ECOLOGICAL SEGREGATION OF BURROWING PETRELS (PROCELLARIIDAE) AT MARION ISLAND

by

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SUMMARY

1. Eight burrowing petrel species were found nesting within the area studied in north-eastern Marion Island during April 1979 to May 1980. These were Salvin's Prion Pachyptila vittata salvini, Blue Petrel Halobaena caerulea, Greatwinged Petrel Pterodroma macroptera, Kerguelen Petrel Pterodroma brevirostris, Softplumaged Petrel Pterodroma mollis, Whitechinned Petrel Procellaria aequinoctialis, Grey Petrel Procellaria cinerea and South Georgian Divingpetrel Pelecanoides georgicus. Eighty-one percent of burrows found belonged to Salvin's Prions.

2. The nest site preferences of Salvin's Prion, Blue Petrel, Greatwinged Petrel, Kerguelen Petrel, Softplumaged Petrel and Whitechinned Petrel were investigated. These species had individual preferences with respect to soil depth, soil moisture content, slope angle or slope aspect.

3. The breeding biologies and diets of Greatwinged Petrels, Kerguelen Petrels and Softplumaged Petrels were studied. The species bred at different times of the year with non-overlapping chick-rearing periods. Incubation periods were similar but, relative to adult size, Kerguelen Petrel chicks grew fastest. All three species took mainly cephalopods although Kerguelen Petrels took the most crustaceans and fish.

4. Subantarctic Skuas Catharacta antarctica were important predators of petrels. They preyed upon whatever petrel species were most abundant in an area, although large petrels (Whitechinned Petrel) and those breeding in winter (Greatwinged Petrel) were seldom taken.

5. Similar petrel species had the bulk of their breeding populations spread over different habitats thus reducing any competition for nest space. At the same time, staggered timing of breeding, and particularly the non-overlapping chick-rearing periods of the three _Pterodroma_ petrels, helped to minimize competition for food.

GENERAL INTRODUCTION

The Prince Edward group of islands (46° 50'S, 37° 45'E) in the Southern Ocean consists of two volcanic islands, Prince Edward (44 km^2) and Marion (290 km^2). Their climate, geology and vegetation have been recently described by Gremmen (1981) (see Chapter 1 for a summary). Out of the 23 island groups in the Southern Ocean, the Prince Edward Islands have the second highest number of breeding seabird species (Williams et al. 1979). These include 12 species of "burrowing petrels", nocturnally active procellariiform seabirds from the families Procellariidae (petrels and prions), Oceanitidae (stormpetrels) and Pelecanoididae (divingpetrels) which nest below the ground in either burrows or natural cavities.

There have been several studies of ecological segregation amongst co-existing seabird species in tropical and temperate areas (e.g. Ashmole 1968, Pearson 1968, Cody 1973) but more recently in the sub-Antarctic at South Georgia (Croxall & Prince 1980). The latter study included six burrowing petrel species, three of which are found at Marion Island. Observations on petrel distribution and breeding at Marion Island have been published by Crawford (1952), Rand (1954) and van Zinderen Bakker Jr (1971).

This study aimed to describe quantitatively the distribution and nest site segregation of burrowing petrels at Marion Island and to identify differences in the breeding biologies and feeding ecology of three Pterodroma petrels which aid their further ecological segregation. In order to determine chick feeding frequency, an automatic recorder was developed which could record the number and timing of nest visits by petrels (Appendix 1).

The introduction of House Cats *Felis catus* to Marion Island between 1949 and 1951 (van Aarde 1979) has led to the extermination to of at least one petrel species and to a general reduction in the petrel populations (van Aarde 1980, Berruti *et al*. 1981). However, the effects of cat predation can only be assessed by knowing the extent of natural predation on petrels, which is mainly by Subantarctic Skuas *Catharacta antarctica*. For this reason, skua predation on petrels was also investigated.

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CHAPTER 1

Distribution and abundance of burrowing petrels (Procellariidae) at the Prince Edward Islands

Distribution and Abundance of Burrowing Petrels (Procellariidae) at the Prince Edward Islands

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Summary. The distribution of burrows of six petrel species - Salvin's prion _Pachyptila vittata salvini_, blue petrel _Halobaena caerulea_, great-winged petrel _Pterodroma macroptera_, Kerguelen petrel _Pterodroma brevirostris_, soft-plumaged petrel _Pterodroma mollis_ and white-chinned petrel _Procellaria aequinoctialis_ - within the north-eastern part of Marion Island in the Prince Edward Island group (southern Indian Ocean) was determined with respect to six habitat characteristics. These were geology, vegetation type, slope aspect, slope angle, soil depth and moisture content. Great-winged and white-chinned petrels, which excavate the largest burrows, were restricted to areas with deep soil. Only Kerguelen and white-chinned petrels, whose burrows are adapted to allow water drainage, nested in marshy areas. soft-plumaged and blue petrels favoured steep, exposed slopes where enhanced lift facilitated rapid take-off and reduced vulnerability to predation on the ground. Salvin's prion occurred in the widest range of conditions and used both natural cavities and burrows for nesting. It was the most abundant

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species within the study area (81 % of burrows, with a maximum density of 279 burrows ha^{-1}). Burrow densities at Marion Island were 6-32 times lower than in comparable areas at neighbouring Prince Edward Island. Predation by feral house cats *Felis catus*, absent from Prince Edward Island, is assumed to be largely responsible for this difference.

Introduction

Many small procellariiform seabirds from the families Procellariidae, Pelecanoididae and Oceanitidae breed underground, usually in burrows, but occasionally in natural cavities. These birds are collectively called burrowing petrels.

Quantitative data on the abundance of selected burrowing petrel species have been published or the following sub-Antarctic breeding localities : South Georgia (Croxall & Prince 1980; Croxall & Hunter 1982); the Crozet Islands (Derenne & Mougin 1976); and Macquarie Island (Brothers 1984).

However, the relationships between the distribution of petrel burrows and the vegetation and physical characteristics at breeding localities have not received attention, but have been examined for one species of burrow-nesting auklet (Alcidae) in the northern hemisphere (Vermeer *et al*. 1979).

At Marion Island some observations on petrel distribution have been published (Crawford 1952; Rand 1954; van Zinderen Bakker Jr 1971). Since the introduction of house cats *Felis catus* to Marion Island during 1948 to 1951 (van Aarde 1979) the petrel population has been reduced and at least one species has been exterminated through predation (van Aarde 1980; Berruti *et al*. 1981). This paper reports the distribution and abundance of petrels in north-eastern Marion Island with respect to various habitat characteristics and compares burrow densities with those of nearby cat-free Prince Edward Island.

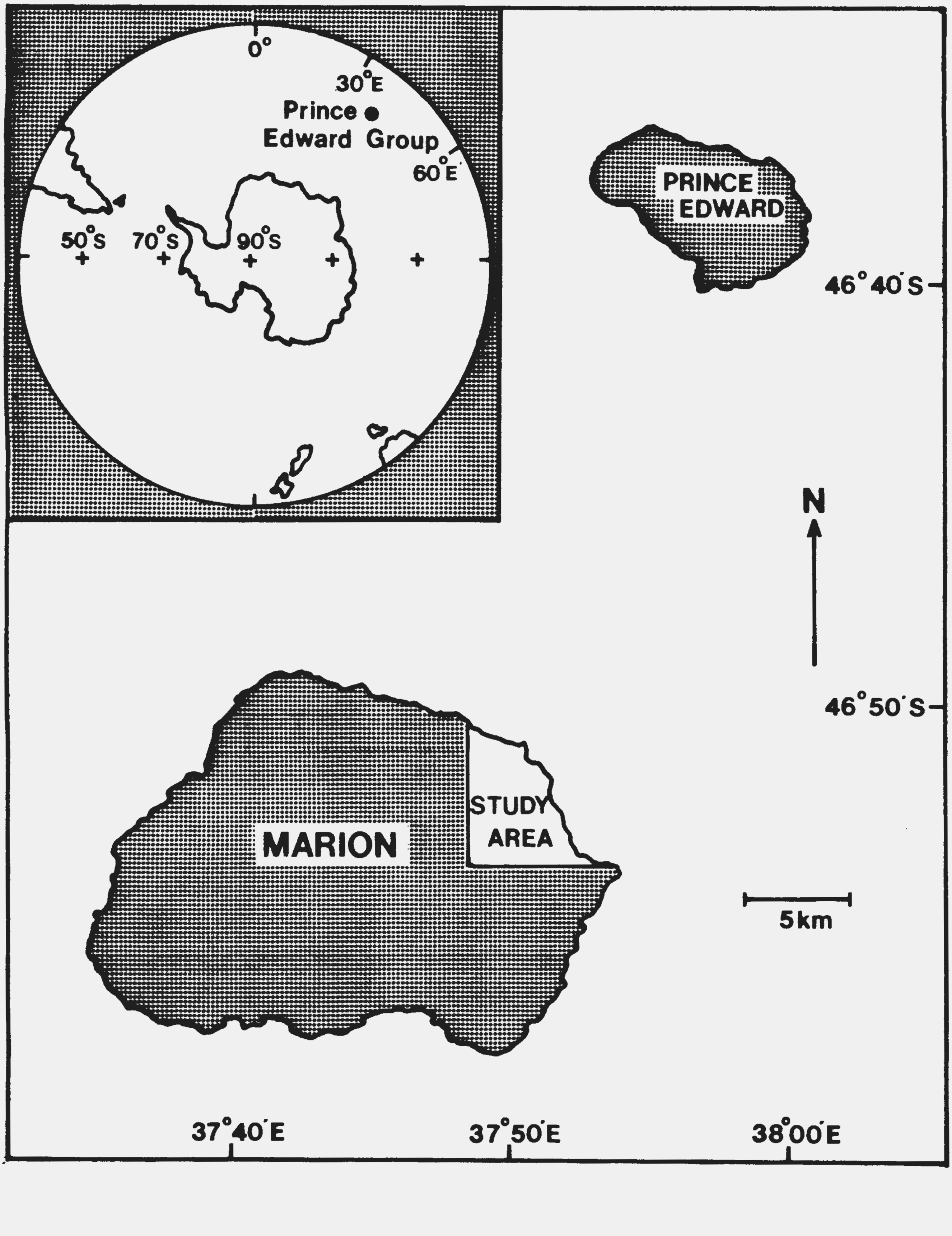
Study Area and Methods

The Prince Edward Island group (46° 50'S 37° 45'E) comprises two islands, Marion Island (area: 290 km^2; maximum altitude: 1 230 m a.s.l.) and Prince Edward Island (44 km^2; 672 m a.s.l.) and several small stacks (Fig. 1). The islands are the summits of submarine shield volcanoes and have similar geological histories (Verwoerd 1971). Glaciation has eroded the original "grey" lavas and produced glacial deposits (Hall 1980). At Marion Island the grey lava and its associated glacial deposits now form elevated ridges, up to several hundred hectares in extent, which radiate from the centre of the island. Subsequent to glaciation (after 12 000 B.P.), several volcanic eruptions have resulted in the production of scoria cones, volcanic ash deposits and extensive areas of hummocky broken "black" lava flows which now cover 80 % of Marion Island (Verwoerd 1971).

The climate is characterized by a low mean annual temperature (5 °C), high precipitation (2 576 mm y^{-1}) and strong, predominantly westerly, winds (Schulze 1971). The islands are treeless but lowland areas are well vegetated with mosaics of tussock grassland, herbfield and fernbrake. Higher and more exposed areas have a sparse *fjaeldmark* vegetation. The vegetation community structure has been recently reviewed by Gremmen (1981).

During April 1979 to May 1980 petrel burrows were sampled in quadrats at 13 sites in an area of approximately 1040 ha in north-eastern Marion Island. The sample sites covered five

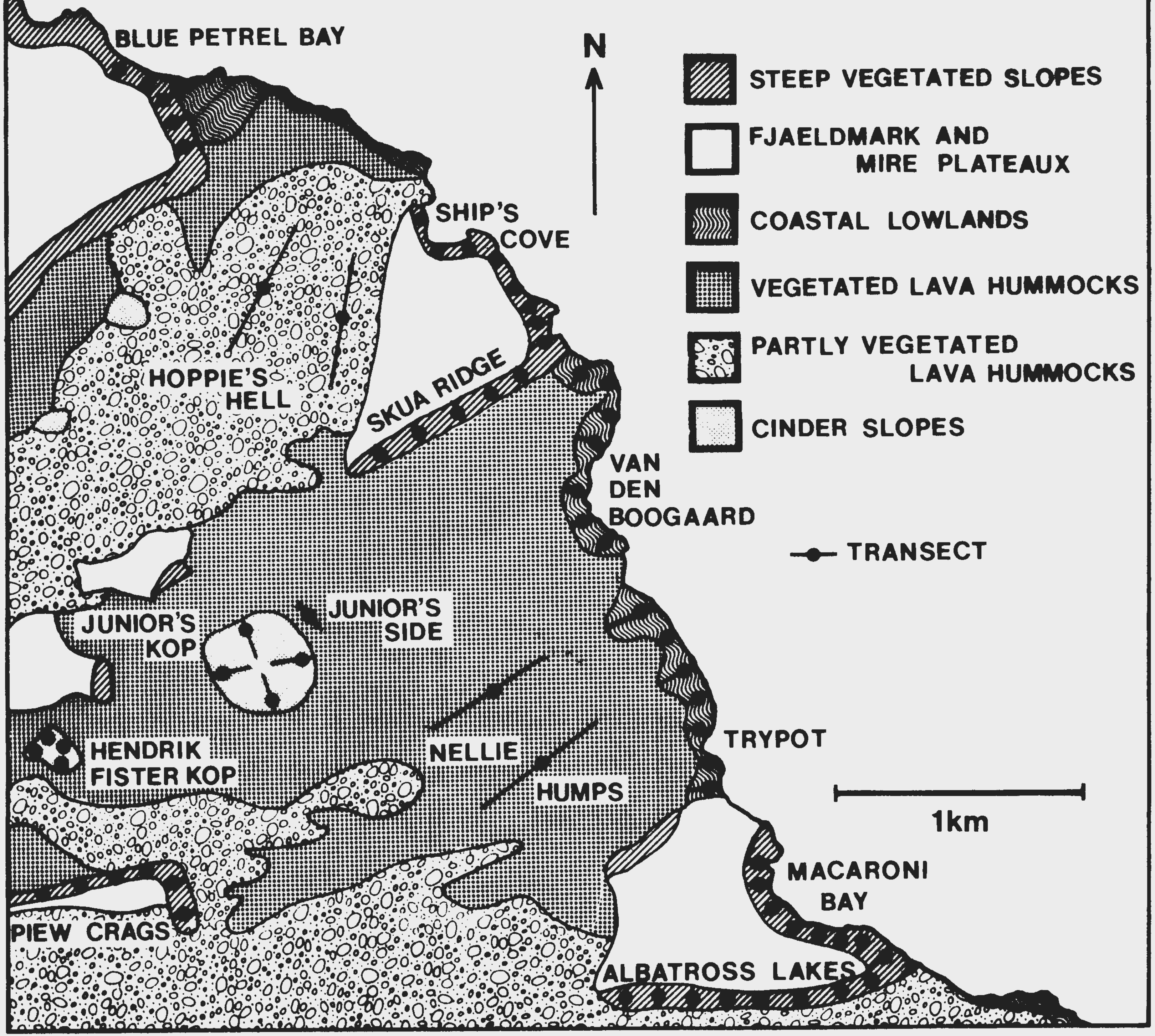
Fig. 1. The Prince Edward Islands, showing their position in the Southern Ocean (inset) and the position of the study area at Marion Island


0°
30°E
Prince Edward Group
60°E
50°S
70°S
90°S
PRINCE EDWARD
46°40'S
N
46°50'S
STUDY AREA
MARION
5km
37°40'E
37°50'E
38°00'E

habitat types: Steep vegetated slopes of the grey lava ridges; vegetated lava hummocks and partly vegetated lava hummocks overlying the oldest and youngest black lava respectively (as distinguished by Verwoerd (1971)); coastal lowland, a narrow flat marshy area on the seaward fringe of the black lava hummocks; and cinder slopes of scoria cones. A sixth habitat, fjaeldmark and mire plateaux, on the tops of grey lava ridges was searched at the beginning of the study but was devoid of petrel burrows and was not sampled further (Fig. 2). At each sample site, quadrats, measuring 30 x 10 m, were laid out at 25 m intervals on transect lines 200 m apart, except at sites in the vegetated and partly vegetated lava hummocks where two random transects were chosen and quadrats were positioned at 50 m intervals for more extensive coverage. Each quadrat was divided into three 10 x 10 m plots and within each plot utilized burrows were identified and counted. Utilized burrows were characterized by the presence of faeces and/or cropped vegetation at the burrow entrance. Initially, burrows were dug-up to determine the specific identity of their owners but later they could be identified by the relative size and shape of the entrance tunnel. No distinction was made between burrows of breeders and non- or failed breeders, or between excavated burrows and natural cavities used for nesting.

Within each 10 x 10 m plot the following were determined: slope aspect (using a compass); soil depth (using a graduated metal rod); and vegetation type (based upon Huntley 1971; Smith 1976a). Duplicate soil samples were collected using a corer in a randomly selected third of the plots. Samples were stored frozen and percentage soil moisture (weight loss upon drying at 100°C) was determined upon return to South Africa. The values

Fig. 2. The study area at Marion Island, showing the six habitat types and the positions of transects


BLUE PETREL BAY
N
STEEP VEGETATED SLOPES
FJAELDMARK AND MIRE PLATEAUX
COASTAL LOWLANDS
VEGETATED LAVA HUMMOCKS
PARTLY VEGETATED LAVA HUMMOCKS
CINDER SLOPES
TRANSECT
SHIP'S COVE
HOPPIE'S HELL
SKUA RIDGE
VAN DEN BOOGAARD
JUNIOR'S SIDE
JUNIOR'S KOP
HENDRIK FISTER KOP
NELLIE HUMPS
TRYPOT
1km
MACARONI BAY
PIEW CRAGS
ALBATROSS LAKES

of the above parameters were used to describe the sample plot and hence the nest sites of all the burrows within that plot. A one-way analysis of variance of nest site characteristics (slope angle, soil depth and moisture content) was performed for burrows of each petrel species and differences between means tested using the Newman Keuls multiple range test (Zar 1974). Slope aspects were analysed using the Watson-Williams test for circular data (Zar 1974). A significant difference between the mean of a particular parameter, for instance soil depth, at a species' nest sites and the mean soil depth in all sample plots was interpreted as the species selecting nest sites with either deep or shallow soil. Conversely, a non-significant difference suggested that the species was randomly distributed with respect to soil depth.

Neighbouring Prince Edward Island, 22 km away, was visited for four days in May 1979 and for four days in September 1979. Transects were positioned randomly at five sites in habitats similar to those at Marion Island. Quadrats were positioned at 25 m intervals and in each plot vegetation type was recorded and burrows were counted but not identified.

Results and Discussion

Eight species of burrowing petrels nested within the study area. These were Salvin's prion *Pachyptila vittata salvini*, blue petrel *Halobaena caerulea*, great-winged petrel *Pterodroma macroptera*, Kerguelen petrel *P. brevirostris*, soft-plumaged petrel *P. mollis*, white-chinned petrel *Procellaria aequinoctialis*, grey petrel *P. cinerea* and South Georgian diving petrel *Pelecanoides georgicus*. Fairy prion *Pachyptila turtur* was the only Marion Island breeding species not recorded, but it is found outside the study area (Berruti 1981). Too few burrows of grey petrels or South Georgian diving petrels were found for statistical analysis of their nest site preferences.

Nest Site Selection

Since petrels are subterranean breeders, soil conditions are important in determining the suitability of an area for burrowing. Burrow size is related to the size (weight) of the bird (Table 1) and consequently the two largest petrels, great-winged petrel and white-chinned petrel, required deep soil to accommodate their large nest chambers (Table 2). The small Salvin's prion made extensive use of natural cavities for nesting and could therefore nest in areas with poor soil cover (Table 2).

The high rainfall at Marion Island renders petrel burrows vulnerable to flooding. Burrows of Kerguelen and white-chinned petrels apparently are adapted to allow for nesting in wet and waterlogged soil. The egg is laid on a mound in the nest chamber and excess water runs off the mound and out through the entrance tunnel. In contrast, great-winged petrels favoured nest sites with relatively dry soil (Table 3). This species breeds in winter and dry soil may improve the burrow microclimate and facilitate thermoregulation of the chick.

Surface features at the nest site are also important in determining its suitability for burrowing. Vermeer et al. (1979) found that burrowing auklets (Alcidae) with a high wing-loading required steep slopes for nesting since insufficient lift was generated from gentle slopes to permit take-off. Petrels in this study have wing-loadings from 0.39 g cm^{-2}

Table 1. Mean body weight (g) and nest chamber dimensions (mm) for six petrel species at Marion Island

	Salvin's prion	Blue petrel	Great-winged petrel	Kerguelen petrel	Soft-plumaged petrel	White-chinned petrel
Body weight						
$\bar{x} \pm$ S.D. (range) n	162 ± 18.7 (106 – 238) 590	204 ± 16.5 (163 – 251) 90	588 ± 69.9 (435 – 745) 71	357 ± 43.2 (255 – 451) 126	312 ± 34.5 (250 – 380) 86	1 144 ± 81.3 (940 – 1 300) 41
Nest chamber height						
$\bar{x} \pm$ S.D. (range) n	111 ± 12.7 (80 – 150) 10	115 ± 10.5 (80 – 150) 10	197 ± 29.7 (150 – 250) 59	153 ± 11.8 (150 – 200) 17	155 ± 22.3 (150 – 200) 19	293 ± 49.5 (250 – 400) 7
Nest chamber width						
$\bar{x} \pm$ S.D. (range) n	147 ± 24.3 (120 – 250) 10	151 ± 21.1 (120 – 260) 10	391 ± 70.4 (200 – 600) 59	368 ± 48.3 (300 – 500) 17	308 ± 46.6 (200 – 400) 19	636 ± 83.3 (500 – 700) 7
Source	This study	This study	Schramm (1983)	Schramm (1983)	Schramm (1983)	This study

Table 2. Mean soil depth (mm) at nest sites of six petrel species at Marion Island. Broken lines connect means not significantly different (*P* >0.05) using the Newman Keuls multiple range test

	Great-winged petrel	White-chinned petrel	All plots	Kerguelen petrel	Blue petrel	Soft-plumaged petrel	Salvin's prion
Mean	826	799	586	545	514	508	430
(Sample size)	(79)	(72)	(535)	(22)	(170)	(40)	(382)

Table 3. Mean percentage soil moisture at nest sites of six petrel species at Marion Island. Conventions are given in Table 2

	White-chinned petrel	Soft-plumaged petrel	Kerguelen petrel	Blue petrel	all plots	Salvin's prion	Great-winged petrel
Mean	84.3	81.2	81.0	75.9	75.1	71.7	67.4
(Sample size)	(40)	(23)	(16)	(107)	(163)	(103)	(36)

(Salvin's prion) to 0.78 g cm^{-2} (white-chinned petrel) (Warham 1977). However, soft-plumaged and blue petrels which have medium wing loadings (0.48 g cm^{-2}) (Warham 1977) favoured the steepest, most exposed nest sites available (Tables 4,5). Although able to utilize more sheltered sites, the enhanced lift generated from steep exposed areas enables them to take-off directly from outside their burrows (pers. obs). Since both species are vulnerable to attack by Subantarctic skuas *Catharacta antarctica*, particularly when on the ground (Schramm in press), nesting in sites which permit rapid escape may reduce their vulnerability to predation. Great-winged and white-chinned petrels, which are seldom preyed upon by skuas (Schramm in press), nested in the most sheltered sites and usually had to run a short distance before take-off (Table 5).

Petrel Distribution and Vegetation Type

No petrel burrows were found in unvegetated parts of the study area, whereas the highest density of burrows was in *Poa cookii* tussock grassland (Table 6). *Poa* grows only where manuring by birds (primarily petrels and penguins) and/or seals enhances nutrient levels in the soil (Huntley 1971, Smith 1976b, 1979). Therefore in areas without seals or penguins, tussock grassland usually indicates the presence of a petrel colony.

Other vegetation types are good indicators of soil conditions and exposure (Gremmen 1981), which are both important determinants of petrel distribution. Therefore, vegetation type may indicate the suitability of an area for burrowing. *Cotula plumosa* grows only where it receives sea spray (Huntley 1971) and such exposed sites were favoured by blue petrels (Table 6). At Macquarie Island most blue petrel colonies are also in *Cotula plumosa* herbfield (Brothers 1984). Closed *Blechnum penna-marina*

Table 4. Mean slope angle (degrees) at nest sites of six petrel species at Marion Island. Conventions are given in Table 2

	Soft-plumaged petrel	Blue petrel	Kerguelen petrel	Salvin's prion	Great-winged petrel	White-chinned petrel	All plots
Mean	34.4	32.6	26.1	20.2	18.8	16.8	16.8
(Sample size)	(42)	(178)	(22)	(395)	(81)	(72)	(550)

Table 5. Mean slope aspect (degrees and compass direction) at nest sites of six petrel species at Marion Island. Broken lines connect means not significantly different ($\underline{P} > 0.05$) using the Watson-Williams test for circular distributions

	Great-winged petrel	White-chinned petrel	all plots	Salvin's prion	Blue petrel	Soft-plumaged petrel	Kerguelen petrel
Mean	155° SSE	134° SE	95° E	95° E	69° ENE	68° ENE	66° ENE
(Sample size)	(80)	(74)	(555)	(394)	(190)	(44)	(23)

Table 6. Mean burrow densities (no. ha^{-1}) of eight petrel species in seven vegetation types at Marion Island

Vegetation type	Salvin's prion	Blue petrel	Great-winged petrel	Kerguelen petrel	Soft-plumaged petrel	White-chinned petrel	Other petrels	All petrels	No. plots (0.01 ha)
Cotula herbfield	22.2 ± 71.2	188.9 ± 262.2	11.1 ± 45.8	5.6 ± 22.9	0	5.6 ± 22.9	0	233.4 ± 242.7	18
Poa tussock grassland	87.8 ± 168.5	104.9 ± 317.2	45.5 ± 112.1	4.1 ± 19.8	17.9 ± 54.2	30.9 ± 89.4	0	291.1 ± 352.5	123
Closed fernbrake	115.2 ± 227.1	0	21.2 ± 59.1	1.5 ± 12.2	0	9.1 ± 37.9	1.5 ± 12.2*	148.5 ± 225.9	66
Open fernbrake	135.2 ± 181.7	0	9.3 ± 34.8	0	0	0	3.7 ± 18.9*	148.1 ± 185.3	54
Acaena herbfield	100.8 ± 174.4	22.5 ± 119.3	2.5 ± 15.6	11.7 ± 36.9	18.3 ± 57.7	15.0 ± 55.8	0	170.8 ± 235.7	120
Agrostis mire	6.7 ± 25.0	0	0	1.5 ± 12.1	0	8.2 ± 32.4	0	16.4 ± 42.7	134
Azorella *fjaeldmark*	8.0 ± 54.8	0	1.1 ± 10.1	0	0	0	5.7 ± 27.6**	14.8 ± 64.9	88
Unvegetated	0	0	0	0	0	0	0	0	138

* Grey petrel

** South Georgian diving petrel

fernbrake is found on sheltered slopes with deep well-drained soils (Smith 1976a), conditions suited to great-winged petrels (Table 6). Open fernbrake develops where soil is shallower, or slopes more exposed (Smith 1976a). The large number of Salvin's prions recorded in this vegetation type mostly nested in natural cavities (Table 6). *Acaena magellanica* herbfield, which is found on wet slopes, particularly along drainage lines (Smith 1976a) had a high density of Kerguelen and white-chinned petrels (Table 6). Their burrows allow drainage in these wet soil conditions. However, soft-plumaged petrels which have unspecialized burrows, were also able to nest in *Acaena* herbfield (Table 6). *Azorella selago fjaeldmark* in exposed wind desert areas with little soil and *Agrostis magellanica* mires in flat waterlogged sites were apparently unsuitable for burrowing and few petrels nested in them (Table 6).

Petrel Distribution and Habitat Type

Differences in petrel burrow density and species composition within the same habitat were nearly as large as differences between habitats (Table 7). Nevertheless, the steep vegetated slopes of grey lava ridges offer conditions very suitable for burrowing, with deep well-drained soil. The highest density and diversity of petrels was recorded here (Table 7). Vegetated lava hummocks have many small slopes which have good soil development and hence a high number and diversity of petrels (Table 7). Conversely the partly vegetated lava hummocks have little soil but an abundance of natural cavities. The high density of petrels recorded here is a result of Salvin's prions making extensive use of natural nest sites (Table 7). The marshy coastal lowland is too wet for most species, but was

Table 7. Burrow densities (no. ha^{-1}) of eight petrel species at 13 sample sites at Marion Island

Habitat type and Sample site	Salvin's prion	Blue petrel	Great-winged petrel	Kerguelen petrel	Soft-plumaged petrel	White-chinned petrel	Other petrels	All petrels	No. plots (0.01 ha)
Steep vegetated slopes	64.6 ± 130.4	77.3 ± 254.4	17.5 ± 71.8	7.3 ± 30.0	17.9 ± 55.6	14.6 ± 48.0	0	199.2 ± 298.9	246
Blue Petrel Bay	8.9	277.8	8.9	20.0	20.0	6.7	0	342.3	45
Ship's Cove	66.7	6.1	4.5	6.1	16.7	19.7	0	119.8	66
Skua Ridge	33.3	10.1	96.7	0	3.3	23.3	0	166.6	30
Macaroni Bay	103.0	169.7	0	12.1	48.5	15.2	0	348.5	33
Albatross Lakes	14.8	7.4	25.9	0	0	29.6	0	77.7	27
Piew Crags	140.0	0	0	2.2	15.6	0	0	157.8	45
Coastal lowland	23.9 ± 72.8	0	2.2 ± 18.9	3.6 ± 18.7	0	24.6 ± 85.8	0	54.4 ± 118.0	138
Van den Boogaard	25.0	0	5.0	3.3	0	28.3	0	61.7	60
Trypot	23.1	0	0	3.8	0	21.8	0	48.7	78
Vegetated lava hummocks	44.9 ± 137.8	1.5 ± 12.0	37.7 ± 83.6	0	0	4.4 ± 20.4	2.9 ± 16.8*	91.4 ± 164.0	69
Nellie Humps	62.5	0	29.2	0	0	0	4.2*	95.9	48
Junior's Side	4.8	4.8	57.1	0	0	14.3	0	81.0	21
Partly veg. lava hummocks	279.2 ± 274.6	0	0	0	0	0	2.1 ± 14.3*	281.3 ± 275.9	48
Hoppie's Hell	279.2	0	0	0	0	0	2.1	281.3	48
Cinder slopes	16.7 ± 89.3	0	3.8 ± 32.1	0	0	0.4 ± 6.4	2.1 ± 17.0**	22.9 ± 100.5	240
Junior's Kop	5.1	0	5.8	0	0	0.6	3.2	14.7	156
Hendrik Fister Kop	38.1	0	0	0	0	0	0	38.1	84

* Grey petrel

** South Georgian diving petrel

favoured by white-chinned petrels (Table 7). Cinder slopes of scoria cones have little or no soil development and petrels nesting here were restricted to the sheltered side where there is some vegetation. This was the only habitat where South Georgian diving petrels nested, although very few were found (Table 7). They are apparently more abundant on cinder slopes at higher altitudes (van Zinderen Bakker Jr 1971).

Lack of a suitable habitat map precludes an estimate of petrel abundance for the whole of Marion Island. However, based on Fig. 2 and Table 7 there were approximately 156 000 petrel burrows within the study area (Table 8). In view of the large standard deviations of burrow density this is at best a crude estimate. Salvin's prion made up 81 % of the petrels (Table 8). Its ability to nest under a wide range of environmental conditions in both burrows and natural nest sites partially explains its high population. At l'île aux Cochons (Crozet Islands) Salvin's prion nests in a similar range of habitats and also uses natural cavities for nesting (Derenne & Mougin 1976).

Comparison with Prince Edward Island

Prince Edward Island was visited when only the winter breeding great-winged and grey petrels were nesting. It was therefore not possible to identify positively all burrows found, although it appeared that the blue petrel was the dominant species, particularly in tussock grassland (Adams 1982, FitzPatrick Institute unpubl. data, pers. ob). Petrel burrow densities were significantly greater ($\underline{P} < 0.001$) than in the same vegetation (Table 9) and habitat types (Table 10) at Marion Island. In addition, at least one species had a higher breeding success than at Marion Island. Thirty per cent (n=30) of fresh

Table 8. Estimated numbers of burrows of eight petrel species within the study area at Marion Island

Habitat type (Approximate area)	Salvin's prion	Blue petrel	Great-winged petrel	Kerguelen petrel	Soft-plumaged petrel	White-chinned petrel	Other petrels	All petrels
Vegetated slopes (71 ha)	4 587	5 488	1 243	518	1 271	1 037	0	14 144
Fjaeldmark and mire plateaux (147 ha)	0	0	0	0	0	0	0	0
Coastal lowland (38 ha)	908	0	84	137	0	935	0	2 064
Vegetated lava hummocks (397 ha)	17 826	596	14 967	0	0	1 747	1 151*	36 287
Partly vegetated lava hummocks (367 ha)	102 466	0	0	0	0	0	770*	103 236
Cinder slopes (21 ha)	351	0	80	0	0	8	44**	483
Total (1 041 ha)	126 138	6 084	16 374	655	1 271	3 727	1 965	156 214
Percentage composition	80.7 %	3.9 %	10.5 %	0.4 %	0.8 %	2.4 %	1.2 %	

* Grey petrel

** South Georgian diving petrel

Table 9. Mean density of petrel burrows (no. ha^{-1}) in four vegetation types at Prince Edward Island

Vegetation type	Burrow density	No. plots (0.01 ha)	Petrel species recorded in burrows
Poa tussock grassland	8 341.7 ± 5 681.5	27	Salvin's prion, blue petrel, great-winged petrel, soft-plumaged petrel
Closed fernbrake	872.7 ± 54.5	11	Salvin's prion, great-winged petrel, Kerguelen petrel, soft-plumaged petrel
Acaena herbfield	3 250.0 ± 3 011.0	6	Salvin's prion
Azorella *fjaeldmark*	475.0 ± 363.2	4	-

Table 10. Mean density of petrel burrows (no. ha^{-1}) at five sample sites at Prince Edward Island

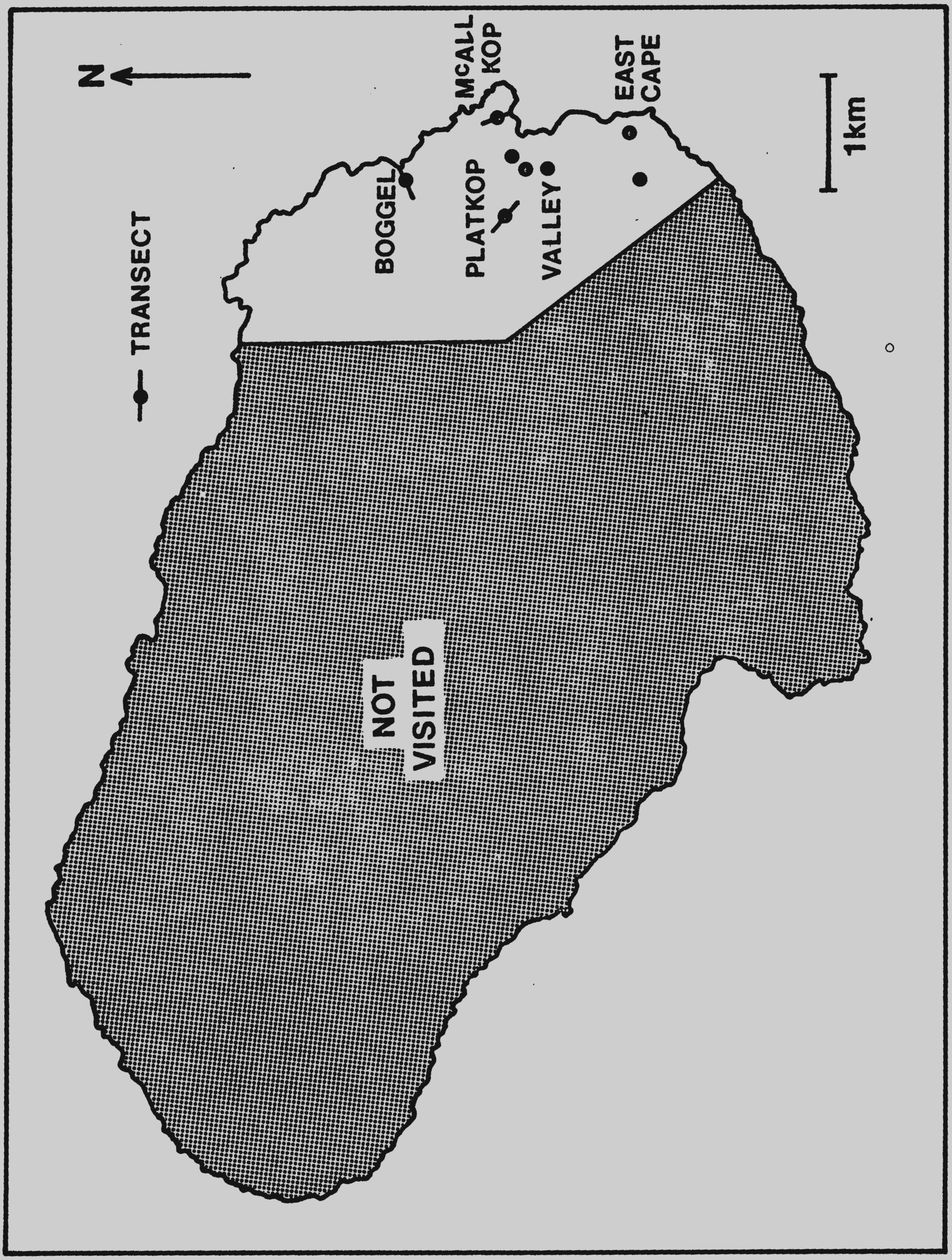
Habitat type and Sample site	Burrow density	No. plots (0.01 ha)	Petrel species recorded in burrows
Steep vegetated slopes	5 919 ± 5 771.0	42	
McAll Kop	5 881.1	9	Salvin's prion, great-winged petrel
Boggel	10 980.0	15	blue petrel, great-winged petrel, soft-plumaged petrel
Platkop	733.3	6	-
Platkop Valley	2 266.7	12	great-winged petrel, Kerguelen petrel
Vegetated lava hummocks	1 226.7 ± 368.2	6	
East Cape	1 226.7	6	Salvin's prion, great-winged petrel, soft-plumaged petrel

great-winged petrel burrows examined at Prince Edward Island during September 1979 contained chicks compared to only 1 % (n=109) at the same time at Marion Island (Schramm 1983).

The greater burrow densities at Prince Edward Island might suggest that the habitat is more suitable for nesting by petrels. There are some geological differences between Marion and Prince Edward Islands, although they have similar geological histories (Verwoerd 1971). Tuff is more evident on Prince Edward Island and the steep vegetated slopes of Platkop and on the seaward side of Boggel (Fig. 3) are covered in tuffaceous soil (Verwoerd 1971), which is very suitable for burrowing. However, differences in burrow density were also apparent between similar vegetation types, vegetation being a better indicator of the suitability of an area for burrowing than the physical appearance of a habitat.

Petrel densities at Marion Island seem extremely low. In tussock grassland blue petrels nested at a density of 105 burrows ha^{-1} (Table 6). Estimates of blue petrel density at Prince Edward Island range from 2 600 burrows ha^{-1} (FitzPatrick Institute, unpubl. data) to 8 300 burrows ha^{-1} (although not all blue petrels) (Table 9), which is similar to the 7 200 burrows ha^{-1} reported from tussock grassland at cat-free South Georgia (Croxall & Prince 1980). On stacks off Macquarie Island, which are free of alien predators, blue petrels reach densities of 20 000 burrows ha^{-1} (Brothers 1984), compared to the maximum density of 278 burrows ha^{-1} at Blue Petrel Bay at Marion Island (Table 7). In addition, densities of white-chinned petrels in tussock grassland at Marion Island were lower (31 burrows ha^{-1} (Table 6)) than at South Georgia (400 burrows ha^{-1} (Croxall & Prince 1980)). At three sites at l'île aux Cochons (cat-free),

Fig. 3. Prince Edward Island, showing the positions of transects


N
TRANSECT
BOGGEL
McALL KOP
PLATKOP
VALLEY
EAST CAPE
1km
NOT VISITED

Salvin's prion nested at densities of 173, 232 and 1 043 burrows ha^{-1} (Derenne & Mougin 1976), compared to densities of 5 to 279 burrows ha^{-1} at Marion Island (Table 7).

It seems likely that predation b eral cats at Marion Island (van Aarde 1980), absent from Prince Edward Island, is largely responsible for the differences in density and breeding success of petrels at the two islands.

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CHAPTER 2

The breeding biologies of the petrels *Pterodroma macroptera*, *P. brevirostris* and *P. mollis* at Marion Island

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THE BREEDING BIOLOGIES OF THE PETRELS *PTERODROMA MACROPTERA, P. BREVIROSTRIS* AND *P. MOLLIS* AT MARION ISLAND.

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SUMMARY

SCHRAMM, M. 1983. The breeding biologies of the petrels *Pterodroma macroptera, P. brevirostris* and *P. mollis* at Marion Island. Emu 83: 75-81.

The Great-winged Petrel *Pterodroma macroptera*, Kerguelen Petrel *P. brevirostris* and Soft-plumaged Petrel *P. mollis* breed in different habitats at different times of the year at Marion Island. *P. macroptera* breeds in inland slopes during winter, *brevirostris* breeds in flat marshy areas during early summer and *mollis* breeds during late summer in coastal slopes. Nesting-burrows of *macroptera* and *mollis* have a similar simple design but burrows of *brevirostris* have a drainage system to cope with their waterlogged breeding habitat.

Incubation periods are similar (56, 49 and 50 days in *macroptera, brevirostris* and *mollis* respectively), but fledging periods are very different (61 days in *brevirostris* and 91 days in *mollis*). The species rear chicks at different times, presumably to help reduce interspecific competition for food. In all species, the chicks are fed mostly squid, but meals of *brevirostris* chicks contain most crustaceans and fish. Differences in quality of meals in part explain the faster growth of *brevirostris* compared to *macroptera* or *mollis*. The timing of breeding influences the vulnerability of each species to predators, which is reflected in differences in breeding success (53%, 7% and 0% in *brevirostris, mollis* and *macroptera* respectively).

INTRODUCTION

The Great-winged Petrel *Pterodroma macroptera*, Kerguelen Petrel *P. brevirostris* and Soft-plumaged Petrel *P. mollis* breed sympatrically at the Prince Edward Islands (46°50′S, 37°45′E) (Rand 1954; Berruti *et al.* 1981). The only other localities where they breed together are the Crozet Islands (Despin *et al.* 1972) and Gough Island (Swales 1965) and possibly also Tristan da Cunha (Elliott 1957).

Aspects of the breeding biology of *macroptera* have been studied on islands off Western Australia (Warham 1956; 1957) and New Zealand (Imber 1976), and *brevirostris* has been studied at the Crozet Islands (Mougin 1969). There are few published data on the breeding of *mollis* in the sub-Antarctic although there is some information for populations in the northern hemisphere (Jouanin *et al.* 1969). This study, carried out at Marion Island in the Prince Edward group, compares the basic breeding biologies of the three species in an attempt to identify some of the ways in which they may be segregated ecologically.

STUDY AREA AND METHODS

Marion Island is the larger (290 km²) of two islands forming the Prince Edward group. The island is volcanic and made up of two lava successions: an old grey lava forming ridges radiating from the centre of the island; and a younger black basaltic lava which is dotted with scoria cones (Verwoerd 1971). Mires are found on the black lava coastal plain and on the tops of grey lava ridges.

I visited Marion Island during April 1979 - June 1980 and for two weeks in September 1980. Adult petrels were captured and weighed, measured (culmen length, depth at the gonys, tarsus and wing chord lengths) and banded. Petrel burrows were measured for tunnel length (from the entrance to the back of the nest chamber), depth from the ground to the floor of the nest and the height and width of the entrance and nest chamber. Breeding success and chick growth were measured in fifty-seven *macroptera* burrows, forty-nine *brevirostris* burrows and thirty-one *mollis* burrows. Nest contents were investigated via a hole dug just in front of the nest chamber and kept plugged with a turf. Burrows were checked once a week during incubation but more frequently when laying or hatching was expected. Eggs were measured, and a sample of freshly laid eggs was collected and weighed in the laboratory. Lengths of culmen, tarsus and wing (chord) and weights of chicks were recorded at every fifth day of age.

Size of meals given to *brevirostris* and *mollis* chicks were determined on four occasions during the middle of their fledging periods. Chicks were weighed at dusk and again at midnight and any weight increase was taken as meal size.

Incubation period (time from laying until hatching), fledging period (time from hatching until final departure from the nest) and breeding success (proportion of eggs giving rise to fledged chicks) were calculated. Failures thought to be related to human disturbance were excluded from the calculations.

RESULTS

Breeding habitat

The three species had their main breeding populations in different habitats. Most *macroptera* bred inland in the slopes of grey lava ridges, but some were found in black lava areas and in the lower slopes of scoria cones. Most *mollis* bred at the coast in grey lava slopes but a few also bred inland. *P. brevirostris* nested in the mires on the grey lava ridges and black lava coastal plain.

Burrow structure

Pterodroma burrows typically had a long curved tunnel leading to a large round nest chamber. Burrows of *brevirostris* and *mollis* were similar in size but smaller than those of *macroptera* (Table I), which is consistent with size differences between the species (Table II). In *macroptera* and *mollis* burrows, the floor of the nest chamber was lined with plant material. In 84% (N = 159) of burrows, the dominant plant used in lining the nest was the one growing most abundantly at the burrow entrance. *P. brevirostris* burrows were modified to cope with their marshy breeding habitat. The egg was laid on a mound of soil and vegetation. A drainage channel around the nest mound led excess water out through the burrow entrance.

Burrows with multiple tunnels and nest chambers were found. Ten per cent (N = 59) of *macroptera* burrows had two tunnels. A *brevirostris* burrow was found with two nest chambers, one was used by a White-chinned Petrel *Procellaria aequinoctialis*. Similar associations have been recorded between *brevirostris* and Salvin's Prion *Pachyptila salvini* (Van Zinderen Bakker 1971). All *mollis* burrows (N = 69) had a single tunnel and nest chamber.

Eggs and incubation

The three species had different breeding seasons: *macroptera* laid in late May; *brevirostris* in early October; and *mollis* in mid-December. Their breeding schedules are similar to other sub-Antarctic localities (Table III). Eggs of *brevirostris* and *mollis* were not significantly different in weight ($p > 0.05$) but were lighter and smaller than those of *macroptera* ($p < 0.001$) (Table IV). One *mollis* burrow was found with two eggs attended by at least three birds. All *macroptera*

TABLE I

Measurements (mm) of the burrows of Pterodroma macroptera, P. brevirostris *and* P. mollis *at Marion Island.*

	P. macroptera				*P. brevirostris*				*P. mollis*			
	$\bar{X}$	± S.D	(Range)	N	$\bar{X}$	± S.D.	(Range)	N	$\bar{X}$	± S.D.	(Range)	N
Entrance height	142	± 22.4	(100-200)	60	111	± 16.1	(80-140)	15	98	± 12.0	(80-120)	16
Entrance width	194	± 34.9	(140-300)	60	168	± 22.8	(140-200)	15	165	± 24.0	(140-200)	16
Nest chamber height	197	± 29.7	(150-250)	59	153	± 11.8	(150-200)	17	155	± 22.3	(100-200)	19
Nest chamber width	391	± 70.4	(200-600)	59	368	± 48.3	(300-500)	17	308	± 46.6	(200-400)	19
Tunnel length	1500	± 473.8	(600-2900)	63	1528	± 491.2	(800-2800)	29	1485	± 561.6	(600-2800)	69
Depth below ground	528	± 18.5	(300-1200)	59	345	± 63.2	(250-500)	28	416	± 97.0	(250-550)	67

TABLE II

Weights (g) and linear dimensions (mm) of adult Pterodroma macroptera, P. brevirostris *and* P. mollis *at Marion Island.*

	P. macroptera				*P. brevirostris*				*P. mollis*			
	$\bar{X}$	± S.D	(Range)	N	$\bar{X}$	± S.D.	(Range)	N	$\bar{X}$	± S.D.	(Range)	N
Weight	587	± 69.1	(460-745)	61	357	± 43.2	(255-451)	126	312	± 34.7	(250-380)	85
Culmen length	36.3	± 0.98	(33.6-38.8)	54	26.7	± 1.47	(23.0-36.6)	118	28.3	± 1.31	(23.7-30.7)	85
Culmen depth at gonys	15.4	± 0.69	(14.5-16.9)	21	11.0	± 0.41	(10.0-12.0)	49	11.5	± 0.47	(10.0-12.6)	56
Tarsus	44.4	± 1.09	(42.2-46.7)	53	39.5	± 1.24	(36.5-42.0)	121	36.5	± 1.58	(34.0-42.5)	85
Wing	307	± 6.8	(289-321)	52	257	± 6.4	(239-272)	121	250	± 0.61	(233-263)	90

(N = 64) and *brevirostris* (N = 50) burrows had only one egg, but elsewhere Imber (1976) found 3-6% of *macroptera* burrows with two eggs attended by four birds.

Mean incubation period was 56 days for *macroptera*, 49 days for *brevirostris* and 50 days for *mollis*. These are similar to values from other localities (Table V). Temporary abandonment of eggs during incubation has been discovered in *macroptera* (Imber 1976) and several other species of petrels (Boersma & Wheelwright 1979). During this study one *mollis* egg was deserted on two occasions for at least two days.

Chick growth and fledging

Mean fledging period was 61 days in *brevirostris* and 91 days in *mollis*. No *macroptera* chicks survived to fledging but elsewhere fledging period is 118-131 days (Table V).

TABLE III

Breeding cycle of Pterodroma macroptera, P. brevirostris *and* P. mollis *at various localities.*

	Laying	Hatching	Fledging	Source
P. macroptera				
Marion Island	late May	late July	no data	This study
Eclipse Island	late May	late July	late Nov.	Warham (1956)
Tristan da Cunha	mid-June	early Aug.	mid-Nov.	Elliott (1957)
Gough Island	mid-June			Swales (1965)
Whale Island	early July	late Aug.	late Dec.	Imber (1976)
P. brevirostris				
Marion Island	early Oct.	late Nov.	late Jan.	This study
Gough Island			early Feb.	Swales (1965)
Crozet Island	early Oct.	late Nov.	early Feb.	Mougin (1969)
P. mollis				
Crozet Islands		late Jan.		Despin *et al.* (1972)
Tristan da Cunha			May	Elliot (1957)
Gough Island	early Nov.			Clancey *et al.* (1981)
		mid-Feb.		Swales (1965)
Marion Island	mid-Dec.	early Feb.	early May	This study

TABLE IV

Weights (g) and linear dimensions (mm) of eggs of Pterodroma macroptera, P. brevirostris *and* P. mollis.

	Weight $\bar{X}$ ± S.D. (Range)	N	Length $\bar{X}$ ± S.D. (Range)	N	Breadth $\bar{X}$ ± S.D. (Range)	N	Source
P. macroptera							
Marion Island	80.8 ± 5.94 (74.0-90.5)	16	65.6 ± 2.46 (62.1-69.8)	16	48.6 ± 2.24 (45.4-55.9)	16	This study
Whale Island	86	60					Imber (1976)
P. brevirostris							
Marion Island	57.1 ± 3.91 (53.0-63.3)	4	57.4 ± 1.48 (55.5-60.5)	28	44.9 ± 0.94 (43.0-46.6)	28	This study
	*55.6 (50-63)	19	56.7 (54.7-60.2)	19	44.8 (43.6-46.7)	19	Rand (1954)
Crozet Island			55.7 (53.2-62.4)	6	44.1 (42.3-45.9)	6	Mougin (1969)
Kerguelen			59.5	1	46.0	1	Paulian (1953)
P. mollis							
Marion Island	54.4 ± 3.92 (50.0-59.5)	3	59.7 ± 2.41 (55.8-65.1)	22	43.0 ± 1.29 (40.3-45.8)	22	This study
Cape Verde Islands	*59.5 ± 0.50 (59-60)	2	58.4 ± 1.01 (57.4-59.9)	4	43.6 ± 1.06 (41.8-44.6)	4	Jouanin *et al.* (1969)

* may not be weights of freshly laid eggs.

TABLE V

Incubation and fledging periods (days) of Pterodroma macroptera, P. brevirostris *and* P. mollis.

	Incubation Period				Fledging Period				Source
	X̄	± S.D.	(Range)	N	X̄	± S.D.	(Range)	N	
P. macroptera									
Marion Island	56	± 1.0	(55-57)	2			no data		This study
Eclipse Island	53			1	131	± 3.0	(128-134)	2	Warham (1956)
Whale Island	55		(53-57)	36	118		(108-128)	28	Imber (1976)
P. brevirostris									
Marion Island	49	± 2.1	(46-51)	3	61	± 1.1	(59-62)	4	This study
Crozet Island	49		(47-51)	4	*ca* 60				Mougin (1969)
P. mollis									
Marion Island	50			1	91	± 1.0	(90-92)	2	This study

Patterns of weight increase and growth of appendages were similar for *brevirostris* and *mollis* chicks but, relative to adult size, *brevirostris* grew faster than *mollis* or *macroptera*, although there are few data for the latter (Figs 1, 2, 3 and 4). Culmen and tarsus growth of *brevirostris* and *mollis* chicks reached an asymptote two-thirds into the fledging period (Figs 1 and 2) but their wings kept growing until fledging. Chick weight reached a maximum equal to mean adult weight in *brevirostris* and 11% greater than adult weight in *mollis*. Chick weights then decreased until fledging.

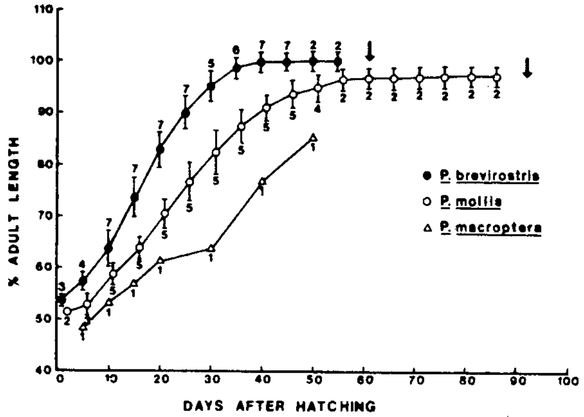

Figure 2. Tarsus growth in *Pterodroma macroptera, P. brevirostris* and *P. mollis* chicks. Conventions are given in Figure 1.

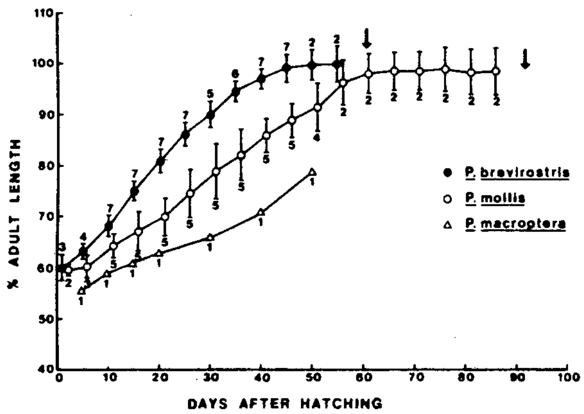

Figure 1. Culmen growth in *Pterodroma macroptera, P. brevirostris* and *P. mollis* chicks. Mean (point) ± standard deviation (bar) and sample size (number) are indicated. Arrows show mean age at fledging. The data for *P. mollis* are offset by one day for presentation purposes.

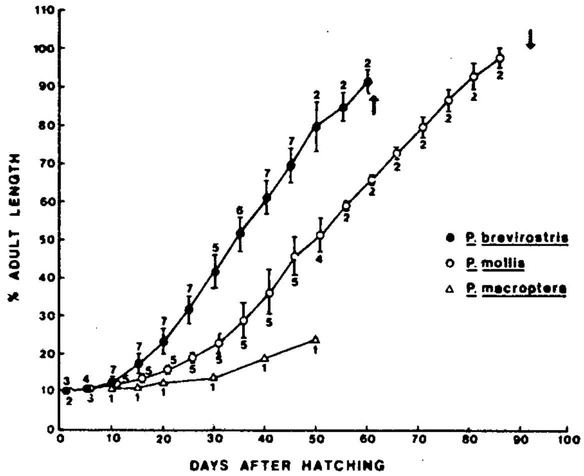

Figure 3. Wing growth in *Pterodroma macroptera, P. brevirostris* and *P. mollis* chicks. Conventions are given in Figure 1.

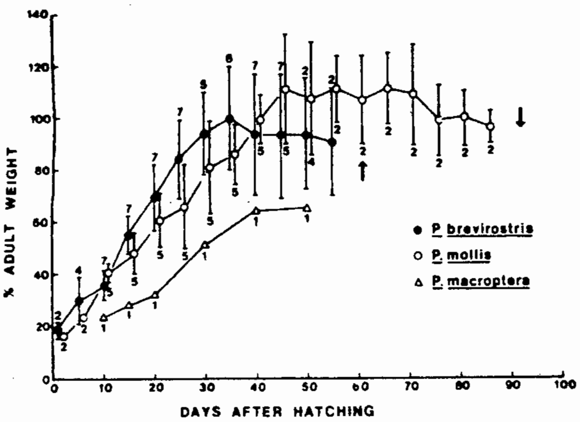

Figure 4. Weight increase in *Pterodroma macroptera, P. brevirostris* and *P. mollis* chicks. Conventions are given in Figure 1.

Meal size and composition

Mean meal size was 73 g (S.D. = 19.0, range = 20 - 100, N = 22) for *brevirostris* chicks. One 180 g chick increased by 200 g overnight, presumably owing to two feeds, and consequently all weight increases over 100 g were interpreted as double feeds. On this basis, 31% of feeds were double feeds. Mean meal size for *mollis* chicks was 74 g (S.D. = 12.5, range = 50 - 90, N = 8), and 33% were double feeds. No data were obtained for meal sizes of *macroptera*, but elsewhere it is recorded as 86 g (Imber 1976).

In all three species, meals comprised mostly squid but *brevirostris* was fed more crustaceans and fish than *macroptera* or *mollis* (Table VI) (Schramm unpubl.). The liquid fraction (oil) comprised 18.4%, 16.0% and 18.7% by weight in *macroptera, brevirostris* and *mollis* meals respectively.

TABLE VI

Percentage composition by weight of squid, crustaceans and fish in stomach samples of Pterodroma macroptera, P. brevirostris, *and* P. mollis *chicks at Marion Island (Schramm unpubl.).*

	P. macroptera	*P. brevirostris*	*P. mollis*
Squid	89.5	70.2	89.0
Crustaceans	6.3	23.8	9.6
Fish	4.2	6.0	1.4
Sample size	20	22	9

Breeding success

Breeding success was 53% in *brevirostris*, 7% in *mollis* and 0% in *macroptera* (Table VII). Most losses were due to eggs being abandoned or chicks disappearing although a high percentage of *macroptera* eggs also disappeared. No direct cases of predation were observed at study burrows but feral House Cats *Felis cattus* and Great Skuas *Stercorarius skua lonnbergii are major* petrel predators at Marion Island and take adults, eggs and chicks (Van Aarde 1980; Schramm unpubl.).

TABLE VII

Egg losses, chick losses and breeding success of Pterodroma macroptera, P. brevirostris *and* P. mollis *at Marion Island.*

	P. macroptera				*P. brevirostris*		*P. mollis*	
	1979		1980		1979/80		1979/80	
	N	%	N	%	N	%	N	%
EGGS								
laid	17	100.0	40	100.0	49	100.0	31	100.0
human caused losses	0	0	1	2.5	3	6.1	1	3.2
infertile	0	0	0	0	0	0	6	20.0
abandoned	7	41.2	5	12.8	11	23.9	12	40.0
disappeared	5	29.4	17	43.6	4	8.7	3	10.0
hatched	5	29.4	17	43.6	31	67.4	9	30.0
CHICKS								
hatched	5	100.0	17	100.0	31	100.0	9	100.0
human caused losses	0	0	0	0	1	3.2	2	22.2
found dead	1	20.0	4	23.5	3	10.0	0	0
disappeared	4	80.0	13	76.5	3	10.0	5	71.4
fledged	0	0	0	0	24	80.0	2	28.6
OVERALL BREEDING SUCCESS	0/17	0	0/39	0	24/45	53.3	2/29	6.9

DISCUSSION

The three *Pterodroma* species studied differ in choice of breeding habitat. Habitat preference and the physical characteristics of the burrows are co-related. The drainage channel in *brevirostris* burrows is an adaptation for nesting in marshy areas, whereas *macroptera* can only nest in habitats with soil deep enough to accommodate their large burrows (Schramm unpubl.). Different habitat preferences might indicate some past competition for nesting space as suitable breeding habitat does not seem to be limiting at present.

The differences in the total length of breeding season are partly a result of differing fledging periods. Fledging period is a function of growth rate and is related to the quantity of food delivered to the chicks (Lack 1968). Differences in growth rate could therefore be attributed to differences in the size of individual meals or the frequency of delivery or both. Meal sizes of *brevirostris* and *mollis* were not significantly different ($p > 0.05$) and, although feeding frequency may be different, differences in the quality of meals may explain the differing chick growth rates.

Food quality has been suggested to explain the differing growth rates of Black-browned Albatross *Diomedea melanophris* and Grey-headed Albatross *D. chrysostoma* chicks (Prince 1980). Although whole squid, fish and crustaceans (krill) taken from meals of albatross chicks have similar energy contents, the liquid fraction associated with krill meals has five to six times more energy than liquid with squid or fish meals (Clarke & Prince 1980). The calcium content of meals, which may limit the growth of birds breeding in calcium deficient environments (Houston 1978), is three to four times higher in fish and crustaceans than in squid (Clarke & Prince 1980). Therefore, meals of *brevirostris* chicks, which have a higher percentage of crustaceans and fish, are likely to contain more energy and calcium than meals fed to *mollis* or *macroptera*. This may explain the faster growth and shorter fledging period of *brevirostris*.

Differences in the timing of breeding in the three *Pterodroma* petrels, and particularly their non-overlapping chick rearing periods, could be a means of reducing any competition for food. Similar differences in breeding seasons are shown by both the Dove Prion *Pachyptila desolata* and Blue Petrel *Halobaena caerulea*, and the South Georgian Diving Petrel *Pelecanoides georgicus* and Common Diving Petrel *P. urinatrix* breeding at South Georgia (Croxall & Prince 1980).

Breeding success may have been influenced by human disturbance, which may account for some cases of abandonment. The disappearance of eggs and chicks can probably be attributed to predation by cats, which regularly enter burrows, even those of the smaller petrel species, in search of food (Van Aarde 1980; pers. obs.). That the prey remains of cats accumulate in their lairs (Van Aarde 1980, pers. obs.) suggests that cats remove their prey from where it was killed for devouring elsewhere. This would explain the absence of any petrel remains in the study burrows. The timing of breeding influences the vulnerability to predation by skuas or cats, which is reflected to some extent by differences in breeding success between the three *Pterodroma* species. *P. brevirostris* breeds when alternative prey, such as penguins, prions and Blue Petrels, are freely available to predators, whereas most summer breeding species have begun leaving the island by the latter part of the *mollis* breeding season. Consequently, *brevirostris* forms only 1% and *mollis* 13% of the petrels taken by skuas (Schramm unpubl.) and may explain the better breeding success of *brevirostris*. *P. macroptera* breeds during winter when there is little alternative prey available to cats. During a visit to neighbouring cat-free Prince Edward Island in September 1979, 33% (N = 30) of fresh *macroptera* burrows contained chicks compared to 1% (N = 109) at cat-infested Marion Island. It therefore seems that cats were largely responsible for the heavy predation and resultant breeding failure of *macroptera*, as skuas are absent from the islands during winter.

Lack (1971) suggested that ecological isolation among congeneric species is achieved through differences in habitat utilization or feeding ecology or both. Several species of sub-Antarctic seabirds at South Georgia differ in these respects (e.g. Croxall & Prince 1980). Differences in breeding habitat and in the timing of breeding are two of the ways in which the three *Pterodroma* species at Marion Island are segregated ecologically.

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CHAPTER 3

Diet of the petrels *Pterodroma macroptera*, *P. brevirostris* and *P. mollis* at the Prince Edward Islands

DIETS OF THE PETRELS _PTERODROMA_ _MACROPTERA_, _P_. _BREVIROSTRIS_ AND _P_. _MOLLIS_ AT THE PRINCE EDWARD ISLANDS

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SUMMARY

SCHRAMM, M. 1980. Diets of the petrels _Pterodroma_ _macroptera_, _P_. _brevirostris_ and _P_. _mollis_ at the Prince Edward Islands. _Ostrich_ 50: 00-00.

Stomach contents of chicks of Greatwinged Petrels _Pterodroma_ _macroptera_, Kerguelen Petrels _P_. _brevirostris_ and Softplumaged Petrels _P_. _mollis_ collected at the Prince Edward Islands were analysed. Chicks of all three species were fed primarily on cephalopods (90 %, 70 % and 89 % by mass of stomach contents, respectively) supplemented by crustaceans (6 % in _macroptera_, 24 % in _brevirostris_ and 10 % in _mollis_) and fish. The diets were similar and differences may be due to seasonal variation in prey availability. Potential interspecific competition for food is presumably reduced, since the petrels have different breeding seasons with non-overlapping chick-rearing periods.

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INTRODUCTION

Gadfly petrels *Pterodroma* spp. (Procellariidae) feed mainly at night (Imber 1973), seizing their prey at the sea surface (Ashmole 1971). Three species, Greatwinged Petrel *Pterodroma macroptera*, Kerguelen Petrel *P. brevirostris* and Softplumaged Petrel *P. mollis*, breed sympatrically at the Prince Edward Islands (46°50'S; 37°45'E) during winter, early and late summer, respectively (Schramm 1983).

Aspects of the feeding ecology of *macroptera* have been studied at Whale Island, off New Zealand (Imber 1973). Little has been published on the diet of *brevirostris* (Paulian 1953; Mougin 1969) and *mollis* (Hagen 1952; Despin *et al*. 1972; Williams & Imber 1982). This paper reports quantitative information on the food of these three petrel species while breeding at the Prince Edward Islands.

METHODS

Quarter- to half-grown chicks of *macroptera*, *brevirostris* and *mollis* were collected from their burrows at Marion Island (Prince Edward Island group) during August 1979, December 1979 and late February 1980 respectively. An additional 10 *macroptera* chicks were collected at neighbouring Prince Edward Island (22 km away) in September 1979. All chicks were made to regurgitate into a plastic bag, by inverting and squeezing their stomachs, and then were killed. In the laboratory, regurgitations and stomach contents were weighed separately, pooled and any oil was then decanted off and weighed. Food remains were sorted into cephalopods, crustaceans and fish, weighed separately, and preserved in 50 % ethyl alcohol.

Additional prey items were obtained from a few adults and from chicks which occasionally regurgitated while being handled. Other workers have used regurgitations from adults returning to feed chicks for diet analyses (Payne & Prince 1979; Prince 1980a) but this was not practicable at Marion Island where Pterodroma petrels have very scattered nests (pers. obs).

The majority of prey items from macroptera were identified from reference collections established by M.J. Imber, New Zealand Wildlife Service, and by the Port Elizabeth Museum, South Africa. Cephalopods were identified from their lower beaks. Lower rostral length was measured for each beak (except in Alloposus for which hood length was measured) and the estimated mass of the cephalopod calculated from length-mass regressions in Clarke (1962, 1980). For intact crustaceans, the total length (tip of rostrum to tip of telson) was measured and, where applicable, carapace length (to tip of rostrum). Fish were identified from otoliths.

RESULTS AND DISCUSSION

The percentage of the total stomach contents regurgitated by chicks was 69 % (range 0-100 %) for macroptera, 29 % (3-73 %) for brevirostris and 7 % (0-89 %) for mollis. It was therefore necessary to kill chicks to obtain representative samples of stomach contents. Twenty-one macroptera, 22 brevirostris and nine mollis chicks were collected. Owing to the low breeding success of macroptera (0 %) and mollis (7 %) (Schramm 1983) and since brevirostris and mollis are not very abundant at Marion Island (600 and 1 300 nests per 10 km^2, respectively; unpubl. data), few chicks were available.

Stomach contents

The liquid fraction of the stomach contents was an orange-coloured oil, which made up 18 %, 16 % and 19 % by mass of macroptera, brevirostris and mollis samples, respectively.

Cephalopod remains, mainly beaks, eye lenses and spermatophores, were found in almost all stomachs and made up 90 % by mass of the solid fraction in macroptera, 70 % in brevirostris and 89 % in mollis samples (Table 1). Twenty-seven species of cephalopods were identified in the 124 lower beaks in the macroptera stomach contents and regurgitations (Table 2). Despite examining similar total amounts of diet material, only 12 and 11 lower beaks (8 nd 7 species) were recovered from brevirostris (Table 3) and mollis (Table 4) samples, respectively.

Estimated mean masses of these cephalopods were 146 g, 68 g and 73 g in macroptera, brevirostris and mollis, respectively. These estimates, potentially inaccurate due to lack of species specific lower rostral length - body mass regressions (Clarke 1962, 1980), are probably higher than the true means, since the smallest squid beaks would be more easily digested and thus under-represented in the stomach samples. Imber (1973) found that the small squid Spirula (mean mass 10 g) formed 25 % of intact cephalopods in macroptera regurgitations but accounted for only 0,3 % of regurgitated beaks. Rapid elimination of smaller beaks might explain their scarcity in the samples from brevirostris and mollis, since these species seem to take smaller prey than macroptera. Many individual cephalopods taken by macroptera had estimated masses greater than the bird (590 g; Schramm 1983). These large cephalopods are probably already dead when taken. Is is well known that Procellariiformes

TABLE 1

PERCENTAGE COMPOSITION (BY MASS AND FREQUENCY) OF STOMACH SAMPLES OF *PTERODROMA MACROPTERA*
P. BREVIROSTRIS AND *P. MOLLIS* CHICKS AT THE PRINCE EDWARD ISLANDS

Prey category	*P. macroptera*	*P. brevirostris*	*P. mollis*
MASS			
Cephalopods	90	70	89
Crustaceans	6	24	10
Fish	4	6	1
FREQUENCY			
Cephalopods	100	95	100
Crustaceans	71	100	77
Fish	33	43	33
SAMPLE SIZE			
Total mass (g)	321	245	282
No. stomachs	21	22	9

TABLE 2

CEPHALOPOD LOWER BEAKS IDENTIFIED IN STOMACH SAMPLES AND REGURGITATIONS FROM *PTERODROMA MACROPTERA* CHICKS AT THE PRINCE EDWARD ISLANDS. MEAN LOWER ROSTRAL LENGTH AND MEAN ESTIMATED MASS (CLARKE 1962, 1980) AND PERCENTAGE CONTRIBUTION BY FAMILY ARE GIVEN

FAMILY Species	No.	Lower rostral length (mm) x̄ ± S.D.	(range)	Estimated mass (g) x̄ ± S.D.	(range)	Contribution of family (%) Number	Mass
ENOPLOTHEUTHIDAE	2					2	2
Ancitrocheirus lesueuri	2	4,3 ± 0,70	(3,6-5,0)	167 ± 87,5	(79-254)		
OCTOPOTEUTHIDAE	2					2	2
Octopoteuthis sp.	2	8,4 ± 0,05	(8,3-8,4)	159 ± 2,0	(157-161)		
ONYCHOTEUTHIDAE	2					2	9
Moroteuthis knipovitchi	1	6,2		555			
Moroteuthis robsoni	1	7,6		1 131			
CYCLOTEUTHIDAE	10					8	18
Discoteuthis sp. C	10	7,1 ± 2,19	(5,1-13,0)	331 ±230,8	(158-979)		
GONATIDAE	21					17	23
Gonatus antarcticus	21	5,9 ± 0,73	(4,3- 7,9)	200 ± 94,5	(67-507)		
HISTIOTEUTHIDAE	31					25	20
Histioteuthis atlantica	14	3,5 ± 0,54	(2,5- 4,7)	73 ± 23,4	(37-133)		
Histioteuthis ?dofleini	2	5,0 ± 0,75	(4,2- 5,7)	151 ± 45,0	(106-196)		
Histioteuthis eltaninae	6	2,6 ± 0,08	(2,4- 2,6)	39 ± 2,3	(34- 40)		
Histioteuthis macrohista	5	2,8 ± 0,22	(2,8- 3,1)	47 ± 7,6	(37- 58)		
Histioteuthis meleagroteuthis	1	4,6		127			
Histioteuthis miranda	3	6,4 ± 0,33	(6,0- 6,8)	561 ± 69,1	(471-639)		
BRACHIOTEUTHIDAE	5					4	4
Brachioteuthis picta	5	4,1 ± 0,33	(3,5- 4,5)	144 ± 30,8	(92-186)		
CHIROTEUTHIDAE	17					14	6
Chiroteuthis capensis	2	5,4 ± 0,15	(5,2- 5,5)	73 ± 5,5	(67- 78)		
Chiroteuthis picteti	13	5,0 ± 0,78	(3,6- 6,4)	64 ± 25,4	(25-118)		
Chiroteuthis veranyi	1	5,0		61			
Chiroteuthis sp.E	1	4,1		35			
MASTIGOTEUTHIDAE	1					1	21
Mastigoteuthis ?agassizi	1	3,2		34			
CRANCHIIDAE	31					25	12
Taonius belone	2	5,8 ± 0,05	(5,7- 5,8)	101 ± 2,0	(99-103)		
Taonius cymoctypus	6	7,1 ± 0,87	(5,6- 8,2)	143 ± 73,9	(96-220)		
Taonius pavo	9	4,8 ± 0,25	(4,3- 5,2)	67 ± 7,6	(54- 81)		
Teuthowenia antarctica	5	3,3 ± 0,27	(2,9- 3,7)	31 ± 5,4	(23- 39)		
Teuthowenia megalops impennis	2	4,7 ± 0,2	(4,5- 4,9)	65 ± 6,0	(59- 71)		
Phasmatopsis sp.	1	4,6		62			
Galiteuthis armata	1	3,2		28			
Galiteuthis glacialis	4	3,3 ± 0,72	(2,1- 4,1)	31 ± 13,1	(11- 48)		
Unidentified sp.	1	3,2		28			
ALLOPOSIDAE	2					2	3
Alloposus mollis	2	8,3 ± 2,25 (Hood length)	(6,0-10,5)	267 ±102,5	(164-364)		

TABLE 3

CEPHALOPOD LOWER BEAKS IDENTIFIED IN STOMACH SAMPLES AND REGURGITATIONS FROM *PTERODROMA BREVIROSTRIS* CHICKS AT THE PRINCE EDWARD ISLANDS. MEAN LOWER ROSTRAL LENGTH AND MEAN ESTIMATED MASS (CLARKE 1962, 1980) AND PERCENTAGE CONTRIBUTION BY FAMILY ARE GIVEN

FAMILY Species	No.		Lower rostral length (mm) $\bar{x}$ ± S.D.	(range)	Estimated mass (g) $\bar{x}$ ± S.D.	(range)	Contribution of family (%) Number	Mass
CYCLOTHEUTHIDAE	1						8	25
Discoteuthis sp.C		1	5,8		203			
GONATIDAE	2						17	44
Gonatus antarcticus		2	5,8 ± 0,35	(5,4- 6,1)	179 ± 35,5	(143-214)		
HISTIOTEUTHIDAE	1						8	5
Histioteuthis ?macrohista		1	2,5		37			
CHIROTHEUTHIDAE	2						17	6
Chiroteuthis sp.E		1	4,1		35			
Chiroteuthis sp.		1	2,8		13			
CRANCHIIDAE	6						50	21
Taonius pavo		1	2,9		23			
Teuthowenia antarctica		4	3,2 ± 1,52	(1,1- 4,8)	35 ± 27,4	(3- 68)		
Unidentified sp.		1	1,6		6			

TABLE 4

CEPTALOPOD LOWER BEAKS IDENTIFIED IN STOMACH SAMPLES AND REGURGITATIONS FROM *PTERODROMA MOLLIS* CHICKS AT THE PRINCE EDWARD ISLANDS. MEAN LOWER ROSTRAL LENGTH AND MEAN ESTIMATED MASS (CLARKE 1962, 1980) AND PERCENTAGE CONTRIBUTION BY FAMILY ARE GIVEN

FAMILY Species	No.	Lower rostral length (mm) $\bar{x}$ ± S.D.	(range)	Estimated mass (g) $\bar{x}$ ± S.D. (range)	Contribution of family (g) Number	Mass
CYCLOTEUTHIDAE	1				9	23
Discoteuthis sp.C	1	5,5		183		
GONATIDAE	1				9	36
Gonatus antarcticus	1	6,7		293		
CHIROTEUTHIDAE	5				45	22
Chiroteuthis picteti	1	5,0		61		
Chiroteuthis sp. E	4	3,8 ± 0,26	(3,4- 4,1)	29 ± 5,1(21- 35)		
MASTIGOTEUTHIDAE	1				9	6
Mastigoteuthis ?agassizi	1	3,6		48		
CRANCHIIDAE	3				27	13
Teuthowenia antarctica	2	3,7 ± 0,60	(3,1- 4,3)	40 ± 14,0(26- 54)		
Galiteuthis armata	1	2,9		23		

scavenge cephalopods (Imber & Berruti 1981), and that their well developed olfactory sense (Grubb 1972; Hutchinson & Wenzel 1980) makes it possible for petrels to locate dead animals at great distances.

Histioteuthid and cranchiid squids were numerically dominant in macroptera samples (Table 2). Off New Zealand, macroptera also takes large numbers of histioteuthids and cranchiids, as well as many spirulids (Imber 1973) which were not represented in the Marion Island samples. Although fewer beaks were found, cranchiids also dominated the brevirostris samples (Table 3), and chiroteuthids and cranchiids the mollis samples (Table 4). A preponderance of cranchiids amongst the squid beaks is a feature of the diets of most of the large petrels and albatrosses studied in the Southern Ocean (Imber 1978).

Crustacean remains were mainly whole amphipods and the carapaces of decapods and mysids (Table 5). No significant differences (t-test, P >0,05) were found between the sizes of the amphipod Eurythenes obesus or the decapod Parapasiphae taken by the three petrel species (Table 6). Too few specimens of the other crustacean species were found for statistical comparison. Since many of the crustaceans had only the exoskeleton remaining, individual masses were not recorded.

The fish material was mostly in an advanced state of digestion and comprised mainly bones and small silvery, scale-like pieces. No whole fish were found and few otoliths. Duffy & Laurenson (1983) found that Cape Cormorants Phalacrocorax capensis totally digested 66 % of otoliths within a day and severely eroded the remainder. Nevertheless, otoliths of five myctophids (two Diaphus? danae and three Electrona subaspera) and one morid were identified in the macroptera stomach contents. The otoliths of a Diaphus were found in a

TABLE 5

PERCENTAGE COMPOSITION (MASS AND NUMBERS) OF CRUSTACEANS IN STOMACH SAMPLES AND REGURGITATIONS FROM PTERODROMA MACROPTERA, P. BREVIROSTRIS AND P. MOLLIS AT THE PRINCE EDWARD ISLANDS.

ORDER Species	Composition by mass (%) P.macroptera	 P.brevirostris	 P.mollis	Composition by numbers (%) P.macroptera	 P.brevirostris	 P.mollis
AMPHIPODA	38,5	25,1	64,8	44,4	33,8	66,7
Eurythenes obesus	38,5	21,5	42,6	44,4	25,4	50,0
Eurythenes sp.	0	2,0	13,0	0	2,8	5,6
Vibilia sp.	0	1,7	9,3	0	5,6	11,1
ISOPODA	0	7,6	0	0	1,4	0
Unidentified parasitic sp.	0	7,6	0	0	1,4	0
MYSIDACEA	48,7	11,2	1,9	22,2	8,5	5,6
Gnathophausia gigas	48,7	11,2	1,9	22,2	8,5	5,6
DECAPODA	12,8	56,2	33,4	33,4	56,3	27,8
Parapasiphae sp.	6,8	43,2	27,8	16,7	49,3	22,2
Sergestes sp.	6,0	7,6	5,6	16,7	5,6	5,6
Acanthephyra sp.	0	5,4	0	0	1,4	0
SAMPLE SIZE	11,7 g	41,0 g	5,4 g	18	71	18

TABLE 6

DIMENSIONS(MM) OF INTACT CRUSTACEANS FOUND IN STOMACH SAMPLES AND REGURGITATIONS FROM *PTERODROMA MACROPTERA*, *P. BREVIROSTRIS* AND *P. MOLLIS* CHICKS AT THE PRINCE EDWARD ISLANDS

ORDER Species	*P. macroptera* Carapace length	*P. macroptera* Total length	*P. brevirostris* Carapace length	*P. brevirostris* Total length	*P. mollis* Carapace length	*P. mollis* Total length
AMPHIPODA						
Eurythenes obesus		27,5±5,99 (18-37) n=6		26,7±10,14 (10-42) n=11		21,6±5,87 (12-32) n=8
Eurythenes sp.		Not taken		25,0±0 (---) n=2		27,0 (---) n=1
Vibilia sp.		Not taken		23,7±1,89 (21-25) n=3		21,0±3,00 (18-24) n=2
ISOPODA						
Unidentified parasitic sp.		Not taken		55,0 (---) n=1		Not taken
MYSIDACEA						
Gnathophausia gigas	---	---	31,0 (---) n=1	76,0 (---) n=1	---	---
DECAPODA						
Parapasiphae sp.	36,0±4,00 (32-40) n=2	---	30,1±4,48 (20-41) n=23	95,5±11,50 (84-107) n=2	31,0±5,00 (26-36) n=2	---
Sergestes sp.	8,0 (---) n=1	38,0 (---) n=1	12,8±3,49 (8-15) n=4	47,5±9,63 (36-58) n=4	11,0 (---) n=1	---
Acanthephyra sp.	Not taken	Not taken	29,0 (---) n=1	---	---	---

brevirostris stomach and an Electrona was identified from the mollis material.

Samples collected from chicks are not ideal for diet analysis because the material is more digested than that taken from adults. Moreover, chicks have a tendency to accumulate material resistant to digestion. Differences in digestibility may also exaggerate the importance of those prey items which have digestion-resistant parts. Furness et al. (in press) found that in a captive Shy Albatross Diomedea cauta squid beaks persisted for up to seven weeks but otoliths were digested within a day.

Although the diet samples from the three petrels in this study can be compared with one another, because they were collected in the same manner, caution is needed when comparing the results with those from other studies. For example, fish comprised 28 % by mass of macroptera samples off New Zealand (Imber 1973) compared to only 4 % in this study (Table 1). Although the samples were collected at different times of the year (December compared to August-September in this study), the samples from New Zealand contained intact and partly intact fish (and squid) and were therefore probably less digested than those from this study. Nevertheless, most of the species of cephalopods, crustaceans and fish taken by macroptera at the Prince Edward Islands were also taken by macroptera off New Zealand (Imber 1973). No euphausiids were found, although they are taken elsewhere by macroptera (Imber 1973) and at Marion Island by Eudyptes penguins (Williams & Laycock 1981) and Broadbilled Prions Pachyptila vittata salvini during summer (pers. obs). At sea, brevirostris apparently ignores dense surface swarms of euphausiids (Griffiths 1982).

There is little information on the diets of brevirostris and mollis elsewhere. At the Crozet Islands eight out of nine stomachs from brevirostris adults and chicks contained cephalopods (Mougin 1969), where Eurythenes obesus is also taken (Bellan-Santini & Ladoyer 1974 in Imber 1976). Six mollis stomachs from the Crozet Islands all contained cephalopods (Despin et al. 1972) and two from Tristan da Cunha contained cephalopods and fish (Hagen 1952). Two adults from Gough Island contained squid beaks of the family Histoteuthidae, Cranchiidae and Mastigoteuthidae (Williams & Imber 1982).

Bioluminescence of prey items

Several studies of petrel and albatross diet have noted the preponderence of bioluminescent prey items and it has been suggested that the birds use this bioluminescence to locate their prey (Imber 1973; Imber & Russ 1975; Imber & Berruti 1981). However, at South Georgia, Todarodes, a non-bioluminescent species, represented 83 % and 66 % of cephalopods taken by Greyheaded Albatrosses Diomedea chrysostoma and Blackbrowed Albatrosses D. melanophris, respectively (Prince 1980b). This shows that certain Procellariiformes are indeed able to locate large numbers of non-bioluminescent cephalopods.

Twenty-five (77 %) of the 28 cephalopod species taken by Pterodroma petrels at the Prince Edward Islands are bioluminescent (Roper 1969; Herring 1977). However, of the three non-bioluminescent cephalopods (Gonatus, Brachioteuthis and Mastigoteuthis), Gonatus antarcticus accounted for 17 % of the beaks taken from macroptera, more than any other species (Table 2). This is contrary to the findings of Imber (1973) and Imber & Russ (1975) who found Gonatus was unimportant to either *macroptera* or Wandering Albatrosses *Diomedea exulans* off New Zealand. These authors suggest that although *Gonatus* is the most abundant squid in the surface waters of the Southern Ocean (Roper 1969), seabirds have difficulty locating it since it is non-bioluminescent.

Competition between the three species

The diets of the three petrels appear similar. All species of squid and fish taken by *brevirostris* and *mollis* are also taken by *macroptera*. The crustacean prey of all three species is similar. However, sample sizes are probably too small to show up quantitative differences clearly.

The mean sizes of cephalopods taken by the three species, although different, are in keeping with differences in the birds' sizes and probably reflect a tendency of the large *macroptera* (590 g) to kill large cephalopods more frequently than do the smaller *brevirostris* (360 g) or *mollis* (310 g).

The most apparent differences in diet are in the relative amounts and types of crustaceans taken. Mysids and amphipods dominated in *macroptera* samples, *brevirostris* took most crustaceans overall, principally decapods, and *mollis* took mainly amphipods (Table 5). Ashmole (1968) suggested that surface-feeding seabirds are relatively non-selective with respect to the taxonomic affinities of their prey and catch any suitably sized prey at the sea surface. Since each of the *Pterodroma* species was sampled at a different time of the year, the above differences may result from seasonal variation in prey abundance and composition. Imber (1973) found many *Eurythenes* in food samples taken from *macroptera* in September but none in samples collected at the same locality off New Zealand in December.

The similarities in diet suggest there is potential for competition between the three *Pterodroma* petrels. Similar species of sympatric seabirds apparently have several mechanisms to reduce competition for food. For instance, at South Georgia Blue Petrels *Halobaena caerulea* and Dove Prions *Pachyptila vittata desolata* have partially separate breeding seasons, concentrate on different types of prey, and feed in different areas (Prince 1980a). Although the three *Pterodroma* petrels at the Prince Edward Islands may have different feeding grounds, they take similar sizes and types of prey. However, they rear their chicks at different times of the year: from late July to November in *macroptera*; late November to late January in *brevirostris*; and early February to early May in *mollis* (Schramm 1983).

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CHAPTER 4

Predation by Subantarctic Skuas *Catharacta antarctica* on burrowing petrels at Marion Island

Predation by subantarctic skuas *Catharacta antarctica* on burrowing petrels at Marion Island

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Petrel remains were collected from around 27 subantarctic skua Catharacta antarctica nests at Marion Island. Skuas took seven species of burrowing petrels, with Salvin's prion Pachyptila salvini forming the dominant prey item. The use of skua remains as indicators of petrel was shown for two areas where the density and composition of petrel burrows had been determined. Although the composition of the remains was related mainly to the abundance of the petrels, breeding season and size also determined how well different species were represented.

Stormvoëloorblyfsels was rondom 27 bruin roofmeeu Catharacta antarctica neste op Marioneiland versamel. Roofmeeue het op sewe spesies van grawende stormvoëls geprooi, met Salvinse stormvoël Pachyptila salvini die dominante prooi-item. Die verbruik van roofmeeu prooi-oorblyfsels as aanwysers van stormvoël volopheid is bewys vir twee areas waar die digtheid en samestelling van stormvoël nesgate alreeds bepaal was. Alhoewel die samestelling van die oorblyfsels hoofsaaklik aan die relatiewe volopheid van die stormvoëls verwant was, het broeiseisoen en grotte ook bepaal hoe goed verskillende spesies verteenwoordig was.

Introduction

Subantarctic skuas *Catharacta antarctica* are major predators of burrowing petrels (subterranean nesting Procellariiformes from the families Procellariidae, Pelecanoididae and Oceanitidae) (Watson 1975). Skuas are opportunistic feeders, foraging close to their nests and breeding adults are highly territorial (Carrick & Ingham 1970, Sinclair 1980). At Marion Island (46°54'S, 37°45'E) in the Prince Edward group there are *c.* 400 pairs of subantarctic skuas (Williams *et al.* 1979) mostly concentrated along the coast (pers. obs.) but some are found inland up to 600 m above sea level (A. Berruti *in litt.*). Ten species of burrowing petrels have been recorded breeding at Marion Island (Williams *et al.* 1979).

Skua predation on petrels has been described for Macquarie Island (Jones 1980) and for the Antipodes (Moors 1980). Jones (1980) used the prey remains left by skuas and feral house cats *Felis catus* as indicators of the status (distribution and relative abundance) of burrowing petrels at Macquarie Island. At Marion Island, aspects of skua predation on petrels have been documented by Sinclair (1980), van Aarde (1980) and Grindley (1981). This paper describes the burrowing petrel component of the skuas' diet and assesses the use of skua prey remains for deriving information about the status of petrels.

Study Area and Methods

Marion Island is volcanic and two lava types can be recognized viz. an old grey lava eroded by glaciation and a younger post glacial black lava (Verwoerd 1971). The grey lava and associated glacial deposits form ridges which radiate from the centre of the island. These ridges have steep well vegetated slopes with deep well drained soils suitable for burrowing by petrels. In contrast, black lava areas generally have poor soil cover and less vegetation. The lava is often very broken with many natural cavities which some petrel species are able to use for nesting.

During February and March 1980, towards the end of the skua breeding season, a strip approximately 2 km wide along the north east coast of Marion Island between Macaroni and Blue Petrel Bays was searched for skua nests. Prey remains, including casts, within a 50 m radius of each nest were collected. The remains of skua prey were distinguished from possible cat prey remains by the lack of tooth marks on the long bones (van Aarde 1980). Casts were broken apart and examined macroscopically. Petrel species were identified by the size, shape and colour of wings, legs or skulls. The minimum number of birds represented by the remains was recorded. Penguin remains were identified mainly from the heads and feet of adults and chicks but were not counted.

During April 1979 to May 1980 information was collected on the distribution and density of petrels in the north east part of Marion Island. Transects were positioned at 200 m intervals on the slopes of grey lava ridges, along the black lava coastal plain and inland. Quadrats 30 X 10 m were laid out at 25 to 50 m intervals on the transects. Within each quadrat all utilized burrows - those containing eggs, chicks or the remains thereof or burrows undergoing renovation - were counted and identified. Natural holes used for nesting were also included.

In order to assess the extent to which skua prey remains reflect the status of the surrounding petrel population, prey remains were grouped into those from skua nests in grey lava areas and those from nests in black lava areas. For each group the species composition of the remains was compared to the composition of the petrel burrows found in that area and the Chi-square test was used to test for significant differences.

Results

Prey remains were collected from around 27 skua nests, 15 from grey lava areas and 12 from black lava areas (Fig. 1). The remains of at least 649 petrels of seven species were found ($\bar{X}$ = 24,0; S.D. = 23,38; range = 2 - 100 petrels per skua nest). Salvin's prion *Pachyptila salvini* comprised 70,1 per cent of the burrowing petrels taken and this species was found at 96,3 per cent of the skua nests (Table 1).

Penguin remains, mainly eggs and chicks, were found at 70,3 per cent of skua nests. King penguin *Aptenodytes patagonicus* and gentoo penguin *Pygoscelis papua* remains were found at 22,2 and 3,7 per cent of nests respectively. The remains of macaroni penguins *Eudyptes chrysolophus* and rockhopper penguins *E. chrysocome*, which could usually not be separated, were found at 63,0 per cent of skua nests. The remains of a lesser sheathbill *Chionis minor* and an unidentified *Phoebetria* albatross chick were found. Hair from southern elephant seals *Mirounga leonina* was found in two of the 103 casts examined. There was no evidence in any of the remains or casts to suggest that skuas preyed upon the house mouse *Mus musculus* which is abundant at Marion Island

Fig. 1. Marion Island showing the study area and subantarctic skua *Catharacta antarctica* nest sites

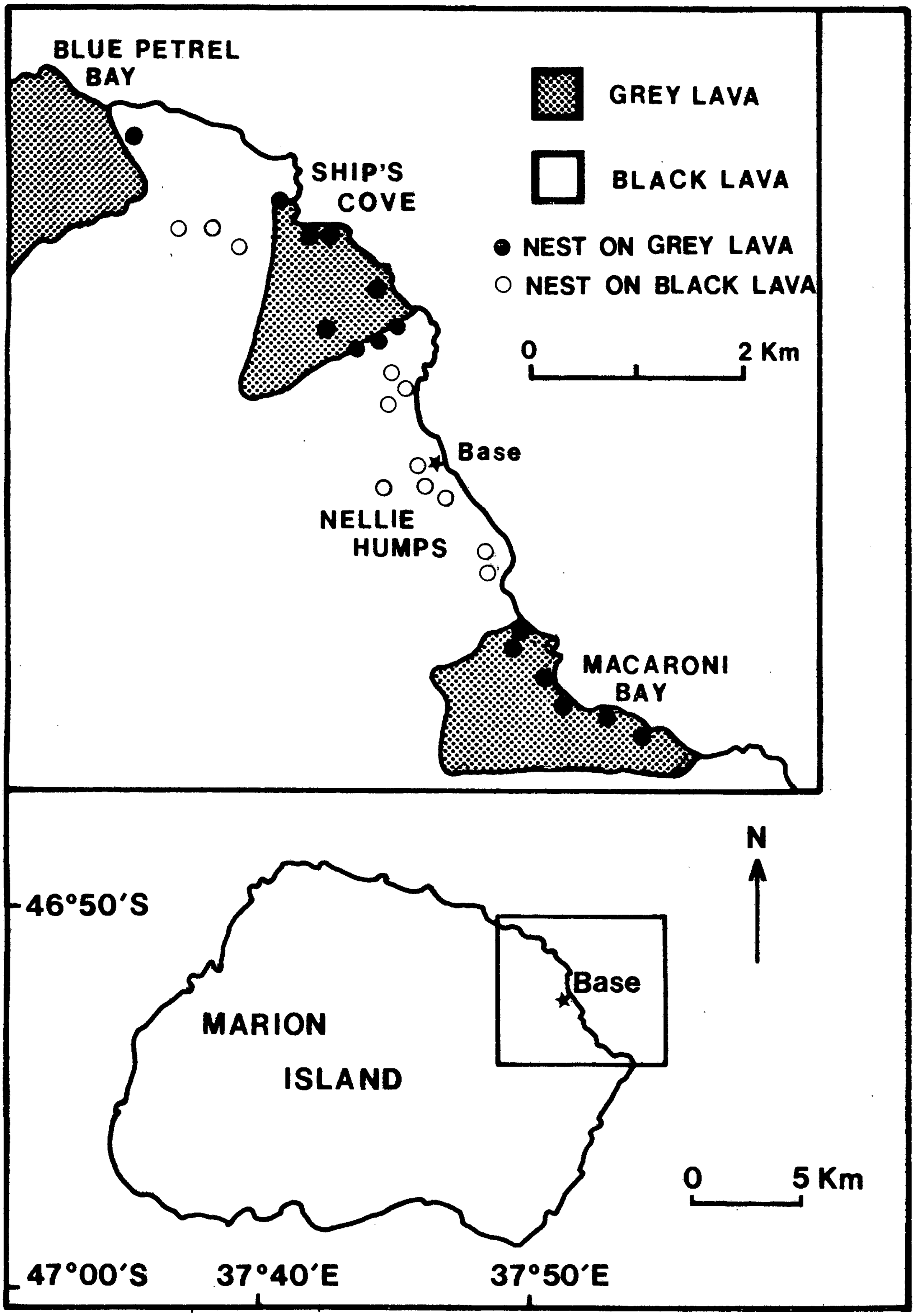
BLUE PETREL BAY
SHIP'S COVE
GREY LAVA
BLACK LAVA
● NEST ON GREY LAVA
○ NEST ON BLACK LAVA
0
2 Km
Base
NELLIE HUMPS
MACARONI BAY
N
46°50'S
Base
MARION ISLAND
0
5 Km
47°00'S
37°40'E
37°50'E

Table 1

Percentage composition of burrowing petrel remains from subantarctic skua *Catharacta antarctica* nest sites at Marion Island.

	Species	Percentage composition	
		Numbers	Frequency of occurrence
Salvin's prion	*Pachyptila salvini*	70,1	96,3
Blue petrel	*Halobaena caerulea*	12,2	37,0
Greatwinged petrel	*Pterodroma macroptera*	1,1	22,2
Kerguelen petrel	*Pterodroma brevirostris*	1,1	18,5
Softplumaged petrel	*Pterodroma mollis*	12,8	63,0
Whitechinned petrel	*Procellaria aequinoctialis*	1,1	18,5
Diving petrels	*Pelecanoides* sp.	1,7	7,4
Sample size		649 remains	27 nest sites

(Anderson & Condy 1974), although A.J. Williams (*in litt.*) reports finding the remains of a mouse in a skua regurgitation.

There were large significant differences (*P* <0,001; chi-square test) between the frequencies of Salvin's prion, blue petrel *Halobaena caerulea*, softplumaged petrel *Pterodroma mollis* and diving petrel *Pelecanoides* sp. remains from skua nests on grey lava compared to black lava (Table 2). The small sample of remains of greatwinged petrel *Pterodroma macroptera*, Kerguelen petrel *P. brevirostris* and whitechinned petrel *Procellaria aequinoctialis* precluded their statistical analysis.

In black lava areas 276 burrows were found in 78 quadrats (353,8 burrows per hectare) and of these 72,4 per cent belonged to Salvin's prion. This species also dominated (90,5%) the petrel remains from the 12 skua nests on black lava (Table 2). Greatwinged and whitechinned petrels were of negliglble importance of skuas although they made up 13,4 and 12,3 per cent of burrows found in black lava areas. In grey lava areas petrel burrows were confined to the vegetated slopes of the grey lava ridges and in 67 quadrats 418 burrows (623,9 burrows per hectare) were found, 45,5 per cent were blue petrel and 23,0 per cent Salvin's prion. These were also the two dominant species taken by skuas nesting in grey lava areas.

Discussion

The preponderance of prions in the prey remains is not unexpected since they are the most widely distributed and abundant petrels nesting on Marion Island (Williams *et al.* 1979, pers. obs.). In an earlier study of the remains of 251 burrowing petrels taken by

Table 2

Percentage composition of burrowing petrel remains from subantarctic skua *Catharacta antarctica* nest sites in grey and black lava areas compared to the percentage composition of petrel burrows found in these two areas.

	Percentage composition					
	Grey lava areas			Black lava areas		
	petrel remains	petrel burrows		petrel remains	petrel burrows	
Salvin's prion	50,9	23,0	**	90,5	71,4	N.S.
Blue petrel	23,1	45,5	**	0,6	0	-
Greatwinged petrel	1,2	10,3	**	1,0	13,4	**
Kerguelen petrel	0.9	4,1	N.S.	1,3	1,8	N.S.
Softplumaged petrel	21,9	8,6	**	3,2	0	-
Whitechinned petrel	2,1	8,6	**	0	12,3	**
Grey petrel	0	0		0	1,1	-
Diving petrels	0	0		3,5	0	**
Sample size	334 remains	418 burrows		315 remains	276 burrows	
	(15 skua nests)	(67 quadrats)		(12 skua nests)	(78 quadrats)	

** differences highly significant (*P* <0,001)

N.S. differences not significant (*P* >0,01)

\- expected frequencies too small for statistical comparison skuas at Marion Island, Grindley (1981) found Salvin's prion formed 71,4 per cent of the total, a figure similar to that obtained during the present study (Table 1).

No comparison has been made between the relative importance of petrels and penguins to skuas, owing to differences in digestibility. Many penguin eggs are swallowed whole and penguin chicks have fewer indigestable components, such as quill feathers and long bones, than the adult birds which make up most of the petrel component of the skuas' diet. Therefore, penguins would tend to be under represented in the remains.

Since skuas forage close to their nests (Carrick & Ingham 1970) regional differences in subantarctic skua diet have been related to the local availability of food (Jones & Skira 1979). Consequently, Jones (1980) used petrel remains left by predators as indicators of the status of petrels. This study at Marion Island provided a means of testing the technique used by Jones (1980) since both the density of petrel burrows and the diet of skuas were known for two areas. If prey remains indicate prey status, the petrels should be represented in the same proportion in the remains as in burrows.

Whereas it was found that most of the abundant petrels were well represented in the prey remains and the remains of both Salvin's prion in black lava areas and Kerguelen petrels were very good indicators of their relative abundance, the remains of many species were poor indicators of their status. For example, whitechinned petrels were not heavily preyed upon, comprising only 1 per cent of the remains, but they nest abundantly in both black lava areas and on the slopes of grey lava ridges (43,5 and

53,7 burrows per hectare, respectively) making up about 10 per cent of the burrows found. Van Aarde (1980) found that this species comprised only 0,8 per cent of the birds taken by feral cats, which are major predators of the other petrel species at Marion Island. It is likely that the whitechinned petrel's large size (mean mass 1 144 g as compared to 1 638 g for skuas - FitzPatrick Institute unpublished data) and aggressive nature renders it less vulnerable to predation. However, in the absence of small more suitable prey such as prions, skuas will regularly take whitechinned petrels (Despin _et_ _al_. 1972). On the Antipodes, where there are few small petrels, whitechinned petrels form up to 21 per cent of the petrels taken by skuas (Moors 1980).

Most skuas arrive at Marion Island during August, breed during mid-summer and depart again in April (Williams 1980). Therefore, only petrels nesting during this time would be vulnerable to predation. Greatwinged petrels breed during winter (Schramm 1983) which would explain why so few remains of this abundant species were found.

The time at which the prey remains are collected appears to influence how well different species are represented. In the remains from grey lava areas, blue petrels were significantly under-represented (Table 2). Since blue petrels nest in early summer, with chicks fledging from late January to early February (pers. obs.), most birds would have left the island by the time the remains were collected in February and March. This might explain why, in relation to the number of blue petrel burrows in grey lava areas (45,5% - 283,8 burrows per hectare), only 23,1 per cent of the remains belonged to this species. Salvin's prions and softplumaged petrels which breed during mid and late summer respectively (Schramm 1983) would therefore tend to be over- represented in remains collected at this time of year (Table 2).

A few diving petrels (probably South Georgian diving petrels *Pelecanoides georgicus*), which were not found breeding in the study area, appeared in the prey remains from two skua nests in Nellie Humps. This area is used as a flyway by petrels *en route* to inland nest sites (pers. obs.) and the birds were probably taken as they flew over the skuas' territories.

The composition of skua prey remains reflects the relative abundance of petrels occurring around the time of collection of the remains. However, skuas tend to undersample larger species (e.g. whitechinned petrels) and winter breeding species (e.g. greatwinged petrels). Nevertheless, analysis of skua prey remains could be useful during short visits to Prince Edward Island and to the remote parts of Marion Island.

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SYNTHESIS

Co-existing burrowing petrel species share two resources while breeding: nesting space on land, and food from the surrounding ocean. This study has tried to identify some of the ways in which the petrels at Marion Island partition these resources.

At Marion Island petrels nest in a wide range of habitats. However, individual species have particular nest site preferences (steep slopes, dry soil, etc.). Furthermore, some species are able to nest in areas unsuitable for most petrels through adaptations in burrow design (Whitechinned Petrels Procellaria aequinoctialis and Kerguelen Petrels Pterodroma brevirostris) or by using natural cavities for nesting (Salvin's Prion Pachyptila vittata salvini). Although there are areas where several petrel species nest together, similar species have the bulk of their breeding populations spread over different habitats (Chapter 1, Table 8). Similar spatial segregation of nest sites has been observed at the Crozet Islands between Salvin's Prion and Fairy Prion Pachyptila turtur (Derenne & Mougin 1976) and at South Georgia between South Georgian Divingpetrel Pelecanoides georgicus and Common Divingpetrel P. urinatrix (Payne & Prince 1979). Although such segregation serves to reduce any interspecific competition for nest sites, there seems to be no shortage of suitable burrowing habitat at Marion Island, an observation also made at South Georgia (Croxall & Prince 1980). Nest site segregation may be a continuing response to reduce competition that occurred in the past.

Studies on seabirds at South Georgia which included petrels have shown that differences in breeding biology (timing of breeding), food and feeding ecology (feeding techniques and foraging ranges) help to reduce any interspecific competition for food (Croxall & Prince 1980).

At Marion Island, similar petrel species have staggered breeding seasons although the degree of overlap in timing varies: Blue Petrel *Halobaena caerulea* and Salvin's Prion have partially separate chick rearing periods (Cooper 1984, pers. obs.), the three *Pterodroma* petrels, Greatwinged Petrel *P. macroptera*, Kerguelen Petrel *P. brevirostris* and Softplumaged Petrel *P. mollis*, have completely separate chick rearing periods (Chapter 2), and the two *Procellaria* species have entirely separate breeding seasons - Whitechinned Petrels nest in summer and Grey Petrels *P. cinerea* nest during winter (Cooper 1984, pers. obs.). During chick rearing the competition for food is probably greatest owing to the increased food demands and because at this time the birds are restricted to foraging within the vicinity of the island since they must return regularly to feed their young. Although staggered breeding helps to reduce any competition for food, this alone is probably insufficient to lead to total ecological isolation.

However, further resource partitioning may result from differences in feeding technique among Marion Island petrel species. Divingpetrels feed below the sea surface by pursuit diving, while the other petrel species feed at or near the surface, *Procellaria*, *Pterodroma* and Blue Petrels by surface seizing and Salvin's Prion by filter feeding (Ashmole 1971). In this way a variety of niches is exploited.

The diets of Pterodroma petrels appear very similar with few differences in either size or species of prey taken, although Kerguelen petrels take more crustaceans overall (Chapter 3). Competition may be reduced by the differences in timing of breeding (see above) but the species may have different foraging areas. The importance of differences in foraging areas or ranges in reducing competition has been highlighted in several studies of seabird feeding ecology (e.g. Pearson 1968, Cody 1973, Croxall & Prince 1980). Differences in foraging range may be inferred from differences in chick feeding frequency. The automatic nest visit recorder (Appendix 1) was installed in two Softplumaged Petrel burrows and in this species mean chick feeding frequency was 3,5 days (range 1-7 days, n = 8). No comparative data were collected for the other two Pterodroma species owing to the breeding failure of Greatwinged Petrels and practical problems with installing the recorder in the flooded entrances of Kerguelen Petrel burrows.

Subantarctic Skuas Catharacta antarctica are largely opportunistic predators, taking whatever petrels are most abundant in an area (Chapter 4). However, burrowing petrels have several habits which aid in predator avoidance: they nest underground, usually emerge only at night, some nest in areas permitting rapid escape (Chapter 1), and some nest in winter when predators are absent. These habits are of little help in avoiding predation from feral House Cats Felis catus. Cats can get down all but the smallest burrows (van Aarde 1980), are nocturnally active and are present throughout the year. The winter-breeding Greatwinged Petrel is particularly vulnerable to predation by cats. It is one of the few suitable prey items available to cats during winter since the summer breeding petrels are only sporadic visitors to the island at this time of year (pers. obs.). Grey Petrels which also breed in winter are not preyed upon by cats (van Aarde 1980), possibly because of their large size.

The cats seem to be responsible for reducing the numbers of petrels, extirpating at least one species (Common Divingpetrel) and lowering the breeding success of at least one species (Greatwinged Petrel) (Chapter 1). However, there has been a decrease in the cat population from 2 139 ± 290 in 1974/75 (van Aarde 1979) to 406 ± 75 in 1981/82 (van Rensburg 1982). Consequently, breeding success of Greatwinged Petrels has increased from 0 % in 1979 and 1980 (Chapter 2) to 20,7 % in 1982 (I.P. Newton unpubl. data in Cooper 1984).

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APPENDIX 1

Automatic recording of nest visits by burrow-nesting birds

Automatic Recording of Nest Visits by Burrow-Nesting Birds.—During a study of the breeding biology of burrow-nesting petrels (Procellariidae) at the Prince Edward islands (46°54'S, 37°45'E) data were required on the frequency and timing of nest visits by adult birds. The nocturnal habits of petrels and their irregular feeding of nestlings dictated the use of an automatic recording system capable of registering the passage of a bird both in and out of the burrow. The system had to be inexpensive, but robust enough

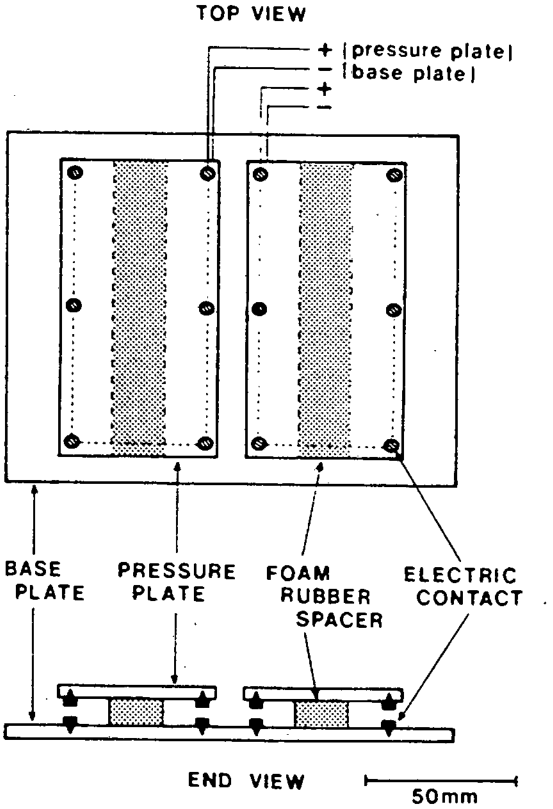

FIGURE 1. Design of a sensor for monitoring the nest visits of burrow-nesting birds.

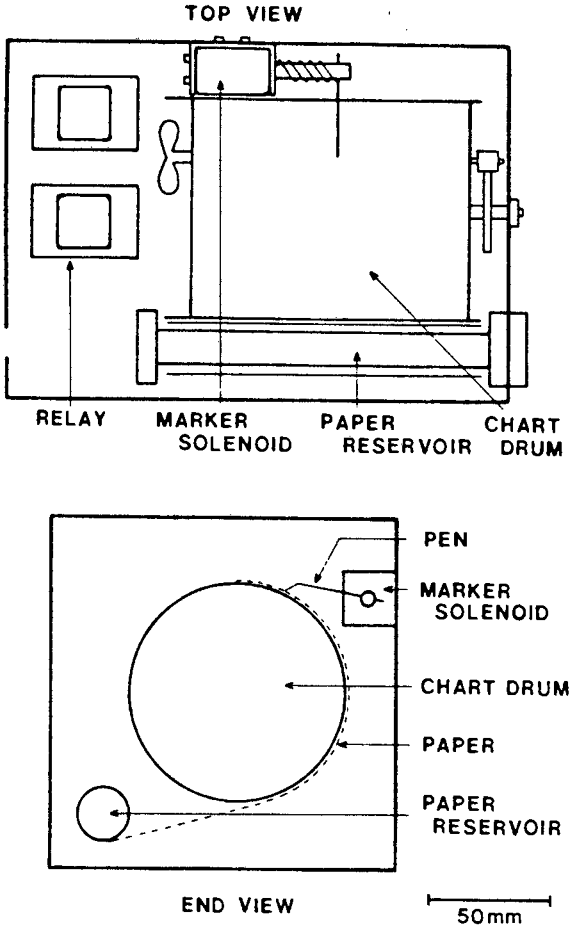

FIGURE 2. Design of a chart-recorder for recording the nest visits of burrow-nesting birds.

to withstand the extreme Subantarctic climate, requirements not met by locally available commercial systems. I used a sensor, placed inside the nest-tunnel, linked to a chart recorder outside, and powered by a rechargeable battery.

The sensing device (Fig. 1), made of plastic, included 2 pressure plates mounted over a base plate. Six electrical contacts made from self-tapping screws were positioned around the edge of each pressure plate and kept apart from the matching contacts on the base plate by a foam-rubber spacer. If a bird stood on almost any part of the sensor, it tilted the pressure plate on the foam rubber and closed one or more of the contacts.

The recorder (Fig. 2) was mounted in a weatherproof box and consisted of a clockwork chart-drum, revolving once every 24 h at a speed of 12mm/h. The chart-drum chosen was a type used by meteorological stations for recording daily pressure changes. Pressure sensitive chart paper around the drum was fed from a paper reservoir, made from a pipe, and allowed 3–4 days of continuous running. The sensing device in the tunnel was connected via 2 relays to a marker-solenoid (Fig. 3) and the whole system was

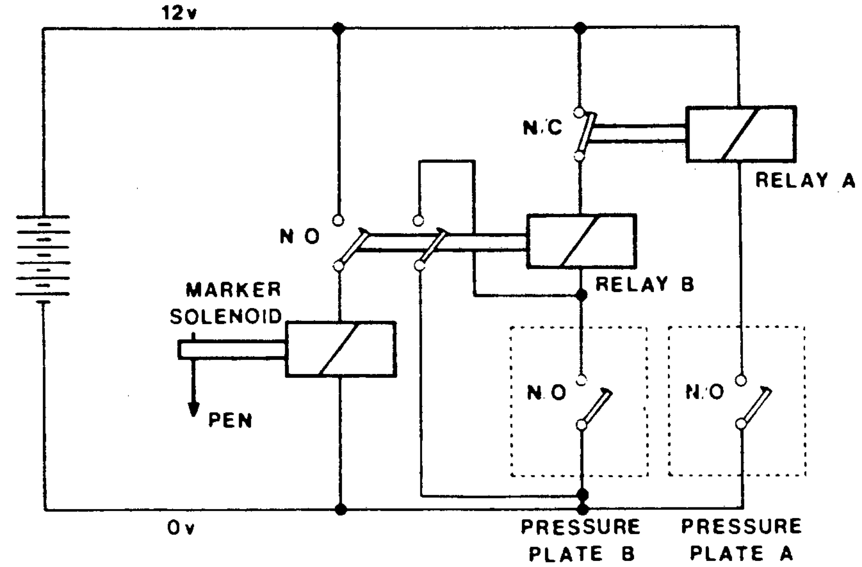

FIGURE 3. Circuit diagram of apparatus for monitoring the nest visits of burrow-nesting birds (N O = switches normally open; N C = switches normally closed).

powered by a 12-volt battery which lasted about 10 days without recharge. A dissecting needle attached to the marker-solenoid was used as a pen on the pressure sensitive paper. A light spring kept the pen depressed so that it made a continuous trace across the paper on the drum. As a bird entered the burrow and walked over both pressure plates, the pen made a mark on the chart and only returned to its original position once the sensor had been reactivated as the bird left the nest.

This automatic monitoring system proved reliable and occasional cleaning of the contacts on the sensor was the only maintenance required. The clockwork chart-drum was very satisfactory and kept the total cost of the recorder and sensor to under $200 (1982 prices). The system obviously has wider application than just tunnel-nesting birds and could be used for recording the passage of any animal which uses a regular pathway.

I wish to thank K. Achleitner for his technical advice. Financial and logistic support was provided by the South African Department of Transport, Antarctic Division.—MICHAEL SCHRAMM, *FitzPatrick Institute, University of Cape Town, Rondebosch, 7700, South Africa.* Present Address: *Zoology Department, University of Transkei, Private Bag X5092, Umtata, Transkei.* Received 16 Apr. 1981; accepted 13 Sept. 1982.