FOOD AND FORAGING BEHAVIOUR OF LESSER SHEATHBILLS AT MARION ISLAND

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1. INTRODUCTION

Sub-Antarctic Islands are characterised by terrestrial ecosystems with low species diversity and relatively simple food webs (Van Zinderen Bakker 1971). The islands are used as breeding and moulting areas by very large populations of seabirds (Williams *et al.* 1979), but typically have few or no breeding species of land-foraging birds (Watson 1975). This has been attributed to a paucity of suitable food and vegetation cover, the isolation and the inhospitable climates (Watson 1975, Burger *et al.* 1980).

Sheathbills (Chionididae) are the most successful group of land birds in overcoming the problems of living and breeding in the Antarctic and Sub-Antarctic, and their breeding ranges fall entirely within these regions: the Wattled Sheathbill *Chionis alba* on the Antarctic Peninsula and three island groups, and the Lesser Sheathbill *C. minor* on four island groups (Watson 1975). Sheathbills have seldom been studied (Jones 1963, Burger 1979) and this paper reports a first attempt at a detailed analysis of the food and foraging behaviour of a population of Lesser Sheathbills, at Marion Island (46° 54′ S, 37° 45′ E). The Lesser Sheathbill is the only avian resident at Marion Island which is entirely dependent on terrestrial and intertidal food resources. The remaining 28 avian species breeding there are seabirds (Williams *et al.* 1979).

2. METHODS

Lesser Sheathbills were studied during January—November 1974 and April 1976—May 1977, in a 100 ha area, 200 m wide, along 5 km of the north-eastern coast of Marion Island. There were, on average, 197 sheathbills in the area. The birds' foraging activities were recorded at ten-day intervals in 1976—1977 during censuses made on foot, between 08h00 and 15h00. The following data were collected for each bird when encountered: age, recorded as adult, subadult or juvenile (Burger 1980); flock size; mean minimum distance of the bird or flock to the sea; and the food being eaten. Most birds were foraging when encountered. Individuals which were not foraging were linked with a particular food type determined by what other members of the group were eating and what food was available at the site of observation. Sub-Antarctic Skuas *Catharacta skua lonnbergi* within the study area were also counted every 10 days.

Similar censuses were made over periods of several weeks to cover entirely the accessible parts of the island's coast and coastal plain in winter (July to September) and also in summer during the early part of the sheathbill's breeding season (November and December). These censuses probably included over 90% of the island's sheathbill population.

Typical flock size (TFS) of foraging birds was calculated as follows (from Jarman 1974):

$$TFS = \frac{n^2_1 + n^2_2 + n^2_3 \ldots n^2_i;}{N}$$

where n_1, n_2, n_3 etc. are the numbers of birds in each flock and N is the total sample population. The TFS is the flock size in which the average individual occurs and provides a better estimate of social grouping than the mean flock size (Jarman 1974).

The number of adult penguins, and their eggs and chicks within the study area were estimated by means of censuses, regular photography of colonies and from the demographic data given by Siegfried *et al.* (in press). The relative abundance of intertidal algae was measured at intervals throughout the year at five sites in the study area. The index

of abundance used was the percentage cover of algae (estimated from photographs) on 42 selected boulders multiplied by the mean oven-dried mass (g) of algae scraped off five 10 × 10 cm quadrats centred on patches of the algal carpet at each site. The numbers of amphipods within each quadrat were also counted.

Representative samples of food items were analysed for their energy content, using a Gallenkamp ballistic bomb calorimeter; protein content, using standard Kjeldahl methods; and fat content, using a hot hexane soluble reflux method. Protein and fat determination were made in duplicate from pooled samples.

3. FOOD AND FORAGING AREAS

3.1. WITHIN THE STUDY AREA

Estimates of the importance of various food types in the diet were based on analysis of the gut contents of 35 Lesser Sheathbills (Table 1) supplemented by over 600 hours of observation during 25 months in the field (Table 2). The gut contents were too few to be fully representative of the wide range of food eaten but larger samples were precluded because the island is a nature reserve. The usefulness of gut contents was limited, since much of the food eaten was soft and unrecogniseable in the oesophagus or stomach. The food most commonly taken within one of five major foraging areas was usually fairly specific to that area (Tables 1 and 2). If Lesser Sheathbills were to move to a different area their diet would also change.

Lesser Sheathbills foraged in colonies of King Penguins *Aptenodytes patagonicus*, Macaroni Penguins *Eudyptes chrysolophus*, Rockhopper Penguins *E. chrysocome* and Gentoo Penguins *Pygoscelis papua*. In these colonies they ate flesh, blubber and skin from the carcasses of adult and chick penguins (small

Table 1. Analysis of oesophagus and stomach contents (combined) of Lesser Sheathbills at Marion Island. The % mass of food eaten in penguin colonies could not be determined due to problems in identifying soft food mixed in the gut

	Habitat where the birds were collected from				
	Coastal vegetation		Intertidal zone		Penguin colonies
Food items (%)	Occurrence %	Mass (%)	Occurrence (%)	Mass (%)	Occurrence (%)
Terrestrial invertebrates					
Earthworms	100	17.3	0	0	12
Earthworm cocoons	31	0.2	0	0	0
Lepidoptera adults and pupae	31	1.1	0	0	12
Lepidoptera larvae	62	14.4	0	0	0
Weevil adults	39	18.3	0	0	0
Weevil larvae & pupae	23	0.1	0	0	0
Spiders	23	0.7	0	0	6
Snails	8	0.1	0	0	0
Intertidal organisms					
Porphyra algae	8	3.8	100	47.9	18
Other algae spp.	0	0	20	1.1	0
Amphipods	0	0	20	4.7	0
Chitons	0	0	20	3.9	0
Limpets	0	0	100	13.8	6
From penguin colonies					
Penguin flesh	15	0.7	40	5.3	59
Penguin excreta	8	traces	40		88
Penguins eggs	0	0	0	0	12
Pelagic crustaceans and fish	0	0	0	0	12
Eggshells	31	2.0	0	0	76
Squid beaks (from excreta)	8	traces	0	0	65
Small pebbles	85	12.3	100	8.5	59
Vegetable matter	54	0.1	0	0	0
Unidentified matter	77	28.6[1]	40	14.9	41
No. of birds examined	13	10	5	4	17

[1] Most of this was probably earthworms.

Table 2. A summary of the food eaten by Lesser Sheathbills at Marion Island. The food types were rated as common (×××), occasional (××), rare (×) and not recorded (–)

Food type	Penguin colonies	Seal colonies	Intertidal zone	Kelp jetsam	Inland vegetated areas
Eggs	×××	–	–	–	–
Excreta	××	×	×	–	–
Carcasses	×××	××	–	–	–
Placentae	–	×	–	–	–
Small chicks	××	–	–	–	–
Food robbed from penguins	×××	–	–	–	–
Porphyra algae	–	–	×××	–	–
Limpets, chitons and starfish	–	–	×	×	–
Amphipods	–	–	×	–	–
Kelp flies & larvae	×	×	–	××	–
Terrestrial invertebrates	×	×	–	–	×××

penguin chicks were killed by the Lesser Sheathbills); eggs, either discarded by or stolen from incubating penguins; freshly voided penguin excreta; and, krill (pelagic euphausids, amphipods and copepods), fish and squid spilled by penguins while feeding their chicks, and obtained from the penguins by kleptoparasitism (see Burger 1979). Lesser Sheathbills also ate insects and ectoparasites found in penguin colonies, but these were very minor food items.

The breeding sites of albatrosses (four species, Williams *et al.* 1979) and the Imperial Cormorant *Phalacrocorax albiventer* were visited by small numbers of Lesser Sheathbills which took spilled food, regurgitated pellets and excreta. The Lesser Sheathbills might also have preyed upon eggs and small chicks in the cormorant colonies.

Elephant Seals *Mirounga leonina* bred and moulted within the study area, and the Lesser Sheathbills ate their placentae, flesh from pup carcasses, occasionally sipped milk from nursing cows and picked at wounds and nasal mucous on adults and pups. Fur Seals *Arctocephalus tropicalis* and *A. gazella* did not breed in the study area but Lesser Sheathbills were sometimes seen foraging near these seals elsewhere on Marion Island. Seal excreta was occasionally eaten but generally ignored. Carcasses of adult seals and Killer Whales *Orcinus orca* occured extremely rarely on beaches, but they were eaten by avian scavengers, including Lesser Sheathbills, when available.

The membranous alga *Porphyra* sp., which was pulled and scraped off rocks, was the major food eaten in the intertidal region. Other algae species were not eaten, although *Rhodymenia* sp. was as common as the *Porphyra* (De Villiers

Table 3. Mean (± S.D.) percentages of adult, subadult and juvenile Lesser Sheathbills foraging in various areas in winter (May to October) and summer (November to April) within the study area

Foraging area	Winter			Summer		
	Adults	Subadults	Juveniles	Adults	Subadults	Juveniles
Penguin colonies	17 ± 7^{s}	9 ±11	15 ± 7	31 ± 6	53 ±17^{aj}	36 ±20
King						
Macaroni	4 ± 3^{sj}	0	1 ± 2	11 ± 6^{sj}	1 ± 1	1 ± 3
Rockhopper	5 ± 5^{sj}	1 ± 2	2 ± 3	36 ±13^{sj}	9 ±10	13 ±19
Seal Colonies	4 ± 7	6 ±10	4 ± 8	–	–	–
Intertidal zone	23 ±17	26 ±22	28 ±20	5 ± 6	7 ±10	13 ±13^{a}
Kelp jetsam	9 ± 4	7 ± 8	7 ± 5	7 ± 5	12 ±19	18 ±17^{a}
Coastal vegetation	37 ±19	50 ±33	41 ±22	9 ± 7	17 ±14^{a}	18 ± 7^{a}
Kitchen	1 ± 1	2 ± 3	1 ± 1	1 ± 2	1 ± 3	1 ± 2
No. censuses	17	17	17	17	17	11[1]
Mean no. birds/census	150 ±22	32 ±10	30 ± 8	139 ±10	20 ± 9	32 ±14

^{sj}: Mean values are significantly higher than those of adults $^{(a)}$, subadults $^{(s)}$ and juveniles $^{(j)}$, respectively ($P < 0.05$, t-test).

[1] Between January and mid-March all juveniles (chicks) were in nests and not censused.

1976). Amphipods *Hyale* spp. which were numerous in the algal carpets were ingested along with the algae but the Lesser Sheathbills did not seem to actively seek these prey. Amphipod densities in the *Rhodymenia* patches, which were ignored, were as high as in the *Porphyra* (Fig. 3). Other intertidal organisms which were eaten opportunistically were limpets *Nacella delersserti* and *Kerguelenella lateralis*, chitons *Hemiarthrum setulosum* and starfish *Anasterias rupicola.*

Lesser Sheathbills ate larvae, pupae and adults of kelp flies *Paractora dreuxi* and *Apetenus litoralis*, and small oligochaetes which lived in the piles of rotting kelp jetsam common on the rocky shore. The birds probed amongst the kelp fronds and small stones, and often pulled them aside to get at their prey. They never used their feet to scratch or dig for prey.

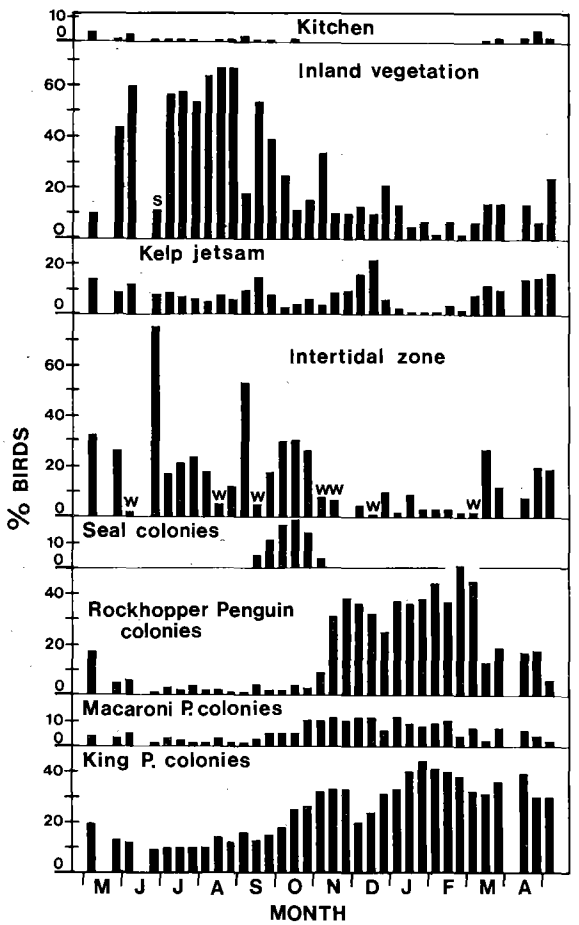


Fig. 1. Percentage of Lesser Sheathbills within the 200 ha study area (average population 197 birds) foraging in different areas during 34 one-day censuses throughout the year. Days with exceptionally heavy waves on the shore (W) or with heavy snow and frozen ground (S) are indicated where applicable.

Lesser Sheathbills ate a wide variety of terrestrial macro-invertebrates, mainly earthworms and insects, taken from vegetated areas on the coastal plain (Table 1, Burger in press). The birds obtained their fossorial invertebrate prey by pulling away grass and moss and less frequently by probing into the substrate. They also picked up prey on the vegetation surface.

Lesser Sheathbills, Sub-Antarctic Skuas and Kelp Gulls *Larus dominicanus* were attracted to the meteorological station for discarded kitchen scraps. During this study these scraps were thrown to the sea to prevent this but a few Lesser Sheathbills persistently foraged around the buildings.

Colonies of penguins provided most of the food to Lesser Sheathbills from November to April, whereas terrestrial invertebrates and intertidal algae were the most common foods eaten from May to October (Fig. 1). These two periods are termed "summer" and "winter" respectively, for convenience. At both times of the year the foraging patterns of adults, subadults and juveniles were broadly similar, with certain notable exceptions (Table 3). The King Penguin colonies were used by proportionately more adults than subadults in winter but by more subadults than adults or juveniles in summer. This was due to the greater numbers of King Penguins occuring outside the territories of adult Lesser Sheathbills in the summer but not in winter (see below). Proportionately more adults occured in Rockhopper and Macaroni Penguin colonies in both summer and winter. Colonies of these penguins in the study area were comparatively small and were usually wholly within the defended territories of the adult Lesser Sheathbills. There was a tendency for more juveniles and, to a lesser extent, more subadults to forage outside penguin colonies than adults, in summer.

3.2. AROUND THE WHOLE ISLAND

In summer, 90% of the island's Lesser Sheathbills foraged in penguin colonies (Table

4). At this time most Lesser Sheathbills occurred in colonies of Rockhopper Penguins (Table 4 and 5). Rockhopper Penguins, being smaller, might have been kleptoparasitised more easily by Lesser Sheathbills than the other penguin species. Rockhopper Penguin colonies were small and situated on steep, broken lava slopes; for the Lesser Sheathbills this enabled free movement between the penguins, facilitated foraging for eggs and chicks and provided nest sites. Eighty-four percent of the island's King Penguins occurred in three very large colonies (over 20000 pairs each) and over 90% of the Macaroni Penguins occurred in two such colonies (Siegfried *et al.* in press). Much of these very large colonies were unsuitable for Lesser Sheathbills when they were packed with penguins for the summer, but attracted large numbers of Lesser Sheathbills when they were partially or wholly deserted by penguins in winter. Hundreds of carcasses of Macaroni Penguins, which died during breeding or moulting, provided food for Lesser Sheathbills for many weeks after the penguins had left for the winter. This was not true for the small Macaroni Penguin colonies in the study area.

Proportionately fewer of the island's Lesser Sheathbills used the shoreline than in the study area (Table 4). Outside the study area there were relatively fewer beaches and the coast was considerably more exposed to heavy surf (De Villiers 1976). In winter almost a third of the island's Lesser Sheathbills foraged for terrestrial invertebrates.

Table 4. The use of foraging areas by Lesser Sheathbills in all accessible parts of Marion Island, and the typical flock sizes of these birds, in summer (November/December) and winter (July to September). N.D.: not determined

Foraging area	% of count		Typical flock size (range in parentheses)	
	Summer	Winter	Summer	Winter
Penguin colonies				
King	38	48	N.D.	N.D.
Macaroni	12	10	N.D.	N.D.
Rockhopper	40	3	1.9 (1–4)	1.9 (1–3)
Intertidal zone and kelp jetsam	5	8	5.5 (1–19)	3.3 (1–13)
Coastal vegetation	5	31	2.9 (1–7)	11.1 (1–44)
No. of birds	3528	3457	–	–

Table 5. Numbers of Lesser Sheathbills counted in colonies of various penguins at Marion Island in November and December 1976, immediately prior to egg laying by the sheathbills, in relation to the current annual breeding populations of the penguins

Penguin species	No. of pairs of penguins[1]	Sheathbills counted	
		No. birds	No. per 1000 penguin pairs
King	215 230	1347	6.3
Macaroni	450 000	406	0.9
Rockhopper	93 290	1426	15.3

[1] From Williams *et al.* (1979).

4. FACTORS AFFECTING FORAGING

4.1. FOOD QUALITY AND AVAILABILITY

Penguin colonies provided food which, except for excreta, had higher energy, protein and fat contents than the algae and invertebrates which were the most common alternative items eaten (Table 6). Lesser Sheathbills sought food in penguin colonies whenever this was readily available, and the many birds foraging there in summer (Fig. 1, Table 4) corresponded to the peak period of maximum densities, and of breeding, of King, Macaroni and Rockhopper Penguins (Fig. 2). The presence of small colonies of Gentoo Penguins had little effect on the foraging of Lesser Sheathbills and most of the birds seen near these penguins ate terrestrial invertebrates. Lesser Sheathbills bred when high-quality food supplies were most abundantly available from the penguin colonies (Fig. 2; Burger 1979).

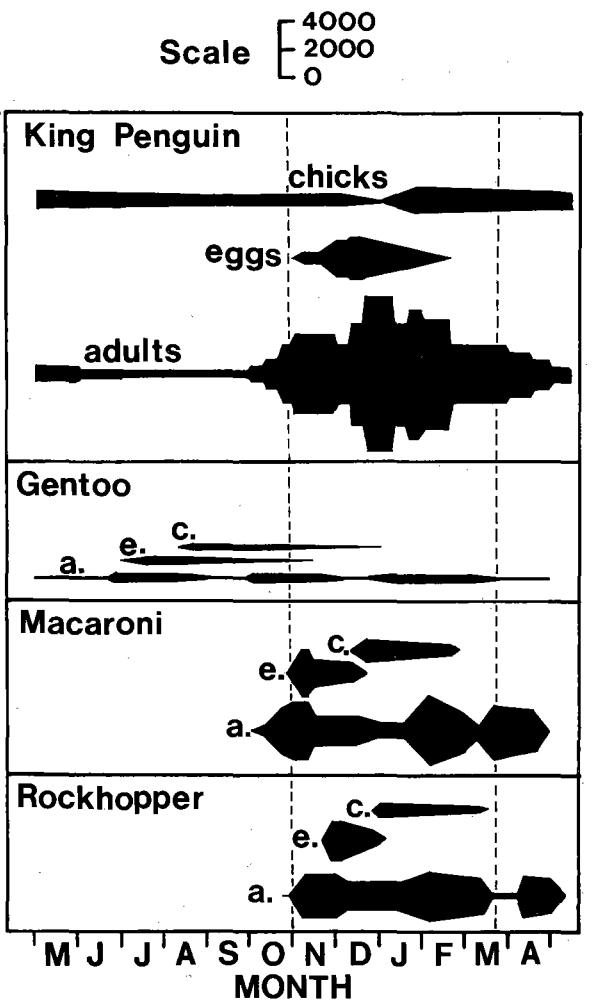
The placentae and carcasses of Elephant Seal pups were also attractive food sources to Lesser Sheathbills but were available only between mid-September and mid-November (Condy 1979), which was the only time that the birds foraged intensively amongst the seals (Fig. 1).

The invertebrates amongst the rotting kelp jetsam represented food items which were small, probably of low nutritional value, spa-

Table 6. Mean (± S.D.) energy, protein and fat contents of fresh and dried (in parentheses) food items available to Lesser Sheathbills at Marion Island

Food type	Energy (kJ g^{-1})		Protein (% mass)	Fat (% mass)
	Mean	No. samples		
From penguin colonies				
Egg contents	5.5 ± 0.4 (26 ± 2)	18	10.4 (50)	7.4 (36)
Carcass: skin and blubber	11.6 ± 0.4 (30 ± 1)	2	19.1 (49)	16.9 (43)
Carcass: meat and sinews	4.9 ± 0.1 (26 ± 1)	2	13.1 (69)	2.9 (15)
Crustaceans (taken from Rockhopper Penguins)	6.8 ± 0.1 (25 ± 1)	2	18.3 (68)	2.8 (10)
Squid[1]	4.5 ± 0.2 (20 ± 1)	15	no data	no data
Fish[2]	5.5 ± 0.3 (21 ± 1)	36	14.9 (58)	9.5 (37)
Excreta	2.1 ± 0.3 (14 ± 2)	30	3.4 (22)	0.5 (3)
Intertidal algae				
Porphyra sp.	4.1 ± 0.3 (19 ± 1)	8	7.3 (34)	0.1 (0.5)
Rhodymenia sp.	2.6 ± 0.1 (18 ± 1)	10	4.2 (28)	0.1 (0.2)
Terrestrial invertebrates	3.0 ± 0.2 (18 ± 1)	40	10.7 (64)	1.2 (7)

[1] From Cooper (1979)
[2] Energy contents from Griffiths (1977); water, protein and fat contents of Antarctic fish from Roschke & Schreiber (1977).



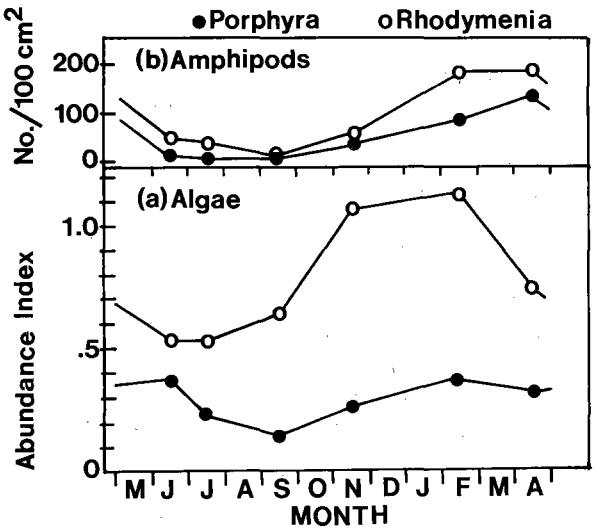


Fig. 3. The relative abundance of *Porphyra* and *Rhodymenia* algae on the intertidal boulders near Transvaal Cove (a), and the densities of amphipods *Hyale* spp. within algal carpets (b). See text for derivation of the index of algal abundance.

tially restricted to small areas and present throughout the year. The deposits of beached kelp which supported the invertebrates were produced by heavy onshore swells (over 2 m) which occurred during all months of the year

Fig. 2. Temporal availability and approximate numbers of adult penguins, eggs and chicks within the study area. The duration of the Lesser Sheathbill's breeding season (nest-building, laying, incubation and rearing chicks) is delineated by the vertical dashed lines.

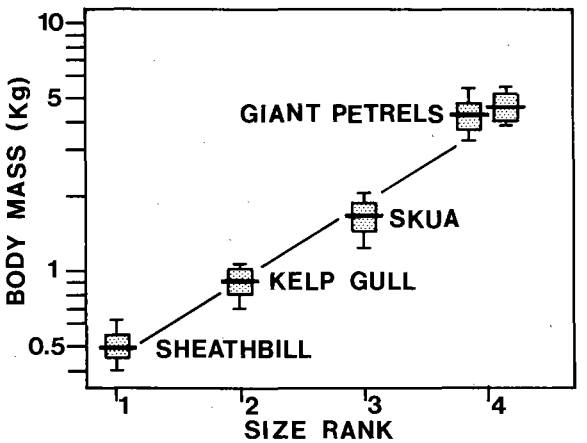


Fig. 4. Mean, S.D. and range (horizontal line, shaded bar and vertical line respectively) of the adult body masses of the predatory-scavenging birds at Marion Island, ranked from smallest to largest. The two species of Giant Petrels have been given equal rank, since their masses are not significantly different (Voisin 1976, Johnstone 1977).

(De Villiers 1976, pers. obs.). Small numbers of Lesser Sheathbills ate these invertebrates in the kelp throughout the year (Fig. 1).

Porphyra algae were available in the intertidal zone of the study area all year (Fig. 3), but the Lesser Sheathbills ate the algae intensively only during the winter (Fig. 1). Little was eaten in summer (November to April) when the algae and amphipods were most abundant.

The densities, biomasses and mean item masses of terrestrial invertebrates were relatively constant all year, with no marked seasonal trends (Burger in press), but the Lesser Sheathbills foraged in large numbers for this food only in winter (Fig. 1). It is clear that algae and invertebrates were important food only during the period when there was lesss food available from penguins.

4.2. INTERSPECIFIC COMPETITION

Penguins provided the bulk of the food taken at Marion Island by avian predators and scavengers, mainly in the form of carcasses, live birds and eggs (Williams *et al.* in press, Siegfried *et al.* in press). This food was eaten by Northern and Southern Giant Petrels *Macronectes halli* and *M. giganteus*, Sub-Antarctic Skuas, Kelp Gulls and Lesser Sheathbills. Although all these birds used alternative food resources, particularly in winter, they were potential competitors in penguin (and seal) colonies. Feral cats *Felis catus* also ate carcasses and eggs of penguins, but in negligible amounts (Van Aarde 1977).

In guilds in which species show large overlaps in the use of habitat, differences in body size might confer differences in diets to allow coexistence in a competitive environment. This has been shown for certain birds (Storer 1966, Hespenheide 1975, Cody 1975, Diamond 1975) and rodents (Brown 1975, Withers 1979). MacArthur (1972) pointed out that interspecific differences between body size of such consumers tended to be uniform on a logarythmic scale, within the guild. The five species in the predator-scavenger guild at Marion Island can be ranked into four non-overlapping size classes which differ from each other uniformly on a logarythmic scale (Fig. 4). It is not known to what extent the size differences conferred dietary differences in this guild but the size of penguin (adult or chick) each species was able to kill appeared to correlate with predator body size. In addition, the specific sequence of feeding at large, fresh carcasses appeared to be linked to the size-related dominance of each species. Very little overt or ritualised aggression occurred at carcasses, except between the similarly sized species of Giant Petrels (Johnstone 1977, pers. obs.).

Lesser Sheathbills could not handle some of the prey or carcasses eaten by the larger predator-scavengers. They could kill only the very smallest penguin chicks and had great difficulty in ripping open the skins of large chicks, adult penguins and seals. Conversely much of the food eaten by Lesser Sheathbills such as tiny pieces of flesh picked off skeletons was too small to be profitably eaten by larger birds. The Lesser Sheathbills in fact benefited by the presence of Giant Petrels and skuas which killed large penguins and ripped open the tough skins of penguins and seals. At carcasses, Lesser Sheathbills appeared to fill a similar "bone-picking" role as the Hooded Vultures *Necrosyrtes monachus* and Egyptian Vultures *Neophron percnopterus* did in the six-species guild of vultures in East Africa (Kruuk 1967).

The larger predator-scavenger species could not move amongst breeding penguins to search

for eggs, small chicks, carcasses or spilled penguin food as freely as Lesser Sheathbills. No other birds attempted to rob food from penguins feeding their chicks.

No birds, other than Lesser Sheathbills, ate intertidal algae at Marion Island. Limpets and other shore organisms were frequently eaten by Kelp Gulls which obtained most of their prey by swimming and diving in shallow subtidal water. These organisms were not, however, important in the diet of Lesser Sheathbills.

Lesser Sheathbills, Kelp Gulls and Kerguelen Terns *Sterna virgata* ate terrestrial invertebrates. The terns seldom ate this food and numbered fewer than 150 birds at Marion Island. Kelp Gulls ate large numbers of invertebrates and might have competed for this food with Lesser Sheathbills in a few localised areas, but the gulls appeared to eat only the larger prey. Introduced House Mice *Mus musculus* also ate the terrestrial invertebrates (J. Gleeson, pers. comm.) but the amounts eaten are not yet known.

4.3. WEATHER AND WAVES

The climate is typical of oceanic Sub-Antarctic islands, with frequent gales (on more than 100 days per year), low temperatures (averaging 5.3° C) and high precipitation (2600 mm annually) most of which falls as rain (Schulze 1971). Gales impeded the locomotion and feeding of Lesser Sheathbills but cold and rain appeared to have little effect. Heavy snow and frozen ground, which prevented Lesser Sheathbills from foraging for terrestrial invertebrates (Fig. 1) occurred on only 5% of days in the year on the coast. Prolonged periods of frozen ground resulted in the starvation of small numbers of Lesser Sheathbills (Burger 1979).

The tidal range at Marion Island is slight, with a spring maximum of 70 cm (De Villiers 1976). The effective intertidal zone is greatly extended by wave action so that Lesser Sheathbills could still eat algae at high tide. Onshore swells of 2 m or more, which prevented the birds from foraging in many intertidal areas (Fig. 1) occurred in the study area in every month but averaged only 10% of days in the year (unpubl. meteorological data). Big waves were considerably more frequent in other parts of the island's coast.

4.4. PREDATORS

Flocks of Lesser Sheathbills foraging further than 20 m from the shore almost invariably took flight towards the shore at the approach of a Sub-Antarctic Skua, even though the skuas seldom killed Lesser Sheathbills (Burger 1979). There was a significant inverse correlation between the mean distance from the shore that Lesser Sheathbills foraged for terrestrial invertebrates and the numbers of skuas present ($r = -0.57$, $P < 0.01$); when the skuas left the island for the winter the Lesser Sheathbills ventured further inland (Fig. 5). Lesser Sheathbills foraging on the shore or in penguin colonies kept a safe distance (a few metres) from skuas and giant petrels but the presence of these predators did not otherwise affect their foraging.

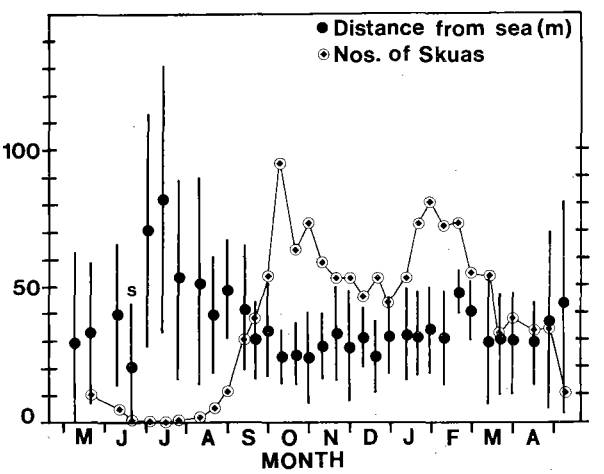


Fig. 5. Variations in the numbers of Sub-Antarctic skuas and the mean (± S.D.) distance from the shore of Lesser Sheathbills foraging for terrestrial invertebrates in the study area in 1976—1977. A day of heavy snow cover which prevented foraging by sheathbills in many areas is shown with an S.

5. FLOCK SIZE OF FORAGING BIRDS

Territories were maintained only by pairs of adult Lesser Sheathbills and only within penguin colonies. Breeding birds and their chicks derived virtually all their food from within their territories and nests were always within or

adjacent to penguin colonies (Burger 1979). The large aggregations of Lesser Sheathbills at King Penguin colonies (Fig. 6) also included non-territorial adults and immatures, which foraged solitarily in the undefended portions of the colonies and by intruding into territories. At the very large King and Macaroni Penguin colonies outside the study area, day-roosts of up to 300 non-territorial Lesser Sheathbills were seen. Groups of Lesser Sheathbills within Rockhopper Penguin colonies and the small Macaroni Penguin colonies in the study area remained small all year (Fig. 6, Table 4). In summer these colonies were almost exclusively occupied by territorial pairs and in winter very few Lesser Sheathbills foraged there (Fig. 1).

Most Lesser Sheathbills foraging on the intertidal zone or amongst kelp jetsam were solitary or in small flocks and the typical flock size for these habitats averaged three birds within the study area (Fig. 6) and was 3—6 birds

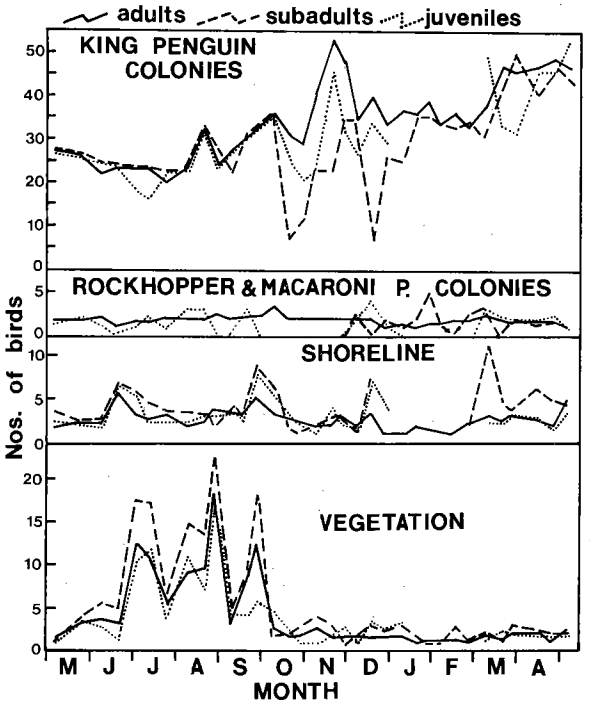


Fig. 6. Typical flock sizes of Lesser Sheathbills foraging in penguin colonies, the shoreline (including the intertidal zone and kelp jetsam, but excluding the beaches of the King Penguin colonies) and the coastal vegetated areas. Note that the ordinate of the data from King Penguin colonies is double that of the other data.

on the island as a whole (Table 4). Foraging flocks remained small even when large numbers of birds were using these habitats in winter (Fig. 1, Table 4). The flocks occurring on the vegetated coastal plain in winter were considerably larger (Fig. 6, Table 4) and a maximum flock of 80 birds was recorded there. The small numbers of Lesser Sheathbills foraging on the coastal plain in the summer precluded the formation of large flocks at that time.

6. DISCUSSION

6.1. THE BROAD TROPHIC NICHE

Lesser Sheathbills regularly ate portions of all food resources exploitable by land birds at Marion Island, with the exception of certain algae species, terrestrial plants, seeds and micro-invertebrates. Sheathbills of both species appear to have similarly broad diets at other locations (Table 7), although the data are scanty. Birds on species-poor islands generally have broad trophic niches, particularly with regard to the use of habitats (MacArthur *et al.* 1966, MacArthur & Wilson 1967, Diamond 1970, Morse 1971) but Sub-Antarctic or Antarctic Islands have not been studied in this respect (Abbot 1974). There are three major factors which make a broad trophic niche adaptive to Lesser Sheathbills at Marion Island.

Seasonality of the preferred food. Great seasonal fluctuation in food supply favours phenotypes with broad ecological niches and morphologies which allow them to exploit one set of resources in one season and another at a different time (Cody 1974).

According to Cody (1974) a species should concentrate on that part of the resource span which has a mean level of high predictability, within a certain period, and ignore other neighbouring resources at that time. These generalisations appear to apply to Lesser Sheathbills at Marion Island. Penguins supplied large amounts of food which was spatially concentrated, predictable and had high energy, protein and fat contents. When penguins were occupying their colonies, Lesser Sheathbills usually foraged there and tended to ignore other resources. The Lesser Sheathbills could

Table 7. A summary of the food eaten by *Chionis minor* and *C. alba* at six localities. The numbers refer to the references given below and the letters in parentheses (a or c) refer to albatrosses or cormorants respectively

Food items	*Chionis minor*				*Chionis alba*	
	Marion Island	Crozet Islands	Kerguelen Island	Heard Island	South Orkney Islands	Falkland Islands
Kleptoparasitised seafood						
From penguins	1	3	8	9, 10	12	14
From other birds	1(a)	2(a)				14(a)
Eggs						
Penguins	1	2, 3	4, 5, 6	10, 11	12, 13	14,15
Other birds	1(c)	2(ac)	5&6(c), 8		13(c)	14&15(c)
Small chicks						
Penguins	1	3, 4	4	10	12	
Carcasses						
Penguins	1	2, 3, 4	4, 5	10	12, 13	15
Other birds	1	2, 4	4, 5		12	15
Seals	1	2, 4	4, 5	10		15
Whales	1	2				
Seal placentae, blood & wounds	1	2	11	12, 13		
Seal milk	1	4	4	11		
Excreta						
Penguins	1	2, 3		10, 11	12	15
Other birds	1					15
Seals	1	2		10, 11	12, 13	14, 15
Unspecified		4	4			
Terrestrial invertebrates	1	2, 4	4	10		
Kelp flies, larvae & pupae	1	2, 4	4	10		
Intertidal organisms						
Algae	1	2, 4	5, 6, 7	10	12	
Mulluscs and crustaceans	1	2, 4	4, 5, 6	10	12	15
Human kitchen refuse	1	2, 4	4, 5	10	12	

References: 1 (this study); 2 (J.-F. Voisin, *in. litt.* 1978); 3 (Barrat 1976); 4 (Prevost & Mougin 1970); 5 (Paulian 1953); 6 (Sharpe (Kidder 1875); 8 (Hall 1900); 9 (M. C. Downes *in litt.* 1980); 10 (Ealey 1954 a, b); 11 (Downes *et al.* 1959); 12 (Jones 1963); 1: Clark 1906); 14 (Woods 1975); 15 (Cobb 1933).

not, however, specialise on any of the food items produced by penguins, since all were available in large quantities for only a fraction of the year. The birds were forced to be generalists within the penguin colonies. When the majority of the penguin colonies were deserted by penguins, the Lesser Sheathbills turned to resources in other habitats which required modification of feeding methods. These alternative resources (terrestrial, intertidal and shoreline invertebrates and algae) had less seasonality in availability than the food associated with penguins but the Lesser Sheathbills ate them only as a second choice.

Relative to most waders and plovers (Burton 1974) sheathbills do not appear to have morphologies which are specialised for any particular feeding method, although no study of the functional aspects of their anatomies has been attempted.

Low levels of interspecific competition. Small isolated islands usually have relatively few species due to problems of immigration and colonisation (MacArthur & Wilson 1967). As a result, island birds frequently have relatively broad foraging niches in response to low levels of interspecific competition for certain available resources (MacArthur & Wilson 1967, Diamond 1970, 1975, Lack 1976). Lesser Sheathbills at Marion Island appear to exploit many food resources without encountering significant interspecific competition. Only in penguin colonies did these birds encounter potentially high levels of interspecific competition. Even here, however, the exploitation of resources was probably mediated by the size differences between the members of the predator-scavenger guild. The Lesser Sheathbills' resource spectrum was as much restricted by their small body size, and thus the size of items

they could handle or kill, as by direct or diffuse interspecific competition. The predator-scavenger guild appeared to form a closed set, from which immigrants using the same resources might be excluded by diffuse competition (Diamond 1975).

Short-term weather variation. Weather can directly affect the availability of food resources, apart from indirectly affecting the seasonality and predictability of the resources (Cody 1974). This was certainly true in winter at Marion Island. Heavy snow or frozen ground and heavy onshore storm waves reduced the availability to Lesser Sheathbills of terrestrial invertebrates and intertidal organisms, but the birds were usually able to turn to other resources in these circumstances.

At islands with colder climates than Marion Island, continuous snow cover and frozen seas make terrestrial and intertidal food resources unavailable in winter and many sheathbills at these islands are forced to migrate northwards once the penguins and seals depart (Murphy 1936, Jones 1963). The combination of extreme isolation, precluding regular migration, and severe winters is probably the reason why no sheathbills occur on Bouvetøya which lies midway between the present ranges of *Chionis alba* and *Chionis minor* (Watson 1975).

6.2. SOCIAL ADAPTATIONS FOR EXPLOITING FOOD RESOURCES

Lesser Sheathbills foraged in territories, in flocks and solitarily. These variations in social behaviour appeared to be adaptations for exploiting food resources which had different qualities, spatial and temporal distributions and defendability.

Food available in penguin colonies had high energy, protein and fat contents, was spatially and temporally concentrated and was fairly predictable in supply. These are all characteristics which favour territoriality in birds competing for food resources (Brown 1964, Brown & Orians 1970, Davies 1978). Territorial behaviour was dependent on continued supply of food while penguins were present; Lesser Sheathbills abandoned territories in colonies of Macaroni and Rockhopper Penguins, when these penguins left the island for the winter (Burger 1980b). These Lesser Sheathbills then foraged solitarily or in flocks in other areas. Similar shifts from territorial behaviour to flocking in response to changes in food availability have been described for other bird species (Crook 1965, Zahavi 1971, Davies 1976).

Lesser Sheathbills feeding on terrestrial invertebrates on the coastal plain usually foraged in flocks. They were exploiting resources which were individually small objects, spatially scattered and patchy and which were either fossorial or cryptic (Burger in press). Sampling of areas was needed to find profitable patches. The predation risk to the Lesser Sheathbills in these areas was greater than elsewhere. Flocking has been shown to be adaptive in birds for locating and exploiting patchy food supplies (Cody 1971, Ward & Zahavi 1973, Krebs 1974), or for reducing predation risk (reviewed by Bertram 1978) or perhaps in attaining both these benefits (Kenward 1978, Rubenstein 1978). Flocking in Lesser Sheathbills is probably an adaptive response to improve food finding and also as an anti-predator measure, as discussed elsewhere.

On the intertidal and kelp jetsam zones, Lesser Sheathbills foraged solitarily or in twos and threes. The food taken here was specially scattered in a linear fashion, of medium to poor quality, occurred in predictable places and could support few birds per unit area. Predation risk was small. The resources were not suitable to support spatially restricted territorial birds. Food intake was limited by handling and digestion time (particularly when eating algae) but not search time. The advantages of flock-foraging did not therefore apply, either with regard to locating or exploiting food or avoiding predation.

6.3. THE IMPORTANCE OF PENGUINS TO SHEATHBILLS

Lesser Sheathbills at Marion Island, and sheathbills of both species at other localities bred only when they had access to food from penguins, or rarely cormorants (Burger 1979). The seasonal changes in foraging habits of Lesser Sheathbills at Marion Island were largely dictated by the availability of food from penguin colonies, and this is likely to be true

elsewhere. One can only speculate on whether the close association between sheathbills and penguins arose prior to the sheathbills' colonisation of the Antarctic and Sub-Antarctic or afterwards. Whatever the case, it is clear that this close association, coupled with the sheathbills' abilities to switch to other resources when necessary, has been fundamental to their success as land-based birds on very inhospitable islands.

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8. SUMMARY

Lesser Sheathbills *Chionis minor* were the only birds at Marion Island, in the Sub-Antarctic, entirely restricted to land-based food. At penguin colonies the sheathbills fed on carcasses, eggs, small chicks, excreta and seafood kleptoparasitised from the penguins. At seal colonies they commonly ate carcasses, placentae and blood. In the intertidal zone the sheathbills took algae (*Porphyra* sp.), amphipods, limpets and other invertebrates, and from kelp jetsam on beaches they took kelp flies and oligochaetes. On the vegetated coastal plain they ate invertebrates, mainly earthworms and insects. Seasonal changes in the foraging habits were dictated by the availability of food from penguins, which provided concentrations of food with high energy, protein and fat contents. Predatory skuas *Catharacta skua lonnbergi* affected the foraging of Lesser Sheathbills on the coastal plain. The foraging habits of adult, subadult and juvenile Lesser Sheathbills were broadly similar but adults fed more commonly in penguin colonies. Three factors which favoured a broad trophic niche in Lesser Sheathbills were: seasonal fluctuations in availability of preferred food from penguin colonies; the paucity of interspecific competition; and short-term weather variations, particularly snow and heavy waves. Co-existence between Lesser Sheathbills and the other four species of predator-scavenger birds at Marion Island was probably facilitated by differences in specific body masses. Lesser Sheathbills foraged in territories, in flocks and solitarily; each social arrangement appeared to be adapted to the nature of the food resource being exploited. The close association with penguins is fundamental to the success of sheathbills as land-based birds on inhospitable islands.

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10. SAMENVATTING

Van alle vogels van Marion Eiland in de subantarctische Indische Oceaan waren de Kleine Zuidpoolkippen *Chionis minor* de enige die uitsluitend voedsel van terrestrische oorsprong of op het land zochten. In pinguinskolonies (vooral Geelkuifpinguins of Rotsspringers) voedden zij zich met dode vogels, eieren, kleine jongen, uitwerpselen en van uit zee afkomstig voedsel dat zij van de voedsel aandragende pinguins stalen (kleptoparasitisme, Tabel 1 en 2; zie Ardea 67 (1979): 14). In zeeleeuwkolonies aten zij ook van dode dieren, placentas en bloed. In de getijdezone aten zij wieren (Porphyra), kleine kreeftjes (Amphipoda), napjesslakken en andere ongewervelde dieren (invertebraten), en tussen de op het strand aangespoelde kelp (grote drijvende wieren) vingen zij vliegen en wormen. Op de begroeide kustvlakte aten zij invertebraten, vooral regenwormen en insecten. Seizoensveranderingen in foerageergewoonten (Fig. 1) werden grotendeels bepaald door de beschikbaarheid van voedsel dat zij van pinguins konden stelen en dat niet alleen van hoge energische waarde was, maar dat ook veel eiwitten en vetten bevatte (Tabel 6). De roofgewoonte van Grote Jagers *Catharacta antarctica* beïnvloedde het voedsel zoeken van zuidpoolkippen op de kustvlakte (Fig. 5). Adulte, subadulte en jonge vogels voedden zich op dezelfde wijze, maar de volwassen vogels zochten meer dan de andere hun voedsel in de pinguinkolonies (Tabel 3). De volgende drie factoren hielpen mee aan het totstand komen van een ruime voedsel-niche: seizoensschommelingen in de beschikbaarheid van voorkeursvoedsel uit de pinguinskolonies, het vrijwel ontbreken van interspecifieke concurrentie, en de snel optredende weersveranderingen, vooral hevige sneeuwval en hoge stormgolven. Het samen voorkomen van Kleine Zuidpoolkippen en vier andere rovende en aasetende vogelsoorten op Marion Eiland, te weten de twee soorten reuzenstormvogels, de Zuidelijke Mantelmeeuw en de Subantarctische (Grote) Jager, werd waarschijnlijk vergemakkelijkt door verschillen in specifieke lichaamsgrootte (Fig. 4). Kleine Zuidpoolkippen zochten hun voedsel alleen of in troepen; de sociale ordening scheen direct te zijn aangepast aan de ter plaatse benutte voedselbron. De nauwe samenhang met pinguins, zo niet hun afhankelijkheid van pinguinkolonies, is de grondslag van het succes van zuidpoolkippen als aan land gebonden vogels levend op onherbergzame eilanden in een stormachtige oceaan — KHV.