Mineral and energy contributions of petrels (Procellariiformes) killed by cats, to the Marion Island terrestrial ecosystem

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It has been estimated that in the period October 1974-September 1975, the population of 2 100 cats, Felis catus, *on Marion Island had a total energy requirement of $9{,}97 \times 10^8$ kJ. The cats fed principally on small petrels. The mean energy content of bodies of petrels is 25,4 kJ g^{-1} (dry weight). Assuming that bodies of small petrels provided 90 per cent of the cats' energy requirement in the 1974/75 period, then a minimum 35,4 t (dry weight) of petrel bodies must have been consumed. Over the 207 km^2 in which cats occur, the average input to the ecosystem would be 1,7 kg ha^{-1} yr^{-1}. Extrapolation from prey remains indicates that over 400 000 birds of the seven main prey species were killed. As a by-product 7,9 t (dry weight) of feathers, with an energy content of $1{,}7 \times 10^7$ kJ, passed to the ecosystem. The concentrations of selected mineral elements (Ca, Cd, Cu, K, Mg, Mn, N, Na, P, Sr, Zn) in the bodies and feathers of 12 species of petrels known or believed to fall prey to the cats were determined, and the total quantity of mineral elements in the bodies and feathers of the seven main prey species, which form about 96 per cent of the estimated body mass consumed, was calculated. It is forecast that the predation of petrels by cats is reducing the amount of energy and mineral elements contributed by petrels to the island's ecosystem.*

Introduction

Albatrosses and petrels (Procellariiformes) are adapted for life at sea, but have poor agility on land. All species therefore normally avoid breeding in areas containing terrestrial mammalian predators. The smaller petrels are also vulnerable to avian predators and to avoid these they breed under cover, in holes or burrows and only visit land at night. The sub-Antarctic Prince Edward islands, being truly oceanic, lack indigenous mammalian predators and are an important breeding station for procellariiform seabirds. Ten species of small petrels are known to breed on the islands (Williams *et al.* 1979) and a further five species may also do so (Williams & Burger, 1978).

Since the beginning of the 1950s a population of feral cats, *Felis catus*, has become established on Marion Island (46°54′S, 37°45′E). According to Van Aarde (1977), the population of cats on Marion Island in the period October 1974-September 1975 was 2 100 individuals; the estimated annual energy requirement of the cats was $9{,}980 \times 10^8$ kJ; and small petrels formed the bulk of the cats' diet.

Preliminary studies of the role of seabirds as nutrient and energy transporters are being made on Marion Island (Siegfried, 1978). Procellariiform birds feed solely at sea. When a petrel is killed on land by cats the materials and energy contained in the carcass and in the feathers form a net gain to the terrestrial ecosystem.

This paper reports the mass of carcasses of petrels killed by cats to meet the estimated seabird component of the annual energy requirement of the cats at the 1974/75 population level, assesses the mineral element and energy contents of the bodies and feathers of 12 species of petrels, and calculates the amount of energy and selected mineral elements made available to the Marion Island ecosystem from seven species of petrel frequently killed by cats.

Materials and methods

Specimens of the following 12 species of petrels were collected in 1974-1975: Salvin's prion, *Pachyptila vittatta salvini*; fairy prion, *P. turtur*; great-winged petrel, *Pterodroma macroptera*; Kerguelen petrel, *P. brevirostris*; soft-plumaged petrel, *P. mollis*; blue petrel, *Halobaena caerulea*; grey petrel, *Procellaria cinerea*; white-chinned petrel, *P. aequinoctialis*; black-bellied storm petrel, *Fregetta tropica*; grey-backed storm petrel, *Garrodia nereis*; common diving petrel, *Pelecanoides urinatrix*; and South Georgian diving petrel, *P. georgicus*. All specimens were placed in a deep freeze as soon as possible after collection.

Birds were weighed when taken from the deep freeze and plucked. Feather mass was taken as the difference between the mass of the whole bird and that of the plucked carcass. Carcasses were cut into small pieces and then minced. Mince and feathers were then oven-dried at 60 °C until they achieved constant mass. A sample of dried feathers was cut into small pieces and then ground with a ceramic mortar and pestle.

Energy values of dried mince and powdered feathers were obtained using a Gallenkamp ballistic bomb calorimeter. Concentrations of mineral elements were determined by means of a Varian Techtron AA-6 atomic absorption spectrophotometer, using acetylene fuel and flame spectroscopy (Pringle *et al.* 1968), after the organic material had been treated as described by Watling and Watling (1975). The following element concentrations were determined in this way: copper, cadmium, potassium, magnesium, manganese, sodium, strontium, and zinc. Total calcium was determined by EDTA titration using Erichrome Black T indicator (Vogel, 1939). Phosphorus concentrations were determined by stannous chloride procedure (Taras *et al.* 1971), and nitrogen by standard Kjeldahl procedure (Grodzinski *et al.* 1975). In order to obtain a mean value, three determinations were made on each sample. Only one sample each of body mince and of feathers was analysed per species.

Results

Van Aarde (1977) calculated that the energy requirement of the cat population on Marion Island in the period October 1974-September 1975 was $9{,}97 \times 10^8$ kJ. He used several methods to assess the diet of cats on Marion Island, all of which indicated that petrels formed the bulk of the diet. It has been assumed that 90 per cent ($8{,}98 \times 10^8$ kJ) of the energy requirement of cats in the 1974/75 season was met by petrels, and that all the energy was derived from the bodies of the birds and none from their feathers.

Data on the amounts of energy contained in the bodies of 12 species of petrel found on Marion Island are contained in

Appendix 1

Mean dry weight (g) and energy content (kJ) of bodies and feathers of 12 species of petrels on Marion Island.

	Bodies				Feathers			
	dry weight	(*n*)	energy content	(*n*)	dry weight	(*n*)	energy content	(*n*)
Great-winged petrel	168,0 ± 12,3	(4)	23,7 ± 2,0	(3)	45,2 ± 3,3	(3)	21,8	(1)
Kerguelen petrel	135,6 34,3	(3)	26,1 0,8	(3)	29,2 3,5	(3)	27,1	(1)
Soft-plumaged petrel	111,5 30,9	(6)	27,1 1,9	(6)	20,9 1,7	(3)	22,2	(1)
Blue petrel	80,3 7,1	(3)	25,1 1,7	(3)	15,7	(1)	25,1	(1)
Salvin's prion	51,1 10,4	(5)	24,7 2,8	(5)	12,3 0,9	(4)	21,7	(1)
Fairy prion	34,0 5,8	(3)	23,6 1,7	(3)	7,3 0,6	(3)	18,7	(1)
Grey petrel	— —		— —		77,9 10,0	(3)	22,6	(1)
White-chinned petrel	— —		— —		82,2 1,3	(2)	20,1	(1)
Black-bellied storm petrel	18,4 —	(1)	28,7 —	(1)	4,8 0,4	(2)	28,1	(1)
Grey-backed storm petrel	10,6 1,4	(3)	26,6 2,3	(3)	2,7 0,5	(2)	19,1	(1)
Common diving petrel	45,3 3,5	(4)	24,0 1,8	(4)	8,4 0,7	(5)	18,0	(1)
South Georgian diving petrel	39,4 —	(1)	24,8 —	(1)	7,2 —	(1)	20,5	(1)
Mean values			25,4 ± 2,3	(32)			22,1 ± 3,2	(12)

Appendix 2

Concentration (ppm) of selected mineral elements in the bodies of 12 species of petrels on Marion Island.

	Micro-elements					Macro-elements					
	Cu	Cd	Zn	Mn	Sr	Mg	K	Na	Ca	P	N
Great-winged petrel	25,02	18,85	106,45	3,52	147,36	890	6 790	4 930	42 500	14 980	65 480
Kerguelen petrel	10,29	5,00	84,80	2,83	68,63	1 060	5 540	4 750	37 860	15 560	108 530
Soft-plumaged petrel	9,49	1,61	98,55	4,88	33,91	910	5 740	5 730	26 800	8 430	96 400
Salvin's prion	15,36	11,50	108,85	3,88	93,12	1 140	7 640	6 640	24 000	7 890	82 520
Fairy prion	10,98	13,00	108,68	3,51	84,00	1 110	8 070	6 880	51 720	10 000	97 090
Blue petrel	7,96	4,60	71,50	2,57	48,98	700	4 750	2 040	16 070	10 760	126 070
Common diving petrel	9,64	8,32	94,46	3,32	86,31	940	7 200	4 850	58 950	11 860	97 090
South Georgian diving petrel	9,58	19,75	97,54	3,64	103,91	1 080	7 990	5 680	42 920	—	98 120
White-chinned petrel	6,00	16,00	128,00	5,00	83,00	570	4 990	4 100	37 800	21 000	84 060
Grey petrel	4,78	10,25	71,75	2,22	69,49	810	5 240	4 110	15 210	21 500	68 760
Black-bellied storm petrel	15,60	0,01	105,00	2,80	30,09	1 010	—	4 800	28 450	18 050	65 710
Grey-backed storm petrel	17,78	0,01	94,35	4,18	43,93	1 460	1 050	1 050	28 700	15 340	81 760

Appendix 3

Concentration (ppm) of selected mineral elements in the feathers of 11 species of petrels on Marion Island

	Micro-elements					Macro-elements					
	Cu	Cd	Zn	Mn	Sr	Mg	K	Na	Ca	P	N
Great-winged petrel	49,07	0,01	115,85	2,64	9,65	435,6	95,7	1 058	1 155	1 492	107 142
Kerguelen petrel	14,17	0,16	88,24	1,07	17,38	1 069,5	454,5	5 164	1 540	3 166	90 877
Soft-plumaged petrel	14,42	0,27	103,99	4,06	16,15	303,5	367,1	1 318	3 188	2 531	142 971
Salvin's prion	15,41	0,01	110,00	5,15	16,05	523,6	422,3	2 813	850	2 526	121 578
Fairy prion	17,02	0,15	112,55	2,64	9,65	274,4	1 117,9	1 866	1 099	2 805	145 572
Blue petrel	16,64	3,44	364,00	6,00	15,72	752,0	592,5	3 304	4 238	5 285	102 666
Common diving petrel	22,84	0,02	104,06	2,03	16,50	934,3	964,5	5 076	850	1 725	97 742
South Georgian diving petrel	19,07	0,44	111,88	4,71	17,67	373,8	947,3	4 079	8 269	2 496	102 551
Grey petrel	17,00	0,01	90,00	5,00	10,00	660,0	390,0	3 900	850	22 500	140 000
Black-bellied storm petrel	9,88	8,88	92,50	4,05	55,50	922,4	6 234,1	5 401	1 160	37 500	159 905
Grey-backed storm petrel	11,06	7,92	73,92	9,31	89,06	948,8	6 519,2	4 209	—	—	—

Appendix 1. Employing a mean energy content of 25,4 kJ g^{-1} (dry weight) for all petrel species, then a total of 35 360 kg (dry weight) of petrel bodies is necessary to meet 90 per cent of the energy requirements of the cats. Van Aarde (1977) found that cat density differed in the coastal lowlands (areas below 100 m above sea level) and the interior (100-450 m a.s.l.). Using Van Aarde's zonal densities, the input of dry material resulting from cat-killed petrels was 2,84 kg ha^{-1} and 1,09 kg ha^{-1} in the coastal and interior zones, respectively.

The mineral element content of petrel bodies and feathers, and the mass of feathers per bird, have a greater inter-specific variation than does body energy content (Appendices 1-3). In order to calculate the quantities of those items which enter the island's ecosystem it is necessary to estimate the number of birds of each species which are killed by cats. The best available information comes from analysis of the surface accumulations of bones and feathers of birds eaten by cats. Van Aarde (1977) collected and identified remains representing the bodies of 1 124 birds killed by cats. Small petrels formed 99 per cent of these bodies. The estimated total energy content of the (1 124) petrel bodies is $2,46 \times 10^6$ kJ (Table 1). The total number of birds killed in order to meet the 1974/75 energy intake that cats obtained from petrels can be estimated by applying the percentage energy contribution of each species to the total energy requirement. According to this method, the total number of petrels killed in 1975 was at least 410 430 (Table 1).

Using the numbers of each species killed, calculated in Table 1, then the total mass of bodies of the seven main prey species killed by cats was 39 990 kg (dry weight) (Table 2). As a by-product of the predation by cats, at least 7 908 kg (dry weight) of feathers (Table 2) enter the ecosystem. At a mean energy content of 22,1 kJ g^{-1} (dry weight), these feathers contained $1,7 \times 10^7$ kJ.

The mass of mineral elements contained in the bodies and feathers of cat-killed individuals of the same seven species is given in Table 3.

Discussion

The aim of this paper has been threefold: to provide basic data on the mass, energy and mineral element content of petrel bodies and feathers; to assess the total mass of petrels which the cats needed to kill to obtain 90 per cent of their 1974/75 energy requirement; to attempt to delimit the species concerned and their respective contributions to the ecosystem.

Data on mass, energy and mineral element contents of petrels is useful not only to the present study, but also for other studies. On Marion Island such studies include the

Table 1

Number of birds of eight species needed to meet the energy requirement of cats on Marion Island in 1974/75.

	Occurrence in 1 124 prey items[1]		Mean energy content of individual bodies[2]	Energy in 1 124 prey items		Energy contributed to 90% of cats' total energy requirement[4]	No. of individuals killed to meet energy requirement
	%	(n)		amount	%		
			kJ	kJ		kJ	
Salvin's prion	61,03	(686)	1 273	873 400	35,5	318 842 000	250 430
Kerguelen petrel	12,90	(145)	3 552	515 040	20,9	187 713 000	52 850
Soft-plumaged petrel	9,40	(105)	3 130	328 660	13,3	119 454 000	38 160
Great-winged petrel	10,05	(113)	4 002	452 300	18,4	165 259 000	41 290
Blue petrel	4,00	(45)	2 016	90 740	3,7	33 231 000	16 480
Diving petrel spp.	0,54	(6)	1 089	6 540	0,3	2 694 000	2 470
White-chinned petrel	1,06	(12)	13 262	159 150	6,5	58 380 000	4 400
Lesser sheathbill	1,06	(12)	2 889[3]	34 670	1,4	12 574 000	4 350

[1]Van Aarde (1977). [2]Appendix 1. [3]Burger, A. (pers. comm.). [4]898 146 810 kJ.

Table 2

Dry mass of bodies and feathers of petrels of seven species killed by cats on Marion Island[1].

	Estimated no. killed annually	Body mass		Feather mass	
		mean/individual	total	mean/individual	total
		g	kg	g	kg
Salvin's prion	250 430	54,6 (8)	13 673	12,2 (4)	3 055
Kerguelen petrel	52 850	123,0 (3)	6 500	29,2 (3)	1 543
Soft-plumaged petrel	38 160	111,5 (6)	4 255	20,9 (3)	798
Great-winged petrel	41 290	168,0 (4)	6 936	45,3 (3)	1 870
Blue petrel	16 480	77,3 (4)	1 274	15,7 (1)	259
Diving petrel spp.	2 470	45,0 (5)	111	8,3 (5)	21
White-chinned petrel	4 400	281,7 (2)	1 240	82,2 (2)	362
	406 080		33 989		7 908

[1]Data refers to 1974/75 only.

Table 3

Mass[1] of selected elements contained in the bodies and feathers of 406 100 petrels killed by cats on Marion Island.

	Bodies	Feathers[2]	Total
Macro-elements (kg)			
Nitrogen	2 974	854,7	3 829
Calcium	390	295,0	685
Phosphorus	1 057	246,0	1 303
Sodium	188	20,6	209
Potassium	255	2,6	258
Magnesium	34	4,5	39
Micro-elements (g)			
Copper	509	1 002,4	1 511
Cadmium	354	0,1	354
Zinc	3 457	867,5	4 325
Manganese	126	27,2	153
Strontium	3 061	42,9	3 104

[1]Calculated from data in Table 2, and Appendices 2 & 3.
[2]Excludes element content of white-chinned petrel feathers.

inter-relationships between petrels and the island's avian predators, and assessments of future changes in cat and petrel populations in relation to the functioning of the island's ecosystem.

The assessment of the species of petrels killed by cats has a number of shortcomings. It relies on Van Aarde's (1977) collection of prey remains. Such remains are easily collected and provide a large sample size but one that is not necessarily truly representative of the range of prey killed. The remains consist mainly of pectoral girdles and attached wings. Most cats will have difficulty in breaking and ingesting the bones from the larger species of petrels but the bodies of smaller petrels may be eaten entirely. Thus, although no storm petrels were found among the 1 124 birds identified, they occurred in a limited sample of cat stomach contents (Van Aarde, 1977). Chicks may also be eaten entirely. The size of the predator may also affect the composition of prey remains: small cats and kittens may leave more remains and remains of smaller petrel species, than large adult cats. An obvious error is manifested by the proportion of lesser sheathbills, *Chionis minor*, in the prey remains (Table 1) which indicates that cats should have killed 4 350 sheathbills in 1974/75. This exceeds the total population of sheathbills on Marion Island, that is, 3 157 (Williams *et al.* 1975).

The species composition of cat-killed petrels in 1974/75 cannot be considered representative of the prey of cats throughout the period that they have been on Marion Island. Relatively more vulnerable prey species, notably storm petrels and diving petrels, which can be detected and readily caught by humans when moving on the ground at night (personal observation), may have declined in numbers, and therefore in importance, as cat prey well before Van Aarde's (1977) study. In the period before and immediately after feral cats became established on Marion Island, diving petrels, *P. urinatrix*, were widely distributed and common (Crawford, 1952; Rand, 1954): by 1965/66 Van Zinderen Bakker Jr. (1971) could find no nests. Original population levels of all petrel species on the island are also likely to have been reduced. Although immigration from the adjacent and cat-free Prince Edward Island may occur, it seems unlikely that the numbers of immigrants could balance the numbers of birds killed by cats in the 1970s.

Despite numerous qualifications, the estimates made here are thought to be a valid indication of the potential contribution of cat-killed petrels to the Marion Island ecosystem. Most of the carcasses and the feathers of the petrels are ingested by cats. Materials derived from the petrel bodies and feathers subsequently pass into the ecosystem via the faeces and urine of the cats and through consumption or decomposition of cat carcasses. The surface remains of petrels — pectoral girdles and primary feathers — decompose slowly *in situ*.

Much of the avian material contributing to the Marion Island ecosystem is concentrated along the coast (Siegfried *et al.* 1978; Burger *et al.* 1978; Williams & Berruti, 1979; Williams *et al.* 1978). The energy and nutrients derived from cat-killed petrels have a potentially enhanced importance, because they occur over inland areas which otherwise receive relatively little avian material. This input must be weighed against the potential input of the petrel population, were it not affected by cat predation. Breeding petrels contribute egg shells, the contents of broken or failed eggs, and the carcasses of adults and chicks which die 'naturally'. Most importantly they contribute guano. In other species studied, the annual input of guano from a population exceeds the combined mass of all other avian inputs from the same species (Siegfried *et al.* in preparation). Such inputs of avian material are sustained from year to year. The guano especially is widely distributed over the island. It seems probable that cat predation has already severely reduced the numbers of some, and probably all, the main petrel prey species. Such reduction in populations can only have resulted in a lower overall input of avian material to the Marion Island ecosystem, and the lowered inputs are not compensated by the energy and materials contributed by the cat-killed carcasses.

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References

Burger, A.E., Lindeboom, H.J. & Williams, A.J. Mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.*, **8**, 58-69. 1978.

Crawford, A.B. The birds of Marion Island, South Indian Ocean. *Emu*, **52**, 73-85, 1952.

Grodzinski, W., Klekowski, R.Z. & Duncan, A. *Methods for Ecological Energetics*. I.B.P. Handbook, No. 24. Oxford, Blackwell, 1975.

Pringle, B.H., Hissong, D.E., Katz, B. & Mulawka, S. Trace metal accumulation by estuarine molluscs. *J. Sanit. Engng. Div. Am. Soc. Civ. Engn.*, **94**, 455-475, 1968.

Rand, R.W. Notes on the birds of Marion Island. *Ibis*, **96**, 173-206, 1954.

Siegfried, W.R. Ornithological research at the Prince Edward Islands: a review of progress. *S. Afr. J. Antarct. Res.*, **8**, 29-32, 1978.

Siegfried, W.R., Williams, A.J., Burger, A.E. & Berruti, A. Mineral and energy contributions of eggs of selected species of seabirds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.*, **8**, 74-86, 1978.

Taras, M.J., Greenberg, A.E., Hoak, R.D. & Rand M.C. *Standard Methods for the Examination of Water and Waste Water*. Washington, D.C., American Public Health Ass., 1971.

Van Aarde, R.J. *Voeding, habitatsvoorkeur en voortplanting van die Wildehuiskat (Felis catus Linnaeus, 1758) op Marioneiland.* MSc thesis, University of Pretoria, 1977.

Van Zinderen Bakker, E.M. Jr. Comparative avian ecology. In *Marion and Prince Edward Islands*, edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom, & R.A. Dyer, 161-172. Cape Town, A.A. Balkema, 1971.

Vogel, A.I. *A Textbook of Quantitative Inorganic Analysis.* London, Longmans, 1939.

Watling, H.R. & Watling, R.J. Preliminary preparation of molluscs for trace metal analysis. *FIS Special Rep.*, **76**, CSIR, Pretoria, 1975.

Williams, A.J. & Burger, A.E. Notes on non-breeding seabirds at the Prince Edward islands. *Cormorant*, **5**, 11-14, 1978.

Williams, A.J., Siegfried, W.R., Burger, A.E. & Berruti, A. The Prince Edward islands: a sanctuary for seabirds in the southern oceans. *Biol. Conserv.*, **15**, 59-71, 1979.

Williams, A.J., & Berruti, A. Mineral and energy contributions of feathers of penguins, gulls and cormorants to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.*, **8**, 70-73, 1978.

Williams, A.J., Burger, A.E. & Berruti, A. Mineral and energy contributions of carcasses of selected species of seabirds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.*, **8**, 52-58, 1978.

Williams, A.J., Burger, A.E., Berruti, A. & Siegfried, W.R. Ornithological research on Marion Island, 1974-75. *S. Afr. J. Antarct. Res.*, **5**, 48-50, 1975.

Mineral and energy contributions of carcasses of selected species of seabirds to the Marion Island terrestrial ecosystem

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Sub-Antarctic Marion Island annually receives an estimated 125,9 t (dry weight) of carcasses belonging to 12 species of seabirds. These carcasses are initially deposited within an area of 128 km², almost all of which is coastal lowland. Mortality of adult birds whilst breeding is negligible. Adult penguins which die during their annual moult-fast contribute some 46,9 t (dry weight) of avian material to the ecosystem. More than 165 000 chicks of the 12 species die each year before fledging. They contribute 79,7 t (dry weight) of material to the ecosystem, penguin chicks forming 99 per cent of this. An area of 4 km² receives 77 per cent of the penguin chick carcass material. Over the remaining 124 km² area in which chicks die, the average annual input of chick carcass material is 1,5 kg ha⁻¹. The concentrations of selected mineral elements (Ca, Cd, Cu, K, Mg, Mn, N, Na, P, Sr, Zn) in the bodies of penguin chicks were determined, and the total mass of mineral elements thus contributed to the ecosystem calculated. The energy contributed by penguin chick carcasses alone amounts to 1,57 × 10⁹ kJ per annum.

Introduction

In many terrestrial ecosystems birds are important links in trophic webs (Weiner & Glowacinski, 1975). Seabirds feed primarily or solely at sea. Any avian products — eggs, guano, feathers and carcasses — which seabirds deposit on land whilst breeding or moulting ashore, represent a net transfer of material to the terrestrial ecosystem. Preliminary studies of the role of seabirds as mineral element and energy transporters are being made on sub-Antarctic Marion Island (46°54'S, 37°45'E) in the southern Indian Ocean (Siegfried, 1978).

This paper reports the mass of carcasses of adults and chicks of 12 species of surface-nesting seabirds which breed on Marion Island, and the amounts of energy and selected mineral elements contained in the carcasses of chicks of four species of penguins. The species concerned are: king penguin, *Aptenodytes patagonicus*; gentoo penguin, *Pygoscelis papua*; macaroni penguin, *Eudyptes chrysolophus*; rockhopper penguin, *E. chrysocome*; wandering albatross, *Diomedea exulans*; sooty albatross, *Phoebetria fusca*; light-mantled sooty albatross, *P. palpebrata*; northern giant petrel, *Macronectes halli*; southern giant petrel, *M. giganteus*; imperial cormorant, *Phalacrocorax albiventer*; sub-Antarctic skua, *Catharacta antarctica*; and kelp gull, *Larus dominicanus*.

Materials and methods

Studies of the breeding biology of sub-populations of each species on Marion Island provided data on growth in chick mass, chick mortality, and phenology (Berruti, 1979; Williams, Burger & Berruti, unpublished data). Most of the species are synchronised breeders and for these, seasonal calculations were based on the date by which 50 per cent of the chicks had hatched. Gentoo and king penguins are asynchronous breeders and allowance has been made for this in the calculations. Chick mortality in the king penguin could not be studied closely on Marion Island, nor are data on this topic available in the literature. We have assumed (from Williams & Burger, unpublished data) that 10 per cent of king penguin chicks die between hatching and the end of May at a mean mass of 0,5 kg; a further 30 per cent die during the period June-September at a mean mass of 3 kg; and that a further 5 per cent die between October and January at a mean mass of 5 kg. Mortality of adult penguins during moult was estimated from field observations. The mass of adult penguins which starve to death during moult was assumed to be the same as the minimal individual mass for the species as reported in the literature.

To facilitate the plotting of the distribution of avian