare (71°18′S, 170°15′E). These are small, mean wing 261 (251-269). Only two were taken during the breeding season, in mid-December. Some eggs were also collected at Robertson Bay, near Cape Adare. These too are from small birds.

Wilson (1907) reviewed specimens in the Discovery and Morning collections and also earlier material in the British Museum. Like Sharpe, he commented on the great range in size and that it applied to both sexes. He did not give dimensions for every bird, only the largest, 290 (Ross Sea pack ice), and the smallest, 245 (off Cape

Adare), and remarked: ". . . and between these two extremes every gradation may be observed." Unfortunately, it is impossible to discover from Wilson's paper exactly where these birds were taken. Although Lowe & Kinnear (see below) did give exact locations, they also remeasured the specimens, and so one cannot match their specimens with Wilson's.

Always an outstanding observer, Wilson also commented on large flocks of Snow Petrels off the Balleny Islands on 2 March: "All were uniform in size and of the larger type; not one of the smaller type was seen, but as they seemed to be in flocks and on the move, one could not consider this to be characteristic of the locality." None of these was collected. At this date, most parents have abandoned the chick (Mougin 1968, Isenmann 1970).

Gain (1914) reported on specimens from Petermann Island $(65^{\circ}10'S, 64^{\circ}08'W)$ on the Antarctic Peninsula, and also gave information on behaviour and seasonal movements. Of 22 birds, 7 were large (280-292), and one of these is described as "a juvenile male of 3-4 months" with grey dorsal feathering. Eight other birds were described as juveniles, and as a group they were smaller than the adults. Dates of collection for the whole series were between early April and mid-August.

Snow Petrels were not breeding in the immediate area, and the first appeared in April, when all birds were seen to be travelling northward. From that time until September they were seen regularly, and Gain noted that their numbers increased when the sea ice broke up and open water approached the wintering ship. They took advantage of food sources made available by the presence of the party, including seal carcases and galley scraps, and at times would remain in the area for many days. From early September their numbers began to fall off as they left for the south, and after 3 October only one bird was seen. It is now known that there are breeding colonies further south on the Peninsula (Watson *et al.* 1971).

Gain also recorded large numbers near Peter I Island (68°45'S, 90°40'W) in the following summer, but I can find no subsequent information on possible breeding there.

Lowe & Kinnear (1930) discussed the literature and taxonomy of the species and reviewed not only the Terra Nova collection but also other museum material from the expeditions of Ross, the Southern Cross, Discovery, Morning etc.; 69 specimens in all. Only one of these was taken at a colony in summer; this is one of the two abovementioned Southern Cross birds taken at Cape Adare. They remeasured the specimens and so their measurements cannot be compared bird for bird with those in the original reports, especially as they apparently used a different technique. Thus, three of the birds studied by Wilson have a wing larger than Wilson's largest of 290, and the same applies to some of Gain's collection, part of which is included. Two of the birds from Ross's expedition were also large, 290 and 290+. Both were taken in summer, the former in the Ross Sea, and the latter 400 km from the Balleny Islands and the same distance from Scott Island (67°25'S, 179°50'W); both these latter localities are now known to be breeding places (Kinsky, pers. comm.; Harper, pers. comm.).

One of the *Terra Nova* birds is large (297) and was shot in the pack ice in mid-December, less than 100 km from Scott Island and 500 km from the nearest coast. One of Wilson's large birds (300) was taken in late November, 200 km from Scott Island, 400 km from the coast and 500 km from the Balleny Islands. One of the *Scotia* expedition's birds from the South Orkney Islands (61°S, 46°W) in winter is also large (283).

Lowe & Kinnear refuted the claim of Mathews (1912) that large and small species *(sic)* can be separated on the basis of *discrete* size ranges; they believed that there is a gradation of intermediate sizes, although they conceded that the existence of two species was "highly probable."

Falla (1937) described 33 specimens, some of which were taken during the breeding season at two colonies. There was one large bird (295) shot in the pack ice at 66° S, 73°E, 300 km from the nearest land, on 22 December, that is in the middle of the incubation period. Two adults were taken at the colony at Proclamation Rock ($65^{\circ}51'$ S, $53^{\circ}48'$ E) in mid-January; the male was large (283), the female, from an adjoining nest, was small (258). Falla commented on the range of sizes at this colony and noted that "the larger form predominated in the neighbourhood." Falla used the criterion of wing 280 when speaking of large birds.

He also commented on the homogeneity in size of birds from Cape Denison ($67^{\circ}S$, $142^{\circ}40'E$) which have a wing of 250-275, and suggested that the measurement of the wing may be more reliable than that of the length of bill. Like other writers, he found gradation of sizes, with "no marked gaps such as would justify specific distinctions."

Friedmann (1945) gave dimensions of 14 birds, including some taken during the breeding season at two colonies: Neny Island ($68^{\circ}12'S$, $67^{\circ}02'W$) on the Antarctic Peninsula and the Rockefeller Mountains ($78^{\circ}S$, $155^{\circ}W$) in Edward VII Land. All were small, less than 270.

Dupond (1946) published the ornithological results of the Belgica expedition of 1897-1899. Snow Petrels were seen throughout the winter while the ship was beset in the pack ice. Three specimens were measured; all were small, 270-273, and were collected at about 71°S, and between 83 and 90°W.

Bierman & Voous (1950) described birds taken at sea on whaling expeditions between $26^{\circ}W$ and $9^{\circ}E$, and between 62 and

68°S. Of 19 birds, only one male and one female were classified as definitely breeding birds. Three other males are adult, of which one is a large bird (286) with a correspondingly large bill and tarsus and a weight easily the greatest of the 19. The authors speculated as to which colonies their breeding birds might have come from and suggested the South Sandwich Islands (58°S, 27°W at centre), about 1100 km from where the breeding male bird was taken and 500 km from where the breeding female and the large adult male were taken. All the non-breeders were collected after 1 March, within a very few days of the earliest departures of the juveniles.

Maher (1962), working at Hallett Station (72°19'S, 170°20'E), reported on the weights of 20 birds, and measurements of these were given by Prevost (1969); all were small, less than 260. All were collected at breeding colonies in November.

Brown (1966) reported on breeding colonies near the Australian stations at Davis (68°35'S, 77°58'E) and Mawson (67°36'S, 62°52'E). All the 31 adults collected were small birds.

Pryor (1968) at Haswell Island (66°33'S, 93°01'E) gave egg measurements only. These were clearly from small birds.

Prevost (1964) gave data on the breeding cycle at Dumont, which were expanded by Mougin (1968). Only the usual hidden type of nest of the species was described; no mention was made of nests in more open positions.

Mougin (1968) gave the first detailed account of the breeding of the Snow Petrel and other petrels at Dumont. The emphasis is on comparisons between the species. While the microclimate at ground level was more severe in the Snow Petrel breeding areas than among the Cape Pigeons, Mougin believed that the Snow Petrel, nesting in sheltered tunnels, must confront less severe conditions, and he correlated this with their weight, which was less than that of the Cape Pigeons. He did, however, mention that some Snow Petrel nests were in relatively open positions. He gave a series of measurements of juveniles just before their departure. The mean wing was 250, compared with the local adult mean of 295. The mean weight was 365 g (adults 450 g). The tarsus was the same size as in the adult, and the bill was rather smaller.

Isenmann et al. (1969) reported on birds collected at Cape Denison, and at Cape Hunter, 18 km to the north-west. This area is in King George V Land, about 100 km from Dumont. All are breeding birds; 11 are from Cape Denison and 8 from Cape Hunter. Later, Isenmann (1970) noted that there were "at the most 20 pairs" at each locality. The Cape Denison birds, like those of Falla (1937), are all small (mean wing 263). No mention is made of the large bird (wing 293) collected there in the breeding season by SapinJaloustre (1951). The Cape Hunter birds are less homogenous; the mean wing is 273 (239-295) and 4 of the 8 are large (281-295). The greater homogeneity of the Cape Denison birds is later cited by Isenmann (1970) as evidence for the lessening influence of the large form at Dumont as the distance increases, Cape Denison being a little farther away from Dumont than is Cape Hunter.

Prevost (1969), in reviewing previous literature, mentioned but did not discuss the large birds of Falla and of Bierman & Voous, while most of those of Lowe & Kinnear were not even mentioned. Turning to recent French collections, beginning with those of Isenmann *et al.* from Cape Denison and Cape Hunter, Prevost dismissed the large bird of Sapin-Jalcustre as being without doubt from another colony ("il provenait sans doute d'une zone de reproduction situee a l'Est ou a l'Ouest de Pointe Geologie").

The collections made at Dumont numbered 90 birds in five collections. (There are actually 91, but a printing error deletes one set of measurements.) Most of these measurements were of birds killed at the colonies. Each of the five groups includes some small birds: in all 16 (18%) with a wing less than 280 of which 7 (8%) have a wing less than 270.

Prevost regarded the size of bill as also important and suggested that some large-billed birds may be of the "large form" even though short in the wing. He indicated two populations separated by a wing length of 275 and a culmen height of 11. The Dumont birds exceeded these dimensions, while by contrast those from Hallett, a typically "small" population, fall below them, as do the "rare aberrant birds" of Dumont. (Actually, the diagrams as printed plot the wing length against the cumen *length*, not height.) Prevost concluded by proposing two subspecies; a larger one, *Pagodroma nivea major*, of Terre Adelie and probably the Balleny Islands, and a smaller one, *Pagodroma nivea nivea*, breeding in all other known localities.

Isenmann (1970) followed the hypothesis of two forms of the Snow Petrel and developed the proposals of Prevost while trying to embody in the hypothesis the presence of small individuals among the breeding birds at Dumont.

Isenmann accepted seven groups of birds for comparison, all from breeding colonies in summer. These were: Dumont, 86 birds (see Prevost 1969), excluding some owing to lack of data; Cape Hunter, 8 birds (see Isenmann *et al.* 1969); Cape Denison, 13 and 11 birds (see Falla 1937, and Isenmann *et al.* 1969); Mawson, 10 birds, and Davis, 20 birds (see Brown 1966); and Hallett, 20 birds (see Maher 1962). Actually, Brown had 9 birds from Mawson and 22 from Davis, but this does not alter the facts in any way. Falla's (1937) birds from Proclamation Rock, one of which was large, were not included. Where available, weight, wing, culmen length and tarsus were compared for these seven populations. Weight, of course,

varied greatly during the cycle, especially during shifts of incubation. The Dumont birds were significantly different in all four dimensions from the other six populations, with a security of 95%, and none of these six showed such differences from one another.

Isenmann drew attention to the *large spread of dimensions* in the Dumont birds, which is the key statement in understanding the hypothesis of two forms. The Dumont birds' wing lengths cover 87% of the total range of all seven groups, whereas those at Davis cover only 37%. That is, the typically "small" form, as at Davis, is not only small but homogenous, whereas the "large" form is very variable in size and includes some small birds, which Prevost (1969) dismissed as "aberrant." Comparing available breeding data from Dumont with those of small birds, the Dumont birds produced a larger egg, incubated a little longer but in shorter shifts, and hatched a larger chick.

About 10-15% of the birds at Dumont, mostly large birds, nested in relatively open and exposed sites such as had not been described elsewhere. Isenmann quoted Pryor (1968) (then in litt.) as suggesting population pressure as a possible reason for using such unfavourable sites, although Pryor as published does not say so. Isenmann in any case rejected this theory, believing that large birds would hardly be evicted by small ones, although he seemed to assert that the small birds in such sites had been so evicted. The absence of predation by skuas at Dumont was discussed as a possible factor permitting exposed nesting, although such predation seemed only to be seen at inland colonies (Lovenskiold 1960, Brown 1966), possibly because of the absence there of Adelie Penguin colonies as a preferred food source. Isenmann was unable to correlate climatic differences with differences in the size of birds. Nonetheless, he claimed that Dumont uniquely showed an example of climate affecting size, the "electicism " of some birds in their choice of nest site having tended to fayour by natural selection the development of larger birds better able to withstand the more severe microclimate of the open nest site. Isenmann concluded by proposing that the Snow Petrel is a bitypic species whose two forms show imperfect geographical isolation and some genetic mixing, e.g. at Cape Hunter. The large form shows great variability in size; the small form shows little variability.

Kinsky (1970, and pers. comm.): In an addendum to the lastmentioned paper, Isenmann reported information from Kinsky on 26 specimens collected at the Balleny Islands, and F. C. Kinsky has kindly provided me with details of these birds. This is a unique collection of entirely large birds, the mean wing being 300 (291-311) and other dimensions correspondingly large, which corroborates Wilson's observation. Kinsky points out that because of the difficult terrain he did not actually see breeding, but the observations of large numbers of Snow Petrels landing on cliff faces in February seems conclusive !

Kinsky's data also include the dimensions of specimens from other localities. One of 38 birds taken in November at the breeding colony at Hallett Station, although too early to be on an egg, is a large bird (291), which makes Hallett another probable breeding place of large birds. Four other birds in this group have a wing of 275-280. This collection from Hallett is in fact more numerous than that of Maher, on the basis of whose collection the French authors have continued to regard Hallett as the seat of a typical population of homogeneously small birds with a wing not exceeding 258 (data from Maher quoted in Prevost, 1969).

Watson et al. (1971) and Watson (1975) are two recent publications, which include bibliographies. Both set forth the prevailing view of the French authors, that is, that "large" Snow Petrels breed at Dumont and the Balleny Islands, and typical "small" Snow Petrels breed elsewhere.

DISCUSSION

The vastness of Antarctica is difficult to grasp and has tended to vitiate thinking about the distribution of birds. If one studies distribution maps of known breeding localities of antarctic birds, most of these localities obviously correspond with the vicinity of manned stations or of well-visited areas. For example, the Southern Giant Petrel (Macronectes giganteus) is known to breed at only four places around the coast of the Antarctic Continent, that is, at Casey, Davis, Dumont and Mawson (Watson et al. 1971, Johnstone et al. 1973) ! If you discover the breeding place of unusually large Snow Petrels, you can easily assume that such birds may not occur elsewhere, forgetting the enormous stretches of coast and ocean from which no specimens at all are available (see Fig. 1). The literature contains very little information on the movements of Snow Petrels in winter, of non-breeding birds in summer, or even of the feeding range of breeding birds. The rule for species which breed around continental Antarctica is not to show regional differentiation, and the Snow Petrel has been the single "enigmatic exception" to this rule (Watson 1975). Isenmann (1970) suggested that differing local climates, especially wind conditions, might favour the development of distinct subspecies: and yet, if such an effect exists, why does it not seem to apply to other species ?

Records of large birds fall into the three categories shown in Fig. 6, as follows:

- 1. Those from breeding colonies. Large birds have been shown to breed at Dumont (Prevost 1969, Isenmann 1970), the Balleny Islands (Kinsky 1970), Cape Hunter (Isenmann *et al.* 1969), Cape Denison (Sapin-Jaloustre 1951), Proclamation Rock (Falla 1937), Hallett (Kinsky, pers. comm.) and the Windmill Islands (present paper).
- 2. Those collected at sea in summer and coming presumably from some colony within a few hundred kilometres. Localities where such birds have been collected or reliably reported include the

seas north and east of the Balleny Islands and around Scott Island (Ross 1847, Sharpe 1902, Lowe & Kinnear 1930), the Ross Sea and Great Ice Barrier (Ross 1847, Lowe & Kinnear 1930), the seas off the Amery Ice Shelf (Falla 1937) and near the South Sandwich Islands (Bierman & Voous 1950).

3. Those collected in autumn and winter in the vicinity of wintering ships near islands in the Antarctic Peninsula (Gain 1914) and the South Orkney Islands (*Scotia* collection in Lowe & Kinnear 1930).

While Snow Petrels are known to visit land throughout the year whenever weather conditions bring open water up to the shore (Gain 1914, Prevost 1964, ANARE Station Logs), such visits seem to be concentrated in April and May (Mougin 1968). Watson (1975) states that "in some areas birds are present all the year." At the South Orkney Islands Snow Petrels were "by far the most numerous of



FIGURE 6 — Antarctica. Records of large (over 280 mm) Snow Petrels; when and where collected or recorded.

the few species which remained for the entire winter" (Clarke 1906), and at Petermann Island the birds spent extended periods about the wintering ship (Gain 1914).

The Snow Petrel is confined to the zone of pack ice. Complete circumpolar movements like those of the Wandering Albatross seem unlikely. The tireless glide of the Wanderer on the westerlies contrasts with the fast-beating erratic flight of this much smaller bird among the pack ice, where the winds are easterly but with irregularities in flow (Knox 1970), and where the frequent and violent local blizzards must also tend against consistent movement patterns. Any movements are more likely to be confined within a sector of longitude. Gain, too, believed that the Petermann birds bred at a colony further south, and that their seasonal movements were meridional.

The presence of small birds among the large ones at Dumont was described by Prevost (1969) as "aberrant," but was later incorporated into the hypothesis proposed by Isenmann (1970). Differences in bill size have received only cursory attention and do not seem to be regarded as a reliable sole criterion, varying with age, among other factors, though in general tending to correlate with wing length (Lowe & Kinnear 1930, Bierman & Voous 1950, Prevost 1969).

The paired distribution of dimensions shown in Fig. 4 suggests good correlation in the three dimensions, and, since wing length is easier and more accurate in the field on the live bird, I believe it should continue to be the main standard used.

Prevost (1969) suggested a separation around 275 mm wing length between two groups of birds, the "large" and "small" forms. However, I believe that my series shows a rather continuous size range in all dimensions, that is, that birds of all intermediate sizes occur between the largest and the smallest. As I have also shown, large birds do breed with small birds.

Finally, I have shown that the proportion of large birds (280 mm wing length or above) is widely variable, examples being 100% at the Balleny Islands, 82% at Dumont, 50% (4 of 8) at Cape Hunter, 35% at the Windmill Islands, single birds at Hallett and at Proclamation Rock and 0% at Davis and at Mawson. The evidence indicates a very strong individual size variation in many breeding populations of the Snow Petrel. However, since variability in size cannot be correlated with geographical distribution, the existence of two subspecies is, in my opinion, questionable.

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