

## APPENDIX 4

Average concentrations (ppm) of mineral elements in the combined contents (excluding shell) of eggs of 12 species of seabirds on Marion Island. All values represent an average of three samples and each sample consisted of a composite of at least three eggs of each species except the light-mantled sooty albatross for which only one egg was available.

	Micro elements					Macro elements					
	Cu	Cd	Zn	Mn	Sr	Mg	K	Na	Ca	P	N
King penguin	3,44	0,74	39,80	0,59	14,26	511	6 145	10 703	4 047	7 680	75 135
Gentoo penguin	1,40	0,01	20,70	0,90	0,38	495	6 700	6 300	3 766	8 240	86 716
Macaroni penguin	2,88	0,48	45,35	1,44	18,23	441	5 758	9 724	4 447	4 980	81 060
Rockhopper penguin	1,70	0,01	31,00	1,00	0,55	297	6 100	5 300	4 122	8 060	74 935
Wandering albatross	4,23	0,71	65,85	1,13	13,64	409	4 186	5 174	4 260	9 620	73 428
Sooty albatross	2,40	0,01	27,20	0,50	0,70	123	5 300	6 300	3 861	8 600	80 638
Light-mantled sooty albatross	4,55	0,01	67,17	0,22	0,20	189	4 928	6 181	4 545	9 498	79 460
Northern giant petrel	5,75	0,01	51,98	2,38	11,90	91	5 516	7 040	2 416	6 740	85 885
Southern giant petrel	3,70	0,01	34,70	1,10	0,45	140	4 000	4 000	4 858	6 080	83 083
Imperial cormorant	4,60	0,01	38,10	1,00	0,50	159	2 900	6 000	2 299	4 620	100 000
Sub-Antarctic skua	2,70	0,01	47,00	0,70	0,27	115	4 800	4 600	5 550	5 380	92 465
Kelp gull	1,60	0,01	20,60	0,60	0,40	56	6 000	5 900	3 854	10 180	89 500

## Terrestrial invertebrates: a food resource for birds at Marion Island

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*The density, biomass and energy content of the terrestrial macro-invertebrates (Oligochaeta, Mollusca, Araneida, Lepidoptera and Coleoptera) were measured in 19 vegetation types at Marion Island in the sub-Antarctic. The mean annual density and dried biomass of the combined samples was 1 980*

*organisms m<sup>-2</sup> and 16,86 g m<sup>-2</sup> respectively (weighted in proportion to the percentage area of each vegetation type). Earthworms comprised 86,8 per cent of the biomass, earthworm cocoons 2,2 per cent, Lepidoptera larvae 3,7 per cent, Lepidoptera adults and pupae 0,1 per cent, weevil larvae and*

pupae 2.5 per cent, weevil adults 0.7 per cent, spiders 0.8 per cent, snails 1.9 per cent, and slugs 1.3 per cent. There were no marked seasonal trends in the monthly variations of biomass, density, mean item mass and species composition of the combined samples, nor in the biomass within each vegetation complex. Invertebrate biomass differed greatly between vegetation types, with most species showing clear habitat preferences. The greatest biomass was found in vegetation communities influenced by manuring of birds and seals (particularly *Cotula plumosa* and *Callitriche antarctica* communities) and certain mire communities. Within the 100 ha study area, terrestrial invertebrates supported 27.5 per cent of the resident sheathbills, *Chionis minor*, and 12.9 per cent of the kelp gulls, *Larus dominicanus*. The standing crop of macro-invertebrates in this area was about 16.86 t (dried mass), of which the birds ate about 8 per cent annually. Terrestrial invertebrates are particularly important to the birds during winter when other, more favoured food, is less available.

## Introduction

During the first biological expedition to Marion Island (Van Zinderen Bakker Sr., *et al.* 1971), biologists noted that flocks of sheathbills, *Chionis minor*, and kelp gulls *Larus dominicanus*, sometimes foraged extensively for invertebrates on inland vegetated areas. This phenomenon was recognised as a potentially important pathway in the energy and mineral systems of the island (Van Zinderen Bakker Sr., 1971), since the densities of invertebrates, particularly earthworms and caterpillars, were found to be high in some areas (Huntley, 1971). In addition to preying on the invertebrates, the foraging birds uproot many plants in their search efforts. This may subsequently cause erosion or retardation of vegetation succession (Huntley, 1971).

There are no birds on Marion Island which feed exclusively on terrestrial animals or plants. The sheathbill is the only species breeding on the island which is not a seabird. Sheathbills and, to a lesser extent, kelp gulls are primarily scavengers at penguin and seal colonies, taking carcasses, eggs, chicks, seal placentae, krill and fish stolen from penguins, and guano (Williams *et al.* 1975). The gulls forage extensively for marine invertebrates in the offshore kelp-beds and in the intertidal zone, and may kill small petrels on occasions. Sheathbills also eat considerable quantities of intertidal algae and invertebrates. Both species are thus generalist feeders. Their exploitation of terrestrial invertebrates has apparently evolved in the absence of competition from other vertebrates for these resources on Marion Island. Kerguelen terns, *Sterna virgata*, may also eat terrestrial invertebrates (Berruti & Harris, 1976), but since the population of this species at Marion Island is less than 30 pairs (Berruti & Harris, 1976) and this foraging behaviour is infrequent, the impact of tern predation on the invertebrates is negligible.

This paper reports on the density, biomass and energy content of selected terrestrial invertebrates, and the foraging behaviour of sheathbills and kelp gulls in a study area on the eastern coastal plain of Marion Island. The terrestrial invertebrates studied were earthworms (*Microcolex kerguelarum* Grube), flightless lepidopterans (*Pringleaphaga marioni* Viette and *Embryonopsis halticella* Eaton), coleopteran weevils (Curculionidae, mostly *Ectemorrhinus similis* Waterhouse), spiders (*Myro* spp. Cambridge), snails (*Notodiscus hookeri* Reeve) and slugs (an unidentified species). These larger invertebrates, or macro-fauna (Odum, 1971),

comprise the bulk of the terrestrial invertebrate biomass on Marion Island. The meso-fauna, including rove-beetles (Coleoptera, Staphylinidae), small flies (Diptera), aphids (Hemiptera), Collembolla and acarid mites, were not considered, although these sometimes occurred in large numbers (Burger, 1979). Sheathbills and gulls were not seen to eat these small organisms in appreciable quantities and they were not found in the stomach contents of the birds.

## Methods

Terrestrial invertebrates and the foraging activities of sheathbills and kelp gulls were studied between April 1976 and May 1977 in a 100 ha study area, 200 m wide, along 5.0 km of coastline between Prion Valley and East Cape. The birds in the study area were counted about every ten days and their foraging activities noted at the same time. There were, on average, 198 sheathbills and 66 kelp gulls resident in the study area. These birds very seldom foraged more than 200 m from the shore. The relative areas of 19 vegetation types within the study area were determined along 68 transects, each 200 paces long and perpendicular to the shoreline, spaced regularly throughout the study area. After 10 paces along a transect, the vegetation within a 10 × 10 m area was assigned to one of 19 vegetation types. The percentage area of each vegetation type was calculated from the aggregates.

Sampling for terrestrial invertebrates occurred at randomly selected sites in each vegetation type. Generally, the samples were taken from the same patch of each vegetation type in each month. Five samples were collected from each vegetation type in the second half of each month. Each sample consisted of a core (diameter 8 cm), covering 50.5 cm<sup>2</sup> of substrate and about 10 cm deep. Virtually all the animals were found in the upper 4 cm of substrate. A relatively small core was deliberately chosen to investigate the spatial variability of invertebrate abundance and biomass within sampling areas. Cores included live plants, litter, peat and soil. In the laboratory the cores were sorted through by hand and all the visible macro-invertebrates removed, counted, dried in a convection oven for 48 hours at 60-70 °C and weighed. The samples were stored in a deep freeze until the energy contents were determined. The spiders, earthworm cocoons and weevil adults were analysed using a Phillipson microbomb calorimeter and the remaining samples using a Gallenkamp ballistic bomb calorimeter.

Analysis of the data was facilitated by UNIVAC Statjob computer programs provided by the Madison Academic Computing Centre, Wisconsin. When means of pooled data from all 19 vegetation types were calculated, the variables were weighted in proportion to the percentage area of each vegetation type in the study area.

## Vegetation types

The vegetation was classified according to information supplied by N.J.M. Gremmen (in litt., 1976). The classification provided by Huntley (1971) was found to be incomplete and too generalised, although his description of the physiognomy and edaphic conditions, together with those of Smith (1976a) should be referred to for further details. The following vegetation types were recognised, being arbitrarily numbered for reference within this paper (Plate 1). The list does not include all possible vegetation types on Marion Island, but includes those common on the eastern coastal plain. Figures in parentheses refer to the relative area (percentage) of each vegetation type within 200 m of the shore in the study area.

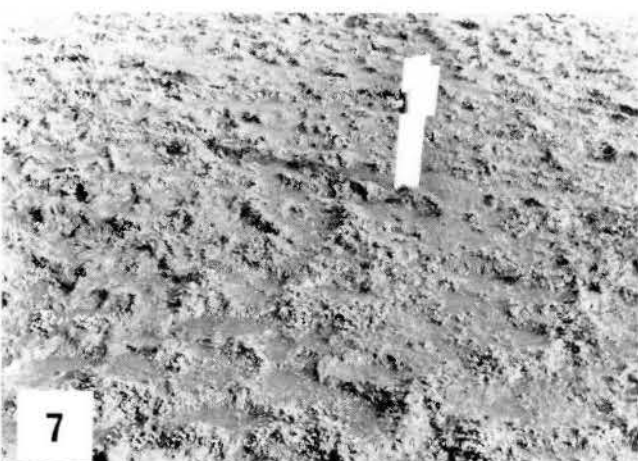
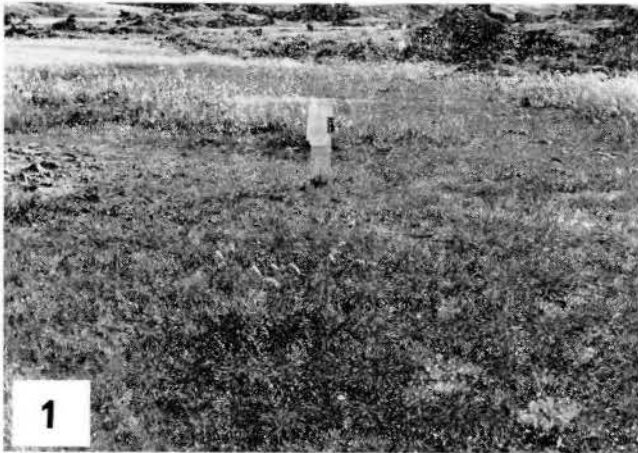


Plate 1. Examples of the 19 vegetation communities where terrestrial invertebrates were studied at Marion Island. The numbers refer to the numbering system used in the text. The marker pole has a width of 10 cm.

#### Mires and bogs

Most abundant on level areas, mires and bogs cover large tracts of the coastal plain. They all have soft, peaty substrates, short vegetation with the water table at or slightly below the surface.

1) *Juncus scheucherooides* bog, (4 per cent of the study area), which has a sparse plant cover of *Juncus scheucherooides* and the grass, *Agrostis magellanica*.

Mire types 2-6 have well-developed, characteristic bryophyte layers with *Agrostis magellanica* invariably dominant in the herb layer. These types could be included in Huntley's (1971) types four and five.

2) *Drepanocladus uncinatus*-*Agrostis magellanica* mire (4 per cent).

3) *Blepharidophyllum densifolium*-*Agrostis magellanica* mire (5 per cent), which is frequently waterlogged.

4) *Clasmatocolea humilis*-*Agrostis magellanica* mire (6 per cent), which is similar in appearance and often on adjacent, slightly drier areas to type three. *Ranunculus biternatus* is often present.

5) *Jamesoniella colorata*-*Agrostis magellanica* mire (3 per cent), which occurs in less waterlogged areas and has a well developed herb layer.

6) Mixed species mire (17 per cent), which has a well-developed herb layer with several species of bryophytes present. This mire usually occurs on slightly raised ground which is possibly better drained than the other mires.

7) Degenerated bog (2 per cent). Eroded and sparsely vegetated, peaty bogs with *Agrostis magellanica* and occasionally *Ranunculus biternatus* present.

8) *Uncinia diki*-*Ptychomnion ringianum* mire (11 per cent). Characterised by relatively dense vegetation dominated by the sedge, *Uncinia diki*, and *Ptychomnion ringianum* moss, with *Agrostis magellanica* present.

#### Slope communities

Due to the hummocky nature of the coastal lowlands on Marion Island, there are many small areas of slopes, characterised by well drained soils and fairly tall vegetation (Smith, 1976a).

9) *Blechnum penna-marina* fernbrake (7 per cent). A densely vegetated community of ferns, equivalent to Huntley's (1971) type nine.

10) *Acaena magellanica* herbfield (6 per cent). A densely vegetated community which is equivalent to Huntley's (1971) type eight.

11) *Agrostis bergiana* grass community (2 per cent), which occurs on grey lava slopes and often along the banks of streams.

#### Saltspray communities

These vegetation communities occur where much salt spray is blown inland near the shore. Bryophytes are either absent or sparse.

12) *Tillaea moschata* community (1 per cent), which is a compact mat of *Tillaea moschata*. This is equivalent to Huntley's (1971) type one.

13) *Cotula plumosa*-*Tillaea moschata* community (2 per cent), which is also mat-like and has these two plant species co-dominant.

14) *Azorello selago*-mixed species community (5 per cent), which is characterised by the cushion plant, *Azorello selago*, with *Tillaea moschata*, *Cotula plumosa*, *Poa cookii* and other angiosperms present.

#### Biotically influenced communities

These communities owe their physiognomic and floristic characters to manuring and other influences of birds and seals (Huntley, 1971). These communities generally have taller, more luxuriant plants than in the other nutrient-poor communities.

15) *Callitriche antarctica* community (3 per cent), which occurs on revegetated seal wallows and other highly manured sites. *Poa cookii* grass is usually present.

16) *Poa cookii* tussock grassland (9 per cent), which commonly occurs on slopes bordering penguin colonies and where burrowing petrels nest.

17) *Clasmatocolea vermicularis*-*Marchantia berteroana* mire (3 per cent), which has a well developed bryophyte layer with a sparse herb layer of *Agrostis magellanica*, *Cotula plumosa*, *Poa cookii* and other species.

18) *Cotula plumosa* community (9 per cent), which almost invariably occurs at the borders of penguin colonies and seal wallows. The growth form of *Cotula plumosa* in this community is more luxuriant than in type 13, and *Tillaea moschata* is generally absent.

#### Lowland fjaldmark community

19) Lowland *Azorello selago*-*Andraea* spp. fjaldmark community (1 per cent), which has sparse vegetation cover and little soil and occurs on windswept, rocky hilltops on the coastal plain.

#### Density and biomass of invertebrates

Earthworms were by far the most common invertebrates in the samples, comprising 68,4 per cent of all the organisms and 86,8 per cent of the dried biomass (Table 1). Earthworm cocoons were common, but contributed only 2,2 per cent of the dried biomass.

All the Lepidoptera adults and pupae and almost all of the larvae encountered were *Pringleaphaga marioni*. Some of the smaller larvae may, however, have been *Embryonopsis haiticella* but these probably contribute very little to the biomass. Although Lepidoptera adults were seldom found, the larvae contributed 3,7 per cent of the dried biomass (Table 1). The paucity of adults is partially a sampling error, since adults of both species were caught readily by other means (Burger, 1979). The very low number of adults relative to larvae was, however, not entirely unexpected, since *Pringleaphaga kerguelensis* at Kerguelen, which may be conspecific with *P. marioni* (Vari, 1971), has a larval stage lasting several years while the adults live for only about three weeks (Paulian, 1953). The life-histories of Lepidoptera on Marion Island are still unknown (Vari, 1971).

Weevil larvae and pupae were also more abundant, with a greater biomass than the adults. The life-histories of these beetles on Marion Island are still not known, but at Heard Island weevil larvae are present for far longer periods than adults (Brown, 1964). Spiders were surprisingly common but contributed little to the total invertebrate biomass (Table 1). These data do not support an earlier statement that the density of spiders on Marion Island is commonly between three and ten times that of beetles, and several hundred times that of the flightless Lepidoptera (Smith, 1977).

Slugs were relatively uncommon, yet, because of their bulk,





contributed disproportionately to the total invertebrate biomass (Table 1).

The weighted mean annual density and biomass of all the invertebrates considered was 1 980 organisms  $m^{-2}$  and 16,86  $g m^{-2}$  (dried mass) respectively (Tables 1 and 3). The average fresh mass of the invertebrates was six times their dried mass. The mean fresh biomass of all the invertebrates considered would thus be 101  $g m^{-2}$ . The mean standing crop of macro-invertebrates within the 100 ha study area was thus 1 980 million organisms or 16,86 t (dried mass).

The invertebrates studied were all present throughout the year, and occurred in similar proportions in all months (Table 2). The monthly fluctuations in the combined densities and biomass of invertebrates were irregular, with no clear seasonal pattern being apparent (Fig. 1). There were slightly fewer

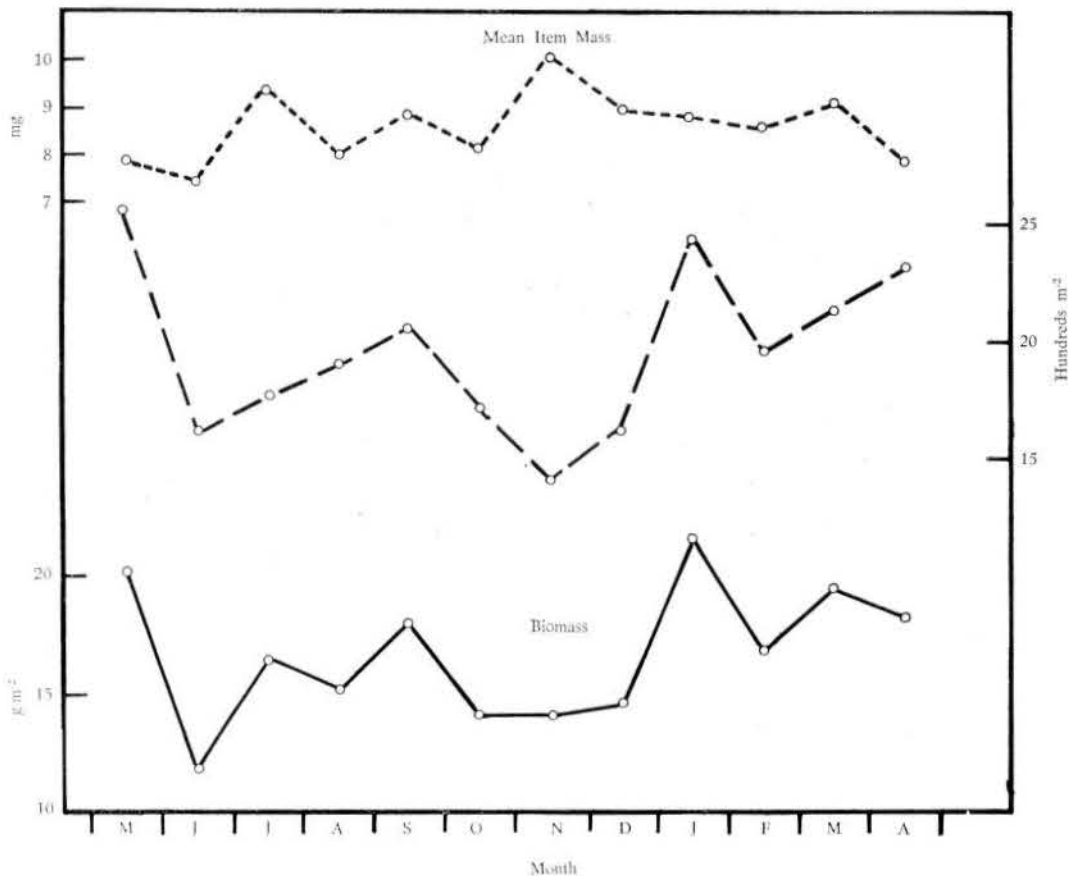


Fig. 1. Weighted monthly means of total biomass, density and mean item mass of terrestrial macro-invertebrates in 19 vegetation types at Marion Island.

Table 1

Mean annual density (no. m<sup>-2</sup>), dried biomass (g m<sup>-2</sup>) and mean individual mass (mg) of terrestrial invertebrates from 1140 cores in 19 vegetation types at Marion Island.

	Density				Biomass				Mean individual mass
	Weighted mean	Max.	CV <sup>1</sup> (%)	% of total numbers	Weighted mean	Max.	CV <sup>1</sup> (%)	% of total biomass	
Earthworms	1354	29800	154	68,4	14,63	421,00	182	86,8	10,8
Earthworm cocoons	356	12600	311	18,0	0,37	14,00	319	2,2	1,0
Lepidoptera larvae	46	800	237	2,3	0,62	26,80	327	3,7	13,5
Lepidoptera adults & pupae	1	200	1507	0,1	0,02	7,37	1600	0,1	20,0
Weevil larvae & pupae	106	3400	202	5,4	0,42	15,00	222	2,5	4,0
Weevil adults	25	800	360	1,3	0,12	4,20	374	0,7	4,8
Spiders	41	800	316	2,1	0,14	3,40	347	0,8	3,4
Snails	33	2800	711	1,7	0,32	31,00	712	1,9	9,7
Slugs	18	1600	444	0,9	0,22	13,00	436	1,3	12,2
Total	1980	42800	146	100,0	16,86	436,40	162	100,0	

<sup>1</sup>Co-efficient of Variation (100 × standard deviation/mean).

Table 2

Monthly percentage composition (by total dried mass) of terrestrial invertebrates in 19 vegetation types at Marion Island. Data from 95 cores per month.

Month	Earthworms	Earthworm cocoons	Lepidoptera larvae	Lepidoptera adults & pupae	Weevil larvae & pupae	Weevil adults	Spiders	Snails	Slugs
May	84	4	4	0,5	2	0,2	1	1	3
Jun.	73	3	9	0,4	6	2	1	3	3
Jul.	84	2	7	0	2	0,2	1	1	4
Aug.	85	3	4	0,4	3	1	0,4	0,5	2
Sep.	85	2	6	0	3	0,4	0,4	0,2	2
Oct.	87	3	3	0	3	0,4	1	2	2
Nov.	89	1	4	0	2	1	1	1	1
Dec.	86	1	5	0	4	1	1	1	1
Jan.	88	2	4	0	3	1	0,3	1	2
Feb.	87	3	4	0	2	1	1	1	1
Mar.	86	2	4	0	3	1	1	2	2
Apr.	82	3	4	0,3	3	2	1	1	3

organisms present, with slightly lower biomass in some winter months (June, July and August) and in early summer (October, November and December). The mean density and biomass peaked in late summer and early winter. The mean mass per item remained relatively constant all year (Fig. 1).

Invertebrate biomass differed greatly between the 19 vegetation types (Table 3). Vegetation types 15-18, which were influenced by manuring and other actions of birds and seals, supported the greatest densities and biomasses of invertebrates. *Cotula plumosa* communities (type 18) and *Callitriche antarctica* communities (type 15) had the most abundant macro-invertebrate fauna. Vegetation growth is taller and more productive in areas where vertebrate excreta fall (Huntley, 1971; Smith, 1976b), providing more varied microhabitats and probably greater food abundance for invertebrates.

The fjaeldmark vegetation (type 19) had low densities and biomass of invertebrate fauna, probably a reflection of the barren, rocky nature of the habitat.

Saltspray vegetation communities (types 12, 13 and 14) supported average to low populations of invertebrates. The saline nature of the substrate and the compact, mat-like structure of the vegetation, particularly in *Tillaea moschata* communities (type 12), appears to be unsuitable for the invertebrates considered here.

Vegetation communities on slopes (types 9, 10 and 11) supported moderate to low invertebrate populations. The *Blechnum penna-marina* fernbrake (type 9) was particularly impoverished, which is perhaps surprising, since the vegetation is relatively tall and apparently productive (Smith, 1976a). Invertebrate densities and biomasses varied considerably within mire communities. Some mires (types 1, 2, 4, 6 and 8) had relatively high biomasses and densities of invertebrates, while these were low in other mires. Several mires appeared very similar in structure (e.g. types 2, 3 and 4, Plate 1) yet differed greatly in the invertebrate populations they supported. A more detailed study of the chemical and physical factors affecting invertebrate distribution, particularly within mires, is needed.

Monthly changes in the invertebrate biomass within each vegetation complex showed no clear seasonal trends (Fig. 2). The biotically influenced vegetation communities supported the greatest invertebrate biomass in all months.

Earthworms occurred in every vegetation type which was sampled (Table 4) and had their greatest biomass in the biotically influenced vegetation types and in certain mires (types 1, 2, 4, 6 and 8). Their cocoons were similarly distributed.

Lepidoptera larvae were most abundant in *Drepanocladus uncinatus*-*Agrostis magellanica* mires (type 2) and in the

**Table 3**

Annual mean density and dried biomass of terrestrial invertebrates in 19 vegetation types at Marion Island. Data from 60 cores per vegetation type.

Vegetation type	Density (animals m <sup>-2</sup> )			Biomass (g m <sup>-2</sup> )			
	Mean	S.D. <sup>1</sup>	C.V.	Mean	S.D. <sup>1</sup>	C.V.	
Mires	1	1237	1039	84	9,83	9,40	96
	2	1860	1852	100	18,87	19,36	103
	3	193	202	104	0,74	1,01	136
	4	1467	1284	88	12,01	12,71	106
	5	263	307	117	1,48	2,13	144
	6	1937	1361	70	17,46	14,00	80
	7	317	439	139	2,82	4,70	167
	8	1887	1343	71	16,67	11,95	72
	9	347	418	121	2,86	3,47	121
Slopes	10	1143	915	80	10,60	9,42	89
	11	1243	997	80	11,10	8,93	80
Saltspray	12	663	453	68	4,20	3,18	76
	13	1540	890	58	9,87	6,28	64
	14	1447	1335	92	9,77	8,91	91
Biotic	15	5027	4932	98	38,30	44,49	116
	16	2670	1466	55	24,50	14,97	61
	17	2697	1973	73	20,67	18,23	88
	18	5553	5754	104	46,86	58,10	124
Fjaeldmark	19	800	706	88	7,24	6,85	95
<i>Weighted mean</i>	1980	—	—	16,86	—	—	

<sup>1</sup>Standard deviation

biotically influenced vegetation, particularly the biotically influenced mires (type 17). Huntley (1971) found similar high densities of these larvae in *Drepanocladus* vegetation, relative to other mires. The present data on the Lepidoptera adults and pupae are insufficient to indicate spatial distribution.

The biomass of weevil larvae, pupae and adults was greatest in *Clasmatocolea humilis*-*Agrostis magellanica* mires (type 4) and in biotically influenced vegetation types. They were also relatively common in lowland fjaeldmark vegetation (type 19). Spiders were most abundant in *Uncinia diki-Ptychomnion ringianum* mires (type 8) and, to a lesser extent, in some other mires (types 2 and 5), in *Cotula plumosa*-*Tillaea moschata* saltspray communities (type 13), in *Poa cookii* tussocks (type 16) and in *Cotula plumosa* hummocks (type 18).

Snails were absent from all saltspray vegetation types, most biotically influenced types and most mires. Their biomass was greatest in *Uncinia-Ptychomnion* mires (type 8), *Poa cookii* tussock vegetation (type 16) and on slope communities. Slugs were found in only seven vegetation types and predominantly in slope communities.

The coefficient of variation (CV = 100 × standard deviation/mean) was used to compare the amount of variation in populations having different means (Sokal & Rohlf, 1969). The CV of density and biomass of all the invertebrates considered was high (Table 1). The CV of total invertebrate density and biomass within each vegetation type was also high (Table 3). In

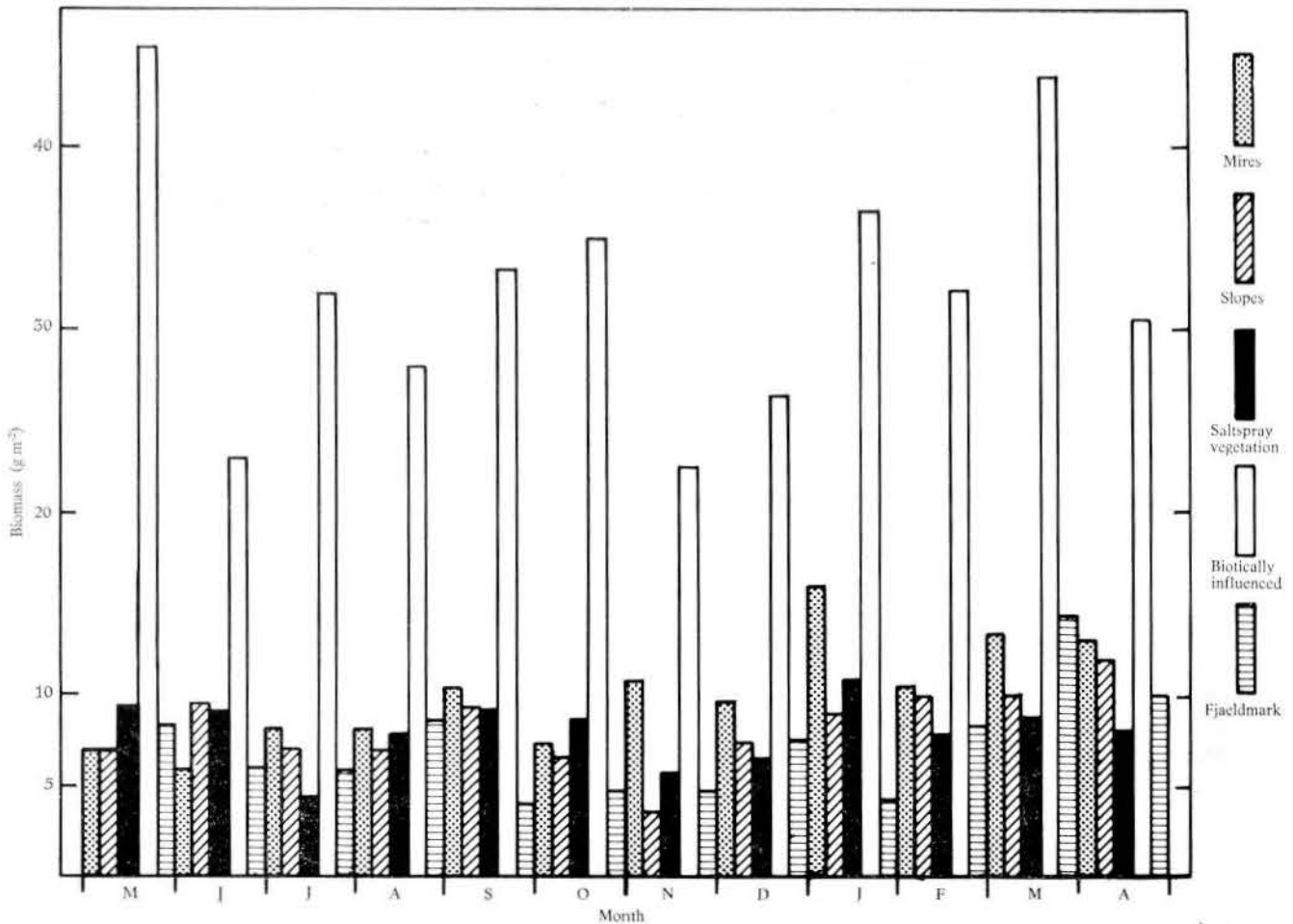


Fig. 2. Monthly values of mean invertebrate biomass in each vegetation-type complex at Marion Island.



**Table 4**  
Annual mean biomass (dried g m<sup>-2</sup>) of terrestrial invertebrates in each of 19 vegetation types at Marion Island.

Vegetation type	Earthworms	Earthworm cocoons	Lepidoptera larvae	Lepidoptera adults & pupae	Weevil larvae & pupae	Weevil adults	Spiders	Snails	Slugs
<b>Mires</b>									
1	9,18	0,22	0,30	0	0,06	0,06	0	0	0
2	15,14	0,28	2,64	0	0,24	0,01	0,16	0	0,40
3	0,10	0	0,14	0	0,32	0,12	0,06	0	0
4	9,84	0,20	0,28	0	1,30	0,38	0,02	0	0
5	0,86	0,02	0,10	0	0,26	0,08	0,16	0	0
6	15,82	0,34	0,54	0,08	0,28	0,08	0,08	0,30	0
7	2,42	0,04	0,12	0	0,18	0,04	0,01	0	0
8	13,92	0,26	0,50	0	0,40	0,10	0,24	1,28	0
<b>Slopes</b>									
9	2,14	0,08	0,04	0	0,08	0,06	0,06	0,16	0,26
10	7,52	0,16	0,14	0	0,48	0,16	0,12	0,06	1,98
11	7,08	0,12	0,50	0	0,08	0	0,10	0,32	2,90
<b>Saltspray</b>									
12	3,06	0,01	0,68	0	0,30	0,10	0	0	0,04
13	8,54	0,24	0,44	0,20	0,18	0,06	0,22	0	0
14	8,00	0,30	0,88	0,06	0,34	0,12	0,08	0	0
<b>Biotic</b>									
15	34,56	1,86	1,02	0,01	0,58	0,18	0,06	0	0
16	21,34	0,24	0,80	0	0,38	0,08	0,40	1,16	0,04
17	17,38	0,36	1,96	0	0,78	0,14	0,04	0	0
18	43,14	1,34	0,97	0	0,75	0,35	0,29	0	0,09
<b>Fjaeldmark</b>									
19	6,12	0,06	0,18	0	0,50	0,14	0,01	0,24	0
<b>Weighted mean</b>	<b>14,63</b>	<b>0,37</b>	<b>0,62</b>	<b>0,02</b>	<b>0,42</b>	<b>0,12</b>	<b>0,14</b>	<b>0,32</b>	<b>0,22</b>

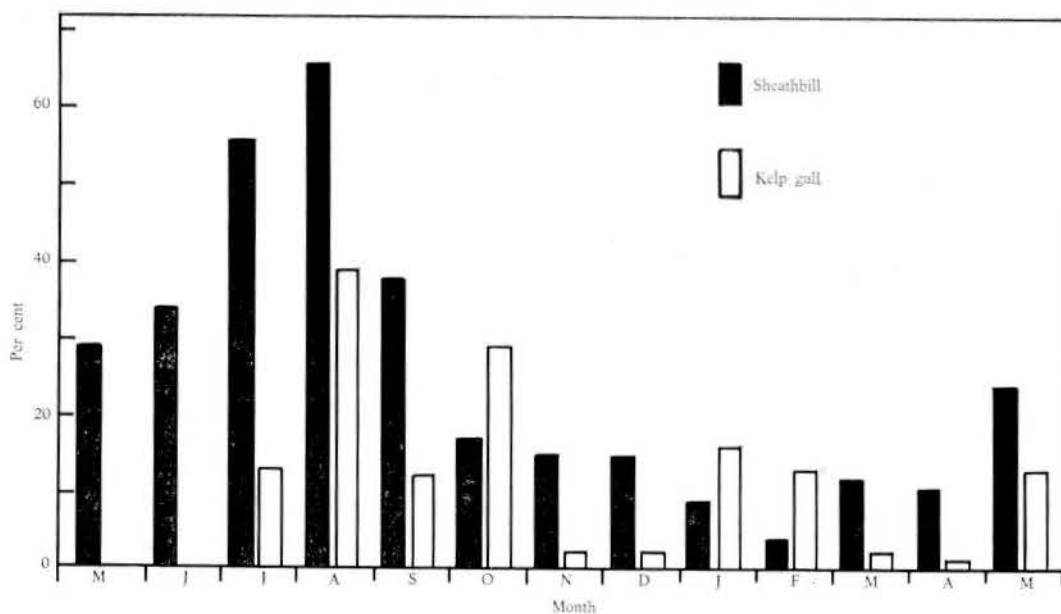


Fig. 3. Monthly percentages of sheathbill and kelp gull populations which foraged for terrestrial invertebrates within the study area. No data were available on kelp gull foraging during May and June 1976.

addition to the differences of density and biomass between vegetation types, there was also thus considerable variation within vegetation types, which was probably the result of micro-habitat preferences by the invertebrates.

The energy contents of terrestrial invertebrates at Marion Island are given in Table 5. The energy contents of earth-

worms from each vegetation type were very similar; significant differences were found between the energy content of earthworms from slope vegetation (types 9, 10 and 11) and those from saltspray vegetation (types 12, 13 and 14) (Student's *t*-test  $P < 0,05$  but  $P > 0,01$ ) but other energy contents of earthworms were not significantly different ( $P > 0,05$ ).

Table 5

Mean ( $\pm$ S.D.) energy contents of terrestrial invertebrates (including ash) at Marion Island.

Organisms	Vegetation type	Energy content (kJ g <sup>-1</sup> dry mass)	n
Earthworms	1	17,60 $\pm$ 0,09	2
	2	18,02 $\pm$ 0,83	3
	3	No data	
	4	18,10 $\pm$ 0,14	2
	5	16,56 $\pm$ 0,71	2
	6	18,57 $\pm$ 0,60	2
	7	17,59 $\pm$ 0,65	2
	8	18,28 $\pm$ 0,28	2
	All mires	17,83 $\pm$ 0,75	15
	9	19,74 $\pm$ 2,51	3
	10	17,44 $\pm$ 0,55	3
	11	18,90 $\pm$ 0,71	2
	All slopes	18,67 $\pm$ 1,76	8
	12	16,24 $\pm$ 0,53	2
	13	17,63 $\pm$ 1,38	4
	14	17,59 $\pm$ 0,65	2
	All saltspray types	17,31 $\pm$ 1,19	8
	15	17,69 $\pm$ 0,73	2
16	17,52 $\pm$ 0,49	2	
17	17,91 $\pm$ 0,54	2	
18	17,37 $\pm$ 0,04	2	
All biotic types	17,62 $\pm$ 0,45	8	
Fjaeldmark 19	17,87 $\pm$ 0,25	2	
All earthworms		17,89 $\pm$ 1,12	41
Earthworm cocoons	All types	20,95 $\pm$ 0,35	2
Lepidoptera larvae	All types	20,33 $\pm$ 2,49	2
Weevil larvae and pupae	All types	18,24 $\pm$ 0,51	4
Weevil adults	All types	18,15 $\pm$ 0,21	2
Spiders	All types	21,40 $\pm$ 0,14	2
Snails	All types	8,08 $\pm$ 0,32	2
Slugs	All types	17,19 $\pm$ 0,08	2

Table 6

The occurrence and mass of food items in the oesophagus and gizzard contents of 13 sheathbills which were foraging on inland areas.

	Occurrence (%)	Dried mass (%)
Terrestrial invertebrates		
Earthworms	100	20,2
Earthworm cocoons	31	0,2
Lepidoptera larvae	62	16,8
Lepidoptera adults and pupae	31	1,3
Weevil larvae and pupae	23	0,1
Weevil adults	39	21,4
Spiders	23	0,8
Snails	8	0,1
Slugs	0	0,0
Unidentified invertebrate matter	77	33,5
Intertidal organisms		
<i>Porphyra</i> algae	8	4,4
Diptera larvae	8	0,1
Other items		
Penguin flesh	15	0,8
Penguin excreta	8	traces
Plant matter	54	0,1

Table 7

Linear correlation coefficients between the occurrence and mass of terrestrial invertebrates in the oesophagus and gizzard contents of sheathbills and their density, biomass and mass per item in the substrate. Data from Tables 1 and 6.

	Invertebrates in substrate		
	Density	Biomass	Mean item mass
Invertebrates in sheathbills			
% Occurrence	0,80 <sup>1</sup>	0,82 <sup>1</sup>	0,14
% Mass	0,46	0,53	0,09

<sup>1</sup>P < 0,05

### Food and foraging of birds

With the exception of slugs, all the invertebrate species considered in this study were found in the oesophagus and gizzard contents of sheathbills (Table 6). The vegetation types in which slugs were the most common (types 9, 10 and 11) were very seldom visited by foraging sheathbills. Most of the unidentified invertebrate matter in the samples appeared to be derived from earthworms and very little from other soft-bodied invertebrates. Earthworms were thus more prevalent in the diet of sheathbills than the data in Table 6 suggest. Sheathbills collected while feeding on vegetated areas had ingested very little food which was not terrestrial invertebrates (Table 6).

The occurrence and mass of invertebrates in the oesophagus and gizzard contents of sheathbills were significantly correlated with their density and biomass in the substrate of the 19 vegetation types (Table 7). There was, however, no significant correlation between the mean mass per item of the invertebrates and their occurrence or mass in the gut contents of sheathbills. Predation by sheathbills on invertebrates was roughly proportional to the abundance of the invertebrates rather than their mean item mass, above a certain minimum size. Although sheathbills were occasionally seen to eat smaller invertebrates than those considered here, these were not found in the gut contents which were analysed, and they appear to be of negligible importance in the birds' diet.

No gut contents from kelp gulls were available for analysis. Lepidoptera larvae and earthworms were found in a few regurgitations obtained from kelp gull chicks at Marion Island. Observation of foraging gulls indicated that these relatively larger invertebrates were eaten frequently.

Sheathbills and kelp gulls showed marked seasonal trends in their foraging for invertebrates (Fig. 3). Both species sought terrestrial invertebrates more frequently in winter than at other times of the year. Short-term fluctuations in their foraging behaviour were partially due to weather conditions. During stormy weather, gulls were observed to forage less at sea and to prey more on terrestrial invertebrates. Sheathbills and kelp gulls preyed less on terrestrial invertebrates on days when snow covered the coastal plain, but these variations have been masked by combining the data into monthly means (Fig. 3).

An annual mean of 27,5 per cent of the sheathbills and 12,9 per cent of the kelp gulls were foraging for terrestrial invertebrates during sampling censuses (Fig. 3). The quantity of invertebrates eaten was estimated, assuming that the energy needs of these proportions of the study populations (on average, 54 out of 198 sheathbills and 9 out of 66 kelp gulls)

were entirely met by terrestrial invertebrates. This assumption was supported by observations that individuals recorded as foraging for terrestrial invertebrates spent little time foraging for other resources (Eurger, in preparation) and that such sheathbills ingested little other food (Table 6).

The energy requirements of these birds were calculated from estimates of their Daily Existence Energy (DEE) using the following formula:

$$\log \text{DEE} = \log 317,7 + 0,7052 \log W \quad (\text{King, 1974})$$

where DEE is in kcal day<sup>-1</sup> (multiplied by 4,187 to obtain kJ day<sup>-1</sup>) and *W* is the fresh body mass of the bird in kg. The energy actually ingested was calculated, assuming an assimilation efficiency of 75 per cent (Wiener & Glowacinski, 1975). The mass of organisms, with a mean energy content of 18 kJ g<sup>-1</sup> (Table 5), needed to supply this energy was calculated. The daily and annual intake of terrestrial invertebrates by an individual bird and by the percentage of the population of sheathbills and kelp gulls which foraged for this food within the study area are given in Table 8. Together, both species ingest  $2,6 \times 10^7$  kJ (1 423 kg, dried mass) annually in the study area.

## Discussion

Few species of terrestrial invertebrates occur at Marion Island and neighbouring Prince Edward Island (Van Zinderen Bakker Sr., *et al.* 1971). For instance, only about 27 species of insects have been recorded at these islands (Dreux, 1971). The low species richness at the Prince Edward group is attributed to the geologically "young" age of the islands, their isolation and the relative simplicity of their ecosystems (Van Zinderen Bakker Sr., 1971).

Although few terrestrial invertebrate species occur on Marion Island, the combined densities and biomass of macro-invertebrates are surprisingly high, approaching those of temperate regions. The biomass of macro-invertebrates in 19 vegetation types on the coastal plain on Marion Island was 16,86 g m<sup>-2</sup> (dried mass) or about 101 g m<sup>-2</sup> (fresh mass). The numbers of smaller invertebrates, such as acarid mites and Collembolla, are also sometimes very high (Burger, 1979), and would significantly add to the total invertebrate biomass. No data on the density and biomass of macro-invertebrates in other sub-Antarctic areas are available for comparison. Terrestrial macro-invertebrates are absent from the Antarctic (Gressitt, 1967) and the total biomass of terrestrial invertebrates is low, probably less than 5,2 g m<sup>-2</sup> (fresh mass), even in the most favourable areas (Holdgate, 1967). By way of comparison, at a moorland site in Britain, the total live biomass of invertebrates, including micro-invertebrates, was about 260 g m<sup>-2</sup> (Cragg, 1961). At grassland and meadow sites in Britain the live biomass of soil and litter invertebrates was about 190 g m<sup>-2</sup> (Macfadyen, 1963).

The dominance of earthworms in the soil and litter fauna of Marion Island is also characteristic of many temperate regions (Wallwork, 1970). The density and biomass of earthworms on the coastal plain of Marion Island are similar to those of natural habitats in temperate regions, but lower than those in temperate agricultural pastures (Table 9). The abundance of earthworms supports Smith's (1977) statement that plant products on Marion Island are primarily used via a detritus, rather than a grazing, food chain.

The density, biomass, mean organism mass and species composition of terrestrial invertebrates on Marion Island

Table 8

Estimates of the energy and dried mass of terrestrial invertebrates required to meet the energy demands of sheathbills and kelp gulls.

	Sheathbill		Kelp Gull	
	One bird	Population in study area	One bird	Population in study area
Body mass (kg)	0,453		0,941	
Daily existence energy (kJ)	761		1274	
Daily ingested energy (kJ)	1015	54 810	1699	15 291
Annually ingested energy (kJ)	$3,7 \times 10^5$	$2,0 \times 10^7$	$6,2 \times 10^5$	$5,6 \times 10^6$
Daily ingested mass (g)	56,4	3046	94,4	850
Annually ingested mass (kg)	20,6	1112	34,5	311

Table 9

Earthworm density and biomass at Marion Island and elsewhere in temperate regions.

Habitat and region	Density (No. m <sup>-2</sup> )	Fresh biomass (g m <sup>-2</sup> )	Reference
Coastal plain, Marion Island	1354	91 <sup>1</sup>	This study
13 Habitat types, U.K. & Europe	0,01-848	0,9-287	Satchell (1967)
Chalk grassland, U.K.	103	23	Chappell <i>et al.</i> (1971)
Montane soils, Australia	7-135	1-82	Wood (1974)
Forest and grassland, U.K.	524	152	Satchell (1967)
Pastures, S. Australia	260-740	39-152	Barley (1959)
Pastures, S. Australia	357	80	Noble <i>et al.</i> (1970)
Pastures, New Zealand	650-1400	140-320	Waters (1955)

<sup>1</sup>Fresh mass at Marion Island was 6,2 times dried mass.

varied from month to month, but there were no clear seasonal trends. On sub-Antarctic Heard Island many insect species have seasonal cycles, with adult emergence occurring only during summer (Brown, 1964). Such seasonal patterns were less evident on Marion Island, although a study of population dynamics is needed to confirm this. The year-round presence of earthworm cocoons and insect larvae cannot be interpreted as reflecting year-round reproduction until the dormancy periods, if any, are known. On Heard Island, the insects often overwinter in larval stages (Brown, 1964).

The monthly variations of biomass and densities were slight, in relation to the great differences found between the mean biomasses of different vegetation types. This might be attributed to the equability of the climate of Marion Island; the temperature, windspeed and rainfall remain remarkably constant throughout the year (Schulze, 1971).

The biotically influenced vegetation (types 15-18) and certain mires (types 2, 4, 6 and 8) supported the greatest total populations of invertebrates. Those vegetation types which were favourable for some invertebrates were generally favourable for all the types considered, with certain exceptions. Snails and slugs, for instance, often had their greatest densities and biomass in vegetation types, such as slope vegetation, which had lower than average total invertebrate densities and biomass.

Differences in the spatial distribution of the invertebrates considered here could be the result of their preference for vegetation structure and factors such as pH and the nutrient, water, oxygen and organic contents of the substrates. Some of these factors have been shown to differ between vegetation types on Marion Island (Smith, 1976a) but a detailed analysis of their effects on invertebrate distribution has not been attempted.

Terrestrial invertebrates represent a patchily distributed food resource, with great differences in biomass between adjacent vegetation types and also considerable variation within vegetation types. The foraging success of the predatory birds could be significantly influenced by their selection of foraging sites. The invertebrates considered in this study include all those of importance in the diet of sheathbills and probably also those important in the diet of kelp gulls. The smallest of these invertebrate organisms apparently represents the minimum item size which is profitable to be included in the foraging effort of these birds. Although individual birds may have prey size preferences that differ from those of others, the population appears to ingest all available invertebrates above a minimum size.

The standing crop of macro-invertebrates within the 100 ha study area was estimated to be 16,86 t (dried mass). The sheathbills and kelp gulls resident in this area annually ingest about 1 423 kg (dried mass) of invertebrates, which amounts to 8,4 per cent of the standing crop. Information on the annual productivity of the invertebrates, applied to the present data on standing crop, would allow a more realistic estimate of the effects of predation by birds. It is already apparent, however, that large amounts of matter and energy pass from the invertebrates to the birds.

Estimates of mass and energy transfer from terrestrial invertebrates to birds on the entire coastal plain must be regarded as tentative. The areas of each vegetation type on the entire coastal plain are not known. The coastal plain of the island is about 100 km<sup>2</sup> in area. The standing crop of macro-invertebrates within this area would be 1 686 t (dried mass), if the proportions of each vegetation type were the same as

those in the study area, which is unlikely. There are 3 500 sheathbills and 923 kelp gulls resident on Marion Island. If the same percentage of birds foraged for invertebrates as in the study area, the annual intake of terrestrial invertebrates on the whole island could be  $3,56 \times 10^8$  kJ (20 t, dried mass) and  $0,74 \times 10^8$  kJ (4 t, dried mass) by sheathbills and kelp gulls respectively. Together they would thus ingest  $4,30 \times 10^8$  kJ (24 t, dried mass) of invertebrates.

Terrestrial invertebrates annually supply about a quarter and an eighth of the energy needs of the sheathbill and gull populations respectively, within the study area, and probably about the same proportion of the energy needs of the total island populations of these birds. Other food items, such as eggs and carcasses of penguins, krill and fish stolen from penguins, carcasses and placentae from seals, and marine organisms, supply most of the food to these two species. Terrestrial invertebrates are, however, important, since they are available in winter, when food from penguins and seals is less abundant. The increase during winter in the numbers of sheathbills and kelp gulls foraging for terrestrial invertebrates was not the result of an increase in invertebrate density, biomass or mean item mass, but was related to a decrease in the availability of other, more favoured food (Burger, in preparation).

The evidence suggests strongly that the availability of terrestrial invertebrates allows the island's populations of these birds, particularly sheathbills, to be larger, by reducing the incidence of starvation during winter. Elsewhere in the sub-Antarctic and Antarctic where terrestrial invertebrates are less abundant, or absent, sheathbill populations emigrate during winter (Jones, 1963), or, where migration is impossible, they subsist on a meagre fare of marine jetsam, algae and penguin and seal faeces (Downes *et al.* 1959).

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#### References

- Barley, K.P. The influence of earthworms on soil fertility. 1. Earthworm populations found in agricultural land near Adelaide. *Austr. J. agric. Res.*, **10**, 171-178, 1959.
- Berruti, A. & Harris, A. Breeding schedules of Antarctic and Kerguelen terns at Marion Island. *Notornis*, **23**, 243-245, 1976.
- Brown, K.G. The insects of Heard Island. *Australian National Antarctic Research Expedition Reports, Series B*, **1**, 1-39, 1964.
- Burger, A.E. Sampling of terrestrial invertebrates using sticky-traps at Marion Island. *Polar Record*, **19**, 618-620, 1979.
- Chappell, H.G., Ainsworth, J.F., Cameron, R.A.D. & Redfern, M. The effect of trampling on a chalk grass ecosystem. *J. appl. Ecol.*, **8**, 869-882, 1971.
- Cragg, J.B. Some aspects of the ecology of moorland animals. *J. anim. Ecol.*, **30**, 205-234, 1961.
- Downes, M.C., Ealey, E.H.M., Gwynn, A.M. & Young, P.S. The birds of Heard Island. *Australian National Antarctic Research Expedition Reports, series B*, **1**, 1-135, 1959.
- Dreux, P. Insecta. La fauna entomologique des Iles Marion et du Prince Edouard. In *Marion and Prince Edward Islands: Report on the South African Biological and Geological Expedition 1965-1966*, edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom &

- R.A. Dyer, 335-343. Cape Town, A.A. Balkema, 1971.
- Gressitt, J.L. (ed.). *Entomology of Antarctica. Antarctic Research Series*, 10. Washington, D.C., American Geophysical Union, 1967.
- Holdgate, M.W. The Antarctic ecosystem. *Phil. Trans. R. Soc. Lond.*, **B252**, 363-383, 1967.
- Huntley, B.J. Vegetation. In *Marion and Prince Edward Islands, Report on the South African Biological and Geological Expedition 1965-1966*, edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom & R.A. Dyer, 98-160. Cape Town, A.A. Balkema, 1971.
- Jones, N.V. The sheathbill, *Chionis alba* (Gmelin), at Signy Island, South Orkney Islands. *Brit. Antarct. Surv. Bull.*, **2**, 53-71, 1963.
- King, J.R. Seasonal allocation of time and energy resources in birds. In *Avian Energetics*, edited by R.A. Paynter. *Publ. Nuttall Ornith. Club*, **15**, 4-70, 1974.
- Macfadyen, A. The contribution of the micro fauna to total soil metabolism. In *Soil organisms*, edited by J. Doeksen & J. van der Drift, 3-17. Amsterdam, North Holland Publishing, 1963.
- Noble, J.C., Gordon, W.T. & Kleinig, C.R. The influence of earthworms on the development of mats of organic matter under irrigated pasture in southern Australia. *Proc., XI Int. Grassld. Congr.*, 465-468, 1970.
- Odum, E.P. *Fundamentals of Ecology*. Philadelphia, Saunders, 1971.
- Paulian, P. Notes biologiques sur le *Pringleophaga kerguelensis*. *End. Rev. franc. Ent.*, **20**, 45-47, 1953.
- Satchell, J.E. Lumbricidae. In *Soil Biology*, edited by A. Burgess & F. Raw, 259-322. London, Academic Press, 1967.
- Schulze, B.R. The climate of Marion Island. In *Marion and Prince Edward Islands; Report on the South African Biological and Geological Expedition, 1965-66*. Edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom, & R.A. Dyer, 16-31. Cape Town, A.A. Balkema, 1971.
- Smith, V.R. Standing crop and nutrient status of Marion Island (sub-Antarctic) vegetation. *J. S. Afr. Bot.*, **42**, 231-263, 1976a.
- Smith, V.R. The effect of burrowing species of Procellariidae on the nutrient status of inland tussock grasslands on Marion Island. *J. S. Afr. Bot.*, **42**, 265-272, 1976b.
- Smith, V.R. A qualitative description of energy flow and nutrient cycling in the Marion Island terrestrial ecosystem. *Polar Record*, **18**, 361-370, 1977.
- Sokal, R.R. & Rohlf, F.J. *Biometry*. San Francisco, Freeman, 1969.
- Van Zinderen Bakker, E.M. Sr. Introduction. In *Marion and Prince Edward Islands; Report on the South African Biological and Geological Expedition, 1965-1966*, edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom & R.A. Dyer, 1-15. Cape Town, A.A. Balkema, 1971.
- Van Zinderen Bakker, E.M. Sr., Winterbottom, J.M. & Dyer, R.A. (eds.). *Marion and Prince Edward Islands; Report on the South African Biological and Geological Expedition, 1965-1966*. Cape Town, A.A. Balkema, 1971.
- Vari, L. Lepidoptera (Heterocera: Tineidae, Hyponomeutidae). In *Marion and Prince Edward Islands; Report on the South African Biological and Geological Expedition, 1965-1966*, edited by E.M. van Zinderen Bakker Sr., J.M. Winterbottom & R.A. Dyer, 349-354. Cape Town, A.A. Balkema, 1971.
- Wallwork, J.A. *Ecology of Soil Animals*. London, McGraw-Hill, 1970.
- Waters, R.A.S. Numbers and weights of earthworms under a highly productive pasture. *N. Z. J. Sci. Technol.*, **A36**, 516-525, 1955.
- Williams, A.J., Burger, A.E., Berruti, A. & Siegfried, W.R. Ornithological research on Marion Island, 1974-1975. *S. Afr. J. Antarct. Res.*, **5**, 48-50, 1975.
- Wiener, J. & Glowaciński, Z. Energy flow through a bird community in a deciduous forest in southern Poland. *Condor*, **77**, 233-242, 1975.
- Wood, T.G. The distribution of earthworms (Megascolecidae) in relation to soils, vegetation and altitude on the slopes of Mt. Kosciusko, Australia. *J. Anim. Ecol.*, **43**, 87-106, 1974.

## Cephalopod prey of the sooty albatrosses *Phoebetria fusca* and *P. palpebrata* at Marion Island

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The sooty albatross *Phoebetria fusca* and light-mantled sooty albatross *P. palpebrata* are largely allopatric in their breeding and pelagic ranges, but breed sympatrically at Marion Island. Regurgitated casts of food remains (mainly cephalopod beaks) were analysed to assess differences in the foods of these two species at Marion Island. Lower beaks of cephalopods were identified to species, and the masses of whole animals were estimated. Thirty-seven cephalopod species were identified from 3 295 beaks derived from both albatrosses. The mean estimated cephalopod prey mass (219 g and 295 g for *P. fusca* and *P. palpebrata* respectively) was high, as digestion tends to eliminate smaller, less resistant beaks. *Kondakovia*

*longimana* was the most important species by mass, and the *Onychoteuthidae*, *Cranchiidae* and *Histioteuthidae* the most important families in the food of both species. Most cephalopod prey species were bioluminescent, but non-bioluminescent cephalopods constituted a higher proportion by mass. Remains of fish, birds and crustaceans were present in small amounts. Differences in species composition and mass of cephalopod prey between the two albatrosses were small, and partitioning of food resources by spatial separation of feeding areas is apparently more significant in the segregation of *P. fusca* and *P. palpebrata* at Marion Island.