BEHAVIOURAL ECOLOGY OF LESSER SHEATHBILLS
CHIONIS MINOR AT MARION ISLAND

BY

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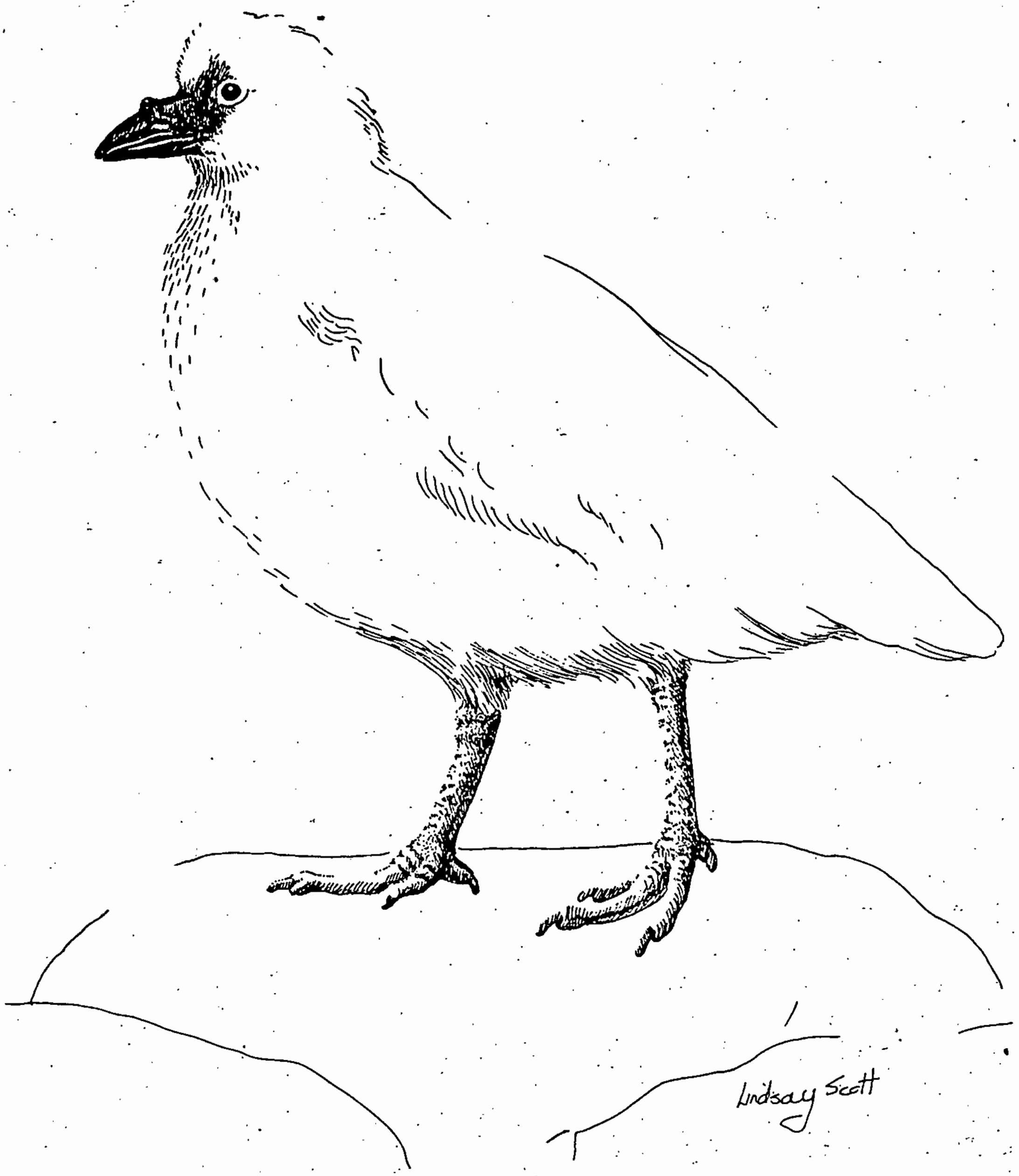
Lindsay Scott

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CONTENTS

ABSTRACT

Adaptations to island life have seldom been studied in birds outside temperate or tropical regions. Lesser Sheathbills *Chionis minor* (Charadriiformes; Chionididae) were studied at Marion Island ($46^{\circ}54'$S, $37^{\circ}45'$E) and the ways in which their feeding ecology, breeding biology and social behaviour were adapted to existence on a sub-Antarctic island were assessed. The birds' reproductive output and post-fledging survival rates were estimated and probable factors limiting the population examined. Seasonal and spatial variations in the diet and foraging habits were related to the quality, availability and distribution of food, and the effects of interspecific competition, the weather and predators. The adaptiveness of the broad trophic niche was investigated. A hypothesis that the variable social behaviour facilitated exploitation of variable food resources to benefit individual birds was examined; particular attention was paid to territoriality among breeding (summer) and non-breeding (winter) adults within penguin colonies and flocking amongst birds foraging on the coastal plain. Time and energy budgets of birds feeding in these habitats were drawn up. Displays by Lesser Sheathbills were described and their functions in territories, flocks, at nest sites and in sexual interactions were quantitatively assessed. Seasonal changes in the frequencies of certain displays were shown. The role of testosterone as a possible mediator of seasonal changes in sexual and territorial behaviour in adult males was examined. The selections of prey, habitats, foraging periods and group sizes by birds eating invertebrates on the coastal plain were examined as possible means of optimising feeding success and/or reducing predation risk. The time and energy demands of pairs rearing chicks were estimated in order to test a hypothesis that access to penguin colonies was essential for successful breeding in Lesser Sheathbills. This allowed an estimate to be made of the amounts of food kleptoparasitised by breeding pairs from the penguins in this particular situation. Morphometric data, aging characters and moult patterns were described. The roles of Lesser Sheathbills within the island's ecosystem were described and the energy taken by a sample population from penguins, seals, intertidal organisms and terrestrial invertebrates was estimated.

BEHAVIOURAL ECOLOGY OF LESSER SHEATHBILLS (*CHIONIS MINOR*) AT MARION ISLAND

INTRODUCTION

Most people visiting Antarctic and sub-Antarctic regions regard sheathbills as unattractive, inquisitive birds usually found in foul-smelling penguin colonies. Early naturalists describe them as having "a strong resemblance .... to the pigeons, in general appearance, gait and mode of flight" (Kidder and Coues 1876) or "like a small white hen" (Moseley 1892). Scientific interest in sheathbills has centred on elucidating their systematic position; they are now accepted to belong to the Charadriiformes but their relationships within the order are still debated (Sibley and Ahlquist 1972, Jacob 1978, Strauch 1978). Their ecology and behaviour have largely been ignored but these aspects are worthy of attention.

Sheathbills (Chionididae) are the only avian family with a breeding range entirely within the Antarctic and sub-Antarctic (Fig. 1). There are two species in the family. The Wattled Sheathbill *Chionis alba* breeds on the Antarctic Peninsula and islands of the Scotia Arc and occurs as a non-breeding migrant at the Falkland Islands, Tierra delFuego and the Patagonian coast. The Lesser Sheathbill *C. minor* is resident on four island groups in the southern Indian Ocean. Sheathbills are perhaps the

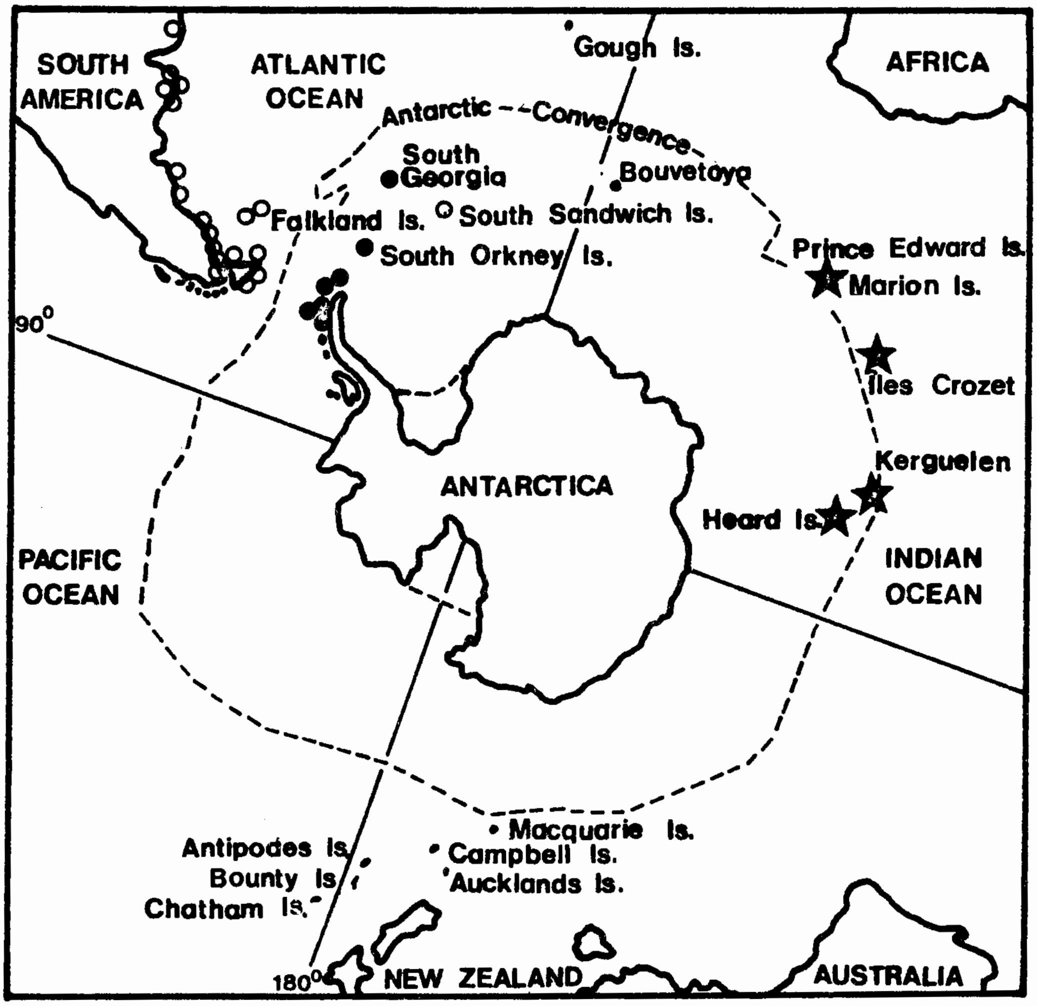

Fig. 1. The Antarctic and sub-Antarctic, showing the location of Marion Island, which is part of the Prince Edward group, the breeding ranges of the Wattled Sheathbill <u>Chionis alba</u> (●) and the Lesser Sheathbill <u>C. minor</u> (★) and the wintering localities of non-breeding <u>alba</u> (○). Data from Watson <u>et al</u>. (1971).

most successful land-based birds in an area where the avifauna is dominated by seabirds (Watson 1975). The islands inhabited by sheathbills have hostile environments, with severe climates, low ecological diversity and few food resources. This study aims to elucidate the characteristics of the behaviour and ecology of the Lesser Sheathbill, which enable it to survive as the only land-based bird at Marion Island in the Prince Edward Islands.

Most of the current ideas related to island biogeography have been formulated and tested in northern temperate or tropical island systems (eg. Darwin 1859, Wallace 1880, MacArthur and Wilson 1967, Lack 1970, 1976, Diamond 1970, 1975, Simberloff 1976). With few exceptions (Abbott 1974, 1978, Abbott and Grant 1976, Burger, Williams and Sinclair in press) the biology of birds on sub-Antarctic and cold-temperate southern islands has not been studied within the context of modern biogeographical theory.

This study examines the effects on Lesser Sheathbills of some of the factors affecting island birds in general, such as reduced interspecific competition and low ecological diversity, and also some factors specifically important on sub-Antarctic islands such as great seasonality in the availability of certain resources and the inhospitable climate.

One of the neglected aspects in the study of island biology is the influence of the environment on the social behaviour of animals (Wallace 1978). Lesser Sheathbills exhibited striking variations in social behaviour, including flocking and territoriality. This study tests the hypothesis that these behaviour patterns are adaptations facilitating the use of food resources with different properties, to benefit the individual bird.

One of the ultimate aims of a multi-disciplinary research programme at Marion Island (Siegfried in press) is the production of quantitative models of the energy and nutrient pathways in the island's ecosystem. My study was designed within the general framework of this programme and some of the important roles played by Lesser Sheathbills in the ecosystem are described. More specifically, however, the major aims of the study were:

1. to describe the breeding biology and survival of Lesser Sheathbills, in an attempt to isolate limiting factors in the Marion Island population;

2. to describe the food, foraging behaviour and social behaviour of the birds in relation to seasonal and spatial variations in food quality and availability;

3. to describe the displays, pair-bonds and territorial systems of Lesser Sheathbills;

4. to examine the possible roles of testosterone in mediating seasonal variations in the birds' sexual and territorial behaviour;

5. to examine the costs and benefits of territoriality, particularly in those adult birds which remained territorial

in winter, outside the breeding season, at a time when other conspecifics had abandoned territories;

6. to examine the behavioural adaptations used by the birds when exploiting terrestrial invertebrates, a resource of small prey objects, which are spatially scattered and patchy;

7. to estimate the birds' costs of breeding at the period of maximum energy demand, ie. while feeding chicks, and to determine the conditions necessary for meeting these energy costs;

8. to provide morphometric data for Lesser Sheathbills at Marion Island; and,

9. to provide data on the biomass, densities and distribution of terrestrial invertebrates which are important prey for Lesser Sheathbills in winter.

Lesser Sheathbills were studied at Marion Island (46° 54'S, 37° 45'E, area 290 km^2) from January to November 1974, May 1976 to May 1977 and April and May 1978. Brief observations were also made at neighbouring Prince Edward Island (46° 38'S, 37° 60'E, area 44 km^2). The islands were formed about 276 000 years ago as the summits of a shield volcano rising from the ocean floor (Verwoerd 1971). For the purposes of this study four habitats were recognised on Marion Island; the barren mountainous interior which is a cold desert; the coastal plain, which comprises areas with tundra-like vegetation interspersed with relatively barren recent lava flows; the shoreline, comprising rocky beaches, cliffs and lava platforms; and penguin colonies, which are generally rocky or muddy and devoid of vegetation. The last three habitats are used by Lesser Sheathbills.

The avifauna at the Prince Edward islands comprises 29 breeding species, of which penguins have the greatest populations and biomass (Williams *et al* 1979). The mammal fauna comprises three seal species, feral cats and feral mice (Skinner in press). The vegetation is dominated by grasses, bryophytes, ferns and low perennial angiosperms and is generally lower than 30 cm (Huntley 1971). The climate is typical of oceanic sub-Antarctic islands (Schulze 1971): it is cool to cold (mean 5°C, maximum range -7° to 22°C), very windy (gales exceeding 34 km hour $^{-1}$ blow on over 100 days p.a.), with frequent precipitation (over 1mm falls on 248 days p.a.) averaging 2 576mm p.a., most of which falls as rain. The recent formation of the islands, their isolation and the harsh climate are believed to be responsible for the low ecological diversity and relatively simple food webs (Van Zinderen Bakker Sr 1971).

Most of the quantitative observations were made within a 100 ha study area, along 5 km of the north-eastern coast of Marion Island (Fig. 2). This area contained a good

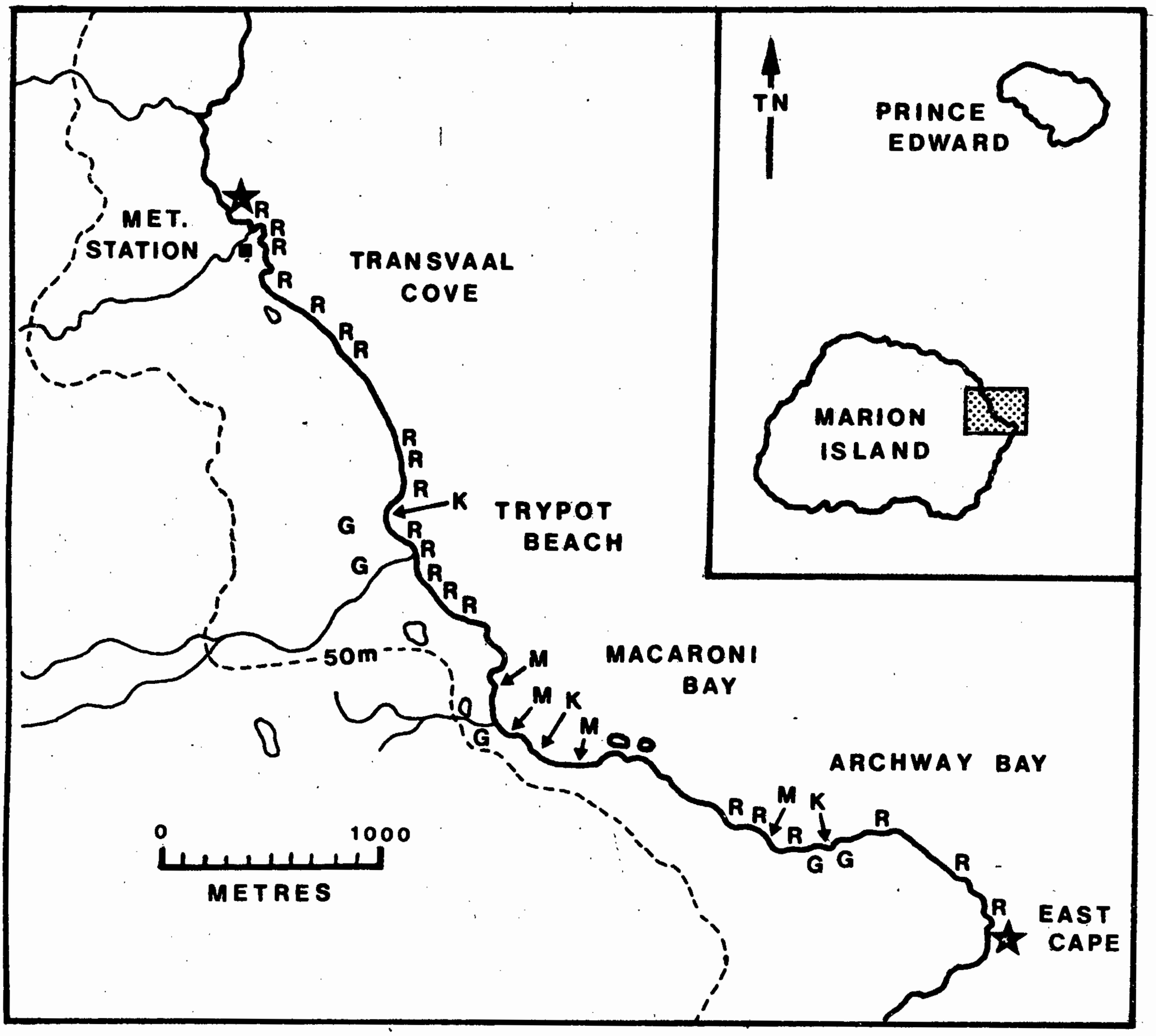

Fig. 2. Map of the main study area at Marion Island showing the limits of the study area (stars), colonies of Rockhopper Penguins Eudyptes chrysocome (R), Macaroni Penguins E. chrysolophus (M), Gentoo Penguins Pygoscelis papua (G) and King Penguins Aptenodytes patagonicus (K), the 50 m altitude contour (stippled line), small streams and ponds.

sub-sample of the habitat available to Lesser Sheathbills and included colonies of all four penguin species and breeding populations of most of the other bird species.

This dissertation comprises a series of papers which have been published or submitted for publication. This format was selected to facilitate rapid communication of the results. I apologise for the minor inconsistencies in style and occasional repetition.

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PART ONE

BREEDING BIOLOGY, MOULT AND SURVIVAL OF LESSER SHEATHBILLS

1. Introduction

Sheathbills are aberrant charadriiform shorebirds which breed in association with penguins in certain Antarctic and sub-Antarctic regions. They have received considerable attention from systematists interested in their relationships within the Charadriiformes (reviewed by Jacob 1977, Strauch 1978). Despite their approachable nature, there have been few studies of these birds in the field, the only detailed work being that of Jones (1963).

The sheathbills are a monogeneric family (Chionididae) of two species. The Wattled Sheathbill *Chionis alba* breeds on the Antarctic Peninsula and islands of the Scotia Arc and occurs as a non-breeding migrant at the Falkland Islands, Tierra del

Fuego and the Patagonian coast (Murphy 1936, Jones 1963). The Lesser Sheathbill Chionis minor (Fig. 1= Frontispiece) has populations at four island groups in the southern Indian Ocean : the Prince Edward Islands, the Crozet Islands, Kerguelen and Heard Island (Watson 1975). The populations of Lesser Sheathbills appear to be genetically isolated at present and are sometimes treated subspecifically (Peters 1934). No sheathbills occur at Bouvet Island which lies midway between the present ranges of the two species.

This paper reports on aspects of the breeding biology, moult and survival of Lesser Sheathbills at Marion Island (46° 54' S, 37° 45' E), part of the Prince Edward group. Comparisons are made, where possible, with sheathbills of both species at other locations. Brief field observations of Lesser Sheathbills have been made at Marion Island (Moseley 1892, Rand 1954), the Crozet Islands (Despin et al. 1972, Derenne et al. 1976), Kerguelen (Kidder 1875, Sharpe 1879, Hall 1900, Paulian 1953), Heard Island (Ealey 1954a, 1954b, Downes et al. 1959) or at several of these islands (Hutton 1865, Falla 1937, Prevost and Mougin 1970).

2. Study area and methods

Marion Island lies 2° lattitude north of the Antarctic

Convergence, and the climate and biota are typically sub-Antarctic (Van Zinderen Bakker *et al.* 1971). Field work totalling 25 months was done between 1974 and 1978 and covered all months of the year. Observations were concentrated in a 100 ha study area, including 5 km of coastline, on the north-eastern side of the island. There were on average 197 Lesser Sheathbills within this area. About 3 000 pairs of King Penguins *Aptenodytes patagonicus*, 2 100 pairs of Macaroni Penguins *Eudyptes chrysolophus*, 1 400 pairs of Rockhopper Penguins *E. chrysocome* and 250 pairs of Gentoo Penguins *Pygoscelis papua* bred within the study area.

Lesser Sheathbills were sexed and aged using size and external appearance criteria (Appendix one). Adults were all birds older than three years, subadults were one or two years old and juveniles were fledged birds less than one year old. Breeding adults were classified as those which were known to have attempted breeding. In April following the breeding season the study population comprised 64% adults, 14% subadults and 22% juveniles.

Estimates of survival, local movements and the age of first breeding were obtained from 480 Lesser Sheathbills which were ringed. Most birds were also individually colour-ringed. The survival of colour-marked breeding adults was monitored from season to season since they returned to breed in the same territories (Part three .). Immature and non-breeding adults were less regular in their habits and an intensive search for ringed birds was made in 1976. It was possible to read ring numbers with binoculars, without capturing the birds. Birds resighted in 1976 had been ringed one or two years previously. This necessitated estimating the annual survival(s) separately for each year of ringing, using the equations :

$$N_1 = N_o s$$

$$N_2 = (N_o s) s$$

where N_o was the total ringed in each year and N_1 and N_2 were the numbers resighted after one and two years respectively. Differences between the percentage survival of two groups were tested for statistical significance using formulae and tables by Cass (1973: 72).

Breeding biology was studied in three seasons but most data were obtained in the 1976/77 season. Nests were visited daily to determine laying and hatching dates. Few eggs were weighed when fresh and fresh weights (W) were thus calculated from the length (L) and breadth (B) using the formula $W = 0.5463\ L\ B^2$ (Romanoff and Romanoff 1949: 107). Newly hatched chicks were marked with thin plastic rings and weighed daily until the 55th day after hatching. The culmen, tarsus and wing lengths were measured on every fifth day of age. Most of the observations were made at Rockhopper Penguin colonies and some at King and Macaroni penguin colonies.

Lesser Sheathbills were examined for moult throughout the year. Stages of growth of the primary remiges were scored using a numerical system (Newton 1966). Other feather tracts were merely examined to see whether any feather growth was in progress.

3. Breeding biology

3.1 The breeding season

Lesser Sheathbills at Marion Island and elsewhere (Hall 1900, Downes *et al.* 1959, Despin *et al.* 1972) breed annually during the austral summer. At Marion Island nest building was first seen on 4 October and by 10 November all nests had fresh material in them. Copulation was seen between 11 November and 30 December.

The earliest egg was laid on 4 December and 95% of all eggs had been laid by 31 December (n = 94 eggs from the 1974/75 and 1976/77 seasons). The modal date of laying of first eggs was 11 - 17 December. The latest clutch was laid in the period 16 - 19 January but these eggs were not incubated. Hatching occurred in January and chicks were independant in the third week in March. Lesser Sheathbills at Marion Island bred at the same time as the three common penguin species (King, Macaroni and Rockhopper penguins) from which the sheathbills obtained most of their food (Fig. 2).

3.2 The age of first breeding

The estimated age of first breeding was three to four years. No ringed birds controlled in their first (n = 15) or second years (n = 11) attempted breeding, but four birds, two of each sex, attempted breeding at the end of their third year. All four were seen to display to other birds; two copulated; two built nests; three defended territories; but only one, a male, successfully reared a chick after mating with a female which was known to have bred successfully in three previous seasons.

During the breeding season there were always small numbers of adults present which did not attempt breeding, probably because they had not established territories. Four adults were recorded as non-breeders for three successive seasons.

3.3 Territories and nest sites

All Lesser Sheathbills seen breeding at Marion Island were territorial and all territories included breeding penguins. Information on the size, location, tenure and defence of territories is given elsewhere (Part three .).

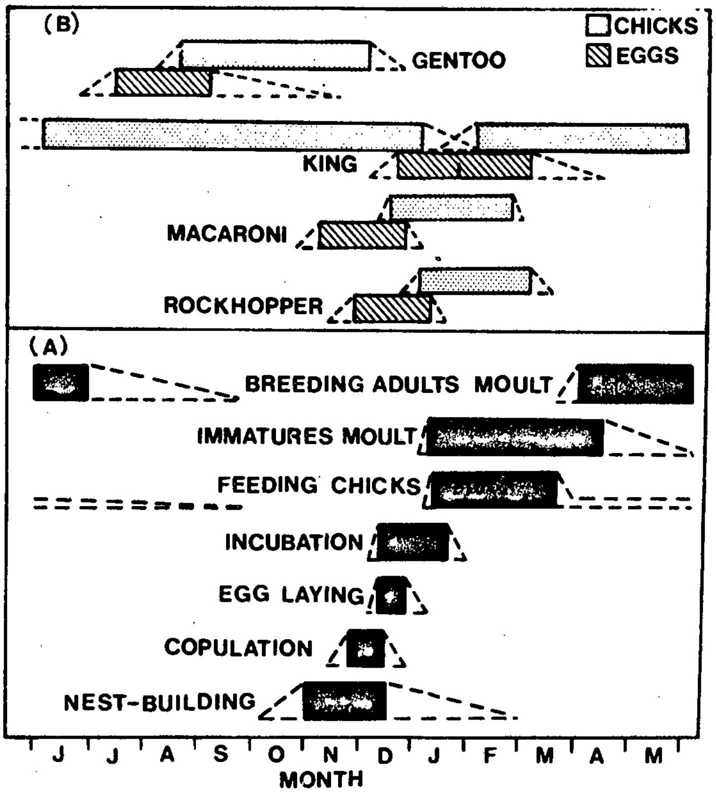

Fig. 2. The timing and duration of breeding and moult of Lesser Sheathbills at Marion Island (A) compared to the breeding activities of the four penguin species at the island (B). The periods of peak activity are shown as solid bars and the known extremes as dashed lines.

Nests were generally situated within the territories used for foraging but about 5% of the pairs had separate nest sites and foraging territories 10 - 50 m apart. Nests were situated in crevices, under lava boulders, in small caves and, rarely, in burrows of the larger species of petrels. Nests were 20 - 100 cm from the surface. The pure white plumage of adult Lesser Sheathbills was often conspicuous amongst the dark lava but when at the nest, the adults were generally hidden from view.

Nests consisted of untidy heaps of kelp debris, feathers and leaves, similar to those of the Wattled Sheathbill (Murphy 1936, Jones 1963). The adults frequently carried shells of penguin eggs to the entrances of the nests, where they dropped them. Many nests were recognisable by the small piles of white eggshells at their entrances. This was also observed at Lesser Sheathbill nests at Heard Island (Downes _et al._ 1959). One pair at Marion Island used white polystyrene fragments in the same way. The significance of this behaviour is not known, but the birds were perhaps using eggshells to signal the presence of an established nest. This might deter other adults seeking breeding sites but could also be disadvantageous if predators, such as Sub-Antarctic Skuas _Catharacta antarctica_, were attracted.

3.4 Eggs and incubation

Clutches ranged between one and four eggs and two and three eggs were most common, as with the Wattled Sheathbill (Table 1). Nest building but not relaying was observed following the loss of a clutch. The laying interval between first (A) and second (B) eggs averaged 3.6 days and between B and third (C) eggs 4.0 days (Table 2). The mean length, breadth and mass of A, B and C eggs did not differ significantly (Paired t-test, $P > 0.05$ in each case, Table 3). The mean size of all Lesser Sheathbill eggs was 54.7 x 37.2 mm (41.7g).

The nest was continuously occupied by one of the parents from the day the first egg was laid, except for brief periods during nest relief or during disturbances (by skuas, etc.) near the nest. Both sexes had two elongated lateral brood patches, each about 19 cm^2, which were unfeathered from the time of laying until the chicks were 50 - 60 days old. These brood patches appeared to be large enough to heat four eggs comfortably, two on either side.

Males had longer diurnal incubation shifts than females. The mean for males was 172 minutes (range 124 - 243 min., $n = 9$) and for females 90 minutes (61 - 158 min., $n = 7$). Females perhaps needed to forage more than males at this time, to replace energy reserves used during ovogenesis. The off-duty bird foraged for most of the time, chased intruders from

Table 1 : Clutch size of *Chionis minor* & *C. alba*

No. of eggs in clutch	Number of clutches			
	C. minor at Marion Island		*C. alba* at Signy Island	
	1974-75	1976-77	1961-62	1962-63
1	0	1	9	3
2	3	15	23	22
3	3	15	13	41
4	0	1	3	0

Data from this study, Jones (1963) and unpublished British Antarctic Survey reports (courtesy of J.P. Croxall).

Table 2 : Laying & hatching intervals between first (A), second (B) and third-laid (C) eggs of Lesser Sheathbills at Marion Island

	Interval (days)									No.
	0	1	2	3	4	5	6	Mean	Mode	clutches
Laying										
A - B	0	0	0	13	9	3	0	3.6	3	25
B - C	0	0	0	3	10	1	1	4.0	4	15
Hatching										
A - B	7	7	3	0	0	0	0	0.8	0-1	17
B - C	0	0	1	4	2	1	0	3.4	3	8

Table 3 : Linear dimensions & masses of Lesser Sheathbill eggs at Marion Island

Dimension	1st egg (A)	2nd egg (B)	3rd egg (C)
Length (mm)			
$\bar{x} \pm$ S.D.	54.7 ±1.7	54.7 ±1.6	54.4 ±2.5
range	52.4 - 58.4	51.7 - 58.5	49.7 - 58.0
Breadth (mm)			
$\bar{x} \pm$ S.D.	37.3 ±0.9	37.2 ±0.6	37.2 ±0.5
range	36.3 - 38.5	36.6 - 38.3	36.4 - 38.0
Mass[1] (g)			
$\bar{x} \pm$ S.D.	41.9 ±1.9	41.7 ±1.8	41.3 ±2.1
range	40.0 - 47.0	39.0 - 44.0	39.0 - 45.0
No. of eggs	26	29	12

[1] Calculated from length and breadth

the territory, or preened while standing outside the nest entrance. No data are available on nocturnal incubation behaviour but both parents were found inside nest cavities at night.

Hatching was asynchronous. On average, the first egg hatched one day before the second which in turn hatched three days before the third (Table 2). Second and third eggs were incubated for an average of 29 days and the first egg for 31 days (Table 4).

The mean hatching success was 68% with no significant differences between first, second and third eggs (X^2 test, $P > 0.05$ in each case, Table 5). Two of the 20 eggs which failed were addled, one cracked and broke, and five were destroyed by waves from stormy seas. The other 12 eggs disappeared without the cause being apparent. Some might have rolled out of the nests. Intraspecific predation is also probable. On several occasions sheathbills were seen to enter nest cavities containing eggs or chicks, which were not their own. In each instance the parent in the nest cavity immediately chased the intruder out. Jones (1963) cited intraspecific predation as a possible cause of egg mortality in *C. alba*.

Table 4 : Incubation periods (days between laying & hatching) of first (A), second (B) and third-laid (C) eggs of Lesser Sheathbills at Marion Island

Eggs	Mean	Range	No. eggs
A	31.4	30 - 33	16
B	29.0	27 - 31	17
C	28.7	28 - 30	7

Table 5 : Survival of eggs & chicks of Lesser Sheathbills at Marion Island. Data on eggs from the 1976-1977 season & on chicks from several seasons.

	Laying sequence					Total
	First (A)	Second (B)	Third (C)	Fourth (D)	Not known	
Egg survival						
No. laid	26	24	12	1	-	63
No. hatched	16	18	8	1	-	43
% survival	62	75	67	100	-	68
Chick survival						
No. hatched	18	16	9	1	4	48
No. fledged	14	6	5	0	2	27
% survival	78	38	56	0	50	56

3.5 Chicks

At hatching Lesser Sheathbill chicks were covered in mottled brown down and were able to walk about the nest cavity although they seldom did so. They were brooded almost continuously for the first 14 days and less after that, until by their 30th day they were brooded for less than 10% of the daylight period (03h45 - 19h30). Both parents brooded the chicks, males for a mean shift of 54 ± 46 (S.D.) minutes (range 8 - 263 minutes, n = 37) and females for 56 ± 78 minutes (8 - 495, n = 43) during daylight. These times did not differ significantly (Student's t-test, $P > 0.05$).

The post-natal plumage changes were very similar to those of the Wattled Sheathbill (Jones 1963). Dark grey mesoptile down replaced the brown natal down from 7 - 14 days of age and white contour feathers erupted from the 12th day to cover the bird by the 50th day.

The parents fed the chicks at the nest for about 50 days and elsewhere in the territory until the 55 - 60th day. The chicks stood at the entrances to the nest cavities for increasing periods from about the 15th day onwards, and they wandered 1 - 2 m from the nest at about the 30th day. By the 50th day chicks frequently wandered 10 m from the nest and undertook brief flights. By the 55 - 60th day they were foraging independently but usually in the company of a parent from whom they still accepted food.

Lesser Sheathbills very seldom foraged outside penguin colonies when breeding. Food was carried in their beaks to the chicks and not regurgitated. During observations at three nests in Rockhopper Penguin colonies the sheathbill parents obtained 97% of the meals (n = 2 362) delivered to chicks during the first 50 days after hatching, from within penguin colonies and the remaining 3% comprised terrestrial invertebrates taken from bordering vegetated areas. During a seven-hour watch at these three nests, 139 meals out of 176 delivered to the chicks, could be identified. These meals consisted of crustaceans stolen from Rockhopper Penguins (91%), flesh from penguin carcasses (7%) and fresh penguin excreta (2%). The adult diet appeared to be similar. Lesser Sheathbills breeding in King and Macaroni penguin colonies also fed their chicks almost entirely on food taken from penguins. Those at King Penguin colonies seemed to feed proportionately more carcass flesh to their chicks than those at Rockhopper Penguin colonies.

Crustaceans (mainly pelagic amphipods, euphuasids and copepods), fish and squid were obtained from regurgitant spilled by penguins feeding chicks. The sheathbills greatly increased the frequency and amount of spillage by leaping or flying against penguins in the act of regurgitation (Fig. 3). The majority of food obtained from penguins was obtained by this kleptoparasitism.

The growth of 13 chicks which fledged from nine nests was measured in 1977. These included seven, two and four chicks from first (A), second (B) and third laid (C) eggs respectively. The tarsus had the most rapid initial growth of the appendages measured and had reached adult size by the 30th day (Fig. 4). This coincided with the time when the chicks began to wander a few metres from the nest. The culmen grew gradually during the first 40 days and very little thereafter. The wing (manus and primary feathers) grew rapidly from the 10th day and was almost adult size at fledging (55 days). Chick weight had a typical sigmoid growth curve (Fig. 5) to reach a mean asymptote of 483 g, equivalent to 98% of the mean weight of breeding adults, on the 48th day. The mean weight at fledging was slightly less than the asymptote.

The masses of chicks from A, B and C eggs, measured within 24 hours of hatching, did not differ significantly (paired t-test, $P > 0.05$ in each case, Table 6). The A chicks were 0 - 2 days old when the B chicks hatched but the differences in mass at that stage were not significant ($P > 0.05$, Table 6). By the time the C chicks hatched, however, both the A and B chicks had grown to be significantly heavier than the newly hatched C

Fig. 3.. Kleptoparasitism by a Lesser Sheathbill. The sheathbill waited until the Rockhopper Penguin was regurgitating food to its chick and then leaped against the penguin to induce spillage of the regurgitant. Lesser Sheathbills obtained most of the food fed to their chicks in this manner.

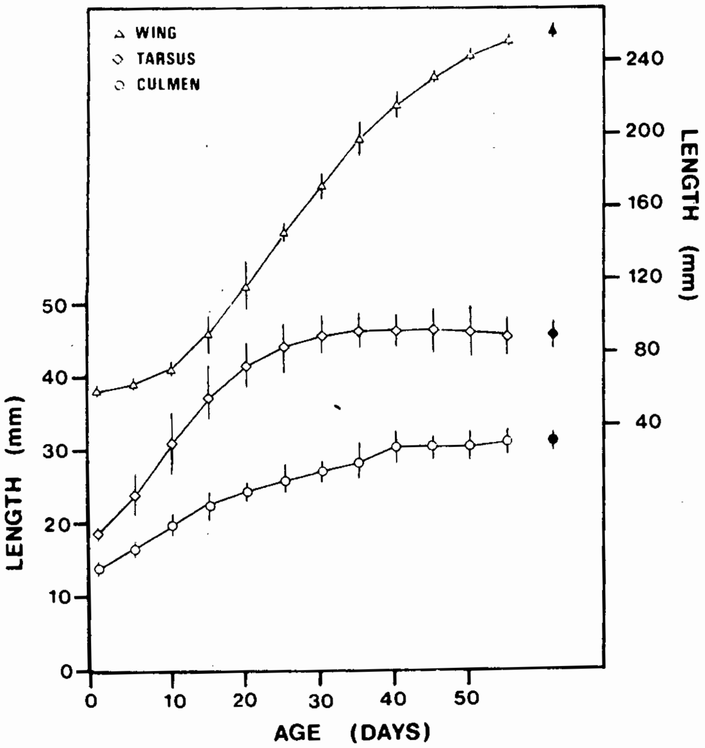

Fig.4

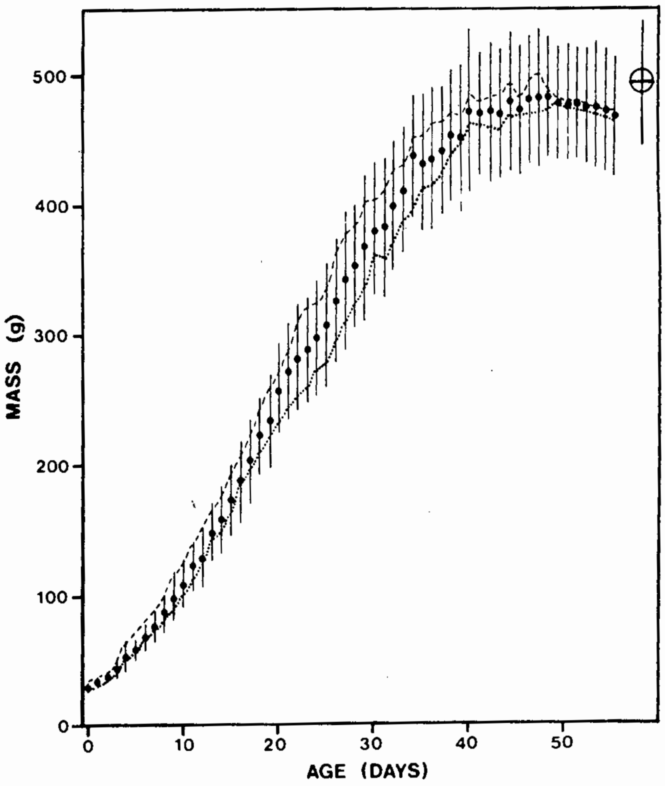

Fig.5

Fig. 4. Growth of the tarsus, culmen and wing (chord) in Lesser Sheathbill chicks. The mean ± S.D. is shown at five day intervals. Adult dimensions are given as shaded symbols.

Fig. 5. Growth in mass of Lesser Sheathbill chicks. The mean ± S.D. of all chicks is given at daily intervals. The mean mass of chicks reared singly (dashed line) is compared to that of chicks reared in broods of two chicks (dotted line). The mean mass (± S.D.) of breeding adults is indicated by the open symbol on the right.

Table 6 : Masses (g) of Lesser Sheathbill chicks on the day of hatching, & on the days when chicks hatched from second (B) and third (C) eggs

Day of measurement	Hatching sequence of chicks		
	A	B	C
Within 24h of hatching			
$\bar{x} \pm$ S.D.	28.3 ± 3.2	26.6 ± 2.7	26.3 ± 0.7
range	23 - 35	23 - 30	25 - 27
No. of eggs	12	10	8
Day when B chick hatched			
$\bar{x} \pm$ S.D.	28.3 - 4.0	26.1 - 2.8	-
range	23 - 35	23 - 30	-
No. of eggs	8	8	-
Day when C chick hatched			
$\bar{x} \pm$ S.D.	52.0 ±15.1	41.6 ± 9.3	26.3 ± 0.7
range	37 - 80	30 - 58	25 - 27
No. of eggs	8	7	8

chicks ($P < 0.01$, Table 6). The A chicks were then heavier than the B chicks but these differences were not significant ($P > 0.05$). The A chicks were heavier than sibling B and C chicks throughout the nestling period at most nests and for the first 35 days at all the nests observed (Fig. 6). Similarly B chicks were generally heavier than sibling C chicks. Chicks reared singly were on average heavier than those reared with siblings, but had similar masses at fledging (Fig. 5).

Survival of chicks prior to fledging averaged 56% (Table 5). Starvation, predation and accidents seemed to be the main causes of chick mortality. Out of 16 chicks monitored daily which died, four underweight chicks (over one S.D. below the mean mass for their age) were found dead and six disappeared, four chicks of average mass disappeared and two were found dead, one was apparently squashed in the nest and the other apparently trampled by a penguin outside the nest. The chicks which disappeared could have been taken by predatory Sub-Antarctic Skuas, which were seen on several occasions to swoop towards Lesser Sheathbill chicks standing at the nests' entrances. Chicks which died of starvation inside the nests might have been removed or eaten by the parents.

Most chick mortality occurred within the first three weeks of hatching (Table 7). Mortality was correlated with hatching sequence : all A chicks and some B chicks apparently died from predation or accidents but all D and C chicks and

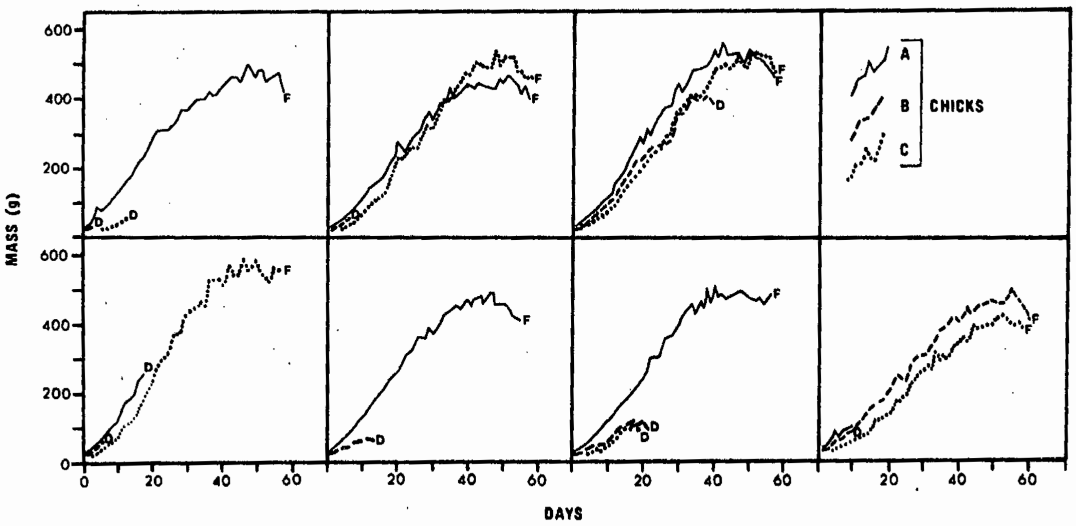

Fig. 6. Comparisons of the growth of chicks from A, B and C eggs in seven broods of Lesser Sheathbills. The time scale is dated from the hatching of the A chicks in each brood. Chicks which died (D) or fledged (F) are indicated.

Table 7 : Numbers of Lesser Sheathbill chicks which died or disappeared at various ages. Numbers of chicks thought to have died of starvation (last mass over one S.D. below mean for their age) are given in parentheses.

Hatching sequence of chicks	Age (weeks)							Total
	0-1	1-2	2-3	3-4	4-5	5-6	6-8	
First (A)	0	1(0)	2(0)	0	0	0	0	3(0)
Second (B)	4(1)	1(1)	1(1)	0	0	1(1)	0	7(4)
Third (C)	2(2)	1(1)	1(1)	0	0	0	0	4(4)
Fourth (D)	1(1)	0	0	0	0	0	0	1(1)
Unknown	1(1)	0	0	0	0	0	0	1(1)
Total	8(5)	3(2)	4(2)	0	0	1(1)	0	16(10)

most B chicks from starvation. The youngest chick in any brood was always the first to die of starvation. No overt sibling aggression was seen but chicks were seen to take food from the beaks of siblings. Starvation of the youngest chick has also been reported for Wattled Sheathbills (Jones 1963).

The proportion of A chicks which fledged was significantly higher than that of B chicks (χ^2 test, $P < 0.05$, Table 5) but the differences between A and C and between B and C chicks were not significant ($P > 0.05$). The relatively high proportion of C chicks which fledged was unexpected, since when they hatched they were lighter than their older siblings. The result was, however, partially an artefact of the small sample of C chicks. Of the five C chicks which fledged, four were from nests where one or both siblings were lost (apparently from predation or accidents since they were not underweight when they disappeared) and one was from a nest in which all three chicks fledged.

3.6 Breeding success

Of the 42 pairs studied, none reared four chicks to fledging, 5% reared three, 26% two, 40% one and 29% no chicks per season (Table 8). Of these pairs, clutch sizes were known in 26 cases. A pair with a clutch of four fledged two chicks, 12 pairs with clutches of three fledged an

Table 8 : Numbers of sheathbill pairs (& percentages in parentheses) which reared 0-3 fledglings per season at Marion & Signy islands. Only pairs which laid eggs considered.

Location and season	Fledged chicks per pair 0	1	2	3	Mean number of fledglings pair^{-1}	No. pairs
Chionis minor at Marion Island						
Rockhopper Penguin colonies						
1973/74	1	1	2	2	1.83	6
1974/75	1	2	1	0	1.00	4
1976/77	3	9	3	0	1.00	15
All years	5	12	6	2	1.20 ± 0.87	25
King Penguin colonies						
1976/77	2	2	3	0	1.14 ± 0.90	7
Adjacent R.P./K.P. colonies						
1976/77	0	2	1	0	1.33 ± 0.58	3
Macaroni Penguin colonies						
1976/77	5	1	1	0	0.43 ± 0.79	7
Total for Marion Island	12(29)	17(40)	11(26)	2(5)	1.07 ± 0.87	42
Chionis alba at Signy Island[1]						
1962/63	13	15	26	16	1.64	70
1963/64	7	2	6	3	1.28	18
Total for Signy Island	20(23)	17(19)	32(36)	19(22)	1.57 ± 1.07	88

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[1] From unpublished British Antarctic Survey Reports, courtesy of J.P. Croxall

average of 1.17 chicks per pair, 12 pairs with clutches of two averaged 0.67 fledglings per pair and one pair with a single egg clutch fledged no chicks.

The mean breeding success per pair was 1.07 fledglings per season (Table 8). The differences in breeding success of pairs in Rockhopper, King and adjacent Rockhopper/King penguin colonies were not significant (Student's t-test, $P > 0.05$ in each case). Breeding success was considerably lower in Macaroni Penguin colonies than elsewhere but these differences were not significant ($P > 0.05$), probably because of the small samples from Macaroni Penguin colonies. The low success in the Macaroni Penguin colonies was due to high seas destroying sheathbill and penguin eggs in the study colonies.

The mean breeding success of Lesser Sheathbills at Marion Island was significantly lower than that of Wattled Sheathbills at Signy Island (Table 8, $P < 0.01$). A relatively greater proportion of pairs reared two or three fledglings at Signy Island, but the reasons for this are not clear. Most pairs of Lesser Sheathbills at Heard Island reared one, and some two fledglings per season but none three (Downes _et al._ 1959). No sheathbills have been reported to rear four chicks per season anywhere.

4. Moult

Lesser Sheathbills moulted all their plumage once annually. Adults which had bred began moulting in the second half of March, once their chicks were independent (Table 9). Their brood patches began to re-feather at this time. Immatures and non-breeding adults began moulting in January during the breeding season. Juveniles moulted for the first time at the end of their first year.

Moult began with the primary remiges, which were replaced in ascending order (Fig. 7). A line fitted by eye to the data for breeding adults in Figure 7 gave an estimate of 70 days for the duration of primary moult in an individual. Replacement of the secondaries began before moult of the primaries was complete. The birds were never flightless at any stage. Moult of the rectrices and body plumage occurred over several months (Table 9) and replacement of accidentally lost feathers occurred at all times of the year.

5. Local movements

Lesser Sheathbills are non-migratory residents at all the islands in their range (Barre _et al._ 1976, Watson 1975). None of the 448 birds ringed at Marion Island between 1951 and

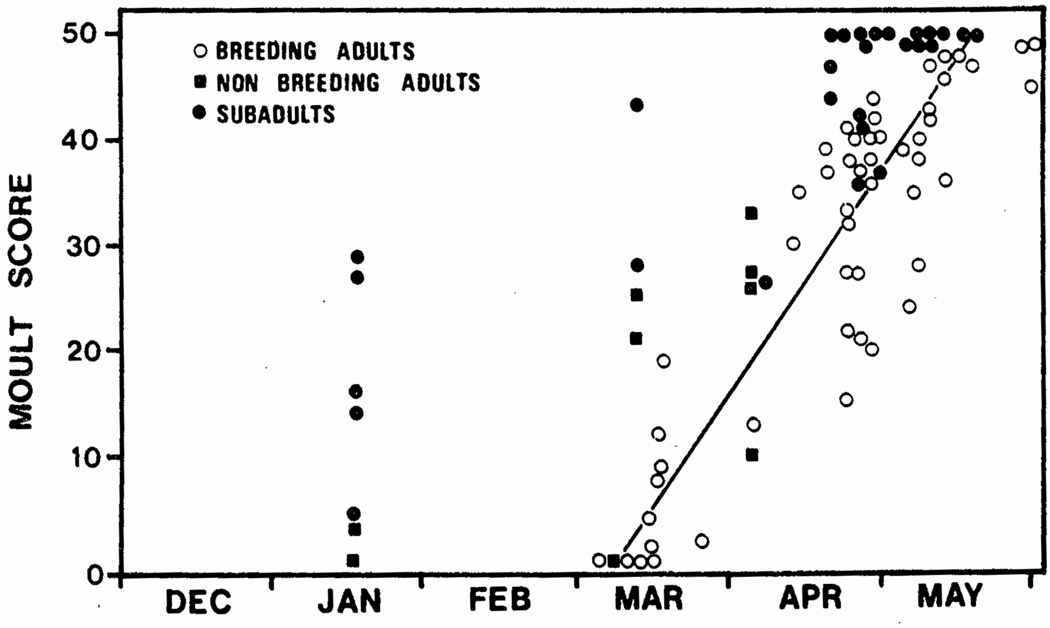

Fig. 7. Primary moult score in breeding adult, non-breeding adult and subadult Lesser Sheathbills. A line was fitted by eye to show the approximate duration of primary moult in a breeding adult.

Table 9 : Moult in breeding adults & in other(non-breeding adults & immature) sheathbills

Month	Percentage of birds growing feathers								Sample size	
	Primaries		Secondaries		Tail		Body plumage[1]			
	Breeders	Others	Breeders	Others	Breeders	Others	Breeders	Others	Breeders	Others
Jan.	0	86	8	71	8	71	0	71	12	7
Feb.	0	-	0	-	33	-	0	-	6	0
Mar.	70	100	20	100	40	83	40	83	10	6
Apr.	100	73	71	82	83	95	83	82	24	22
May	100	57	71	39	94	91	59	26	17	20
June	0	0	20	0	0	0	0	0	5	3
July	7	0	21	0	36	38	29	0	14	16
Aug.	0	0	0	0	80	50	20	0	5	6
Sept.	0	0	0	0	75	67	25	7	8	15
Oct.	0	0	0	0	40	21	0	0	5	19
Nov.	0	0	0	0	20	0	0	0	5	2
Dec.	0	-	0	-	50	-	0	-	2	0

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[1] Omitting birds growing a few accidentally lost feathers

1977 has been reported elsewhere, not even on Prince Edward Island, 22 km distant. Adults, including those not recorded to have bred, very seldom moved more than 1 km from the places where they had been ringed (Table 10). Over 700 sightings of 60 colour ringed breeding adults were made in 1976/77 and these birds were always seen within 1 km, and usually within 500 m, of their breeding territories. Immature birds were more inclined to wander than adults and almost half the subadults and a third of the juveniles were seen 1 km or more from the places where they had been ringed (Table 10).

6. Survival and Predation

6.1 Resightings of ringed birds

On average, 88% of breeding adults returned to their nesting sites in each season (Table 11) and since these birds attempted breeding in each year at the same territories, this was an accurate measure of their mean annual survival. The mean percentage survival of adults breeding in King Penguin colonies did not differ significantly from that of adults breeding in Rockhopper Penguin colonies ($P > 0.05$, Table 11). The samples from Macaroni Penguin colonies were too small for comparison. The survival of adult Wattled Sheathbills breeding at Signy Island was similarly high, being 90% (73

Table 10 : Percentages of ringed Lesser Sheathbills which were resighted (or recovered) at various distances along the coast from the initial ringing site

Age when ringed	Maximum distance moved (km)				No. resighted	No. ringed
	0-1	1-4	4-8	>8		
Adults[1]	96	1	1	2	96	178
Subadults	51	26	6	17	35	47
Juveniles	64	25	5	5	76	180
Mean	77	14	3	6	207	405

[1] Including non-breeding adults

Table 11 : Percentage annual resightings of colour-ringed adult Lesser Sheathbills breeding at Marion Island. The numbers ringed at the start of each period are given in parentheses.

Period between ringing and resighting	Breeding in colonies of			All areas combined
	King Penguins	Rockhopper Penguins	Macaroni Penguins	
1973/74 - 1974/75	100 (7)	79 (14)	-	86 (21)
1974/75 - 1975/76	73 (11)	100 (13)	100 (3)	89 (27)
1975/76 - 1976/77	90 (10)	91 (11)	100 (5)	92 (26)
1976/77 - 1977/78	85 (20)	86 (14)	-	85 (34)
Mean	85 (48)	89 (52)	100 (8)	88 (108)

birds ringed) and 86% (116 birds ringed) in two successive years (Jones 1963, Topliffe 1963).

Significantly fewer non-breeding adults, subadults and juveniles were resighted than breeding adults ($P < 0.001$ for birds of all areas combined, Table 12). These differences were attributed to higher mortality (proportionately more fresh carcass remains were found) and greater mobility (Table 10) of non-breeding adults and immatures. Comparisons of resightings of non-breeding adults and immatures from different areas of Marion Island are not valid since, unlike breeding adults, these birds showed little fidelity to any particular area.

6.2 Causes of mortality

The fresh remains of only 22 full-grown Lesser Sheathbills were found during the 25 months of the study. These included four adults, 16 immatures and two birds of indeterminate age. Seven had been partially eaten by predators or scavangers. Sixteen birds were found after exceptionally cold spells, with snow at sea level, during winter (June - September inclusive). Uneaten dead birds were generally very thin. Their mean mass was 304 ± 55 g (n = 11), considerably lower than the mean mass of living birds (492 ± 48 g for adults, 454 ± 51 g for subadults and 410 ± 60 g for juveniles, Appendix one .). The

Table 12 : Percentage annual resightings of ringed non-breeding & immature Lesser Sheathbills at Marion Island. The numbers ringed at the start of each period are given in parentheses.

Period between ringing & resighting	Non-breeding adults and subadults	Juveniles
1974 - 1976	54 (67)	31 (41)
1975 - 1976	36 (25)	44 (32)
Mean	49 (92)	37 (73)

The apparent causes of mortality were thus the combined effects of starvation and inclement weather and, to a lesser extent, predation.

Sub-Antarctic Skuas and feral cats Felis catus are known to kill Lesser Sheathbills at Marion Island but sheathbills were unimportant in the diets of both predators. Only seven (0.5%) out of 1 558 prey remains which were attributed to cats or skuas were sheathbills, no sheathbills were found in 125 cat stomachs and only one (0.2%) out of 442 prey items at skua nests was a sheathbill (Van Aarde 1977).

Lesser Sheathbills at Marion Island did not show alarm when a cat passed within a few metres of them. At Ile aux Cochons (Crozet Islands) however, cats have apparently severely depleted the numbers of Lesser Sheathbills (Derenne et al. 1976).

Lesser Sheathbills were always wary of Sub-Antarctic Skuas at Marion Island. These predators were seen to catch and kill sheathbills on three occasions and often swooped towards individuals or groups of sheathbills. When foraging farther than 20 m from the shore, groups of sheathbills almost always took flight towards the shore at the approach of a skua (Table 13). The sheathbills appeared to be less vulnerable when foraging amongst the boulders on the shore or

Table 13 : Responses of groups of Lesser Sheathbills foraging on inland vegetated areas to the approach of a flying Sub-Antarctic Skua

Response	Distance from the shore (m)					
	0-20	21-40	41-60	61-80	81-100	100
Group took flight (%)	0	76	100	100	100	66
Birds alert but did not fly (%)	100	24	0	0	0	33
No. groups	8	17	13	4	7	3

in penguin colonies. Here they seldom flew off at the approach of a skua but sometimes adopted alert postures. Downes *et al.* (1959) mentioned that Lesser Sheathbills at Heard Island were reluctant to leave rocky areas to forage on open sandy beaches where they were apparently more vulnerable to skua predation.

Giant Petrels *Macronectes giganteus* and *M. halli* could possibly catch unwary Lesser Sheathbills feeding near them at carcasses although this has not been reported. Kelp Gulls *Larus dominicanus* were rarely observed chasing sheathbill chicks but they could probably not kill a healthy full-grown Lesser Sheathbill. The possibility of intraspecific predation on eggs and small chicks has already been mentioned.

7. Discussion

7.1 Association with penguins while breeding

Lesser Sheathbills at Marion Island bred in close association with Rockhopper, Macaroni and King penguins. Gentoo Penguins which were uncommon and which bred during late winter and spring, were relatively unimportant to breeding Lesser Sheathbills. Penguins supplied most of the food eaten by breeding adults and their chicks and no Lesser Sheathbills attempted breeding without access to breeding penguins. Elsewhere, breeding sheathbills of both species have similar close associations with penguins (Paulian 1953, Downes *et al*. 1959, Jones 1963, Derenne *et al*. 1976) or at a few localities with breeding cormorants (Paulian 1953, Parmelee *et al*. 1977).

Lesser Sheathbills at Marion Island bred when food from penguins was most freely available. They underwent ovogenesis when Rockhopper and Macaroni Penguin eggs were available and their chicks hatched when these penguins were already feeding their chicks and penguin regurgitant was readily available. The long breeding season of the King Penguins started somewhat later than that of the Lesser Sheathbills but carcasses of King Penguins which died during their annual moult (September to March for adults and December to February for immatures) were common at all colonies when the sheathbills were breeding and eggs and penguin chick carcasses were available towards the end of the Lesser Sheathbill's breeding season.

Breeding of Lesser Sheathbills at Heard Island and Wattled Sheathbills at Signy Island is timed so that the chicks hatch when penguins' regurgitant is readily available during most of the Sheathbills' nestling period (Downes *et al*. 1959, Jones 1963, Spellerberg 1975).

Sheathbills of both species appear to breed only when associated with breeding penguins or, far less commonly, with of breeding cormorants. The ultimate factor determining the timing of breeding at Marion Island appears to be the increased food supplies associated with the presence of breeding penguins and the proximate factor might be the actual influx of penguins in spring.

Not all penguin colonies at Marion Island were suitable for the establishment of Lesser Sheathbill breeding territories. Fewer than 20 pairs of Lesser Sheathbills attempted breeding at two very large colonies at Kildalkey Bay and Bullard Beach which contained between them over 400 000 pairs of Macaroni Penguins and 80 000 pairs of King Penguins. These colonies are both situated on smoothed, glaciated grey lava, in contrast to the more broken, younger black lavas most common on the coastal plain. The penguins bred at maximum density on these even surfaces which was perhaps too dense to permit freedom of movement by Lesser Sheathbills between the penguins. Nests sites for Lesser Sheathbills were restricted to the very few areas of broken lava at the perimeters of these colonies.

7.2 Breeding adaptations

Sheathbills have nidicolous, semi-precocial chicks dependent on their parents for at least 50 days and they nest in subterranean cavities and not on the surface. Among the wading and littoral species of Charadriiformes (suborders Charadrii and Lari), these features are shared only with the Crab Plover Dromas ardeola (Lack 1968). For Lesser Sheathbills at Marion Island and probably also for all sheathbills, these features are viewed as adaptations for living in close association with penguins, where climatic conditions are harsh and where predators are a risk.

Lesser Sheathbill chicks are fed food obtained by their parents from penguins which they themselves, lacking sufficient body mass, motor skills and experience, could not exploit alone. The use of cavity nests allows the chicks to obtain some shelter from the prevalent cold, rain and wind, from predatory attacks by skuas and gulls, and from being pecked or trampled by penguins. When these nests are situated within penguin colonies the parents spend less time and energy in transporting food to the chicks and can also increase their territorial vigilence. Although predatory birds are attracted to penguin colonies, the sheathbill nests sited amongst penguins derive some protection from the penguins themselves, which do not tolerate skuas or gulls to walk amongst them.

Most pairs of Lesser Sheathbills fledged fewer chicks than the number of eggs laid. Starvation of chicks from D, C and to a lesser extent B eggs was the single most common cause of mortality. Lesser Sheathbills, in common with many species of birds (Lack 1954, Ricklefs 1968, O'Connor 1978) can evidently rear as many chicks as the average clutch size when conditions are favourable, but have adaptations for eliminating 'excess' chicks when there is insufficient food to rear the full complement. In Lesser Sheathbills brood reduction is facilitated by hatching asynchrony. Sufficient eggs are also laid to provide some insurance against unpredictable losses of eggs and chicks by predation and accidents.

O'Connor (1977) described two adaptations, other than brood reduction, which could maximise reproductive output while minimising waste of parental time and resources. These adaptations are the ability of phenotypes to vary their clutch size in accordance with temporary local conditions, and secondly, the ability of chicks to store sufficient resources to survive short term instability of food supply. Lesser Sheathbills exhibited none of the breeding patterns associated with clutch size adjustment (see O'Connor 1977), and evidence to support or refute resource storage by Lesser Sheathbill chicks is not available. Resource storage adaptations could occur together with brood reduction adaptations (O'Connor 1977).

7.3 Population limitation

Lesser Sheathbills at Marion Island were strongly territorial while breeding; had excess non-breeding adults in the population; low annual mortality of adults (12%); low reproductive output (1.07 fledglings per pair per year); delayed age of first breeding and a long reproductive life-span; and, were relatively sedentary. These features demonstrate a strong tendency towards K-selection (MacArthur and Wilson 1967, Pianka 1970), implying that the population is close to its carrying capacity, like many other long-established insular species. The population appears to be limited by reproductive output rather than by post-fledging predation or other mortality factors. Lesser Sheathbills at Marion Island are apparently obligate commensals with penguins but not all penguin colonies are suitable for breeding sheathbills. The island's population of Lesser Sheathbills appears to be limited by the number of territories which can be established in penguins' colonies and not by the number of penguins _per se_.

8. Acknowledgements

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9. Summary

Lesser Sheathbills Chionis minor were studied at Marion Island in the sub-Antarctic. All breeding adults held territories in penguin colonies; virtually all food eaten by these adults and their chicks was obtained from penguins, mostly by kleptoparasitism; and, the sheathbills bred when food from penguins was most freely available. The minimum age of first breeding was three years and there was a surplus of potential breeding adults. Clutches were one (3%), two (47%), three (47%) or four eggs (3%) and the average laying interval between successive eggs was four days. Eggs within a clutch were similar in size and in hatching success. Growth and survival of chicks, however, differed within broods (first-hatched chicks fared better) and this was related to hatching asynchrony. The adaptive significance of brood reduction is discussed. The mean reproductive output was 1,07 fledglings per pair per year. The advantages of nidicolous chicks and cavity nests are discussed in relation to the sheathbills' close association with penguins, the inclement weather and the presence of predators. Breeding

adults moulted immediately after the breeding season and other, non-breeding birds moulted earlier. Breeding adults had a mean annual survival of 88%, non-breeding adults and subadults (combined) 49% and juveniles 37%. Apparent causes of mortality were starvation, inclement weather and predation by Sub-Antarctic Skuas Catharacta antarctica and feral cats Felis catus. The population on the island appears to be close to its carrying capacity and limited by the number of territories which can be established in penguin colonies.

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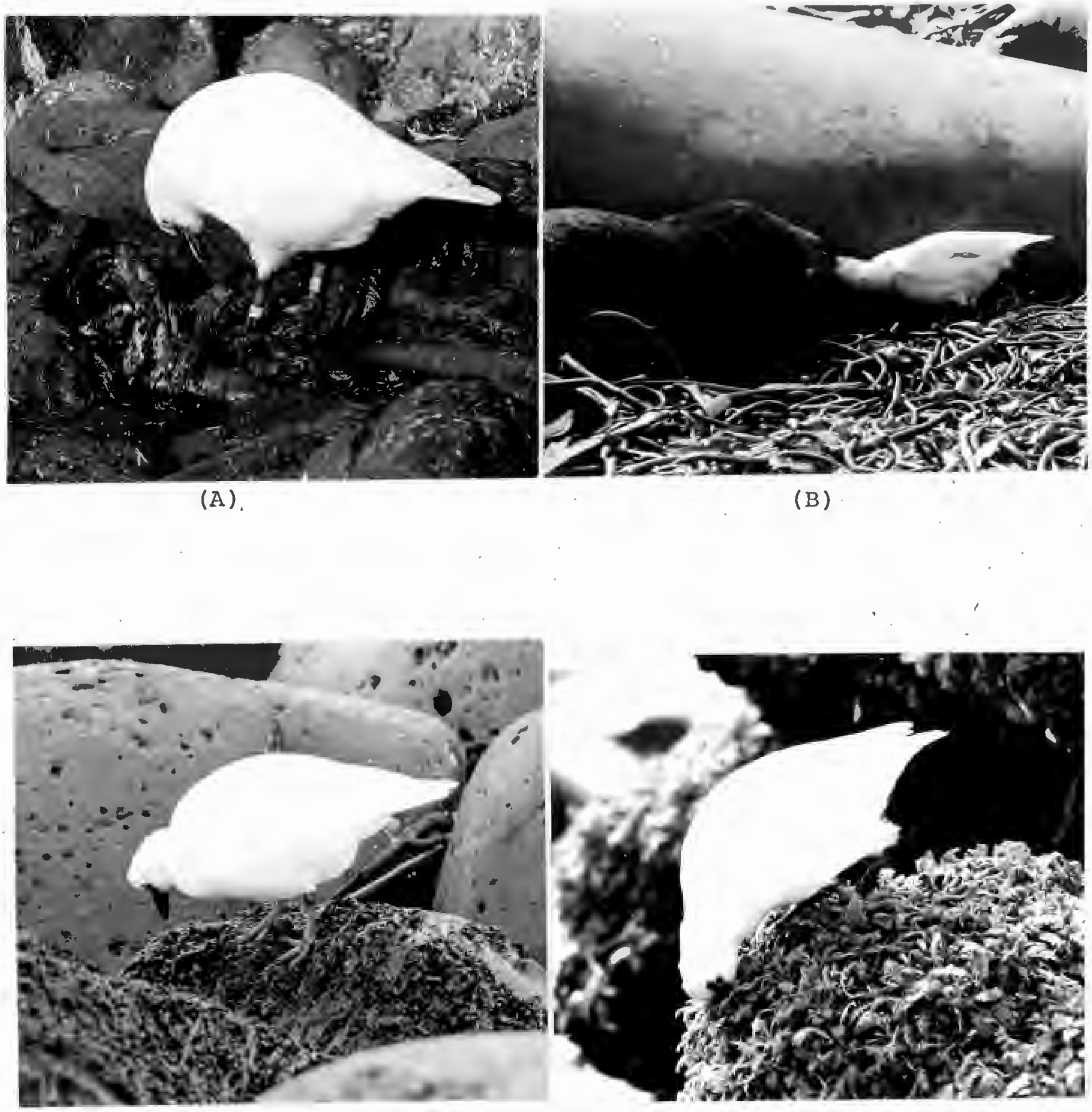
PART TWO

FOOD AND FORAGING BEHAVIOUR OF LESSER SHEATHBILLS


(A) (B)

(C) (D)

Plate 1. The diet of Lesser Sheathbills included carcasses of penguins (A), milk from the mouths of nursing seal pups (B), intertidal algae (C) and fossorial invertebrates from the vegetated coastal areas (D).

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*. in press).

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). 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 5.0km 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 (Appendix one); 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 antarctica 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 from the formula (modified from Jarman 1974):

$$\mathrm{TFS} = \frac{n_1F_1 + n_2F_2 + n_3F_3 \,\ldots\ldots\ldots\, n_iF_i}{n_1 + n_2 + n_3 \,\ldots\ldots\ldots\, n_i}$$

where n is the number of birds in each flock of size F where there are i groups. 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 X 10 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 determinations 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 observations 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 King Penguins <u>Aptenodytes patagonicus</u>, Macaroni Penguins <u>Eudyptes</u> <u>chrysolophus</u>, Rockhopper Penguins <u>E</u>. <u>chrysocome</u> and Gentoo Penguins <u>Pygoscelis</u> <u>papua</u>. In these colonies they ate flesh, blubber and skin from the carcasses of adult and chick penguins (small penguin chicks were killed by the Lesser Sheathbills); eggs, either discarded by or stolen from incubating penguins; freshly voided penguin excreta; and, krill (pelagic euphasiids, amphipods and copepods), fish and squid spilled by penguins while feeding their chicks, and obtained from the penguins by kleptoparasititsm (see Burger in press, a). 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 <u>et</u> <u>al</u>. 1979) and the Imperial Cormorant <u>Phalacrocorax</u> <u>albiventer</u> 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.

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 (%)	Occurence (%)	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
Penguin 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

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[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 (xxx), occasional (xx), rare (x) and not recorded (-).

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

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* occurred 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 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 delerssérti* 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.

Lesser Sheathbills ate a wide variety of terrestrial macro-invertebrates, mainly earthworms and insects, taken from vegetated areas on the coastal plain (Table 1, Appendix two). 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 occurring outside the territories of adult Lesser Sheathbills in the summer but not in winter (see below). Proportionately more adults occurred in Rockhopper and Macaroni

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 King	17 ± 7[s]	9 ± 11	15 ± 7	31 ± 6	53 ± 17[a,j]	36 ± 20
Macaroni	4 ± 3[s,j]	0	1 ± 2[2]	11 ± 6[s,j]	1 ± 1	1 ± 3
Rockhopper	5 ± 5[s,j]	1 ± 2	2 ± 3	36 ± 13[s.j]	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^{-1}	150 ± 22	32 ± 10	30 ± 8	139 ± 10	20 ± 9	32 ± 14

[a,s,j] 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.

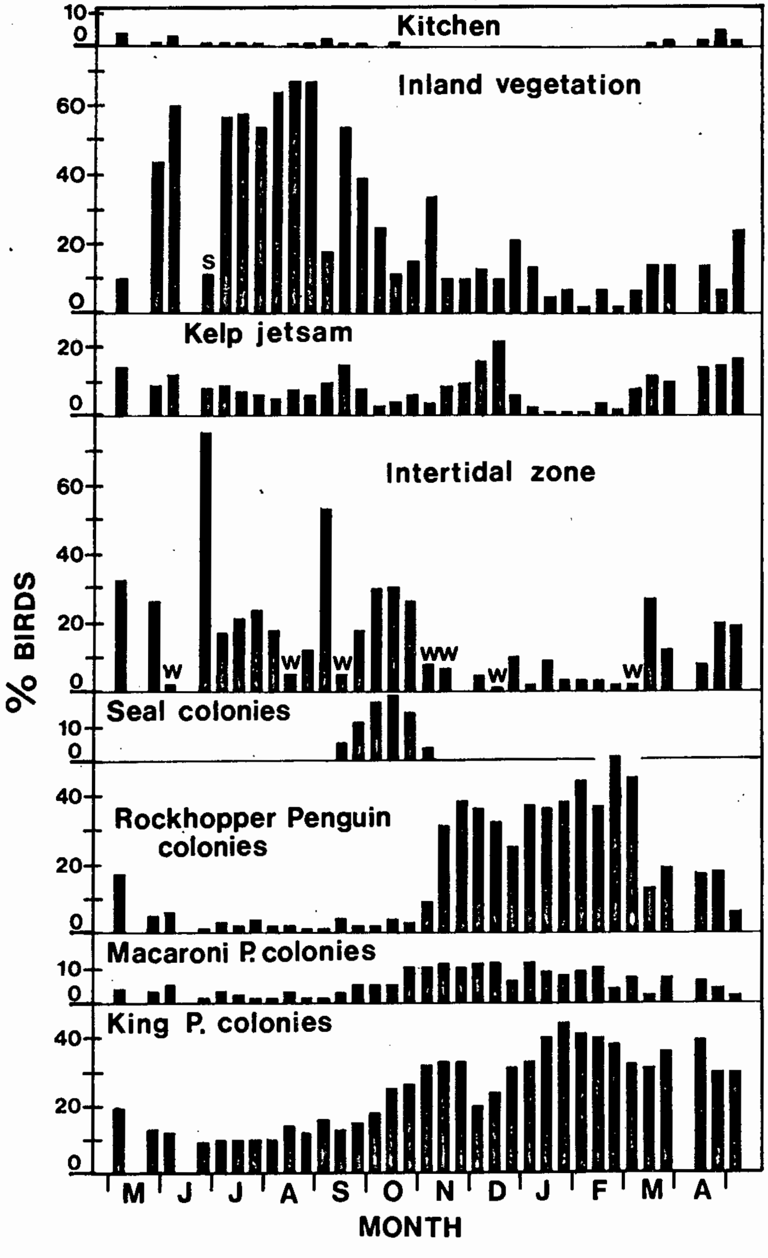

Fig. 1. Percentage of Lesser Sheathbills within the 100 ha study area (average population 197 birds) foraging in different areas during 34 one-day censuses throughout the year. Days with exceptionally heavy waves on the shore (W) or with heavy snow and frozen ground (S) are indicated where applicable.

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 (Tables 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 more nest sites. Eighty-four percent of the island's King Penguins occurred in three very large colonies (over 20 000 pairs each) and over 90% of the Macaroni Penguins occurred in two such colonies (Siegfried et al. in press). Most areas in 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.

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).

Foraging area	% of count		Typical flock size (range in parentheses)	
	Summer	Winter	Summer	Winter
Penguin colonies				
King	38	48	N.D.[1]	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	-	-

[1] Not determined.

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 Penguin	215 230	1347	6.3
Macaroni Penguin	450 000	406	0.9
Rockhopper Penguin	93 290	1426	15.3

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

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.

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).

The placentae and carcasses of Elelphant 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).

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	Fat
	Mean	No. samples	(% mass)	(% mass)
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				
<u>Porphyra</u> sp.	4.1 ± 0.3 (19 ± 1)	8	7.3 (34)	0.1 (0.5)
<u>Rhodymenia</u> 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 and Schreiber (1977).

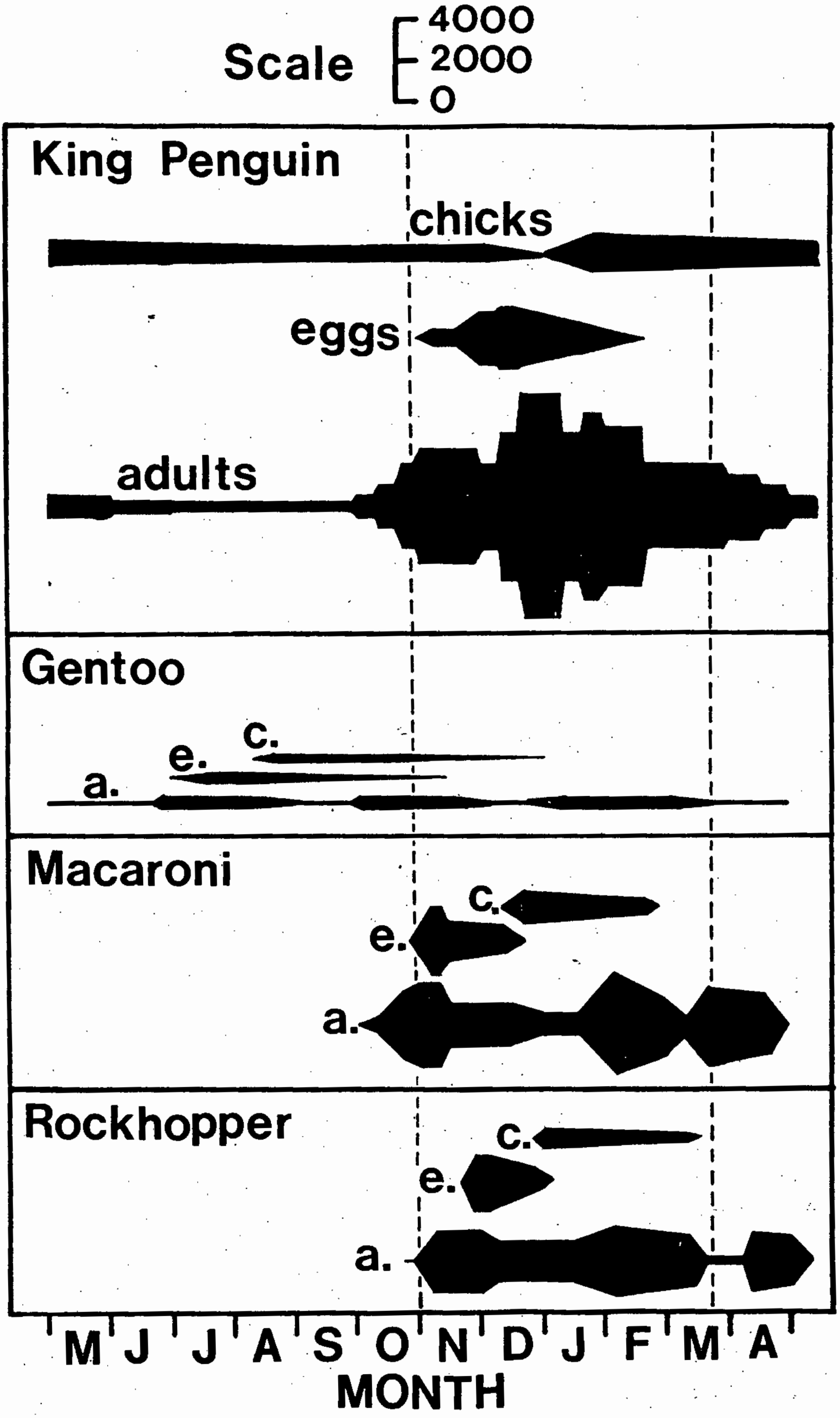

Fig. 2. Temporal availability and approximate numbers of adult penguins, eggs and chicks within the study area. The duration of the Lesser Sheathbill's breeding season (nestbuilding, laying, incubation and rearing chicks) is delineated by the vertical dashed lines.

The invertebrates amongst the rotting kelp jetsam represented food items which were small, probably of low nutritional value, spatially 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 2m) which occurred during all months of the year (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 (Appendix two), 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 less 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,

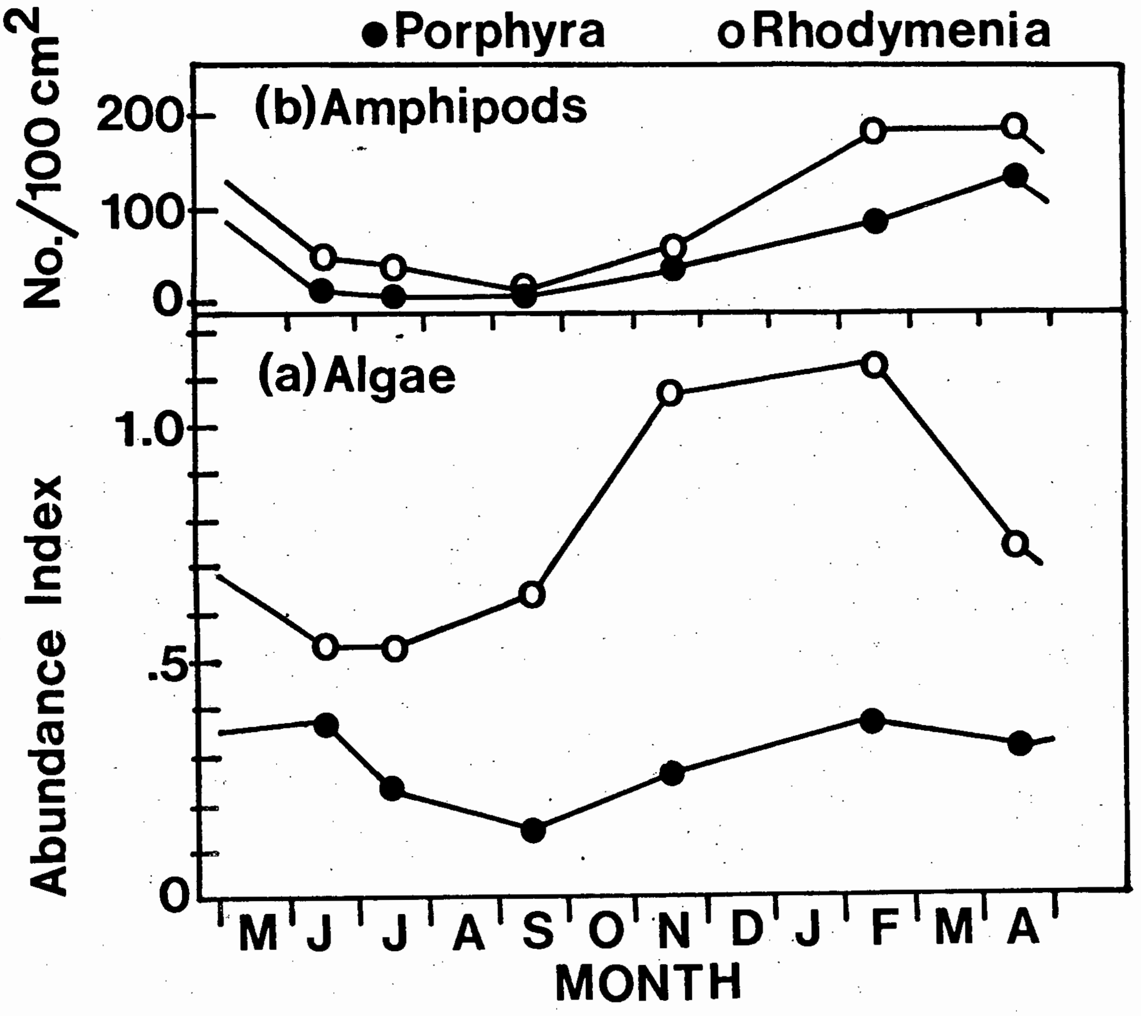

Fig. 3. The relative abundance of <u>Porphyra</u> and <u>Rhodymenia</u> algae on the intertidal boulders near Transvaal Cove (A), and the densities of amphipods <u>Hyale</u> spp. within these algal carpets (B). See text for derivation of the index of algal abundance.

Kelp Gulls *Larus dominicanus* 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 sizes might confer differences in diets to allow co-existence 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 sizes of such consumers tended to be uniform on a logarithmic 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 log. 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 1979, 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.

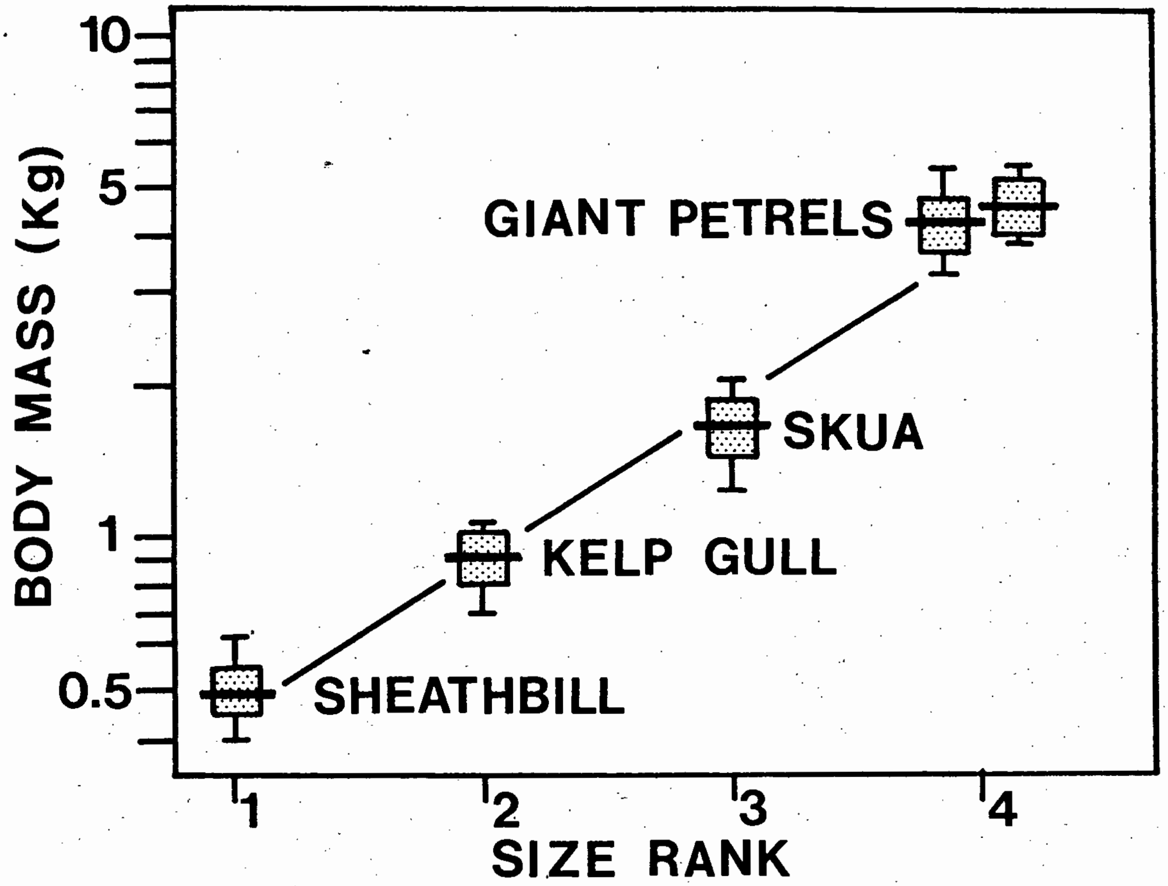

Fig. 4. Mean, S.D. and range (horizontal line, shaded bar and vertical line respectively)of the adult body masses of the predatory-scavenging birds at Marion Island, ranked from smallest to largest. The two species of Giant Petrels have been given equal rank, since their masses are not significantly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

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 (Part one).

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 (Part one). 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.

5. SOCIAL ORGANISATION 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 (Part one). 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

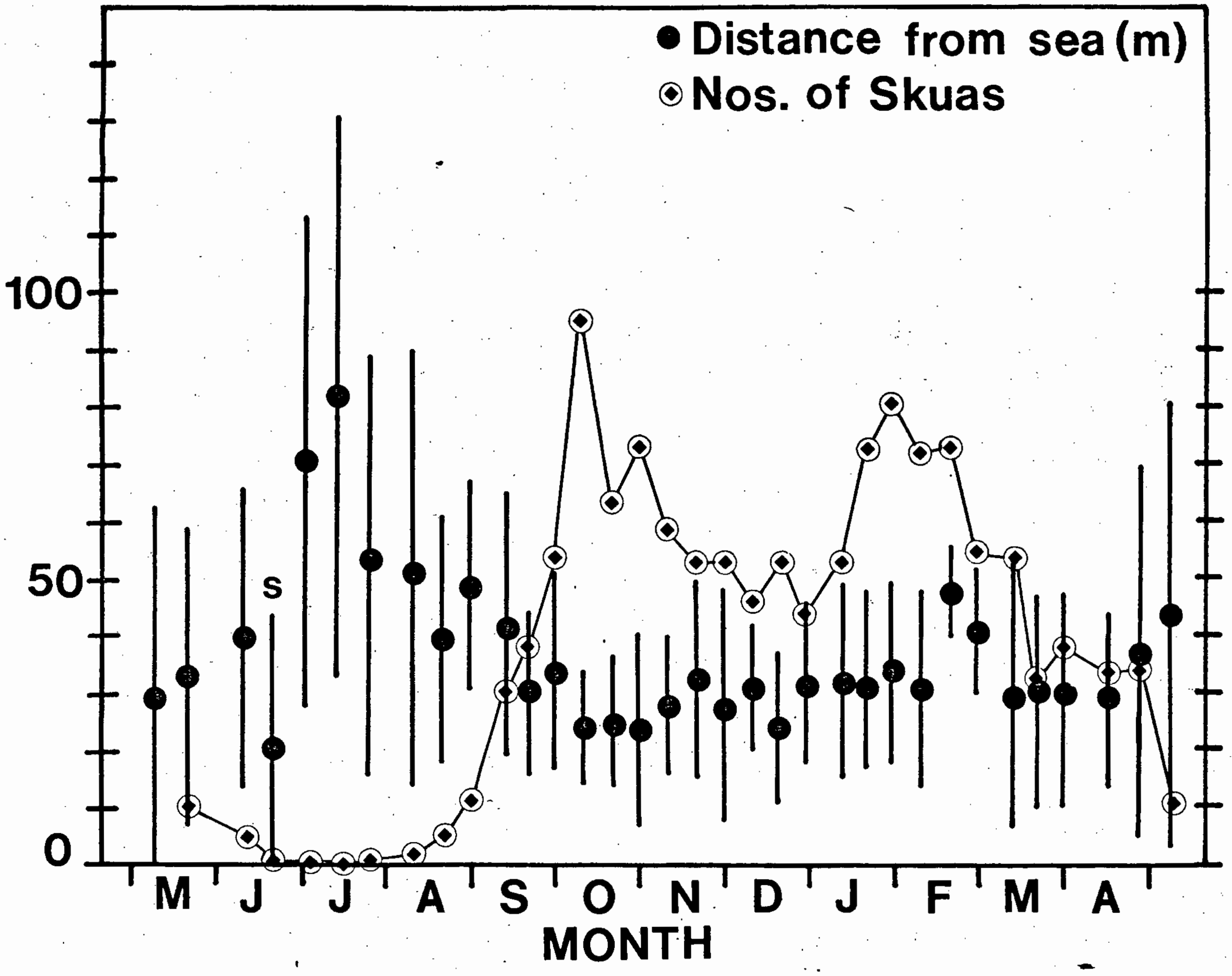

Fig. 5. Variations in the numbers of sub-Antarctic skuas and the mean (± S.D.) distance from the shore of Lesser Sheathbills foraging for terrestrial invertebrates in the study area in 1976 - 1977. A day of heavy snow cover which prevented foraging by sheathbills in many areas is shown with an S.

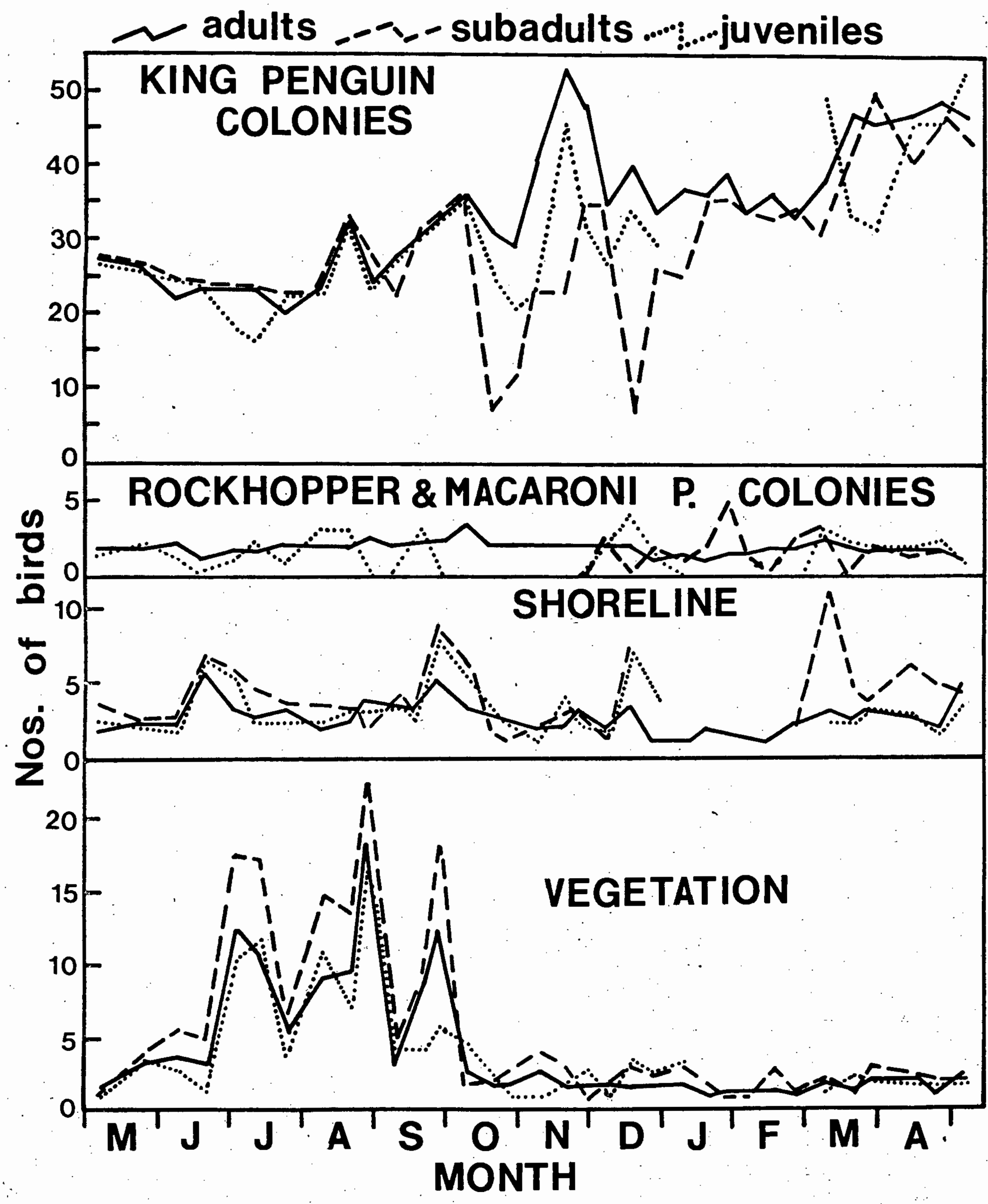

Fig. 6. Typical flock sizes of Lesser Sheathbills foraging in penguin colonies, the shoreline (including the intertidal zone and kelp jetsam, but excluding the beach of the King Penguin colonies) and the coastal vegetated areas. Note that the ordinate of the data from King Penguin colonies is double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

size for these habitats averaged three birds within the study area (Fig . 6) and was 3-6 birds 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 occuring 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, Recher and Cody 1966, Mac Arthur and 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.

(a) 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).

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 and Mougin 1970); 5 (Paulian 1953); 6 (Sharpe 1879); 7 (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); 13 (Eagle-Clark 1906); 14 (Woods 1975); 15 (Cobb 1933).

According to Cody (1974) a species should concentrate on that part of the resource span which had 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 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.

(b) Low levels of interspecific competition

Small isolated islands usually have relatively few species due to problems of immigration and colonisation (MacArthur and 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 and 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 (see Diamond 1975).

(c) Short-term climatic vatiation.

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 Bouvetoya 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 and Orians 1970, Davies 1978). Territorial behaviour was dependant 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. (Part three). 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 (Appendix two . 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 and 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 (Part six).

On the intertidal and kelp jetsam zones, Lesser Sheathbills foraged solitarily or in twos and threes. The food taken here was spatially 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) and did not search time. Possible advantages of flock-foraging did not therefore apply, either with regard to locating or exploiting food or avoiding predation.

7. ACKNOWLEDGEMENTS

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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 kleptoparsitised 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 antarctica* 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 climatic 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.

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PART THREE

THE DISPLAYS AND TERRITORIAL TENURE
OF LESSER SHEATHBILLS

INTRODUCTION

The family Chionididae (Charadriiformes) comprises two allopatric species, the Wattled Sheathbill *Chionis alba* and the Lesser Sheathbill *C. minor*, which breed in Antarctic and sub-Antarctic regions. No study has been made of the ethology of the family, apart from incidental notes on the Wattled Sheathbill by Jones (1963). This paper presents a description and inventory of the displays and comfort behaviour of the Lesser Sheathbill and discusses some aspects of the use of displays in territorial and sexual interactions. Information on the Wattled Sheathbill is included to provide as complete a coverage of the family as possible.

STUDY AREA AND METHODS

This report is part of an investigation into the foraging and social behaviour of Lesser Sheathbills at Marion Island (46°54'S, 37°45'E) in the southern Indian Ocean. Field work totalled 25 months and covered all seasons twice, between 1974 and 1978. Notes were kept on the descriptions, contexts and apparent stimuli of displays, and supplemented by still and 8 mm movie photography. Data on the behaviour of birds of known sex, age and social status were obtained from observations of 210 individuals which had been colour-marked with rings. These birds were aged and sexed using criteria described in Appendix One.

SOCIAL ORGANIZATION

Lesser Sheathbills defended territories of 100 - 300 m^2 within colonies of breeding penguins. Neighbouring territories frequently abutted but appeared to overlap very little. Territories were maintained only by pairs of adults. Juveniles were tolerated within their parents' territories. The principal objective of territorial defence by Lesser Sheathbills was to maintain exclusive use of the reliable and relatively abundant food resources supplied by the penguins, and territories were maintained only while the penguins were present : throughout the year within some colonies of King Penguins *Aptenodytes patagonicus* but only between November and the end of April in colonies of Rockhopper Penguins *Eudyptes chrysocome* (Fig.1).

Non-territorial birds included adults which had temporarily abandoned their territories, adults which had not yet established territories and immatures younger than three years old. These birds foraged in undefended parts of penguin colonies, particularly those of King Penguins, or by intruding into the territories of other Lesser Sheathbills. They also foraged extensively in groups or singly on the shoreline or on vegetated inland areas. Foraging groups varied in size (2 - 80 birds) and in age composition, and appeared to have no rigid social order.

Lesser Sheathbills retained the same mates and territories from season to season and pair-bonds were terminated by the loss of a mate. This was noted for the colour-marked pairs living in 15 territories over four years. During this time six males and five females re-mated, one female twice, on the death or disappearance of their mates. With one exception, re-mating involved the acceptance of a new partner into the established territory, without noticeable changes in its boundaries. New partners had frequented the area, sometimes for years, as non-territorial adults. The one exception was when two neighbouring birds mated after their respective mates had disappeared and the new pair then defended both former territories. The displacement of an established pair by another pair was not recorded. The members of a pair did not necessarily forage together when outside their territory (Fig.1).

Lesser Sheathbills nest in cavities and the nest and attendant parent were usually invisible from outside. Nests were usually within the foraging territory but a few pairs (about 5%, N = 52 pairs) used nest sites separated from the foraging territories by 10 - 50 m. Nestbuilding and nocturnal roosting within cavities commenced six weeks prior to laying and several pairs started nests in more than one cavity within their territory but used only one to breed in. Breeding pairs spent little time together within nest cavities.

DISPLAYS

The nomenclature of Lesser Sheathbill displays is my own but terminology used for gulls (Tinbergen 1959) was used for apparently homologous displays.

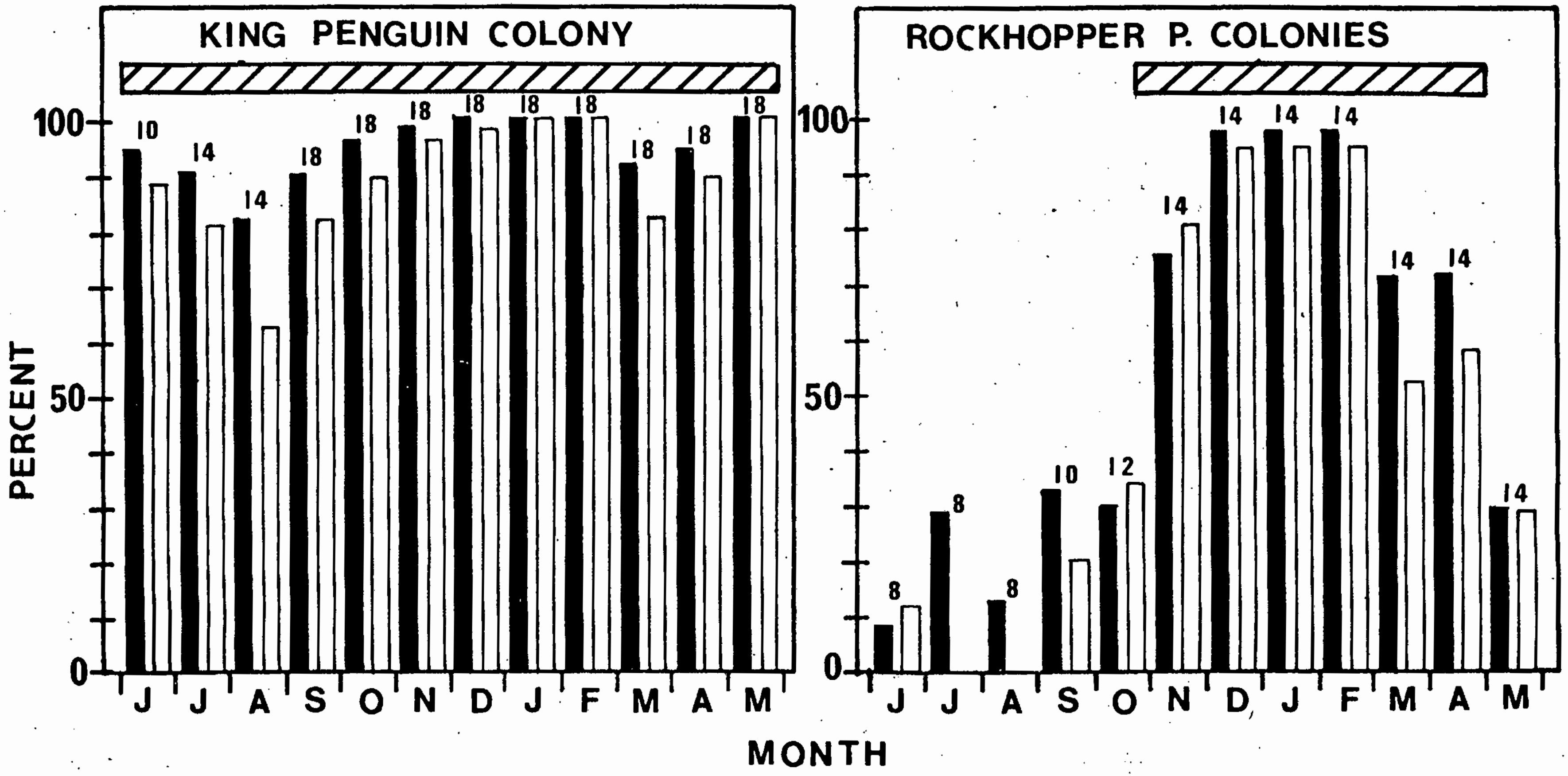


Fig. 1. Mean monthly percentages of colour-marked adult Lesser Sheathbills seen within their territories (black bars) and in the presence of their mates (open bars). The birds observed were all known to have bred or attempted breeding in a colony of King Penguins (left) or in colonies of Rockhopper Penguins (right). The presence of the penguins within the colonies is indicated by the horizontal hatched bar. The mean number of sheathbills, observed every ten days, is given for each month.

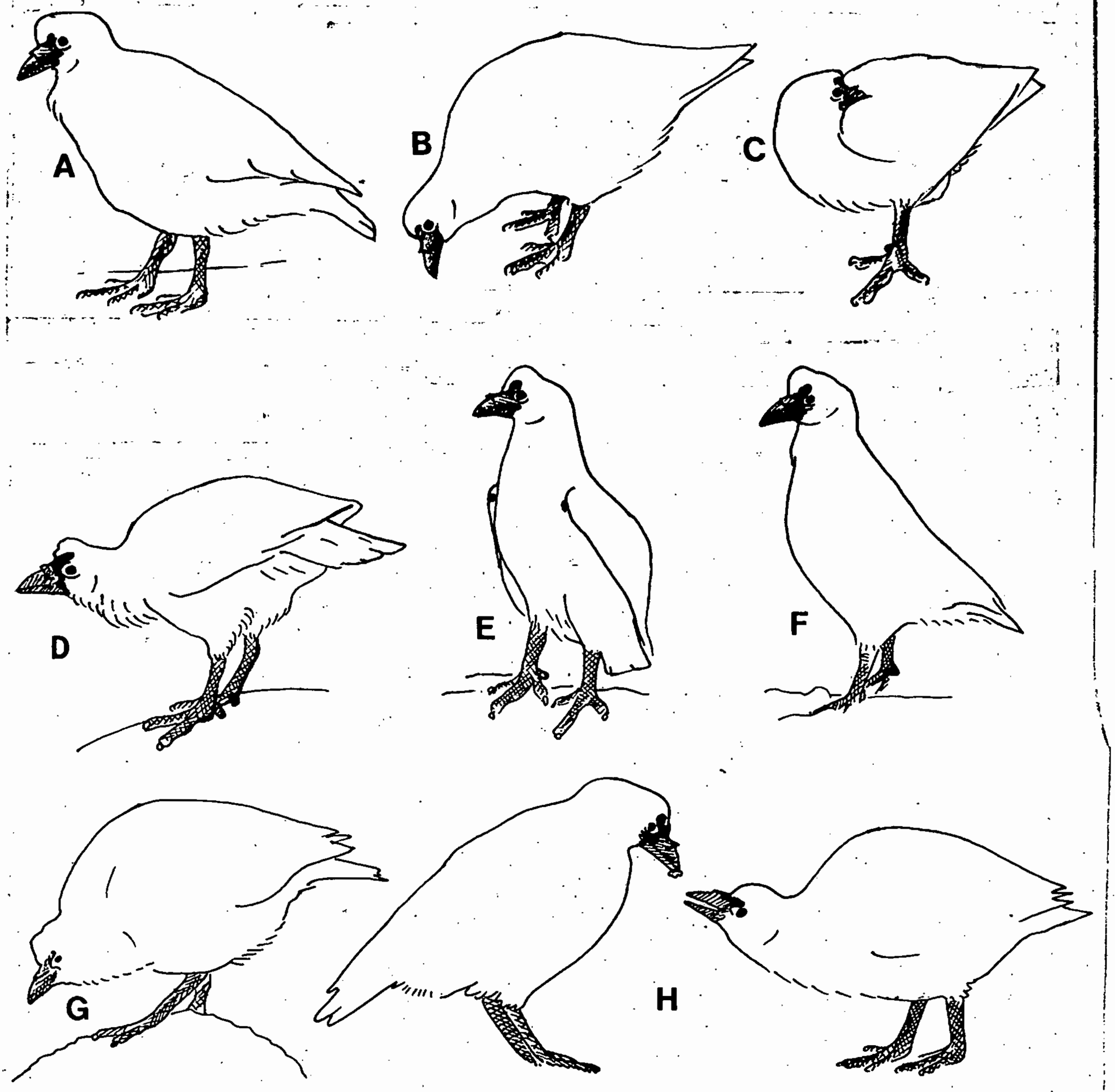


Fig. 2. Normal and display postures of Lesser Sheathbills, including : the normal standing posture (A); foraging (B); roosting (C); the Forward display (D); Aggressive Upright (E); Anxiety Upright (F); the Hunched display (G); and the Hunched display while soliciting food in a juvenile (H). (Drawn from photographs.)

TABLE 1

The relative frequency with which individually-marked territorial male and female Lesser Sheathbills performed various displays. Observations were made in King and Rockhopper Penguin colonies.

Display	No. of displays by		No. of displays
	Males	Females	
Forward			
(with vocalisation)	39	15	54
(without vocalisation)	17	4	21
Chases			
(Running Chase)	46	17	63
(Flapping Chase)	22	3	25
(Unspecified Chase)	49	53	102
All Chases	117	73	190
Boundary disputes	94	7	57[1]
Fights	33	1	21[1]

1) These encounters involve two birds but in some cases only one was colour-marked.

It was given from within a territory, often from a raised rock where the bird was resting or preening and was elicited by the approach or intrusion into the territory by a conspecific and also when neighbouring pairs were calling. The display evidently communicated aggressive threat to an intruder or potential intruder which was at a distance. The threat posture of *C. alba* has been described as a "forward-oblique" pose which is usually accompanied by Bill-wiping and calling (Jones 1963).

The Hunched display

Description : The bird lowers its head with the neck withdrawn and the bill pointing obliquely downwards, so that it appears to have hunched shoulders (Fig. 2). When performed by a juvenile it is usually accompanied by a soft, shrill cheeping call. The bird usually stands at right angles to the dominant bird eliciting the display. The posture is similar to the Forward except that the neck is withdrawn and the bill tends to point downwards and not forwards.

Context : This was an appeasement posture which was most frequently performed by juveniles, particularly those which had just been chased. Adult territorial females also performed the display, rarely, when chased by their mates. A chick or juvenile soliciting food adopted the Hunched posture, called and raised its bill to touch that of its parent (Fig. 2).

Facing Away

Description : A bird standing in a normal or extended upright position turns its head sharply away from a sheathbill standing 10 - 50 cm from it. One or both birds may give the display and it may be repeated 2 - 3 times in succession.

Context : This display was brief and rare and usually occurred when a bird in a non-territorial foraging group approached another. Detailed notes on only 12 performances were made. These involved non-territorial adults and immatures. In eight encounters one bird attacked the other; this followed Facing Away by both birds involved (three times), by the attacking bird (three times) or by the attacked bird (twice). The display was also sometimes performed by females following copulation (see below).

The Upright display

Description : The bird stands in an extended upright posture and extends its neck up to look about (Fig. 2, E & F). Two variations of this posture were apparent : in alarm, the wings are held against the body and single calls may be given (Anxiety Upright); in intraspecific aggressive encounters the wings are held very slightly opened, to expose the black carpal spurs and no calls are given (Aggressive Upright).

Contexts : The Anxiety Upright is adopted when some disturbance or potential danger, such as an approaching Sub-Antarctic Skua *Catharacta antarctica*, is detected. This display was performed by either sex foraging singly, or in flocks and territories. The Aggressive Upright was rarely seen, always in intraspecific aggressive encounters and usually involved neighbouring territorial males. Aggressive Upright was most often seen during or immediately after Fighting (see below) and appeared to communicate defensive threat.

Chasing

Description : Two forms of Chasing were recognised, Running Chase and Flapping Chase, which are believed to have the same function in lower and higher intensity situations respectively. In Running Chase a bird runs rapidly towards another sheathbill, with the head extended forwards. In Flapping Chase the bird runs similarly but the wings are flapped and it may also fly briefly. No vocalisations are made by the chaser but juveniles being chased may utter a plaintive cheeping call. Following a chase, the chaser may adopt the Forward threat posture and the chased bird the Hunched appeasement posture.

Context : Adults of both sexes chased intruders from their territories. The bird being chased invariably fled but occasionally the territorial bird caught the intruder by the wing or tail and held it with its bill until the intruder struggled free. Running Chases were more frequent than Flapping Chases and both were performed more frequently by males than by females (Table 1). Immatures (subadults and juveniles) or non-territorial adults were frequently chased from territories but neighbouring territorial adults seldom were (Table 2).

Both types of Chase are used by territorial adult Wattled Sheathbills to evict intruders (Jones 1963).

Very brief supplanting Chases occurred frequently (2.5 chases bird^{-1} hour^{-1} during 20 hours of focal-animal watching) in foraging groups of non-territorial Lesser Sheathbills. These usually involved one bird running a metre or two to chase another from the spot where it was feeding and the chaser then resumed foraging at that spot.

Bob Call

Description : The display is performed by two birds of opposite sex standing next to each other. Both birds bow the head and neck rapidly up and down, while uttering a long series of staccato calls, "kḗk - kḗk - kḗk - kḗk . . ." (Fig. 3 & 4). A mean frequency of two bows per second was obtained from an analysis of movie film of eight displays.

In 103 visually observed displays, the birds stood facing one another (43% of displays), at right angles to one another with their heads together (43%) or stood next to each other facing in the same direction (15%).

The display is initiated by one of the pair beginning to bob and call, followed by the other. Occasionally (39% of 103 displays) the bird initiating the display pecks at the bill of the other before both display (Fig. 3). The body movements

TABLE 2

Birds chased by male, female and unidentified territorial Lesser Sheathbills. Observations were made at a King Penguin colony and involved ten marked territorial pairs.

Birds chased	Birds chased by			Total
	Males	Females	Unidentified	
Neighbouring territorial adults	1	0	0	1
Non-territorial and visiting adults (1)	2	3	3	8
Subadults	13	9	4	26
Juveniles	5	4	1	10

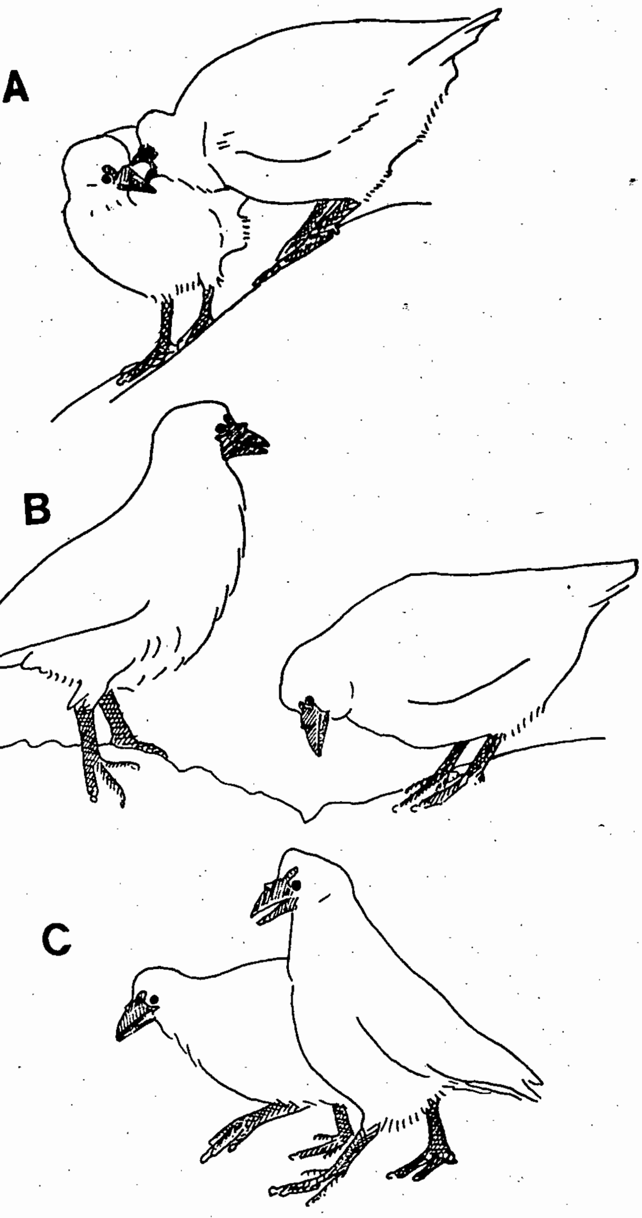
1) Some of the visiting adults had summer breeding territories elsewhere.

of the two birds are not synchronised with each other and neither are the calls synchronised with the movements. Frequently one bird performs more vigorously than the other. Bill-wiping and Run-and-Call displays (see below) were sometimes seen during or after bouts of Bob Call displays.

Context : This is essentially a display by mated pairs within territories but on rare occasions ($< 1\%$) it was performed by two marked adults which were known to have other mates. Ninety-four percent of Bob Call displays occurred within the territories of the birds involved ($N = 103$). The display was initiated equally by either sex (Table 3, $P > 0.05$, Chi-squared test) and when bill-biting was involved, this was also performed equally by either sex (18 times by males, 20 by females, $P > 0.05$).

The display was most often performed when intrusion of the territory occurred or was imminent (48% of displays), or apparently as a greeting signal when a pair met in the territory (29%) but also when some disturbance, such as the presence of a skua or calling by neighbouring pairs took place in the vicinity of a pair (Table 3). The display was also a common sequel to aggressive encounters between neighbouring males (see below). Bill-biting occurred with similar frequency in all situations (Table 3). The display sometimes occurred during nest relief when incubating and it followed 52% of nest reliefs during brooding ($N = 33$).

A homologous pair display, called the "bowing ceremony" by



ig. 3. Bill-biting prior to a Bob Call dis-
ay (A); the Bob Call display (B) showing birds
n the head-up and head-down postures; and,
e Run-and-Call display (C). (Drawn from
otographs and field sketches.)

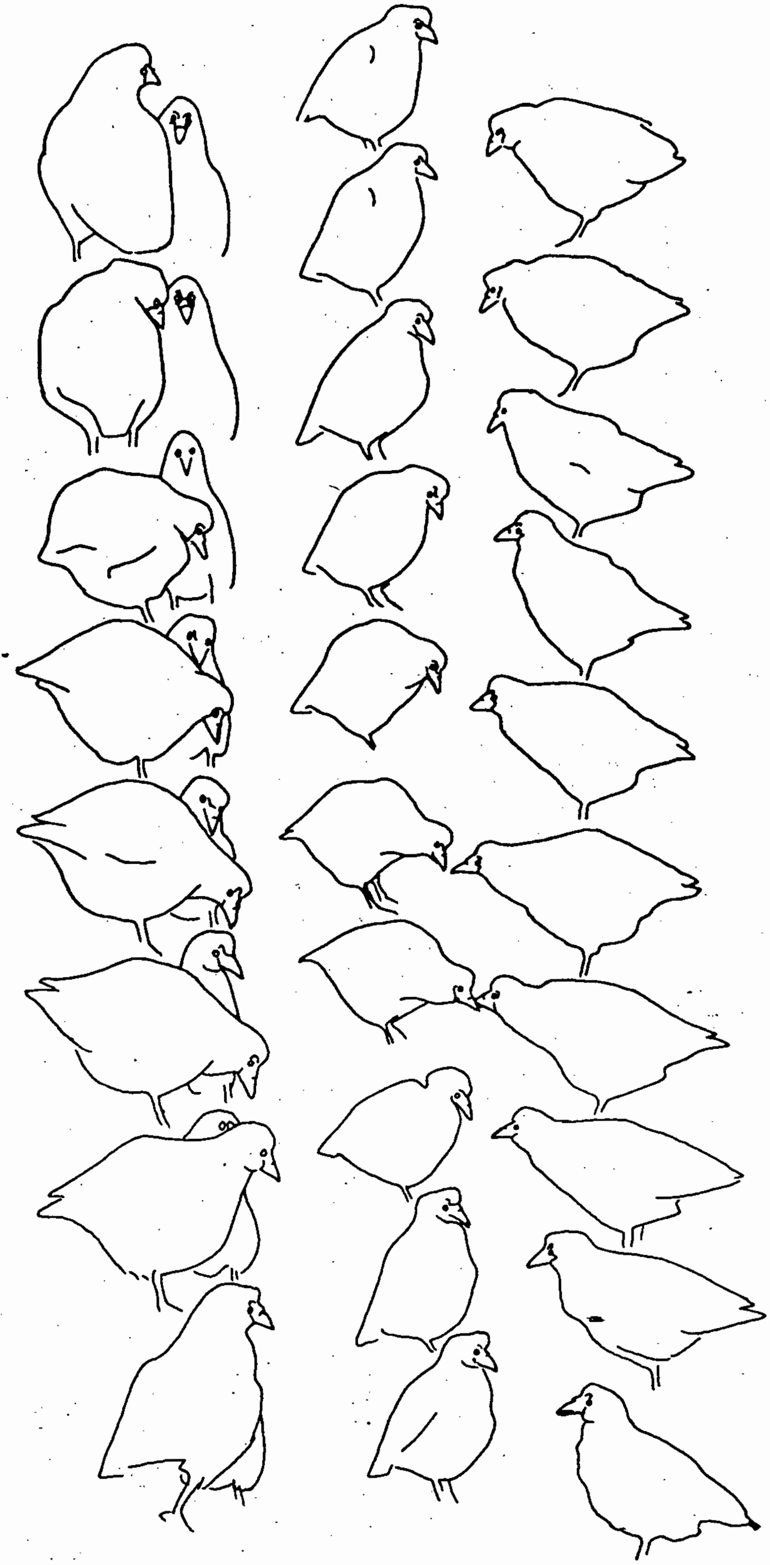


Fig. 4. Two sequences of the Bob Call display (left and right) in Lesser Sheathbills. (Drawn from movie film sequences lasting 0.9 and 1.1 seconds respectively.)

TABLE 3

Analysis of 103 Bob Call displays performed by colour-marked, territorial Lesser Sheathbills of known sex.

Apparent stimulus for the display	% of total	Percentage of displays			
		Initiated by			Bill-biting reported
		Male	Female	Not known	
Following eviction of an intruder	27	57	36	7	43
Intruders near but not chased	21	32	64	4	41
Territorial neighbour chases intruder	7	71	29	0	57
Territorial neighbours give Bob Call display	3	33	67	0	33
Pair meet each other in territory	29	50	50	0	40
Predators in or near territory	6	50	50	0	33
No apparent stimulus	7	72	14	14	0
All displays	100	50	46	4	39

Jones (1963) is the most conspicuous display reported for Wattled Sheathbills and its function is apparently to maintain the pair bond.

Run-and-Call

Description : A pair of birds, both in extended upright postures, run or walk next to each other, occasionally bowing their heads slightly (Fig. 3). The birds utter loud calls similar to those given in the Bob Call display. The wings are held to the sides. The display is interspersed with pauses, when Bob Call displays are given and in many respects Run-and-Call is very similar to that display.

Context : The display was seen to be performed only by the members of mated pairs within or adjacent to their territories. In 39 out of 46 displays observed in detail, the paired birds displayed while moving slowly behind an intraspecific intruder as it left their territory. Intruders most commonly evicted in this manner were non-territorial adults. In this context Run-and-Call displays functioned as low-intensity defence. The display also occurred when neighbouring pairs gave a similar display or the Bob Call display (four of the 46 observations) or for no apparent reason. On rare occasions two pairs displayed simultaneously while moving along their common territorial boundary.

Fly-and-Call

Description : The members of a pair take flight simultaneously and fly, separately, in low circles to land near to where they started. The flight appears to be slower than in normal flight and while in the air one or both birds give loud staccato calls. The flight is often preceded or followed by the Bob Call display.

Context : This behaviour was seen less than 10 times in two years and there is doubt whether it does constitute a display. The behaviour always occurred within a pair's territory. On a few occasions two pairs took flight simultaneously from within 5 m of each other. Single birds returning to their territories after bathing or foraging elsewhere, sometimes flew, calling, in a similar slow, circling manner. No apparent stimuli for the behaviour were observed.

Fighting

Description : Lesser Sheathbills fight by pecking at each other's heads and beating with their wings, apparently using the horny carpal spur to batter the opponent (Fig. 5). One bird may grip its opponent's wing or tail and hold on firmly until the other escapes, usually with the loss of a few feathers. Immediately before attacking, and between bouts of fighting, the birds adopt Aggressive Upright postures.

Context : Fighting occurred between neighbouring territorial adults and almost invariably involved two males (Table 1).

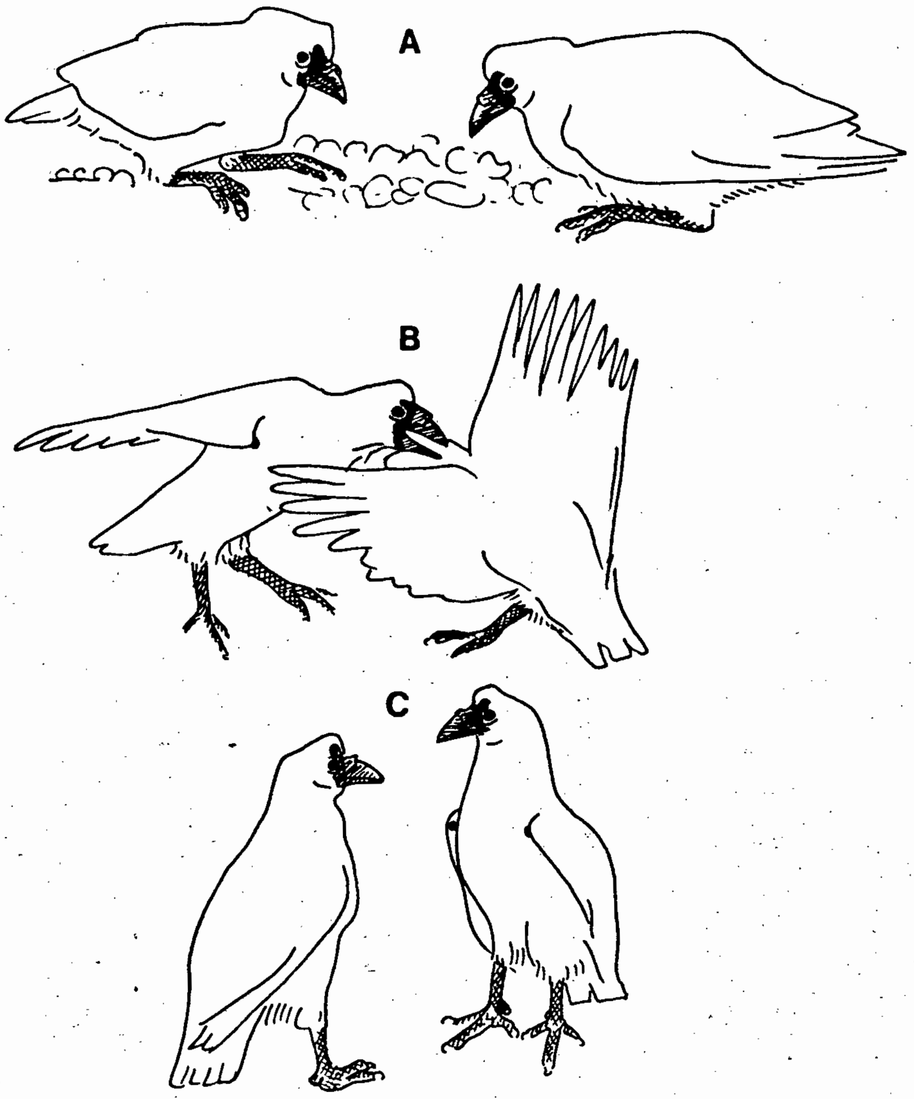


Fig. 5. Displays seen in boundary disputes, including the Crouch-and-Jab display (A); Fighting (B); and, Aggressive Upright postures (C). (Drawn from photographs.)

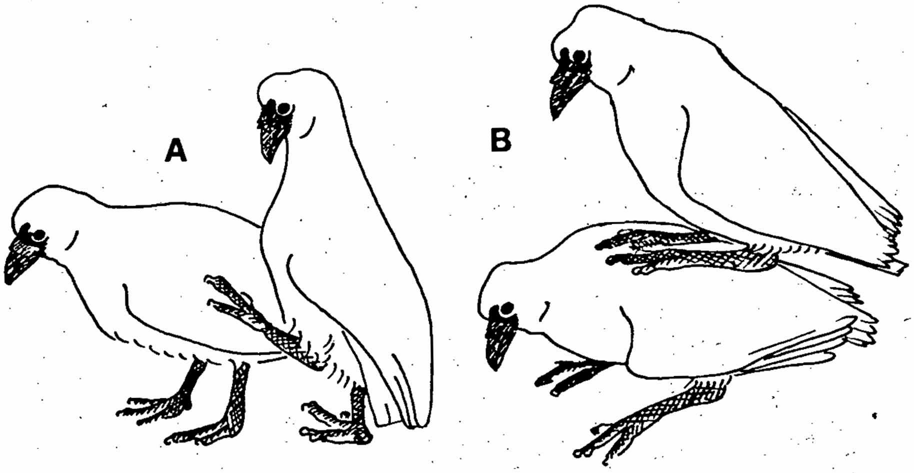


Fig. 6. Pre-copulatory behaviour (A) showing the male Prancing and scratching the flanks of the female and the female in a receptive semi-crouched posture; and, Copulation (B). (Drawn from movie film and field sketches.)

These fights were included in sequences of displays including Bill-wiping, Crouch-and-Jab (see below) and Bob Call displays. Brief exchanges of a few pecks also occurred in non-territorial situations when sheathbills were crowded around a rich food source, such as a seal carcass.

Fights usually only lasted a few seconds and ended before one antagonist was noticeably beaten. Damage to fighting birds was usually nil, sometimes merely muddied and bedraggled plumage and rarely bloodied heads. Fighting in Wattled Sheathbills involves similar pecking and wing-beating and is also seldom damaging (Jones 1963).

Crouch-and-Jab

Description : Two birds, facing directly at each other, crouch low with their bodies parallel to the ground, tarso-metatarsi touching the ground and wings partially opened (Fig. 5). The birds jab with their bills towards each other, sometimes jabbing at stones or debris in front of them or merely jabbing the air. The birds remain crouched in one spot for many seconds but may also shuffle sideways or towards each other. Birds occasionally peck viciously and pull at pieces of kelp debris or feathers in what appears to be redirected aggression.

Context : The display was seen to be performed only by territorial adults at the boundaries of their territories in high intensity boundary disputes (see below). Lesser

Sheathbills probing amongst small pebbles for oligochaete worms and insect larvae crouched and probed with the bill in a manner quite similar to the ritualised Crouch-and-Jab display.

Prancing

Description : The bird stands in an extended upright posture with the bill held almost vertically downwards (Fig. 6). In this posture the bird moves about, to the sides and front of its mate, with its feet treading rapidly in a prancing manner. The bird may scratch repeatedly at the flanks of its mate with a foot. A low-pitched clucking call has been heard from a bird performing the display.

Context : This is a pre-copulatory display given by the male. The female's response to this display was either to crouch slightly whereupon the male mounted, or to move away from the male. Twice females were seen to peck at males' feet before moving away.

Jones (1963) described the pre-copulatory display by male *Chionis alba* as stiff-legged strutting around the female, which stood still with slightly lowered head and raised tail.

Copulation

Description : Following the Prancing display by the male and upon being repeatedly scratched by him on her flank, the female crouches very slightly with a slightly lowered head and the male mounts (Fig. 6). The mounted male treads rapidly, flaps its wings for balance and uses its tail to shift the female's tail aside to make cloacal contact. During the very brief cloacal contact, the female tips forward until her head almost touches the ground. The mounted male does not grip the female's plumage, but one male was seen to peck once at a female's head.

Copulation ends when the female moves away and dislodges the male. Post-copulatory behaviour was very variable. Out of 10 observations of mounting, the female gave : a brief Facing-away movement, while standing very erect, in three cases; a Forward threat facing away from the male on one occasion; a Bob Call display with mutual bill-biting on one occasion; and in all other cases, the pair wandered apart to preen.

Context : Copulation occurred within the territory on level surfaces. Copulation attempts were seen only 16 times during two years of field work, between 21 October and 30 December. Copulation in the Wattled Sheathbill is apparently similar (Jones 1963).

VOCALISATIONS

The calls which accompanied displays by adult Lesser Sheathbills were very similar in pitch and amplitude to the human ear, but varied in the frequency and number of call-notes as described above. No differences could be discerned between the calls of the sexes but juveniles had noticeably shriller and longer call-notes. The voice of an adult Lesser Sheathbill had a high pitch and sufficient amplitude to be heard above the loud background noise of calling penguins.

Short series of calls accompanied take-off when Lesser Sheathbills fled before an approaching Sub-Antarctic Skua. Single "cluck" calls were uttered by Lesser Sheathbills flying to and from roosts and by birds at roosts when others flew in.

BOUNDARY DISPUTES

Several displays occurred during boundary disputes between neighbouring territorial adults. The use of displays varied according to the intensity of the encounter and they were performed in no rigid sequence. Boundary disputes were initiated when neighbouring territorial birds approached within 1 - 5 m of each other while foraging or chasing intruders. In many cases the birds ignored one another and the following analysis concerns only those encounters in which the birds temporarily terminated all other activities in order to display.

In many boundary disputes the birds remained 2 - 5 m apart and stood looking at each other, with frequent Bill-wiping and foraging-like pecks at the ground, before wandering apart. Sometimes neighbours walked parallel with each other along their boundary. Encounters of greater intensity occurred when birds approached closer to each other until in high intensity situations both birds performed Crouch-and-Jab displays while separated by only 10 - 20 cm (Fig. 5). As the distance between the birds decreased, there was an increased tendency for both to crouch rather than stand, for jabbing at the ground or air to increase, and for Bill-wiping and foraging-like pecks to decrease in occurrence (Table 4). Re-directed aggressive pecking and pulling at debris occurred infrequently in all cases.

Boundary disputes led to Fighting, followed by Aggressive Upright postures in 29% of encounters (N = 68) and Fighting occurred in 44% of encounters where the antagonists approached within 20 cm of each other (N = 45). Bob Call displays, by one or both pairs of territorial birds involved, followed 35% of all encounters (N = 68). Occasionally while one adult was involved in a Crouch-and-Jab display, its mate or full-grown chick would stand about 30 cm behind it, vocalizing. Boundary disputes lasted 1 - 13 minutes and 80% of the encounters lasted 2 - 4 minutes (N = 42). Almost all encounters involved territorial males (Table 1) but female-female encounters (two out of 57 instances) and one male-female encounter were seen.

In boundary disputes between territorial adult Wattled Sheathbills the birds "stood facing each other in threatening attitudes, each on its own side of the boundary and usually moved slowly along the boundary in such postures . . ." (Jones 1963).

TABLE 4

The occurrence (and percentage occurrence in parentheses) of certain postures and displays during boundary disputes between neighbouring territorial Lesser Sheathbills.

Posture or display	Distance between birds (cm)			
	⩾ 100	50	30	⩽ 20
Body position				
Crouched	8 (28)	5 (38)	9 (45)	37 (80)
Standing	21 (72)	7 (54)	10 (50)	7 (15)
Not recorded	0 (0)	1 (8)	1 (5)	2 (4)
Head movements				
Jabbing at the air	1 (3)	0 (0)	10 (50)	44 (96)
Jabbing at the ground	0 (0)	3 (23)	1 (5)	18 (39)
Pull and peck at debris	3 (10)	1 (8)	1 (5)	5 (11)
Bill-wiping	19 (66)	9 (69)	7 (35)	16 (35)
Foraging pecks	17 (59)	2 (15)	3 (15)	1 (2)
No. of observations	29	13	20	46

Note: The % occurrences of head movements do not add to 100%, since birds performed several head movements while in one body posture.

COMFORT BEHAVIOUR

The preening, scratching, stretching and bathing behaviour of Lesser Sheathbills was not notably different from other charadriiform birds. Bathing and preening occurred frequently and, although living in muddy areas, the birds kept the plumage remarkably clean. Lesser Sheathbills cleaned their bills, following feeding, by rubbing or wiping them on the ground. This appears to be the only comfort movement to be used in a secondary, ritualised manner as the Bill-wiping display.

DISCUSSION

Morphological adaptations for display

Movements of the head were prominent in many displays by Lesser Sheathbills. In distance-increasing displays (Tinbergen 1959), such as the Forward and Crouch-and-Jab, the bill and face are thrust forwards, whereas in distance-reducing displays such as Facing Away and the Hunched, the bill and face are turned away from other birds. The black facial caruncles and culmen sheath which are present in both sexes contrast with the white plumage, apparently enhancing agonistic signals in a similar manner to the black faces of *Larus ridibundus* and other "masked" gulls (Tinbergen and Moynihan 1952, Tinbergen 1964). Facial features are poorly developed in immature Lesser Sheathbills (Appendix one) and these birds do not hold territories, seldom use the Forward threat display and never participate in boundary disputes. In Wattled Sheathbills the caruncles are pink and the culmen sheath is greenish (Jones 1963) but these features could still enhance the signalling effects of ritualised head movements.

The white plumage of Lesser Sheathbills renders them conspicuous against the background of dark mud, lava or vegetation. It is not known whether this white plumage was selected for its conspicuousness in such habitat or for other reasons, such as for camouflage in snow, but it is an effective advertisement of the bird's presence in a territory or in a flock.

Male Lesser Sheathbills performed agonistic displays more frequently than females, and boundary disputes and Fighting, which involved prolonged physical proximity and contact, were almost exclusively performed by males. Males are significantly larger than females and this has been attributed to selection favouring male dominance in territorial agonistic encounters (Appendix one)

Displays within the territorial context

The full repertoire of displays was used by territorial adults but non-territorial birds were not seen to perform Crouch-and-Jab, Fly-and-Call, Run-and-Call, Prancing, Copulation or Bob Call displays. Nor did they engage in boundary disputes of any form. Anxiety Upright and brief supplanting Chases, rarely accompanied by Facing Away or Fighting, were the only displays to occur regularly amongst non-territorial groups. Intraspecific competition among non-territorial birds usually took the form of unritualised quarrels over ephemeral food items.

Territorial defence usually occupied less than 5% of the daily time and energy budgets of breeding adult Lesser Sheathbills (Part seven), but involved a wide range of behaviour (Table 5). Territorial adults usually rested and preened on raised boulders, which increased their chances of seeing intruders but, since they were very conspicuous, also increased the chances of potential intruders seeing them and being deterred. Active advertisement of territorial occupation was achieved using visually and audibly conspicuous displays. Displays which were apparently used to threaten potential intruders were similarly conspicuous. Active defence of territories at close range did not include vocalisations. When interacting with non-territorial birds, territorial birds usually used overt aggression (Chasing) but when interacting with neighbouring territorial adults, which were likely to retaliate if attacked, they usually used ritualised agonistic signals (Table 5) and resorted to overt aggressive Fighting only in high intensity disputes. This fairly complex array of territorial behaviour is comparable to the three-tiered system of territorial defence found in some song birds, which use long-range warnings to deter potential intruders, visual displays to repel intruders at intermediate range and overt attacks on persistent intruders (Peek 1972, Davies 1978).

Lesser Sheathbills did not compete directly for mates, nests or mating sites, but for the acquisition of foraging territories which were the key to successful breeding (Part one). The birds had no displays which might have functioned purely to attract mates or to advertise nest sites, such as Choking in gulls (Tinbergen 1959). The acceptance of a new partner into an established territory occurred infrequently and the behaviour involved is not adequately known. The Bob Call display, which was seen on rare occasions to be performed by

TABLE 5

Behaviour used by Lesser Sheathbills to advertise and defend territories.

Attributed function	Behaviour
Advertisement	
a) Passive	Preening and resting in conspicuous places
b) Active	Bob Call and Fly-and-Call displays
Distance threat	Forward and Bill-wiping displays
Active defence	
a) Against territorial neighbours	Crouch-and-Jab displays, Re-directed aggressive pecking, Aggressive Upright, Fighting
b) Against non-territorial intruders	Run-and-Call displays, Chasing

birds which were not mated, is probably involved. A new partner had usually frequented the area of the territory as a non-territorial bird and individual recognition between the territory holder and the prospective mate probably facilitated the establishment of a pair-bond.

Pair-bonds did not form outside territories and existing pair-bonds were relevant only within territories. Adults which were temporarily non-territorial in winter tended to ignore their mates. Mutual pair displays were almost always performed within territories, usually in agonistic situations and probably promoted mutual tolerance within the territory. The Bob Call display is possibly comprised of alternating elements of aggression (Aggressive Upright and Bill-biting) and appeasement (Hunched) in a similar manner to the ambivalent Bowing displays in pigeons (Murton and Westwood 1977: 106). Bob Call displays could thus serve to inhibit attack by the mate while demonstrating a measure of territorial aggression.

Pre-copulatory Prancing and Copulation were the only behaviours to which predominantly sexual motivation could be attributed. These behaviours were rare and appeared to be used only for insemination during the breeding season. They were not used at other times of the year to foster pair-bonds, even in birds which remained territorial all year.

Taxonomic implications of displays

The displays of the two species of sheathbills are superficially very similar in form and function, although those of the Wattled Sheathbill are poorly known. It is not known, for instance, whether the frequency of use of the various displays is similar in both species in similar ecological contexts.

The taxonomic affinities of the Chionididae are still ill-defined, despite attention from several taxonomists (reviewed by Shufeldt 1893, Sibley and Ahlquist 1972, Jacob 1977, Strauch 1978). A more detailed survey of the ritualised behaviour of the sheathbills could help to elucidate : the difference between the species, particularly those related to differing ecological conditions; their relationships with other charadriiform families; and, evolutionary trends in the behaviour of the Charadriiformes.

SUMMARY

Agonistic and sexual displays, sequences of displays and comfort behaviour of Lesser Sheathbills *Chionis minor* living in the sub-Antarctic are described. Pairs of adults maintained territories within penguin colonies with the principal objective of defending food resources. Territorial birds of both sexes used a complex array of displays to : (a) advertise their presence; (b) threaten intruding conspecifics; (c) evict non-

territorial intruders; and (d) maintain territorial boundaries, re-inforced by Fighting neighbouring territorial adults. Both members of a pair defended their territory but males did so more frequently. Pair-bonds were formed and maintained only within territories, and mutual pair displays probably promoted mutual tolerance of the mate within the territory. Copulatory behaviour appeared to be used for insemination only. Intraspecific behaviour among non-territorial sheathbills was largely restricted to very brief agonistic interactions over ephemeral food items and involved few and simple displays. The black facial caruncles and culmen sheath apparently serve to emphasize ritualised movements of the head. Vocalizations accompanied many displays and were usually audible above the noise of the penguin colonies. A comprehensive study of the behaviour of both species of sheathbills could provide valuable information on the evolution of displays in the Charadriiformes.

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PART FOUR

SEASONAL CHANGES OF SEXUAL AND TERRITORIAL BEHAVIOUR AND PLASMA TESTOSTERONE LEVELS IN MALE LESSER SHEATHBILLS

Introduction

Most studies of the endocrine basis of avian behaviour have been analyses of the effects of exogenous hormones, or correlations between endogenous hormones and behaviour of birds in laboratories (reviews by Follett 1973; Lofts and Murton 1973; Murton and Westwood 1977). Recently, circulating levels of hormones have been studied in the field in relation to episodic (Harding and Follett 1979) or seasonal changes in behaviour (Temple 1974; Lisano and Kennamer 1977; Wingfield and Farner 1978; Berry, Millar and Louw 1979). These studies have the advantage of using free-living birds exposed to a full range of external stimuli, but involve problems of relating changes in a specific behaviour pattern to changes in levels of a particular hormone. This is particularly so in studies of seasonal events, since territoriality, nest-building and courtship, which are all known to be affected by hormones, are restricted to the same time of year in most birds (Murton and Westwood 1977).

We report on seasonal changes in territorial and sexual behaviour and plasma testosterone levels in free-living, adult male Lesser Sheathbills at Marion Island (46°54'S, 37°45'E). Lesser Sheathbills are omnivorous charadriiform shorebirds, resident on four sub-Antartic island groups (Part one). Breeding in this species is restricted to a brief season in summer (95% of a sample of 94 eggs were laid between 4 and 31 December; Part one).

and all breeding birds are territorial. Territoriality is not, however, necessarily restricted to the breeding season. This characteristic thus affords an opportunity to study the separate role of hormones in territorial as distinct from sexual behaviour.

Pairs of Lesser Sheathbills maintain territories only within penguin colonies and virtually all the food eaten by territorial adults and their chicks is derived from penguins (Part one). Territorial tenure is dependant on the presence of relatively abundant food supplies while the penguins are present. In colonies of King Penguins *Aptenodytes patagonicus*, which are present on Marion Island all year, the sheathbills remain territorial all year, but in colonies of Rockhopper Penguins *Eudyptes chrysocome* and Macaroni Penguins *E.chrysolophus*, which desert the island for the austral winter (May to October), the sheathbills are territorial only during the summer, November to April (Part three).

Methods

Blood samples were collected from living birds, via brachial veins, or from the hearts of birds which had been shot, within 10 minutes of death. The procedures were deemed comparable since in laboratory rats mean brachial vein plasma testosterone was not significantly different from mean cardiac plasma testosterone. The heparinised blood was immediately centrifuged at 2 000 - 2 500 r.p.m.

for 15 min., the plasma aspirated, transferred to Eppendorf reaction vials and stored at -15°C until assay.

Blood samples were collected between 12h30 and 16h30 (local time) in an attempt to obviate possible diurnal fluctuations in testosterone levels (Balthazart 1976). Three samples collected from roosting birds at night (at about 21h00) were, however, also included since the testosterone levels in these samples were similar to those in plasma collected between 12h30 - 16h30 at the same time of year (see Fig. 3). Birds were observed for 20 - 30 minutes prior to sampling to determine whether they were territorial or not and to record displays. All of the sampled birds were adult males which were known to have held territories in either King or Rockhopper Penguin colonies. Some of the birds had, however, temporarily abandoned their territories in Rockhopper Penguin colonies.

Plasma testosterone concentration was estimated in duplicate by radioimmunoassay of ether extracts of samples using an antiserum raised against testosterone-3-carboxy methyl oxime-bovine serum albumin conjugate. The antiserum was highly specific for testosterone and exhibited less than 5,1% cross-reaction with dihydrotestosterone and minimal cross-reaction with other naturally occurring steroids (Millar and Kewly 1976). Intra-assay and inter-assay coefficients of variation were 5,4% and 9,9% respectively.

Behavioural data were collected at a colony of King Penguins occupied by 12 pairs of territorial adult Lesser

Sheathbills and variable numbers of immatures and non-territorial adults. All the territorial birds and most of the others had been sexed, aged (Appendix one) and colour-ringed. The frequencies of conspicuous displays performed by these Lesser Sheathbills were recorded for 30 min. periods, at the same time of day as the blood was sampled, and at intervals of about 10 days between June 1976 and May 1977. Observations were made from an exposed vantage point and weather conditions, (cold, wind and rain) limited observation to 30 min. Additional incidental observations were made between January - November 1974 and April 1976 - May 1977.

Results

Seasonal variation of territorial behaviour

The maintenance of territories in penguin colonies by Lesser Sheathbills included behaviour with three apparent functions: to maintain boundaries between neighbouring territories; to evict intruding conspecifics; and, to advertise the presence of the territorial pair. These objectives were attained with the use of a variety of displays, which are described and analysed elsewhere (Part three).

Boundaries between neighbouring territories in penguin colonies were maintained by ritualised boundary disputes, usually involving only males, which occasionally led to fighting. Boundary disputes and fighting occurred at any time of the year in the King Penguin colony but were always infrequent (Fig. 1, A & B).

The eviction of non-territorial intruders, and very rarely also territorial birds, was achieved by overt chasing and through use of the Run-and-Call display. Chasing and Run-and-Call displays occurred at the King Penguin colony throughout the year (Fig. 1, B & C), and the frequency of occurrence of both activities correlated with the numbers of potential intruders present at the colony ($r = 0{,}71$ and $r = 0{,}54$ respectively, $p < 0{,}01$, $n = 31$).

Advertisement by the territorial pair was largely achieved through a visually and audibly conspicuous mutual pair display, the Bob Call display. This display was also important in maintaining tolerance of the members of the pair for each other's presence in the territory with the use of alternating elements of aggression and appeasement (Part three). Bob Call displays occurred at the King Penguin colony throughout the year (Fig. 1, E) but were most common from mid-September to mid-December, which was when other adults were prospecting for territories and courtship and nest-building was in progress.

The frequency of occurrence of the above displays is evidence that the Lesser Sheathbill pairs in the King Penguin colony actively advertised and defended their territories all year.

Seasonal occurrence of sexual behaviour

Copulation was a rare event among Lesser Sheathbills. During two full years of observations at many parts of the island, copulation or precopulatory behaviour were seen only 18 times, between 21 October and 30 December (Fig. 2).

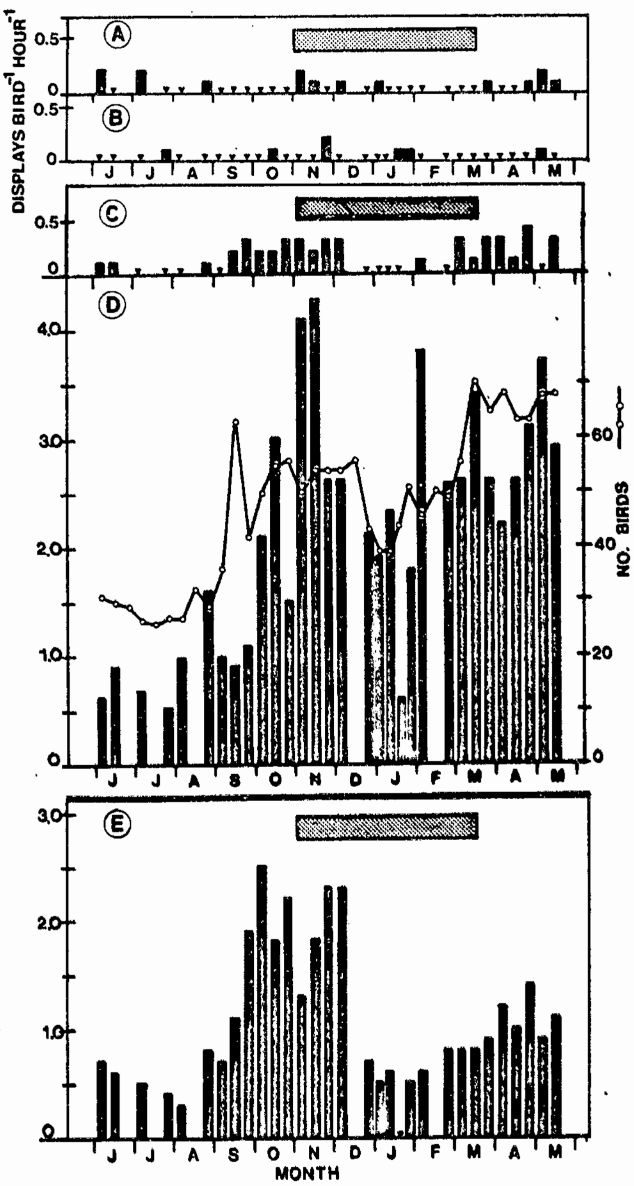

Fig. 1. The frequencies of occurrence of displays by Lesser Sheathbills within a King Penguin colony (solid bars). Triangles indicate no displays recorded in an observation period, the stippled bars delineate the Lesser Sheathbill's breeding season and the open circles the numbers of Lesser Sheathbills counted at the penguin colony. A : Boundary disputes; B : Fighting; C : Run-and Call displays; D : Chasing; E: Bob Call displays.

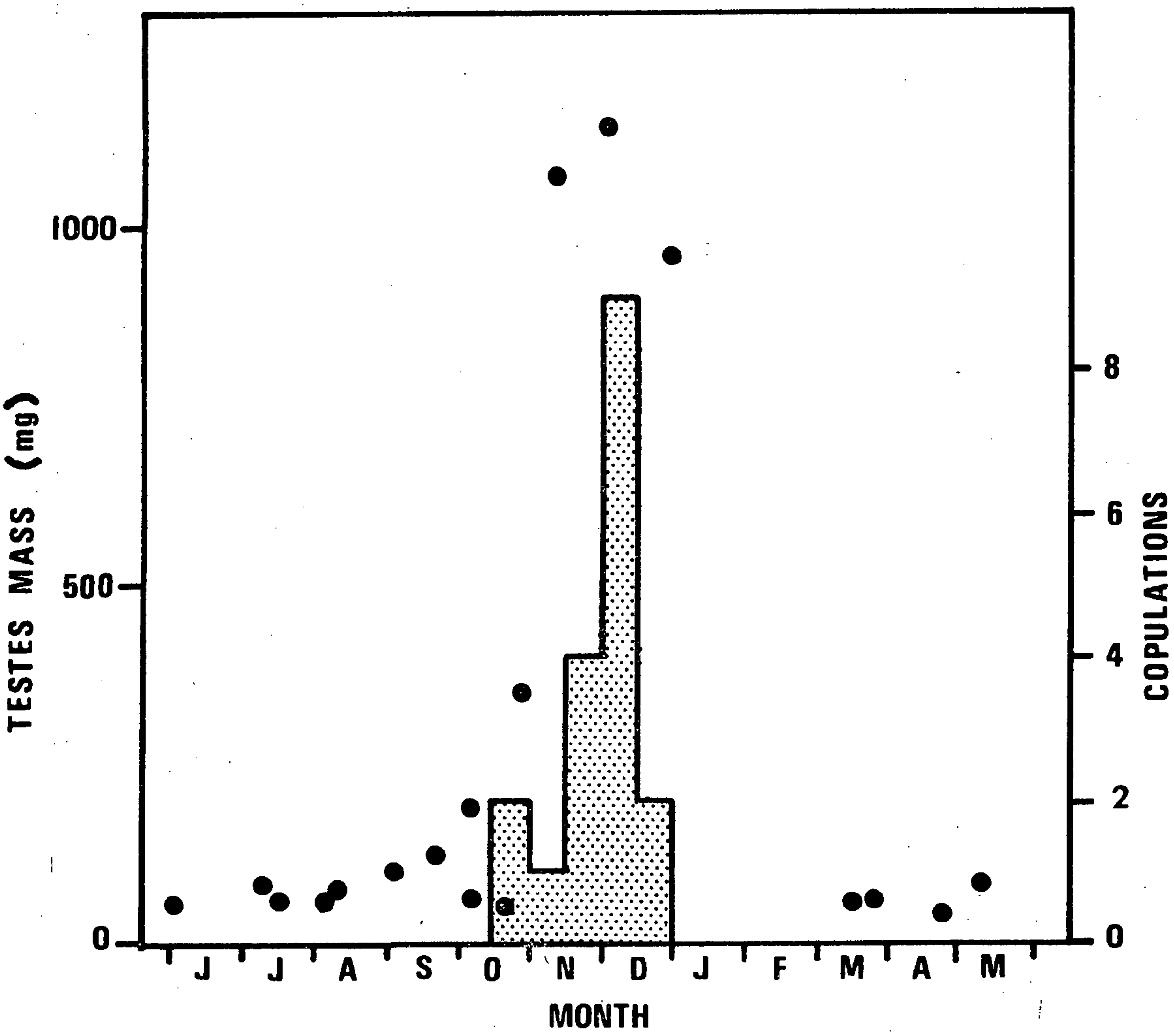

Fig. 2. Seasonal variations in the combined mass of the two testes of individual males (dots), and the incidence of copulation attempts (stippled) in adult Lesser Sheathbills. Data from two full years of observations from many parts of Marion Island.

Copulation was not important outside the breeding season as a means of re-inforcing pair bonds. Copulation was apparently only associated with fertilization and occurred at the time of year when adult males had enlarged testes (Fig. 2).

Plasma testosterone levels

Plasma testosterone levels in adult male Lesser Sheathbills ranged from $< 0,1$ to 7,5 nmoles 1^{-1} and showed a seasonal trend (Fig. 3). Testosterone levels in four months preceding laying (August to November) were significantly higher than at any other time of the year (t-test, $p < 0,01$). The mean testosterone levels in three males which were incubating (sampled late December) or rearing chicks (February and mid-March) were not significantly different from those in nine non-breeding males sampled from mid-March to July (t-test, $p > 0,05$).

Seasonal variations in testosterone levels did not correspond to changes in territorial behaviour. In winter (April to September) when adult Lesser Sheathbills in the King Penguin colony were actively defending and advertising territories, testosterone levels in territorial birds were no higher than in those birds showing no territorial behaviour (Fig. 3).

Testosterone levels were, however, highest at the time of year when nest building and copulation occurred and when the Bob Call pair display was most frequently given. Plasma testosterone levels correlated significantly with the combined masses of the testes in the Lesser Sheathbills

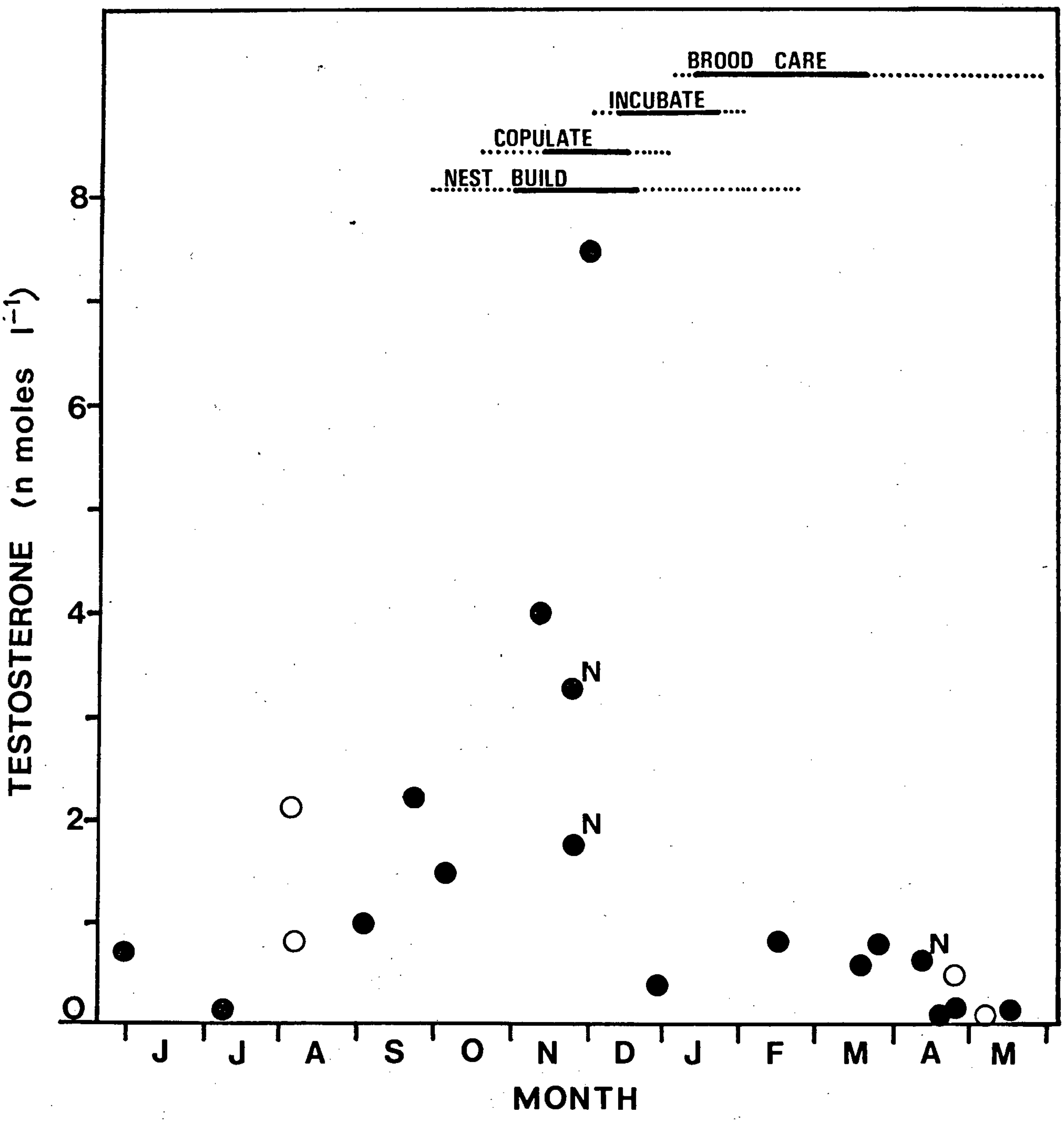

Fig. 3. Levels of testosterone in blood plasma of adult male Lesser Sheathbills which were defending territories (dots) and not defending territories (open circles). The maximum duration (dotted lines) and periods of maximum activity (solid lines) of reproductive events are also shown. Three blood samples collected from birds roosting at night are also indicated (N).

Table 1: Comparison of plasma testosterone levels (nmoles 1^{-1}) in male Lesser Sheathbills which had performed a Bob-call pair display within 20 minutes of being sampled, and those which had not.

	Reproductive activity	Display performed			No display performed		
		Mean	Range	N	Mean	Range	N
Mid-March - July	None (Wintering)	0,4	0,2-0,8	3	0,4	0,1-0,7	6
August - October	None (Pre-breeding)	1,9	1,5-2,2	3	0,9	0,8-1,0	2
November-December	Nest building and courtship	5,8	4,0-7,5	2	2,6	1,8-3,3	2
January - mid-March	Incubation and brood care	0,7	0,6-0,8	2	0,4	-	1

which had been shot ($r = 0{,}74$, $p < 0{,}01$, $n = 14$).

Plasma testosterone levels appeared to vary according to the bird's behaviour immediately prior to sampling. Males which had performed a Bob Call display shortly before being sampled had higher testosterone levels than those males which had not displayed (the ranges did not overlap), in all seasons except the winter (Table 1). This conclusion remains tentative since the data were insufficient for rigorous statistical testing and pooling data from different seasons to increase the sample sizes was not acceptable, due to the seasonal variations of testosterone levels. The highest concentration of plasma testosterone in this study (7,5 nmoles 1^{-1}) was from a male which had copulated 10 minutes before its blood was sampled.

Discussion

Plasma testosterone levels in male Lesser Sheathbills were above 1,0 nmoles 1^{-1} only between August and December. The occurrence of nest-building, copulation, the maximum frequencies of mutual pair displays and the increase in the mass of the testes, which is an index of active spermatogenesis (Murton and Westwood 1977), all co-incided with high levels of plasma testosterone, but incubation and brood-care did not. This suggests that testosterone is important in mediating physiological and behavioural events leading up to egg production in Lesser Sheathbills. Other hormones may also be involved. Testosterone is known to play an important role in spermatogenesis in birds (Lofts and Murton 1973, Murton and Westwood 1977). Injections of testosterone propionate have been demonstrated to modify nest-building, courtship and mating behaviour in several bird species (Crook and Butterfield 1968, Hutchison 1970, Adkins and Pniewski 1978, Balthazart and Hendrick 1978, DeViche 1979), and the seasonal occurrence of these behaviour patterns co-incided with high endogenous levels of plasma testosterone in several species (Balthazart and Hendrick 1976, Lisano and Kennamer 1977, Wingfield and Farner 1978, Berry *et al.* 1979).

It has been suggested that the endocrine system might be important in modulating minute to minute behavioural responses of animals during social interactions (Harding and Follett 1979). We tentatively suggest that short-term increases in testosterone levels in male Lesser Sheathbills co-incided with the performance of Bob Call displays and copulation. This is in accordance with experiments on a variety of species in captivity, in which the concentration of testosterone in males' plasma was higher following sexual stimuli, such as copulation or exposure to the females (reviewed by Harding and Follett 1979). We cannot conclude whether the altered hormone level or the behaviour was the causal factor in Lesser Sheathbills (see Balthazart 1976). Exogenous testosterone is known to affect behaviour and by inference increased endogenous production probably induces behavioural changes. Harding and Follett (1979) have shown, however, that experimentally induced aggression caused significant changes in circulating levels of hormones, including testosterone, within 19 minutes in free living male Red-winged Blackbirds *Agelaius phoenicius*.

Territorial aggression in Lesser Sheathbills was not restricted to the time of year when testosterone levels were high. The year-round availability of food in King Penguin colonies permitted territoriality to persist amongst adult Lesser Sheathbills living in such a colony in winter. Between mid-March to July all adult males sampled had low testosterone levels, whether they were actively defending and advertising territories or not. This indicates that either territorial aggression could be stimulated by testosterone at very low levels, or more probably, that territorial aggression was not influenced by plasma testosterone concentration in this species.

There is conflicting evidence on the role of testosterone in aggressive behaviour in birds. Aggressive territorial defence has often been attributed to the effects of androgens (Davis 1963, Lofts and Murton 1973), but as Davis (1963) pointed out, this was probably due to the seasonal co-incidence of territoriality with courtship, next-building and mating, behaviour which was known to be influenced by testosterone. In laboratories, some authors observed increased aggression following exogenous testosterone treatment (Etienne 1964, Selinger and Bermant 1967, Arnold 1975), but others found very little or no change in aggression (Davis 1957, Vowles and Harwood 1966, Balthazart

1974, DeViche 1979).

It has been suggested that androgens stimulate aggression in birds in "reproductive" situations, when males compete for females or nest sites, but that aggression in other contexts, such as for food in wintering flocks, might not be controlled by testosterone (Crook and Butterfield 1968, Arnold 1975). Our data tend to support this hypothesis. The main objective of territorial behaviour in Lesser Sheathbills was the defence of food resources in penguin colonies. Although breeding was ultimately dependant on the acquisition of a territory (Part one), males did not compete directly for females, nest sites or other objectives of immediate sexual significance.

Since territorial aggression in Lesser Sheathbills appeared to be independant of high testosterone levels, this behaviour might be influenced by other hormones. Exogenous progesterone, perhaps acting indirectly, was found to increase aggressiveness towards conspecifics in breeding males of two species of birds (Vowles and Harwood 1966, Murton, Thearle and Lofts 1969). Several studies have suggested that luteinising hormone, rather than testosterone, mediates intermale aggression in passerine birds (Davis 1963, Mathewson 1961, Crook and Butterfield 1968), although this view has been challenged by Arnold (1975). Recently luteinising hormone-releasing factor was found to directly influence behaviour in rats (Moss and Max McCann 1976) and courtship behaviour in one bird species (Cheng 1977) and might be considered to affect aggression in other birds, as it is produced in the central nervous system and affects neural function (Nemeroff and Prange 1978).

In conclusion, it appears that while high testosterone levels in Lesser Sheathbill males might stimulate reproductive activities, high levels were not essential for territorial aggression to occur.

Summary

At Marion island in the sub-Antarctic all breeding activities of Lesser Sheathbills *Chionis minor* were restricted to a brief summer season and all breeding adults had territories within penguin colonies. Pairs with territories in colonies of King Penguins *Aptenodytes patagonicus* remained territorial in the winter but those in colonies of other penguin species did not.

Plasma testosterone levels in adult male Lesser Sheathbills were significantly higher in the four months preceding laying than at any other time of the year. Nest-building, copulation, the peak frequencies of mutual pair displays and the seasonal increase in testes masses all co-incided with high testosterone levels. Boundary disputes, territorial fighting, eviction of intruders and advertisement of the territory by Lesser Sheathbills occurred throughout the year in a King Penguin colony and were independent of high testosterone levels. In winter both territorial and non-territorial adult males had very low testosterone levels.

The data suggest that in this species high testosterone levels might stimulate reproductive activities but high levels were not essential for territorial aggression to occur.

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PART FIVE

TERRITORIALITY IN NON-BREEDING LESSER SHEATHBILLS

TERRITORIALITY IN NON-BREEDING LESSER SHEATHBILLS (*CHIONIS MINOR*) AT MARION ISLAND IN THE SUB-ANTARCTIC

A. E. BURGER

INTRODUCTION

Territoriality is often interpreted as an adaptation facilitating the use of certain limited resources (e.g. food, nest-sites or mates) to improve the individual's fitness (Brown 1964, Brown and Orians 1970, Davies 1978). Fitness should be measured as the genetic contributions the individual makes to subsequent generations, but in practice this is very difficult to determine. Useful studies have, however, been made by analysing the proximate costs and benefits of territorial behaviour to the individual (e.g. Gill and Wolf 1975, Carpenter and MacMillen 1976).

In this study I examine ways in which territoriality might improve the fitness of adult Lesser Sheathbills *Chionis minor* outside the breeding season, relative to conspecifics living off the same resources at the same time. The assumption is made that a successful bird is one which maximises the net rate of food intake during the time allocated to foraging. This hypothesis is commonly accepted when testing models of optimal foraging (Krebs 1978) and should apply whether the strategy of the bird in a given situation was to maximise its net daily energy gain, to minimise the time spent daily in foraging or to minimise its net daily energy expenditure (see Schoener 1971, Pyke 1979).

At Marion Island (46°54'S, 37°45'E), in the sub-Antarctic, Lesser Sheathbills forage and breed in territories maintained within colonies of penguins during the austral summer, November to March (Part one). Lesser Sheathbills temporarily abandon territories within colonies of Macaroni Penguins *Eudyptes chrysolophus* and Rockhopper Penguins *E. chrysocome* during the winter, April to October, when these penguins desert the island. These sheathbills then forage solitarily or in flocks on the shoreline or on the vegetated coastal plain. King Penguins *Aptenodytes patagonicus*, however, are present throughout the year and this report concerns territorial behaviour in winter by Lesser Sheathbills in a King Penguin colony.

MATERIALS AND METHODS

Observations were made at a colony of King Penguins at Archway Bay, which in early winter (May) contained about 1000 adult penguins and 1200 chicks. The colony supported 40 - 50 Lesser Sheathbills which, for purposes of this study, were grouped into: *territorial adults*, comprising 12 pairs which defended areas of the penguin colony and adjacent beach; *intruders*, comprising non-territorial adults and subadults (Appendix one) which foraged in undefended portions of the colony and by intruding into territories; and *juveniles*, aged 3 - 4 months and independent of their parents. The juveniles were tolerated within their parents' territories where they did most of their foraging.

Instantaneous-scan observations (Altmann 1974) were made from first-light until darkness on three occasions, in June 1976, September 1976 and April 1978, to determine the average time spent foraging amongst the penguins, resting, preening and displaying. The observations were made from a raised vantage point and scans were made every five minutes. Due to difficulties in observing Lesser Sheathbills amongst the penguins, it was impracticable to record the sex, age or status of the birds with each scan.

Focal-animal observations (Altmann 1974) were made in April and May 1978 of individually-marked Lesser Sheathbills which were foraging. Birds which were resting or preening at the edges of the colony (see below) were not sampled. Lesser Sheathbills were unafraid of people and were studied from 20 - 60m range, with aid of binoculars and a tape-recorder. The weather was cold with occasional ice-squalls, limiting observations to 30 min. per bird. The duration and frequency of behaviours were measured from recorded commentary using tally-counters and stop-watches. Handling-and-eating time (Schoener 1971), hereafter referred to as *eating* in Lesser Sheathbills, included the time taken to pull bits off carcasses, extract invertebrate prey from the substrate and to watch for opportunities to kleptoparasitise penguins.

RESULTS

Lesser Sheathbills at the King Penguin colony spent 79% of their daylight time foraging, 10% resting, 10% preening and 1% displaying (Fig. 1). Eighty-two % of the foraging birds were amongst the penguins, 17% on the beach and 1% on the vegetated verges of the colony. Lesser Sheathbills moved out from amongst the penguins to rest or preen; territorial adults and juveniles on to boulders or ridges within their territories and non-territorial birds to the borders of the colony. Lesser Sheathbills recorded as "foraging" in the intantaneous-scans were actually performing one of several activities as revealed by the focal-animal observations.

About 87% of the foraging time of Lesser Sheathbills of each group comprised eating or walking (Table 1). Intruders spent significantly less time eating and more walking than either territorial adults or juveniles ($P < 0.01$, t-test). All birds spent similar amounts of time looking around with the head raised ($P > 0,05$). Other activities combined amounted to less than 5% of the foraging time. Juveniles spent appreciable amounts of time soliciting food from their parents but received very little food. Intruders and juveniles spent significantly less time chasing and more time fleeing than territorial adults ($P < 0.01$).

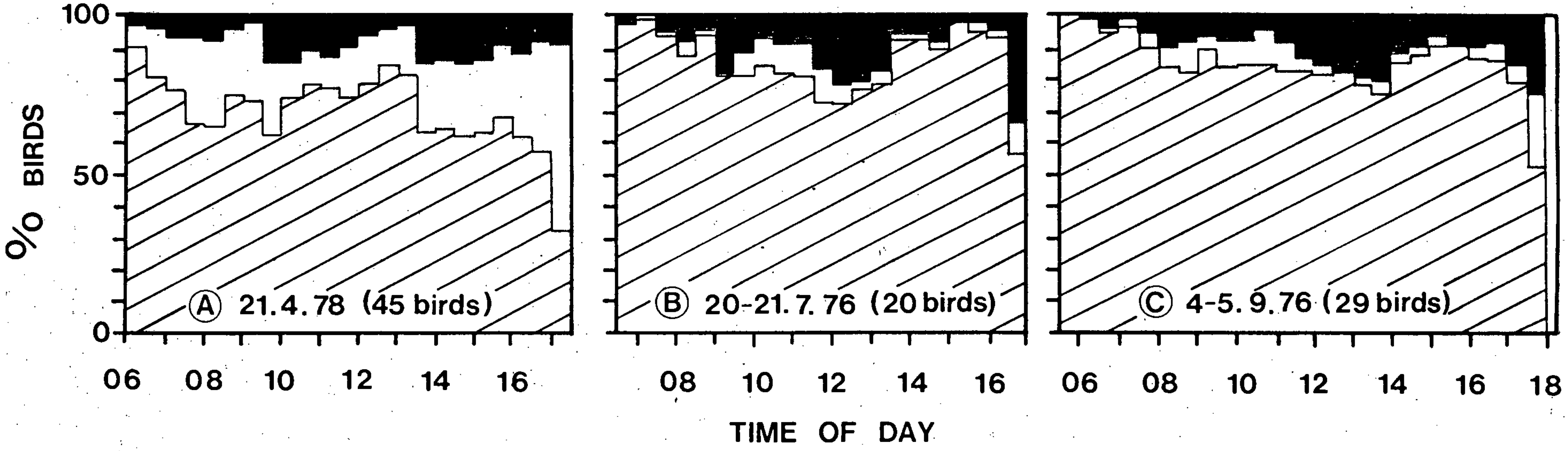

Fig. 1. Average number of Lesser Sheathbills of all ages and statuses engaged in foraging (hatched shading), resting (unshaded) and preening (black) at a King Penguin colony. Display comprised only 1% of the activity records, occurred at any time of day and was included here with foraging. Data from 5-min scans have been pooled into half-hour means and the mean number of birds visible per scan is given. Observations B and C were each made from noon to dark and first-light to noon on successive days.

Table 1

Mean (± S.D.) percentage of time spent by Lesser Sheathbills in various activities while foraging in a King Penguin colony. Data from focal-animal observations in April and May 1978.

Activity	Territorial males	Territorial females	Intruders	Juveniles	All Birds
Eating[1]	45 ± 13	52 ± 18	29 ± 15	49 ± 17	42 ± 18
Walking	44 ± 12	34 ± 18	57 ± 13	40 ± 17	45 ± 17
Looking around	8 ± 4	11 ± 7	11 ± 6	8 ± 5	9 ± 6
Chasing	2.1 ± 1.5	1.4 ± 1.3	0.4 ± 0.6	0.4 ± 0.7	1.1 ± 1.2
Fleeing	0	<0.1	3.3 ± 2.0	0.8 ± 0.7	1.2 ± 1.8
Threatening	0.6 ± 1.9	0.2 ± 0.2	0.3 ± 0.6	0	0.2 ± 0.4
Pair display	0.3 + 0.3	1.4 ± 1.2	0	0	0.4 ± 0.8
Preening	0.7 ± 1.1	0.8 ± 0.8	0.9 ± 1.1	0.3 ± 0.4	0.7 ± 0.9
Soliciting food	0	0	0	3.2 ± 2.5	-
No. birds	10	10	14	10	44
Mean observation time (Min)	30 ± 1	28 ± 3	25 ± 5	28 ± 4	28 ± 4

[1] See text for explanation

It was impossible to measure the absolute quantities of food eaten by Lesser Sheathbills in the King Penguin colony since the diet included very few discrete objects. Consequently the intake of each food type by an individual was taken to be proportional to the amount of time spent eating the food and the frequency of swallowing food per minute of observation time. Five food types were recognised, ranked below in order of decreasing quality, according to energy and protein contents (Part two), average meal sizes and the time needed to find and handle the food.

1) Penguin food. This comprised fish, squid and crustaceans robbed by Lesser Sheathbills from penguins regurgitating to their chicks (Part one). Lesser Sheathbills had to spend, on average, 33 seconds watching the penguins per beakful of food obtained (data from 22 birds). There was also some risk of injury when leaping against the penguin or its chick. When successful, the mass of food per swallow was about 10x that of any other food and the energy and protein content of the food was high, between 4.5 - 6.8 kJ g^{-1} (fresh weight) and 14 - 18% (fresh weight) respectively.

2) Carcasses of penguin adults and chicks, in various stages of decomposition, were concentrated patches of food, easily located by Lesser Sheathbills. They required extended handling time to exploit since the food was pulled off in small pieces. The mean energy and protein

contents of the parts eaten were high, 8.3 kJ g^{-1} and 16% of fresh weight respectively.

3) Invertebrates. Small flies (Diptera), collembolla and mites (Acarina) were widely distributed on the floor of the colony; larger kelp flies (*Paractora* and *Apetenus* sp.), their larvae and pupae and small oligochaetes occurred amongst the rotting kelp on the beach and colony floor, sometimes in dense patches. The exploitation of invertebrates by Lesser Sheathbills involved extended search times, but negligible handling times. The individual food objects were small and had low average energy and protein contents, 3.0 kJ g^{-1} and 11% of fresh weight respectively.

4) Penguin excreta. Lesser Sheathbills occasionally ate freshly voided excreta but did not appear to actively search for it. Handling time was very little but the energy and protein content was very low, 2.1 kJ g^{-1} and 3% of fresh weight respectively.

5) Unidentified small objects, which were probably tiny insects, excreta of the moulted feather-sheaths from penguins. These objects probably had minimal food value.

Territorial adults, intruders and juveniles usually included food of each type in their diets but, on average, all birds spent most time (Table 2) and obtained most food (Fig. 2) at carcasses. The use of each food type varied considerably between individuals but several significant differences between bird classes were noted.

Table 2

Mean (± S.D.) percentage of time spent eating various food resources by Lesser Sheathbills foraging in a King Penguin colony. Data from focal-animal observations in April and May 1978.

Food type	Territorial males	Territorial females	Intruders	Juveniles	All birds
Penguin food	12 ± 15	10 ± 17	4 ± 12	0	6 ± 13
Carcass	20 ± 22	39 ± 26	18 ± 18	31 ± 22	27 ± 22
Invertebrates	10 ± 21	1 ± 1	2 ± 2	2 ± 5	3 ± 11
Excreta	2 ± 2	1 ± 2	2 ± 1	4 ± 4	2 ± 2
Unidentified items	1 ± 1	1 ± 1	3 ± 2	12 ± 15	4 ± 8
Total eating	45 ± 13	52 ± 18	29 ± 15	49 ± 17	42 ± 18

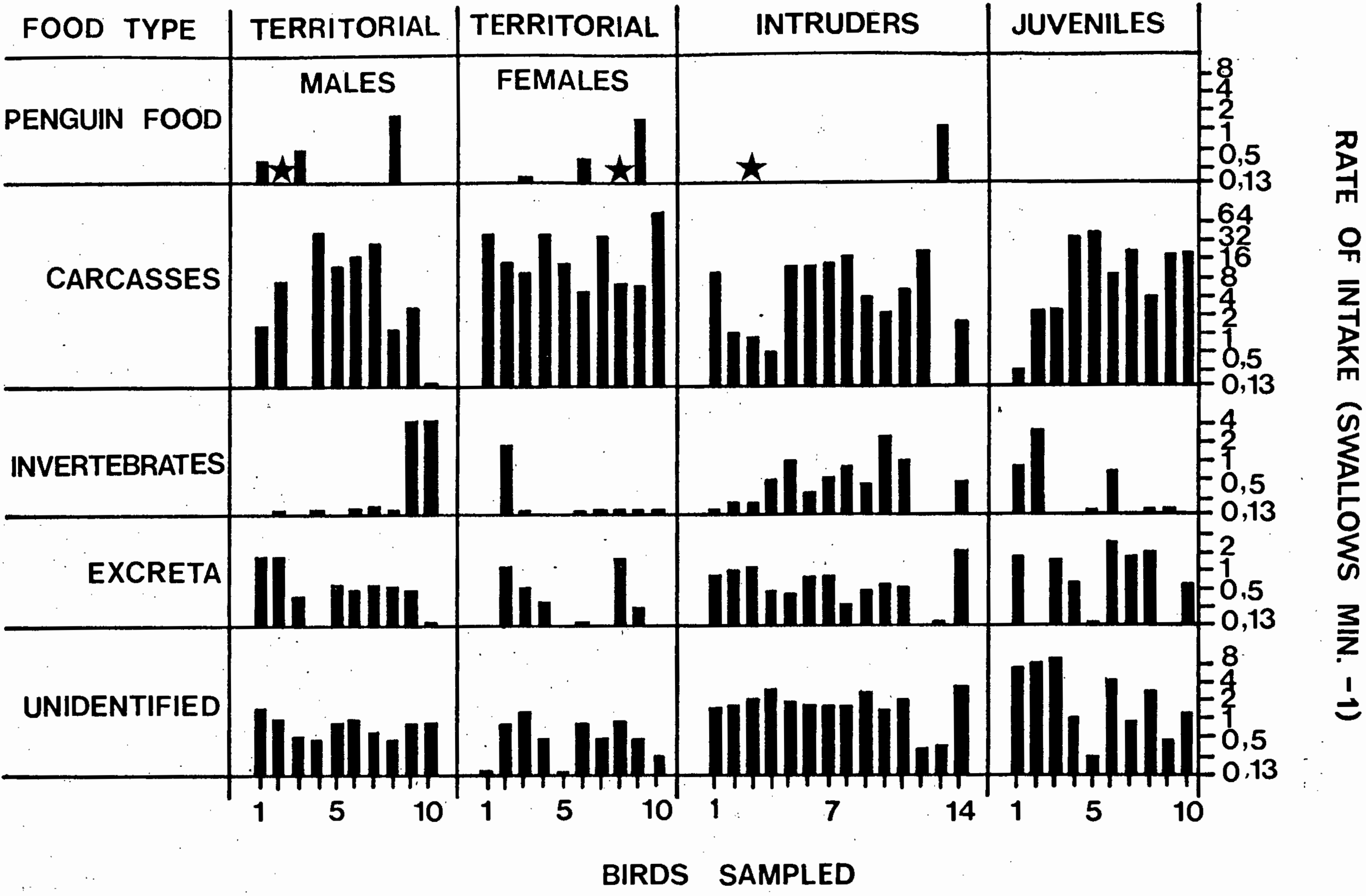

Fig. 2. Frequencies of swallowing food of various types by Lesser Sheathbills in a King Penguin colony. Each vertical set of data represents the diet of an individual bird during a focal-animal watch. Stars indicate birds which tried unsuccessfully to kleptoparasitise penguins. Note that the ordinate has a logarithmic (to the base 2) scale.

Territorial adults spent more time and were slightly more successful at robbing penguins than intruders although the data were insufficient for statistical testing of significance. Juveniles made no attempts to rob penguins, during these observations or at any other time during two years of field work at Marion Island.

The mean rate of intake of small pieces of carcasses by territorial females (25.4 ± 26.3 $min.^{-1}$ of foraging time) was significantly higher ($p < 0,05$, Mann-Whitney test) than that of males (11.2 ± 14.5 $min.^{-1}$) and intruders (7.4 ± 7.3 $min.^{-1}$ but not juveniles (16.2 ± 15.0 $min.^{-1}$, $p > 0.05$). The rate of intake of males was not significantly different to that of intruders and was significantly lower than that of juveniles. Individual males with low rates of intake at carcasses had, however, been successful at robbing penguins (three male sheathbills) or were exceptionally successful at catching kelp flies and their larvae (two male sheathbills), whereas this did not occur amongst intruders and juveniles which were unsuccessful at carcasses (Fig. 2). Juveniles spent more time (Table 2) and had significantly higher rates of food intake at carcasses than intruders.

Birds of all classes ate little of the low-quality food (Fig. 2). The rate of intake of invertebrates by intruders was significantly higher than that of territorial adults ($p < 0.05$, Mann-Whitney test) but the differences between adult males and adult females, adults and juveniles and intruders and juveniles were not significant ($p > 0.05$).

There were no significant differences between the rates of intake of excreta between any groups of Lesser Sheathbills ($p > 0.05$). Intruders and juveniles each had significantly higher rates of intake of unidentified objects than territorial adults ($p < 0.01$ in each case) but there were no differences between adult males and adult females or between intruders and juveniles ($p > 0.05$).

Lesser Sheathbills in the King Penguin colony frequently chased each other (Table 3) but since chases averaged only 4.4 ± 2.5 sec (range 1 - 15 sec, n = 173), chasing demanded very little of the foraging time of any bird (Table 1). Territorial adults did most of the chasing but were very seldom chased (Tables 3 and 4). Juveniles were subordinate to all other birds (Table 4) but were chased less frequently than intruders (Table 3). Juveniles only chased other juveniles, and on one occasion a subadult intruder.

Although chasing and being chased did not take up much time, it frequently disrupted the birds' foraging activities: once every four minutes amongst territorial adults and juveniles and once every two minutes amongs intruders (Table 3). Subordinate birds feeding at carcasses, where they had to remain for relatively long periods in order to get sufficient food, were particularly prone to being chased. Juveniles and intruders ended 47% and 37% of their feeding bouts at carcasses, respectively, by being chased away (n = 65 and 85 bouts respectively). Territorial males were never chased from carcasses and territorial females on

Table 3

Mean (± S.D.) frequencies of aggressive events (per hour) by Lesser Sheathbills foraging in a King Penguin colony. Data from focal-animal observations in April and May 1978.

Behaviour	Territorial males	Territorial females	Intruders	Juveniles	All Birds
Chasing	15.6 ± 8.4	13.4 ± 11.5	3.9 ± 4.8	3.0 ± 5.4	8.6 ± 9.4
Being chased	0	0.2 ± 0.8	28.2 ± 10.3	10.2 ± 9.6	11.3 ± 14.9
Both combined	15.6 ± 8.4	13.6 ± 11.7	32.0 ± 12.9	13.2 ± 9.8	19.9 ± 13.7
No. birds observed	10	10	14	10	44

Table 4

Occurrences of chasing and being chased amongst Lesser Sheathbills foraging in a King Penguin colony in April and May 1978.

Birds	Birds chasing						
being chased	Territorial males	Territorial females	Non-territorial aults	Subadults	Juveniles	Not known	Total
Territorial males	0	0	0	0	0	0	0
Territorial females	2	0	1	0	0	0	3
Non-territorial adults	8	8	0	0	0	9	25
Subadults	30	22	1	8	1	97	159
Juveniles	32	14	7	4	21	11	89
Not known	27	25	4	0	0	0	56
Total	99	69	13	12	22	117	332

only 2% of their feeding bouts (n = 109 bouts). Consequently the mean duration of feeding bouts at carcasses was significantly shorter for intruders and juveniles than for territorial adults (Table 5, $P < 0.05$, t-test).

DISCUSSION

Costs of territorial behaviour.- Territorial Lesser Sheathbills required time and energy to evict intruders and maintain territorial boundaries. However, this cost was low in terms of overt, active behaviour: territorial adults spent less than 2% of their foraging time and similar low proportions of the overall daily time budget in chasing, threatening and other defensive behaviour. Even though chasing involved energetically "expensive" behaviour such as running and flying, the overall energy expended daily in defence would still have been relatively low. The economical defence of the territory was achieved through conspicuous "passive" visual and vocal advertising (Part three). Maintenance of the same territories with stable boundaries from year to year probably facilitated their defence, as has been found for some other species (Southern and Lowe 1968, Davies 1976).

The conspicuousness of territorial Lesser Sheathbills might have increased their risk of predation by Sub-Antarctic Skuas *Catharacta antarctica*. The actual risk was, however, small, since the skuas very seldom attacked Lesser Sheathbills in penguin colonies (Part one).

Table 5

Mean (± SD) duration (seconds) of feeding bouts at penguin carcasses by Lesser Sheathbills. Sample sizes in parentheses.

Territorial adults				
Males	Females	Both sexes	Intruders	Juveniles
54 ± 80	62 ± 63	59 ± 70	37 ± 44	41 ± 46
(64)	(106)	(170)	(98)	(131)

Chasing frequently interrupted the foraging efforts of the territorial individual and even though the chases were very brief, they involved the movement of the individual away from the area where it had been searching for or handling food. This cost could have been partially offset by the territorial bird's familiarity with the resources available within the confines of the defended area. Although all the above cost functions appear to be low, they did represent an investment of energy, time and risk which would have been selected against in the absence of benefits.

Benefits of territorial behaviour - Lesser Sheathbills appear to benefit from territorial behaviour in winter in three ways. Firstly, the territorial adults improved their feeding success relative to their non-territorial conspecifics. Territorial adults ate more of the high-quality and less of the low-quality food than their non-territorial conspecifics. Territorial adults generally had more rapid rates of intake of carcass flesh than intruders, and this was enhanced by the fact that the adults were generally heavier (Appendix one) and could probably tear off larger pieces, and they also appeared to have access to fresher carcasses which yielded larger pieces per beakful. Territorial adults were immediately dominant at any new resources which were deposited within their territories, such as a penguin carcass, and they were able to have longer feeding bouts at such resources than the subordinate juveniles and intruders.

Secondly, by tolerating juveniles within territories, adult Lesser Sheathbills improved the chances of survival of these juveniles, and thus the adults' own genetic investment. Although juveniles were aggressively inferior to non-territorial adults and subadults, they were chased less frequently when in their parents' territories, were able to spend significantly more time feeding, and had significantly higher rates of intake of high-quality food from carcasses than the intruders. Juvenile Lesser Sheathbills were generally thinner than older birds (Appendix one) and more susceptible to death from starvation in winter (Part one), but those within their parents' territories were never found starving. Juveniles partially offset the cost to their parents of their stay in the territories by helping to evict other intruding juveniles.

Thirdly, adults maintaining territories during the winter would have been more likely to have retained these at the onset of the breeding season. This has been shown for Blackbirds *Turdus merula* (Snow 1956). Also, the cost of re-establishing a territory, in terms of time, energy and risk of injury through fighting are likely to exceed the costs of maintaining an established territory (Fretwell and Lucas 1970, Pyke 1979). Territories were essential for breeding in Lesser Sheathbills and as there appeared to be an excess of potential breeding adults at Marion Island, competition for territories occurred

(Part one). Those adult Lesser Sheathbills which had abandoned territories in Rockhopper and Macaroni Penguin colonies for the winter began to re-occupy their territories for several hours a day after mid-October. This involved a reduction in their foraging time since the colonies were still unoccupied by penguins at that time and there was little food for Lesser Sheathbills there. Adults with territories in King Penguin colonies were spared this cost.

Genetic persistance, the ultimate outcome of all successful adaptations, is dependent on two processes: the survival of phenotypes already present, and the production of new phenotypes at a favourable opportunity. Territoriality in Lesser Sheathbills outside the breeding season can be viewed as an adaptation facilitating both processes. The first is facilitated by the improved chances of survival of the territorial adults and also their fledged chicks, relative to non-territorial conspecifics, and the second by the improved chances of future reproduction in the same territory.

Constraints to territorial behaviour - Territoriality should persist only as long as the resources are economically defendable (Brown 1964, Brown and Orians 1970). In the case of Lesser Sheathbills this required a predictable supply of defendable food. The most important food eaten in the King Penguin colonies in winter came from carcasses.

King Penguin chicks have a high mortality during the winter (Stonehouse 1960, Barrat 1976) and their carcasses formed conspicuous patches of high-quality food which was renewed regularly and, within the confines of a territory, was readily defendable. Nevertheless, territorial defence of premium food resources in the King Penguin colony was not 100% successful, and intruders were able to live off undefended resources and by intruding into territories. The "intruder" strategy was not a life-long viable alternative to territoriality in Lesser Sheathbills, however, since only territorial birds reproduced.

SUMMARY

Lesser Sheathbills *Chionis minor* foraging in a colony of King Penguins *Aptenodytes patagonicus* at Marion Island in winter included: pairs of territorial adults; non-territorial adults and subadults ("intruders"); and juveniles, which foraged within their parents' territories. The Lesser Sheathbills spent 79% of the daylight foraging, 10% resting, 10% preening and 1% displaying.

Territorial adults spent less time walking and more time eating than the intruders. They had greater access to and higher rates of intake from sources of high-quality food (Penguin carcasses and food kleptoparasitised from penguins) and ate less of the low-quality food (invertebrates and other small objects) than the intruders. Aggressive chases were frequent but brief and disrupted the foraging of intruders and juveniles more than that of territorial adults. Although juveniles were subordinate to intruders, when foraging within their parents' territories they were chased less frequently, spent more time eating and less walking and had higher rates of intake of high-quality food from carcasses than the intruders.

Costs and benefits of territoriality to Lesser Sheathbills outside their breeding season are discussed. A territorial adult might improve its fitness in three ways: by improving its chances of survival through the winter; by improving the chances of survival of its juvenile offspring; and by improving the adult's chances of retaining

the same territory for future breeding. Territoriality is possible in this situation through the regular supply of defendable food, mainly from carcasses of King Penguin chicks.

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PART SIX

OPTIMAL FORAGING BY LESSER SHEATHBILLS ON THE COASTAL PLAIN

Plate 2. A flock of Lesser Sheathbills foraging for terrestrial invertebrates on the coastal plain.

INTRODUCTION

The behavioural adaptations for island life have seldom been studied in birds outside temperate or tropical regions. Sheathbills (Charadriiformes; Chionididae) are among the very few land-based birds which have overcome the problems of living on Antarctic and sub-Antarctic islands (Watson 1975). Their success is largely due to their close associations with penguins (Jones 1963, Part one). In summer at Marion Island (46^{O}54'S, 37^{O}45'E) in the sub-Antarctic, 90% of the Lesser Sheathbills _Chionis minor_ including all breeding pairs foraged in penguin colonies (Part two). During winter, however, following the exodus of most of the penguins, many Lesser Sheathbills were forced to use other food resources. The most commonly used alternative food was the terrestrial invertebrate fauna on the island's coastal plain. This paper reports on behavioural adaptations used by Lesser Sheathbills for exploiting this resource in winter.

The specific problems facing Lesser Sheathbills seeking the invertebrates include: locating small prey objects which are patchily dispersed, fossorial and cryptic; meeting the time and energy requirements during the short (10 hour) daylight period; inclement weather; and, harassment from predators. No birds at Marion Island feed exclusively on terrestrial invertebrates. Small numbers of Kelp Gulls _Larus dominicanus_ and Kerguelen Terns _Sterna virgata_ use this food, but the Lesser Sheathbills do not encounter significant interspecific competition for this resource (Part two).

MATERIALS AND METHODS

STUDY AREA

Lesser Sheathbills were observed feeding on terrestrial invertebrates in many parts of Marion Island but quantitative observations were confined to a 100 ha study area, 200 m wide, along 5 km of the north-eastern coast of the island, which supported, on average, 197 Lesser Sheathbills. A meteorological station was situated within the study area.

DEFINITIONS

Observations were confined to the period (May to October) when terrestrial invertebrates were most commonly eaten and this was referred to as winter. Foraging areas were vegetated parts of the coastal plain and did not include beaches, penguin colonies or rocky outcrops. Birds active in foraging areas were recorded as foraging and the time spent in these areas as foraging time. All localised searching and eating activities of foraging birds ie, stripping away vegetation, probing, capturing and handling prey have been called feeding and the feeding success was the rate of prey objects swallowed per min. of foraging time.

FIELD OBSERVATIONS

Three methods were used to study foraging behaviour. Firstly, the activities of all Lesser Sheathbills visible within a 6 ha area were recorded, using the instantaneous scan method (Altmann 1974) at five-minute intervals from first-light until darkness. This was done to determine the average time spent on the foraging areas by the birds and the behaviour of each bird was recorded as either foraging or resting/preening/bathing. The distance between observer and the farthest birds (200 m) were too great to make any more detailed observations.

Secondly, the time budgets of foraging birds were determined using focal-animal observations (Altmann 1974) with the aid of binoculars and a tape recorder.Lesser Sheathbills are not afraid of man and it was possible to sit quietly within 15 m of foraging birds without causing any noticeable change in behaviour. The observations were made between 1 June and 6 October 1976. Observations of less than 9 min bird^{-1} were discarded and no observations exceeded 23 minutes. The mean temperature and windspeed during each focal watch was recorded. No observations were made during gales or heavy rain.

Thirdly, the age (Appendix one), foraging habitat and flock size of each Lesser Sheathbill in the study area were recorded during 17 censuses made at roughly 10-day intervals between May to October 1976. The censuses were made on foot between 08h00 and 14h00 on days when the weather was amenable (ie. no gale was blowing or excessive rain.) The foraging habitat was recorded as one of 19 vegetation types, described in Appendix two. The mean densities, biomass and spatial distribution of prey, and physiognomic characteristics of each vegetation type were determined at monthly intervals as described elsewhere (Appendix two). Similarly, the area of each vegetation type and its mean locus relative to the sea were known from strip transects (Appendix two). The average plant canopy height was estimated on an arbitrary scale with 0 indicating no vegetation, 1 = a canopy between 0 - 5 cm, 2 = 5 - 10 cm, 3 = 10 - 15 cm, 4 = 15 - 20 cm and 5 = 20 cm.

The typical flock size (TFS) was calculated from the formula (modified from Jarman 1974):

$$\mathrm{TFS} = \frac{n_1 F_1 + n_2 F_2 + n_3 F_3 \;\; \ldots\ldots\ldots n_i F_i}{n_1 + n_2 + n_3 \;\; \ldots\ldots\ldots n_i}$$

where n is the number of birds in each flock of size F where there are i flocks. The TFS is the flock size in which the average individual occurs and provides a better estimate of social grouping than the simple mean flock size (Jarman 1974).

ANALYSIS

Correlation and stepwise multiple linear regression analyses (Allen 1973) were used to establish which independent variables (environmental and behavioural factors) were related statistically significantly to aspects of the Lesser Sheathbills' foraging behaviour (the dependent variables). The statistical limitations of regression analyses in ecological studies are discussed by Sepkoski and Rex (1974): difficulties in the interpretation of results arise when the independent variables are intercorrelated and/or not normally distributed; causal relationships between variables are determined by inference only and are not directly demonstrated.

In the focal-animal data, the dependant variables were the percentage of foraging time spent on each activity (PCFEED, PCLOOK, PCWALK, etc.) and the rate of feeding success (RFS). Independent variables included the mean prey density for the relevant vegetation types for the months of observation (DENSITY), flock size (FLOCK), estimated distance of the focal-bird to its nearest neighbour (DNNEIGH) and to the sea (BIRDSEA), date (DATE), time of day (TIME), and weather (TEMP, WIND).

The dependent variables in the census data were the relative densities (% birds ha^{-1}) on each vegetation type within the study area,of adults (FORAD), subadults (FORSUB), juveniles (FORJUV), and all ages (FORALL). Independent variables included, for each vegetation type, the projected canopy cover of grass and herbs (HERBS), and of bryophytes (BRYO), average canopy height (VEGHT), mean density (DENSITY)and biomass (BIOMASS) of the combined prey items,and three measures of prey spatial distribution, the co-efficient of variation (Sokal and Rohlf 1969) of prey density (CV1) and biomass (CV2), and Lloyd's index of patchiness (Lloyd 1967, Pielou 1974) applied to the prey densities (PATCHY).

RESULTS

PREY AND FEEDING METHODS

Prey taken by Lesser Sheathbills included nine categories of terrestrial macro-invertebrates: earthworms, earthworm cocoons, lepidoptera larvae, lepidoptera adults and pupae, coleoptera larvae and pupae, coleoptera adults (weevils), spiders, snails and slugs. These animals had a mean dried mass of 10 mg, their spatial distribution was irregular and patchy but their mean densities, biomass and individual animal mass varied little through the seasons (Appendix two). These were not very active animals and were either fossorial in the upper 4 cm of the soil-peat substrate or were cryptic surface dwellers. Lesser Sheathbills ate the nine prey types roughly in proportion to their densities and biomass in the substrate but did not appear to select prey of any particular size within the range taken. (Table 1). Micro-arthropods,(including mites, Collembolla and staphylinid beetles) were not found in stomach contents and were very rarely taken by Lesser Sheathbills although they were often very common in the substrate (Burger 1979).

Lesser Sheathbills stripped away the vegetation to reveal the fossorial prey, rarely probed with their bills into the substrate and picked up prey on the surface. Pursuit time (Schoener 1971) was essentially nil, handling-and-eating time was about one second per prey object but the search time per object was about 12 seconds (see below).

Table 1. Linear correlation co-efficients between the occurrence and mass of terrestrial invertebrate types in the gut contents of 13 Lesser Sheathbills (Part two) and their density, biomass and mass per animal in the substrate (Appendix two).

	Invertebrates in the substrate		
Invertebrates in gut contents	Density	biomass	Mean animal mass
% occurrence	0.80[1]	0.82[1]	0.14
% mass	0.46	0.53	0.09

[1] $p < 0.05$, df = 8.

Areas where Lesser Sheathbills had fed intensively were recogniseable, having a 'ploughed' appearance as a result of the plants being uprooted. Samples from these areas had densities and biomass of prey which were significantly lower than in neighbouring unexploited areas (Table 2).

HABITAT SELECTION : THE USE OF VEGETATION TYPES

Lesser Sheathbills encountered 19 vegetation types (Appendix two) in which the plant species composition, physical and physiognomic properties, prey abundance and prey distribution differed (Table 3). The birds preferred certain vegetation types and the densities of birds per vegetation type correlated significantly with mean prey DENSITY and BIOMASS of the vegetation types (Table 4). Stepwise multiple regression analysis showed that bird densities were related to prey DENSITY, VEGHT, and VEGDSEA (Table 5). These variables accounted for 78% or more of the variability in the selection of habitat by birds of all classes ($R^2 \geq 0.78$, Table 5). Prey BIOMASS which was intercorrelated significantly with DENSITY was not included in the final equation.

SOCIAL ARRANGEMENT OF FORAGING AND ROOSTING BIRDS

During winter 83% of all Lesser Sheathbills eating terrestrial invertebrates occurred in flocks of 2 - 33 birds (Fig. 1). The typical flock size (TFS) was 8.3 birds and the modal size was two. In summer, when far

Table 2. The effects of heavy predation pressure by Lesser Sheathbills on mean (±SD) prey densities within <u>Agrostis magellanica</u> - <u>Clasmatocolea humilis</u> mire (type 4) during the months July-September.

	Prey density (organisms m^{-2})		Prey biomass (g m^{-2} dried mass)	
Prey item	Unexploited areas	Exploited areas	Unexploited areas	Exploited areas
Earthworms	810 ± 887	318 ± 334[1]	9.05 ± 8.63	3.20 ± 4.13[1]
Earthworm cocoons	94 ± 197	40 ± 153	0.09 ± 0.20	0.04 ± 0.15[1]
Lepidoptera larvae	40 ± 82	0	0.19 ± 0.40	0
Coleoptera larvae	304 ± 249	106 ± 147[1]	1.43 ± 1.34	0.41 ± 0.58[1]
Total	1248 ± 997	464 ± 342[1]	10.76 ± 8.44	3.65 ± 4.12[1]
No. samples[2]	15	15	15	15

[1] Significantly less than unexploited ($p < 0.05$, t-test)

[2] Each sample was a core of area 50 cm^2 (Appendix two).

Table 4. Matrix of linear correlation co-efficients between variables of the foraging habitat and the occurrences of Lesser Sheathbills in 19 vegetation types, during winter (May to October). See text for explanation of abbreviations. Correlations were significant $(p<0.01)$ if $r \geqslant 0.56$ or $(p<0.05)$ if $r \geqslant 0.44$.

	FORAD	FORSUB	FORJUV	HERB	BRYO	VEGHT	DENSITY	CV1	BIOMASS	CV2	PATCHY	ITEMASS	VEGDSEA
FORALL	.99	.89	.90	.30	-.25	-.30	.81	.03	.75	.08	.31	.02	-.05
FORAD	—	.83	.86	.34	-.29	-.26	.79	.06	.74	.11	.32	.01	-.04
FORSUB		—	.81	.12	-.05	-.30	.81	.01	.78	.08	.28	.19	.02
FORJUV			—	.30	-.25	-.42	.64	-.10	.56	-.06	.20	-.09	-.18
HERB				—	-.55	.51	.41	-.34	.39	-.39	-.08	.17	.01
BRYO					—	-.16	-.25	-.18	-.21	-.16	-.48	-.02	-.06
VEGHT						—	.07	-.27	.15	-.26	-.13	.41	.36
DENSITY							—	-.09	.99	-.01	.30	.33	.22
CV1								—	-.12	.95	.67	.48	-.22
BIOMASS									—	-.05	.27	.42	.30
CV2										—	.68	-.49	-.23
PATCHY											—	.12	.35
ITEMASS												—	.93

Table 5. Factors influencing the selection of foraging habitat by Lesser Sheathbills in winter. Significant relationships (for which $p < 0.05$) were determined by stepwise multiple regression analyses of census data.

Dependent variable	Independent variable entered	Multiple co-efficient determination (R^2)	Change in R^2
	DENSITY (+)[1]	0.6488	0.6488
FORALL	VEGHT (-)	0.7776	0.1288
	VEGDSEA (-)	0.8451	0.0675
	DENSITY (+)	0.6275	0.6275
FORAD	VEGHT (-)	0.7271	0.0996
	VEGDSEA (-)	0.8033	0.0762
	DENSITY (+)	0.6500	0.6500
FORSUB	VEGHT (-)	0.7793	0.1293
	DENSITY (+)	0.4139	0.4139
FORJUV	VEGHT (-)	0.6346	0.2207
	VEGDSEA (-)	0.7997	0.1651

[1] Nature of the relationship (+ve or -ve)

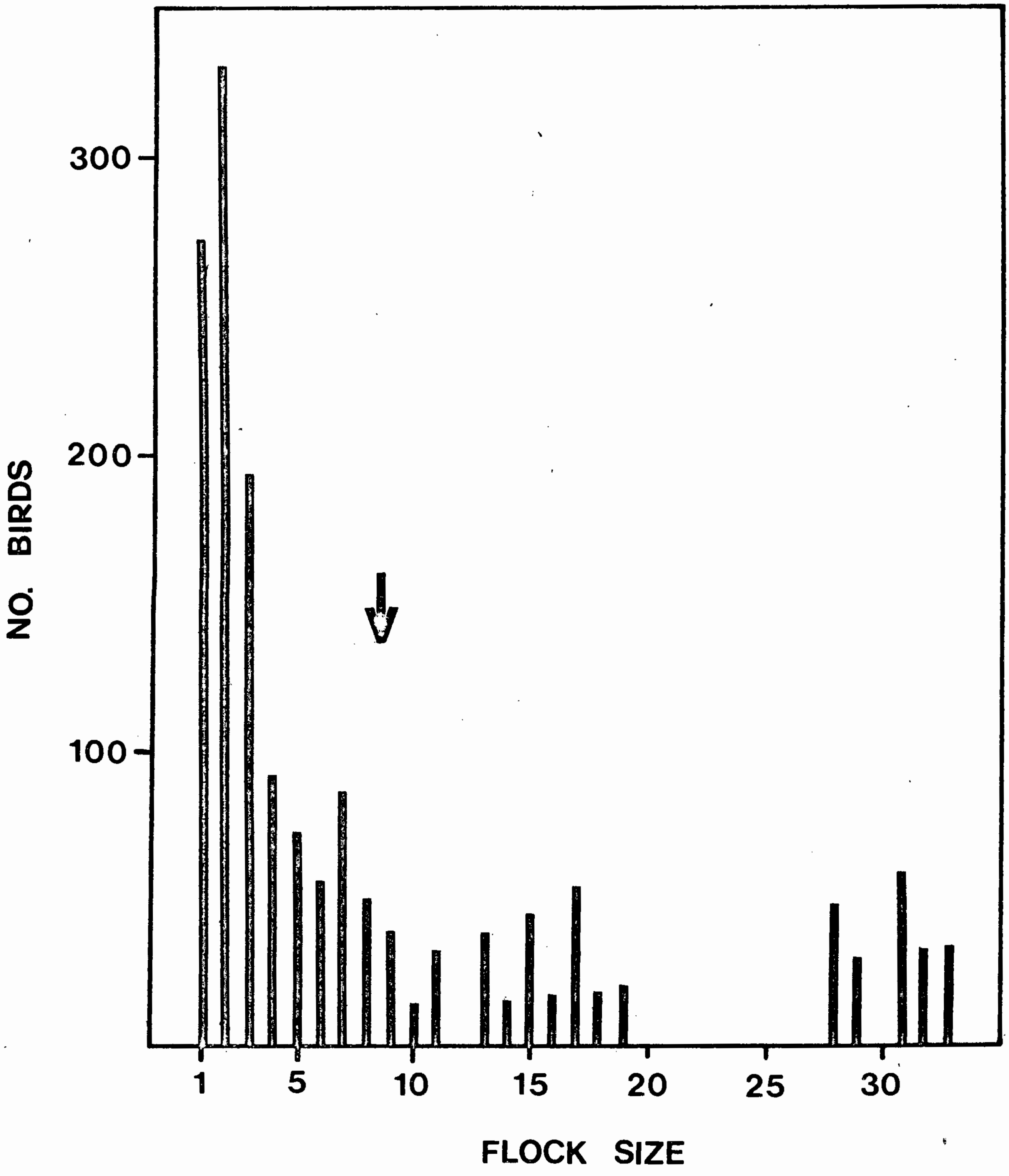

Fig. 1. Flock sizes of Lesser Sheathbills foraging for terrestrial invertebrates in winter (May to October). Data from 1641 sightings during 17 censuses made at ten-day intervals. The typical flock size (TFS) is shown by an arrow.

fewer Lesser Sheathbills foraged on the coastal vegetation, foraging groups were never larger than five birds and the TFS was 2.1 birds (N = 352 sightings from 17 censuses). Foraging flocks included birds of all ages and adults, subadults and juveniles occurred in groups of similar size (Part two).

Lesser Sheathbills which foraged on the coastal plain roosted at night on lava platforms or rocky beaches on the shore. Between May and October 1976, 17 censuses were made at 10 day intervals after dark at 13 roost sites in part of the study area. The average number of birds per census was 38 ± 9 (S.D.), of which 98% were recorded in groups of two or more and the TFS at roosts was 17 birds. On one morning and one evening Lesser Sheathbills were observed departing from and arriving at a communal roost. Out of 166 birds sighted, 77% were in flocks of two or more and the TFS was 16 birds.

TIME AND ENERGY BUDGETS

Lesser Sheathbills spent, on average. 88.3% (9.45 hours) of the daylight hours foraging, fairly uniformly distributed through the day (Fig. 2). The remaining daylight hours (11.7 %) were spent preening, bathing and resting on the shore or on rocky outcrops inland. Movement between the roost sites on the coast and the foraging grounds, which were usually less than 200 m inland, took only a few minutes a

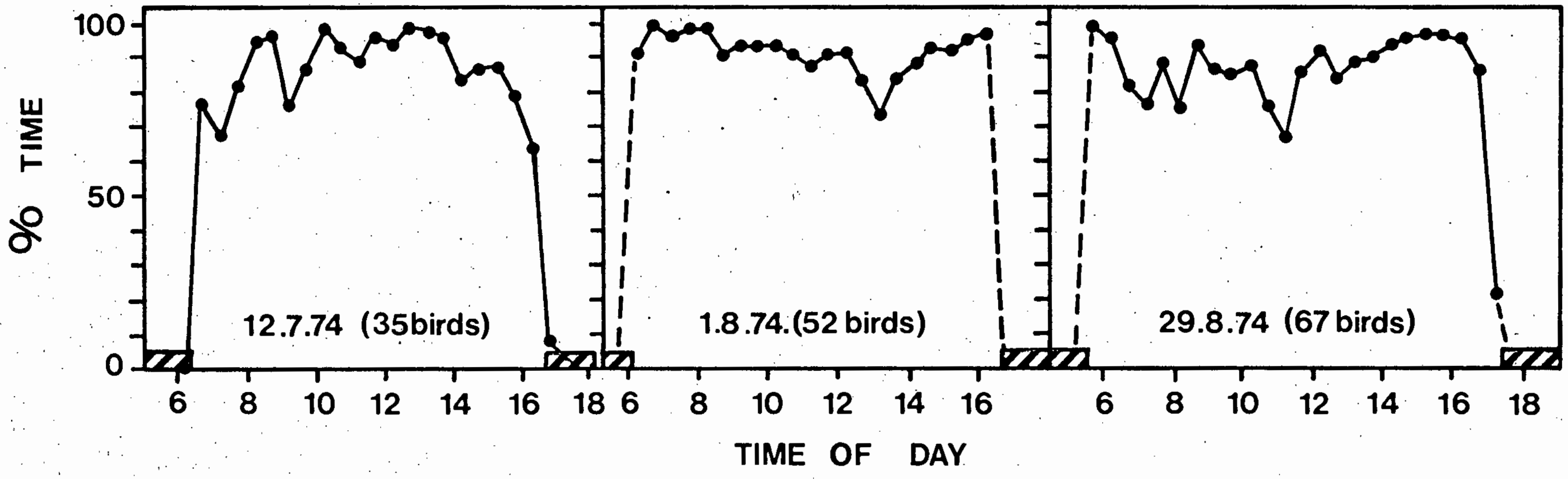

Fig. 2. Percentage of Lesser Sheathbills recorded as foraging during five-min scans from first-light to darkness on three days. The data are given in ½-hour intervals and the mean number of birds visible per scan are given. Hatched areas delineate darkness.

day. Feeding, looking around with the head erect, and walking comprised 99% of the foraging time (Table 6). The activity-time budgets of adults, subadults and juveniles were very similar, the only significant differences were that subadults spent more time walking and being chased and less time feeding than adults, and juveniles spent more time walking than adults (Table 6).

Using the data from Fig. 2 and Table 6 it was possible to construct the daily time budget of a Lesser Sheathbill in winter (Table 7). These estimates were then converted into energy output using the metabolic costs of each activity. The basal metabolic rate (BMR) of a 470 g Lesser Sheathbill was calculated to be 8.37 kJ hour^{-1} using equation 5.5 of Kendeigh, Dol'nik and Gavrilov (1977). Roosting, resting, preening and looking around were estimated to cost 1.5 X BMR, walking, feeding and display 4 X BMR and chasing and fleeing 12 X BMR in Lesser Sheathbills (Part seven). The mean daily (24-hour) energy output was thus estimated to be 487 kJ bird^{-1} (Table 7). This compares favourably with the estimated daily existence metabolism (EM) of 473 kJ bird^{-1} for a 470g non-passerine, in a 10-hour photoperiod at 4.5^{o}C, including 7% of EM added for the cost of free-living (Kendeigh, Dol'nik and Gavrilov 1977: 202).

FEEDING SUCCESS AND THE FACTORS AFFECTING IT

Lesser Sheathbills ingested an average of 5.11 ± 1.57 S.D.

Table 6. Mean (±SD) percentage allocation of foraging time to various activities by Lesser Sheathbills eating terrestrial invertebrates. Data from focal-animal observations.

Activity	Adults	Subadults	Juveniles	All birds
Feeding	90.1 ± 5.2	83.8 ± 14.9[1]	88.4 ± 4.3	88.9 ± 7.3
Looking around	5.5 ± 3.2	7.9 ± 6.6	6.1 ± 3.2	6.0 ± 3.8
Walking	3.0 ± 2.0	7.8 ± 9.4[1]	4.9 ± 2.8[1]	4.1 ± 4.2
Preening	1.4 ± 3.7	0.1 ± 0.3	0.3 ± 0.8	1.0 ± 3.1
Chasing conspecifics	0.2 ± 0.5	0.1 ± 0.1	0.1 ± 0.4	0.2 ± 0.4
Fleeing conspecifics	0	0.5 ± 1.0[1]	0.1 ± 0.3	0.1 ± 0.4
Display	0.1 ± 0.4	0	0	0.1 ± 0.3
No. birds	50	10	15	75
Mean observation time (min)	15.9 ± 3.7	13.5 ± 3.0	17.0 ± 2.9	15.8 ± 3.6

[1] Significantly different from adults (t-test, $P < 0.05$)

Table 7. Daily time and energy budgets of Lesser Sheathbills eating terrestrial invertebrates in winter at Marion Island. Data derived from Fig. 2 and Table 6.

Activity	Time % daylight	 Hours day^{-1}	Metabolic rate[1] (kJ hour^{-1})	Daily energy output (kJ)
Nocturnal roosting	-	13.30	12.56	167.1
Rest/preen/bathe	11.7	1.25	12.56	15.7
Foraging :-	(88.3)	(9.45)	-	-
Feeding	78.2	8.37	33.49	280.3
Walking	3.6	0.39	33.49	13.1
Display	0.1	0.01	33.49	0.3
Preening	0.9	0.09	12.56	1.1
Look around	5.3	0.57	12.56	7.2
Chase and flee	0.2	0.02	100.48	2.0
Total	100.0	24.00	-	486.8

[1] See text for derivation of metabolic rates

prey-objects min^{-1} while on the foraging grounds (N = 75 focal-birds). The successes of adults (5.12 ± 1.73, N=50), subadults (4.90 ± 1.25, N=10) and juveniles (5.17 ± 1.67, N=15) did not differ significantly ($p > 0.05$, t-tests). Within the size range eaten by Lesser Sheathbills, the terrestrial invertebrates available had a mean energy content of 0.18 kJ animal^{-1} (Appendix two). The mean energy intake of a Lesser Sheathbill was thus 55.19 kJ hour^{-1} of foraging time or 522 kJ day^{-1}.

Feeding success (RFS) during focal-animal observations wascorrelated significantly with prey DENSITY and the mean distance of the bird to the sea (BIRDSEA)and both variables had very similar correlation co-efficients with RFS (Table 8). A multiple regression analysis selected only BIRDSEA as having a significant influence on RFS (Table 9); DENSITY was not included but this was because it was significantly intercorrelated with BIRDSEA.

The increased energy intake associated with selection of habitats with high prey densities can be estimated (Fig. 3). At five vegetation types with moderate mean prey densities (1140 - 1920 m^{2}) the mean success of 49 birds was 4.67 ± 1.58 (S.D.) prey-objects min^{-1} of foraging time, but at four vegetation types with high mean prey densities (2650 - 5540 m^{-2}) the intake of 26 birds, 5.92 ± 1.20 prey-objects min^{-1}, was significantly higher ($p < 0.01$, t-test). Given an average winter day with 9.45 hours spent on the foraging

Table 8. Correlation matrix of variables considered in the analysis of Lesser Sheathbill focal-animal observations. Correlations were significant ($p < 0.01$) if $r \geq 0.29$ or ($p < 0.05$) if $r \geq 0.22$.

	RFS	PCFEED	PCLOOK	PLWALK	VEGHT	DENSITY	FLOCK	DNNEIGH	BIRDDSEA	DATE	TIME	TEMP	WIND
RFS	—	.11	.03	-.06	.20	.25	.01	-.02	-.27	.19	.19	-.05	.04
PCFEED		—	-.75	-.78	-.09	-.30	.28	-.07	.06	.24	.50	.13	.29
PCLOOK			—	.42	.14	.38	-.43	.35	-.15	-.21	-.34	-.11	-.28
PCWALK				—	.12	.22	-.05	-.13	.02	-.18	-.36	-.13	-.24
VEGHT					—	.50	.00	.10	-.42	.07	.19	-.45	-.18
DENSITY						—	-.26	-.07	-.27	-.08	-.07	-.35	-.32
FLOCK							—	-.42	.38	-.14	.07	.09	.40
DNNEIGH								—	-.04	.01	.08	.01	-.20
BIRDDSEA									—	-.20	-.26	.16	.18
DATE										—	.31	-.08	.03
TIME											—	-.10	.15
TEMP												—	.10
WIND													—

Table 9. Factors influencing foraging behaviour of Lesser Sheathbills on coastal vegetation in winter. Significant relationships (for which $p < 0.05$) were determined by stepwise multiple regression analyses of focal-animal data.

Dependent variable	Independent variable entered	Multiple co-efficient of determination (R^2)	Change in R^2
RFS	BIRDSEA (-)[1]	0.0707	0.0707
PCFEED	TIME (+)	0.2532	0.2532
	DENSITY (-)	0.3238	0.0706
PCLOOK	FLOCK (-)	0.1824	0.1824
	TIME (-)	0.2801	0.0977
	DENSITY (+)	0.3482	0.0681
	DNNEIGH (+)	0.4052	0.0570
PCWALK	TIME (-)	0.1308	0.1308

[1] Nature of the relationship (+ve or -ve)

grounds and a mean prey energy content of 0.18 kJ $object^{-1}$, this could amount to a difference of 228 kJ, or 44% of the estimated 522 kJ daily intake.

The effects of vegetation height on feeding success could not be adequately tested by the focal-animal observations, since the focal-birds were all in vegetation which was lower than 15 cm. However, quantified observations of Lesser Sheathbills suggested that tall plants could restrict locomotion and feeding. Climatic factors, date, and time of day did not apparently affect feeding success (Tables 8 & 9). During gale-force winds, however, the locomotion and feeding of Lesser Sheathbills did appear to be impeded.

The correlation and multiple regression analyses suggested that the feeding success of Lesser Sheathbills was not affected by flock size (Tables 8 & 9). These analyses used linear correlations but the relationship between the two variables was actually more complex (Fig. 4). Feeding success increased linearly with increasing flock size up to flocks of 15 birds but decreased with larger flock sizes. Feeding success of 16 birds in flocks of 16 - 30 was significantly lower than that of nine birds in flocks of 11 - 15 ($p < 0.01$, t-test, Fig. 4). This trend was not an artifact of the effects of mean prey density. The samples from habitats with high mean prey densities were inadequate to be analysed separately but among habitats with moderate mean prey densities the variation of feeding

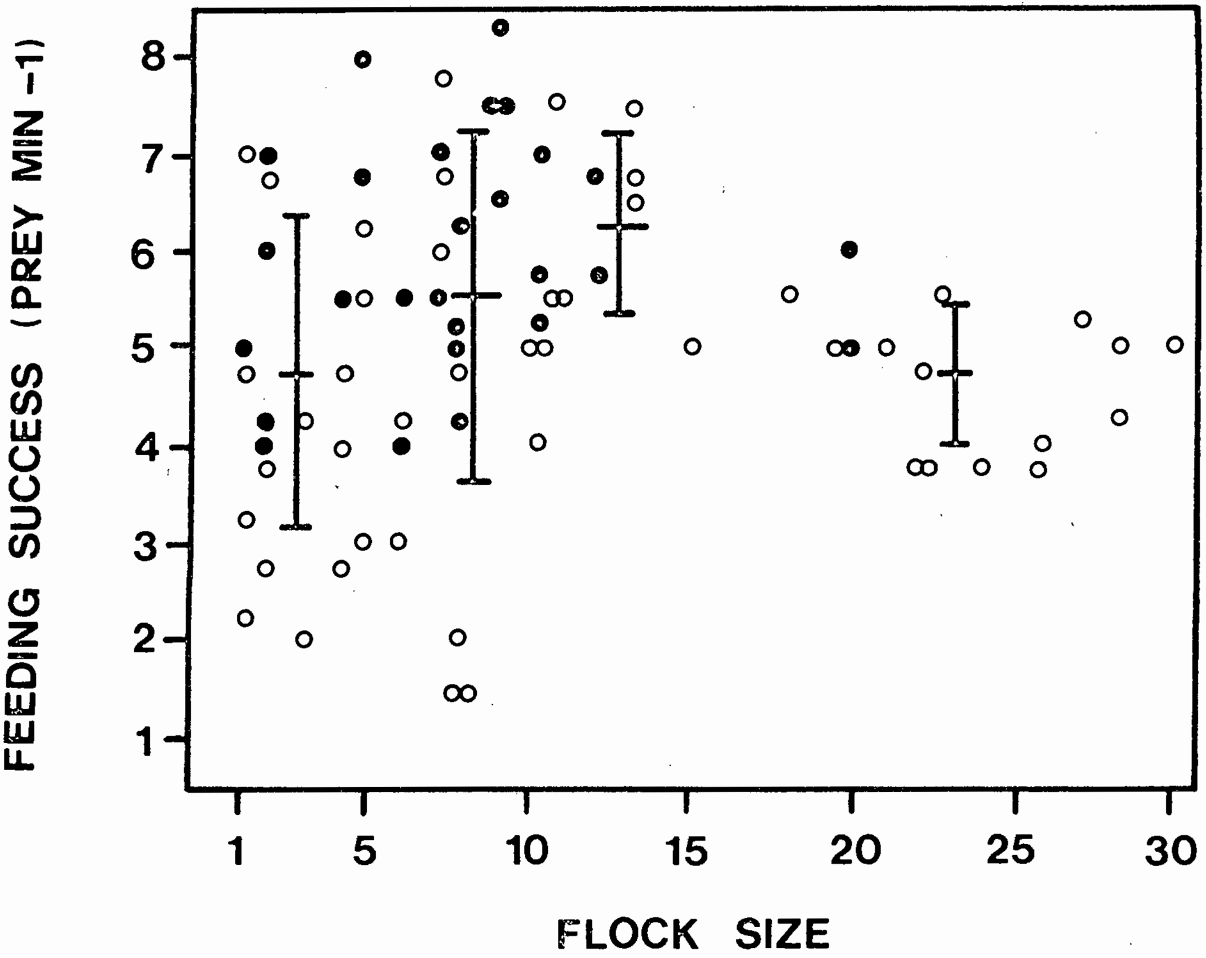

Fig. 4. Relationship between feeding success and flock size in Lesser Sheathbills eating terrestrial invertebrates. Each point is the result of focal-animal observations on an individual bird; birds at vegetation types with high mean prey densities (2650 - 5540 prey m^{-2}) are shown as dots, those at vegetation types with low prey densities (1140 - 1920 m^{-2}) as open circles. The mean ± S.D. success of birds in flocks of 1 - 5, 6 - 10, 11 - 15 and 16 - 30 is shown (horizontal lines and t-bars) and the arrow indicates the typical flock size for birds using this resource in winter.

success with flock size was similar to that of the combined data (Fig. 4). The typical flock size of Lesser Sheathbills in winter falls within the range of flock sizes in which feeding success was fairly high.

FACTORS INFLUENCING TIME BUDGETS OF FORAGING BIRDS

The Lesser Sheathbills could improve their daily energy intake by increasing time feeding proportionate to time looking about or walking. Other behaviours took negligible portions of the foraging time (Table 6). PCFEED was significantly correlated with prey density, flock size, date, time of day and windspeed, PCLOOK with prey density, flock size, distance to nearest neighbour and time of day, and PCWALK with prey density and time of day (Table 8). Many of these independent variables were, however, intercorrelated significantly which makes interpretation difficult. Stepwise multiple regression analysis, which partially corrected for intercorrelations, provided the results shown in Table 9. Lesser Sheathbills spent more time feeding and less time looking around and walking in the late afternoon. The birds appeared to spend less time feeding and more time looking around when prey densities were higher. Important aspects of the time budgets were influenced significantly by flock size and by the mean distance to the nearest neighbour (Tables 8 & 9). As the flock size increased the percentage time spent feeding increased, looking around decreased, but walking was unaffected (Fig. 5).

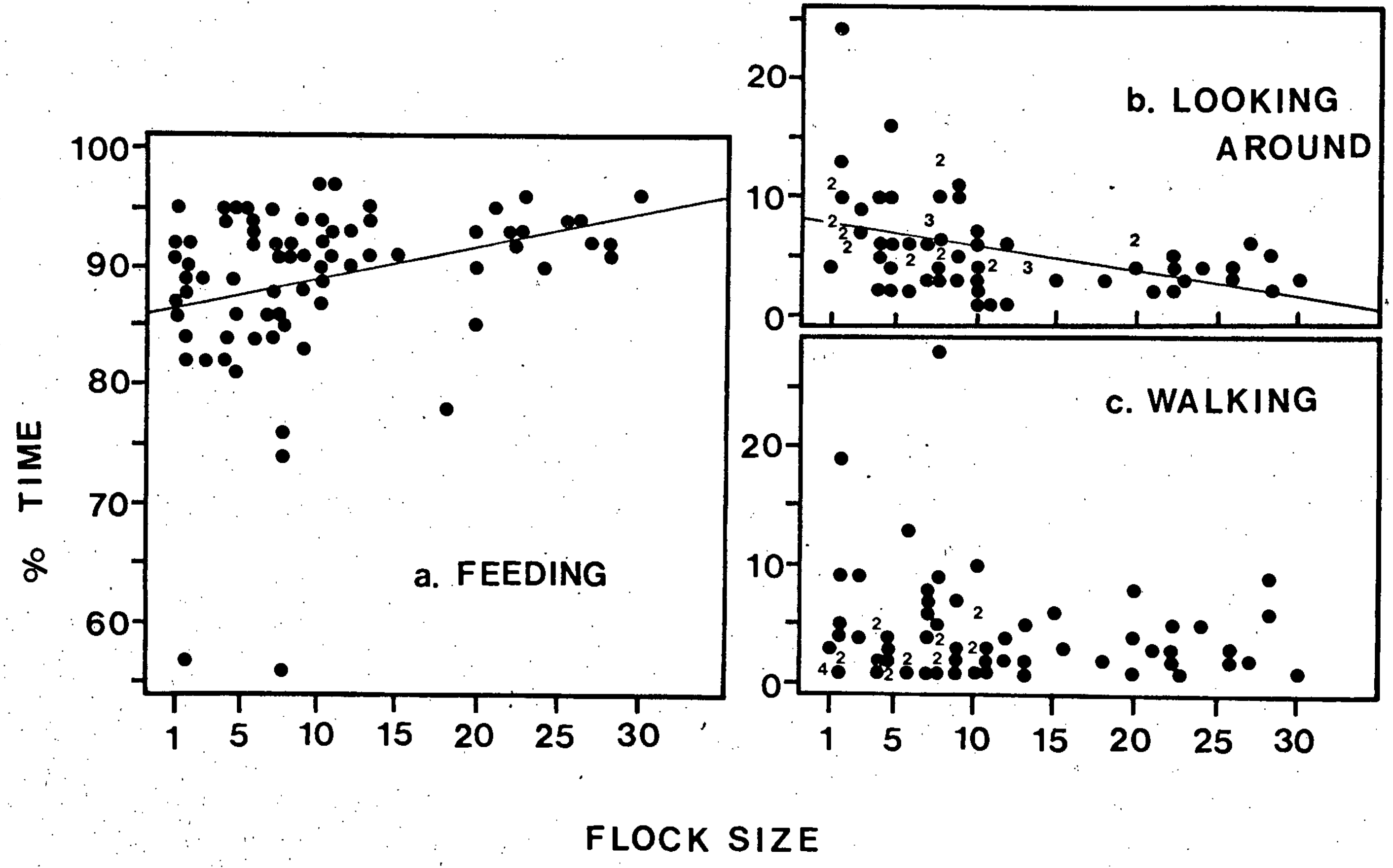

Fig. 5. The relationships between flock size and the percentage time spent feeding (A), looking around (B) and walking (C) by Lesser Sheathbills during focal-animal observations. Feeding and looking around were significantly correlated with flock size and the regression lines are given, ($p < 0.02$ in each case) but walking was not ($p > 0.05$).

AGGRESSION AMONG FORAGING BIRDS

Overt aggression was rare amongLesser Sheathbills foraging for terrestrial invertebrates. The mean frequency of aggressive encounters (chasing and being chased) was 2.5 ± 5.6 $\mathrm{bird}^{-1}\mathrm{hour}^{-1}$ (N = 75 focal-birds). An aggressive encounter rarely lasted more than a second or two. Usually one bird supplanted another at a feeding site and very few displays were involved. The time chasing and being chased amounted to an average of only 0.3% of the foraging time (Table 6).

The percentage time and frequency of aggressive encounters did not increase with increasing flock size (Table 8). Although the estimated mean interbird distance was correlated inversely with flock size (Table 8), Lesser Sheathbills seldom foraged within less than 1 m of each other and the mean interbird distance in flocks of 3 - 30 birds was 4.3 ± 4.7 m (N = 63 focal-birds).

PREDATION AND FLOCK SIZE

Sub-antarctic Skuas <u>Catharacta</u> <u>antarctica</u> seldom killed Lesser Sheathbills but frequently attacked them on the coastal plain (Part one). No empirical data are available on the effects of flock size on the probability of predation of Lesser Sheathbills, but a theoretical model was constructed from probability theory applied to available data. Lesser Sheathbills with their heads down while feeding were considered to be less likely to detect an approaching predator than when performing other behaviour. The vigilance of an individual was taken to be proportional to the foraging time that was not spent feeding. A more usual measure of vigilance, the time spent looking around, was not considered to be adequate, since a bird walking or preening should also have had a good chance of detecting a predator.

The vigilance and vulnerability of flocks of 1 - 30 birds were calculated from the percentage of feeding time of birds in such flocks (Fig. 5A), using probability theory (see Chapter Appendix). Two assumptions were made.

1) Each bird was assumed to organise its vigilance independently of surrounding conspecifics. The birds could actually achieve maximum vigilance by sequentially organising vigilant behaviour of individuals within a flock (Bertram in press), but this was highly improbable within the temporary associations of unrelated birds in flocks of Lesser Sheathbills. The reasons given for independence of vigilance in Ostriches *Struthio camelus* by Bertram (in press) all applied to Lesser Sheathbills.

2) All members of the flock were assumed to benefit if one bird detected the predator, and so the minimal flock vigilance was at least one bird vigilant. Lesser Sheathbills responded to an approaching skua by running rapidly and/or

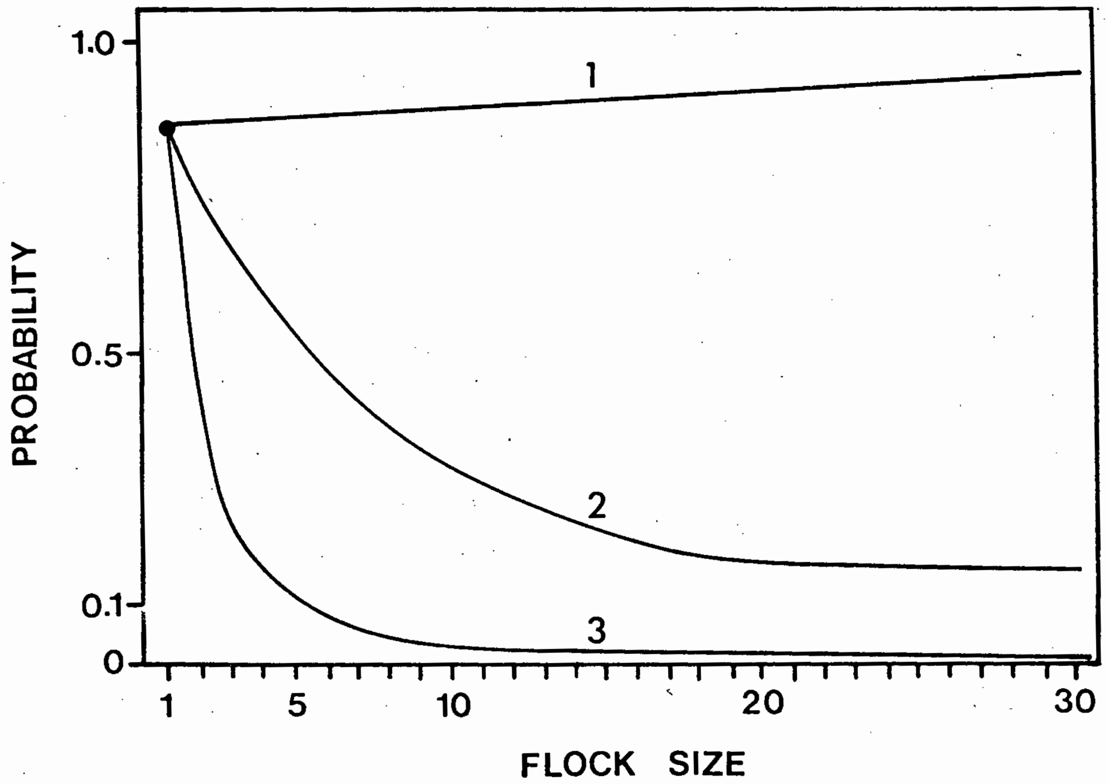

Fig. 6. The effect of flock size on the vulnerability of Lesser Sheathbills to attack from Sub-Antarctic Skuas. Line 1 shows the mean percentage time spent feeding by individuals (from Fig. 5A). Line 2 is the theoretical vulnerability of the flock assuming each individual was behaving independently and had the same % feeding time as in Line 1. (see Chapter Appendix). Since a successful skua could only kill one Lesser Sheathbill within a flock, the theoretical vulnerability of any individual in the flock (Line 3) is simply Line 2 divided by the number of birds in the flock.

taking flight while calling loudly. The sudden movement and sound instantly alerted conspecifics nearby.

The theoretical vulnerability of the flock and the individual decreased sharply as flock size increased while the flocks were relatively small but levelled off rapidly with larger flocks (Fig. 6), which is in accordance with Pulliam's (1973) model. Individual vulnerability improved very little in flocks greater than 5 - 8 birds.

DISCUSSION

DETERMINANTS OF THE FORAGING STRATEGY

It is useful to consider probable proximate determinants of the Lesser Sheathbill's foraging strategy and the constraints acting on the birds, before discussing behavioural adaptation involved in foraging. Since these were non-breeding birds foraging outside their summer breeding grounds, the ultimate factors affecting an individual's fitness are its abilities to meet its daily food requirements, to maintain sufficient reserves to meet unpredictable future food shortages, and to avoid being predated.

Despite the fact that Lesser Sheathbills spent 88% of the daytime foraging and ate one prey-object every 12 seconds during this period, they still appeared to have a precarious energy balance. The estimated energy output was 487 kJ bird^{-1} day^{-1}. The amount of food ingested to meet this cost and to account for energy ingested but not assimilated,lost by excretion, and used for specific dynamic action would be 609 kJ day $^{-1}$(1.25 x 487 kJ day^{-1}; after Ricklefs 1974: 167). The estimated energy intake from the field observations was 522 kJ bird^{-1} day^{-1} which suggests individual birds have a net daily energy deficit of 87 kJ. These estimates admittedly are crude: the greatest source of error being the estimates of metabolic costs (see Furness 1978). Empirical estimates of the costs of walking, feeding and other activities are still very inadequate (King 1974, Ricklefs 1974, Kendeigh, Dol'nik and Gavrilov 1977).

Gales, snow cover and frozen ground impeded or prevented Lesser Sheathbills foraging on the coastal plain. The present observations were largely restricted to periods of favourable weather and on such days the net daily energy balance of the birds should have been positive or at least neutral, for the mean mass of Lesser Sheathbills in winter was not lower than in summer (Appendix two).

Lesser Sheathbills were unlikely to have allocated more time to foraging, since they already spent 88% of the daytime on the foraging grounds. This left little time for essential maintenance such as preening and bathing. The birds foraged in muddy places and needed to preen and bathe frequently. The insulation provided by clean plumage was particularly important in the cold, wet and windy climate of Marion Island. Lesser Sheathbills foraging in other habitats and at other times of the year also spent 10% or more of the daylight preening (Parts five and seven). In addition, increasing the foraging time would incur increased predation risk, since Lesser Sheathbills on the coastal vegetation were more frequently harassed by skuas than those in penguin colonies or on the shore.

Proximate objectives of the Lesser Sheathbill's foraging strategy were thus to minimise the time spent on the foraging grounds, to maximise the net rate of food intake while foraging and to adopt behaviour which reduced the risk of being depredated. This could be achieved by the selection of (a) optimal prey items, (b) optimal periods of feeding, (c) optimal foraging habitat and (d) optimal foraging group sizes (Schoener 1971, Krebs and Cowie 1976). These options are considered below.

SELECTION OF PREY ITEMS

For Lesser Sheathbills eating terrestrial invertebrates, the mean search time per prey-object (12 sec) greatly exceeded the combined pursuit-handling-eating time per object (about 1 sec). Consequently the optimal set of profitable prey could be expected to be broad but unprofitable prey should still be ignored even if they were very common (see review by Krebs 1978). The prey taken by Lesser Sheathbills included invertebrates larger than about 1 mm in diameter (about the size of an earthworn cocoon). They were eaten roughly in proportion to their abundance in the substrate, although this conclusion was based on only 13 stomach contents. The micro-arthropods evidently represented unprofitable prey and were virtually always ignored, although they were often very common (Burger 1979).

SELECTION OF FORAGING PERIODS

Lesser Sheathbills had very little chance to vary their foraging periods since they foraged for 88% of the daytime. The percentage time spent foraging by the birds was in fact similar thoughout the day. Because the prey were sedentary and slow moving and the birds searched the preys' entire habitat in the substrate, the birds were not affected by possible activity periods of the prey. Prey availability should have been similar throughout the day unless the ground was frozen or snow-covered. The risk of predation to Lesser Sheathbills also seemed to be equal throughout the day, since attacks by skuas occurred at any time. There was thus very little benefit to Lesser Sheathbills in attempting to optimise the periods of foraging. Foraging by night was precluded since prey were detected by sight.

SELECTION OF FORAGING HABITAT

Lesser Sheathbills were highly selective in their use of foraging habitats. Out of the possible 19 vegetation types, 97% of the sightings of foraging birds were made in only eight types which together comprised 49% of the study area. The preferred vegetation types were characterised by high mean prey densities, low vegetation height, and were on average close to the shore.

Astute habitat selection was a major factor affecting feeding success and risk of predation of Lesser Sheathbills. Feeding success was significantly higher at vegetation types with high prey densities than in those with moderate prey densities. Feeding success in areas of very low prey densities was not measured, mainly because so few birds foraged there, but it is safe to assume that Lesser Sheathbills could not meet their daily energy requirements if restricted to such habitats. Lesser Sheathbills avoided vegetation with a plant canopy at breast height or higher (15 cm) despite the high prey densities at some of these habitats. Tall vegetation impeded walking, feeding and, probably, the ability to detect predators. The vegetation on Marion Island was nowhere tall enough to provide adequate cover from predators and, unlike the tall tussock grass at some other southern islands (Woods 1970), did not have a clear understory to allow birds to pass between the canopy. Two factors might have influenced the choice of vegetation types near the sea. These were the first habitats to be encountered when Lesser Sheathbills moved inland from the coastal night roosts and the birds reduced the time spent on the foraging grounds by using the nearest suitable habitats. Secondly, birds more than 20 m inland were more vulnerable to harassment by skuas (Part one).

Lesser Sheathbills could have selected habitats with low vegetation and near the sea on simple sensory information but it is not known how they detected high prey densities, the most important habitat criterion in birds of all ages. The prey were small, hidden from view, widely scattered and very patchy. Three possible ways of locating the profitable vegetation types were considered.

(1) The birds could have sampled different areas independently at the start of each day's foraging. This would have been highly inefficient since the mean prey densities varied 50-fold between vegetation types. In fact the birds tended to move directly to foraging areas in the morning and unless disturbed by a skua, an individual's daily foraging range was only about 0.1 ha.

(2) The birds could have identified profitable areas using visual cues based on past experience. It is possible, although unlikely, that the birds were using plant physiognomic cues to indicate high prey densities. Most of the mires and bogs (types 1 - 8) were similar in appearance but their prey densities varied greatly (Table 3). The causes of the clumped distribution of invertebrates are not known (Appendix 2), nor is it known whether Lesser Sheathbills were able to detect the characteristics of the invertebrates' preferred micro-habitats. It is probable that the 'ploughed' areas where Lesser Sheathbills had foraged intensively were used by the birds as indicators of profitable food sources in the vicinity but the disturbed areas themselves often had depleted prey densities.

(3) Profitable patches might have been located by "local enhancement" whereby birds are guided to favourable areas by the behaviour of other birds feeding there (Ward and Zahavi 1973, Krebs 1974). Since birds which were feeding in profitable areas would have been unlikely to have moved away, flocks could have formed by what Hassell and May (1974) termed the "aggregative response". Lesser Sheathbills exploiting terrestrial invertebrates usually foraged, roosted and commuted in flocks, and their white plumage was very conspicuous in foraging and roosting sites. These are all factors believed to facilitate the use of local enhancement in locating scattered and patchy food resources (Siegfried 1971, Ward and Zahavi 1973). It is a very plausible, but as yet untested, hypothesis that Lesser Sheathbills located profitable patches of the invertebrate prey by local enhancement. Even if visual clues were ultimately used to locate high prey densities, these could have been learnt by local enhancement.

SELECTION OF FORAGING GROUP SIZE

Lesser Sheathbills eating terrestrial invertebrates usually foraged in flocks. These flocks did not form for purely social purposes, such as for the establishment of dominance hierarchies or pair bonds. Flocks varied in size and composition from day to day and within a day. Breeding occurred only within penguin colonies and colour-ringed pairs which re-mated each summer, seldom foraged together outside penguin colonies (Part three). Social interactions (displays and aggression) were rare in flocks but very common in penguin colonies. The need to forage efficiently and the risk of predation are the most important forces in the establishment and maintenance of groups of free-living animals (Bertram 1978, Rubenstein 1978).

Flocking facilitated feeding success in Lesser Sheathbills. This behaviour has already been implicated in the successful location of favourable habitats, which resulted in significant improvements of feeding success. Even within favourable habitats, with high or moderate prey densities, feeding success increased with increasing flock size up to flocks of 15 birds but was significantly lower in flocks greater than 15. The increase in feeding success in small flocks was at least partially due to increased feeding time, concomitant with decreased looking around, as flock size increased and, secondly, it might have also been a further example of local enhancement with birds optimising their prey and micro-habitat selection by watching other conspecifics. Both the first (Drent and Swierstra 1977, Inglis and Isaacson 1978, Bertram in press) and the second (Murton 1971, Krebs *et al*. 1972 Krebs 1974) phenomena are known to affect foraging in other bird species.

The feeding success of birds in large flocks has been found to be lowered through increased aggression and interference competition (Silliman *et al.* 1977) or decreased prey availability due to increased bird densities (Goss-

Custard 1970). Aggression amongst Lesser Sheathbills in flocks was rare, demanded negligible time and did not increase with increasing flock size. The birds maintained an interbird distance of several bird-lengths and the small objects they were eating were not worth fighting for. Localised prey depletion, however, did occur following intensive foraging by Lesser Sheathbills and was probably reponsible for the reduced feeding success in flocks of over 15 birds.

An animal reduces its risk of predation by being in a group since predators are likely to be detected sooner by groups than by solitary individuals (Powell 1974, Siegfried and Underhill 1975, Kenward 1978) and since the predator's success is 'diluted' by the presence of nearby conspecifics in the group (Hamilton 1971, Bertram 1978). These two benefits were demonstrated theoretically for Lesser Sheathbills in Fig. 7. This model showed that the advantages to the individual did not improve significantly with flock size in flocks greater than 5 - 8 birds. Birds in larger flocks might in fact have been disadvantaged by the expected increase in "false alarms" or skittishness which Treisman (1975) suggested could outweigh the anti-predator benefits of large flocks.

Lazarus (1972) pointed out that flocking as an anti-predator strategy should be particularly advantageous if the probability of the individual being detected by a predator was great. The white plumage of Lesser Sheathbills was very conspicuous on the coastal vegetation. The habitat provided no cover and the birds actually avoided tall vegetation. A flock or individual Lesser Sheathbill could thus be detected very easily by a passing skua.

The advantages of foraging in flocks could be partly negated if flocks attracted attack more than single birds, although Pulliam (1973), in a theoretical model, showed that flocks conferred advantages even if this was true. Predators are usually at a disadvantage in attacking a flock due to the increased chances of detection and the confusion of sudden movement of many prey in the attack path (Lazarus 1972, Bertram 1978). At Marion Island skuas appeared to swoop on solitary Lesser Sheathbills and small flocks as frequently as on larger groups.

There are so many selection forces acting with different selective pressures on communal foraging that in practice it has been impossible to determine the optimal group size for any animal (Lazarus 1972, Bertram 1978). One might conclude that the optimal group size is the one observed most often but this incurs circular reasoning and does not test the basic premise that animals optimise their foraging behaviour. A better approach is to test whether the observed grouping enhances fitness in the dimensions thought to be most crucial. This study aims to test whether flocking in Lesser Sheathbills was a means of optimising feeding success and the avoidance of predation. Feeding success was greatest in flocks of 11 - 15 birds, was not significantly less in slightly smaller flocks, but was significantly less in flocks greater than 15. The theoretical optimum flock size for avoiding predation was 5 - 8 birds. The observed flock sizes in which most Lesser Sheathbills foraged (the TFS was 8.3 and the modal size was two birds) were within the ranges of flock sizes in which feeding success was high and some reduction of predation risk could be expected.

CONCLUSIONS

Terrestrial invertebrates were eaten by Lesser Sheathbills only when other, preferred food was not available in penguin or seal colonies. The birds exploited the invertebrates without encountering limiting levels of interspecific competition, and this exploitation appears to be an example of trophic niche expansion by a population on a species-poor island. Niche shifts by island birds are believed to occur most readily through behavioural adaptations, particularly with regard to habitat expansion (MacArthur and Wilson 1967, Diamond 1970) and this appears to be true for Lesser Sheathbills. The successful exploitation of the resources on the coastal plain of Marion Island was dependant on behavioural adaptations,particularly critical habitat discrimination and flocking. Since the Lesser Sheathbills which eat invertebrates also eat many other foods and rely on food from penguins when breeding (Part one), genetic change purely to facilitate the exploitation of invertebrates is not adaptive.

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APPENDIX: Calculating vigilance and vulnerability of the flock

The following calculations were similar to those used by Bertram (in press) when calculating vigilance and vulnerability in flocks of ostriches, although he did not give the full method.

The probability that a bird will detect an oncoming predator is proportional to the time it is vigilant. Let the probability of an individual being vigilant be $VI_{ind.}$ and the probability of being vulnerable ($VU_{ind.}$) would then be $1.00 - VI_{ind.}$. In this study birds with their heads down for most of the time while feeding were assumed to be vulnerable so that

$$VI_{ind.} = 1.00 - F_{ind.}$$

where $F_{ind.}$ is the proportion of time the individual spent feeding. The minimal vigilance of a group $VI_{gr.}$ is the probability that at least one bird in the group is vigilant. This assumes that all birds in the group benefit if one of them spots the predator (see discussion of this assumption in the text). Given a mean vigilance $VI_{\bar{n}}$ per bird of flock size n, and assuming that each bird's vigilance is an independent event (see discussion of this assumption in text), then $VI_{gr.}$ can be calculated as follows (Parzen 1960:92):

$$VI_{gr.} = 1 - (1 - VI_{\bar{n}})^n$$

If individual values of vigilance (VI_a, VI_b,......, VI_i) are known for birds A,B, ...i, then

$$VI_{gr.} = 1 - (1-VI_a)(1 - VI_b)\ldots\ldots(1 - VI_i)$$

With Lesser Sheathbills we decided that

$$VI_{\bar{n}} = 1 - F_{\bar{n}}$$

where $F_{\bar{n}}$ is the mean portion of time spent feeding by birds in flock size n, so that

$$VI_{gr.} = 1 - (F_{\bar{n}})^n$$

Similarly the vulnerability of the flock to being surprised is thus

$$Vu_{gr.} = (F_{\bar{n}})^n$$

which is the probability that a predator could attack a flock when none of the birds was vigilant and all were feeding.

SUMMARY

During winter (May to October) many Lesser Sheathbills *Chionis minor* at Marion Island in the sub-Antarctic were obliged to leave their preferred foraging habitat in penguin colonies to forage on the island's coastal plain. The terrestrial invertebrate prey taken there were small, fossorial or cryptic and patchily dispersed. Despite spending 88% of the daytime foraging the birds appeared to have precarious daily energy budgets. The Lesser Sheathbills appeared to optimise their selection of prey, foraging habitats and group sizes to maximise their food intake while foraging, minimise their time on the foraging grounds and reduce the risk of being killed by Sub-Antarctic Skuas, *Catharacta antarctica*.

Only prey larger than 1 mm were commonly eaten, roughly in proportion to their abundance in the substrate. Smaller prey were ignored although often very common.

Out of 19 available vegetation types, 97% of the Lesser Sheathbills foraged in only eight types; these were characterised by high prey densities, low vegetation height and were close to the sea. Feeding success was significantly correlated with prey densities and the habitats with low prey densities could probably not support the birds' needs. Tall vegetation (15 cm) impeded locomotion, feeding and probably predator detection. The birds reduced predation risk and travelling time by feeding near the sea.

During winter 83% of the Lesser Sheathbills on the coastal plain foraged communally and 98% roosted communally;

the typical flock sizes were eight and 17 birds in each situation respectively. Communal foraging and roosting might have facilitated habitat selection by local enhancement. Feeding success increased as flock size increased from 1 - 15 birds; this was partly due to increased time feeding concomitant with decreased time looking around and might have been due to improved selection of prey and micro-habitat by local enhancement. Feeding success in flocks greater than 15 birds however, was significantly less than in flocks of 11 - 15 birds. This was not due to increased aggression or interference competition in the larger flocks, but was probably due to local prey depletions with increased bird densities. Flocking was viewed as a means of reducing predation risk in this species.

The exploitation of terrestrial invertebrates by Lesser Sheathbills appears to be an example of niche expansion on a species - poor island, made possible by optimal foraging behaviour.

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PART SEVEN

TIME AND ENERGY REQUIREMENTS FOR CHICK-REARING IN LESSER SHEATHBILLS

TIME AND ENERGY REQUIREMENTS FOR CHICK-REARING IN LESSER SHEATHBILLS

INTRODUCTION

Reproduction in birds usually requires considerable investment of time and energy above the costs of normal maintenance (King 1973, Ricklefs 1974). In birds with nidicolous chicks the greatest demands of time and energy are generally when feeding the chicks (Ricklefs 1974) and these birds usually breed at times and places of optimum food supply to meet these demands (Lack 1954).

Lesser Sheathbills *Chionis minor* breed in close association with penguins at four island groups in the sub-Antarctic. Pairs of breeding sheathbills maintain foraging and nesting territories centred on colonies of breeding penguins; virtually all the food eaten by the parents and their nidicolous chicks is obtained from penguins, mostly by kleptoparasitism; and, the sheathbills' breeding season occurs when there is most food available for their chicks from suitable penguin species (Part one). Lesser Sheathbills steal food by leaping against a penguin in the act of regurgitating food to its chick, thereby causing food to spill.

In this report I estimate the time and energy demands of rearing chicks of Lesser Sheathbills and discuss whether breeding in these birds is potentially viable if the birds have no access to penguins. The study also provides data on the costs of territorial defence, the role of brooding in the survival of the chicks, the roles of the sexes in the care of the chicks, and the effects of kleptoparasitism on the breeding penguins.

The period of rearing chicks is probably the most demanding phase of the breeding season of Lesser Sheathbills. Their nests are merely heaps of debris requiring little effort to make, their eggs are not large in relation to the size of the female and the clutch is comparatively small, averaging two or three eggs (Part one). Both sexes incubate and the cost of incubation is unlikely to exceed the cost of feeding chicks (King 1973, Ricklefs 1974, Drent 1975).

MATERIALS AND METHODS

FIELD OBSERVATIONS

Lesser Sheathbills were studied at Marion Island (46°54'S, 37°45'E), southern Indian Ocean, in the austral summer of 1976/1977. Observations were concentrated on three pairs (A, B and C) which bred in adjacent colonies of Rockhopper Penguins *Eudyptes chrysocome*. All six parent birds had been sexed (Appendix one) and colour ringed two years before observations commenced. Pairs A and C and the female of pair B had bred successfully in the same territories for at least three seasons; the male from pair B was a three-year old bird breeding for the first time. Pairs A and B fed one chick each from hatching to fledging (about 60 days) and pair C fed three chicks for 39 days and two to fledging.

Diurnal time budgets of these three pairs of parents were determined at roughly weekly intervals from the time the chicks hatched until they left the nest to follow their parents, making observations impracticable. Observations were made from a hide from which the three nests and most of the three territories could be seen. The activities of each adult were recorded at five minute intervals, and one of eight activities was assigned to part or the whole of each interval. The weekly observations were made on successive days to cover the periods dawn to noon and noon to dark. Adult Lesser Sheathbills roosted throughout the night within their territories, and the dawn-dark observations were thus sufficient to construct 24-hour activity-time budgets. Bad weather prevented the gathering of a full set of data on the last week and where necessary, the data from 385 minutes of observations were extrapolated to cover the 871 minutes of daylight on this day.

Samples of the meals fed to Lesser Sheathbill chicks were obtained by means of 'chokers' placed around the chicks' necks to prevent swallowing, and by capturing adults carrying food to their chicks. Food samples were weighed, dried to constant mass in a convection oven at 60 - 70°C and their energy contents were then determined using a Gallenkamp ballistic bomb calorimeter.

PARENTAL ACTIVITIES AND THEIR ENERGY COSTS

The diurnal behaviour of Lesser Sheathbill parents was classified into eight different activities, as follows.

Foraging - This included search effort (walking and watching for penguins to feed their chicks), 'capture' effort (robbing penguins of the food they regurgitated to their chicks, feeding from carcasses and picking up other food items), and carrying food back to the nests.

Resting - Resting birds stood or sat.

Comfort behaviour - This comprised sedentary activities, mainly preening but also stretching and scratching with rare spells of very vigorous bathing.

Brooding - Lesser Sheathbills brooded their chicks within nest cavities and their behaviour there was very difficult to observe. The few observations made of brooding adults indicated that they sat quietly.

Nest building - Adults carried old feathers, kelp and plant matter to the nest.

Territorial defence - Eviction of conspecific intruders from territories involved vigorous chasing activities such as running, flapping, flying and, rarely, fighting.

Antipredator aggression - This involved mock attacks and running about, calling loudly, when Sub-Antarctic Skuas *Catharacta antarctica* and Kelp Gulls *Larus dominicanus*, both potential predators of Lesser Sheathbill chicks, were near nests.

Pair displays - Most displays by Lesser Sheathbills were brief, lasting only a few seconds. Hence, the more prolonged Bob Call and Run-and-Call displays performed by members of mated pairs (Part three) were the only displays to be consistently recorded in these observations. These displays involved vigorous bowing of the body, walking and running.

Crude energy budgets can be constructed from activity-time budgets using estimates of the metabolic cost of each activity (King 1974). Such energy budgets have been made for several species (e.g., Custer and Pitelka 1972, Utter and LeFebvre 1973, Siegfried *et al.* 1976) but all suffer from the paucity of empirical measurements of the metabolic costs of various activities (see King 1974 for a review). The following empirical measures of avian energetics were used as guides : existence energy during long term low level activity by caged birds ranges between 1.2 and 1.8 x Basal Metabolic Rate (BMR) (King 1974); the cost of flight averages 10 - 12 x BMR (King 1974); swimming in ducks averages 4 x BMR (Prange and

Schmidt-Nielsen 1970); and, running in the Greater Rhea *Rhea americana* cost 3.5 - 14 x BMR at speeds of 1 - 10 $hour^{-1}$ respectively (Taylor *et al.* 1971). The predicted BMR of Lesser Sheathbills and the estimated metabolic cost of each activity are given in Table 1. Resting and brooding were estimated to cost 1.5 x BMR by day or night which falls within the range of estimates for resting (Schartz and Zimmerman 1971, Custer and Pitelka 1972, Utter and LeFebvre 1973, Holmes *et al.* 1979) and incubation (Ricklefs 1974, Siegfried *et al.* 1976). Comfort behaviour was more active than resting and was estimated to cost 2 x BMR. Lesser Sheathbills engaged in foraging, nest building, antipredator aggression and pair displays were almost constantly walking or running and occasionally standing or flying and these activities were each estimated to cost 4 x BMR. Hopping in passerines was estimated to cost about 5 x BMR (Holmes *et al.* 1979). The very active spells of territorial defence by the Sheathbills were estimated to cost as much as flight, 12 x BMR.

RESULTS

PARENTAL TIME AND ENERGY BUDGETS

Both sexes performed all eight diurnal activities and, with the exception of comfort behaviour, the mean time allocated to each activity by each sex did not differ significantly (Table 2). The combined activity-time budgets of both members

TABLE 1. Basal Metabolic rates (BMR) and estimated costs of parental activities (kJ $hour^{-1}$) in Lesser Sheathbills

Activities	Male	Female
BMR[1]	8.87	8.11
Resting and brooding (1.5 BMR)	13.31	12.17
Comfort behaviour (2 BMR)	17.74	16.22
Foraging, nest building, pair displays and antipredator aggression (4 BMR)	35.48	32.44
Territorial defence (12 BMR)	106.44	97.32
Mean body mass, October - March[2] (g)	508	450

[1] Based on Kendeigh, Dol'nik and Gavrilov's (1977) equation for non-passerines in summer, day or night.

[2] From Appendix 2.

TABLE 2. Mean (± SD) and percentage (in parentheses) allocations of time (minutes) for diurnal activities by three pairs of Lesser Sheathbills rearing chicks. The observations totalled 83.8 hours.

Birds	Activity							
	Forage	Rest	Comfort behaviour	Brood	Territorial defence	Pair displays	Nest building	Antipredator aggression
Males	3195±73 (64)	50±40 (1)	682±254 (14)	888±286 (18)	63±49 (1)	4±2 (0,1)	64±49 (1)	69±68 (1)
Females	3170±478 (63)	34±28 (1)	512±232 (10)	1096±573 (22)	88±44 (2)	4±2 (0,1)	83±80 (2)	40±28 (1)
Paired t-test	N.S.[1]	N.S.	$P < 0,05$	N.S.	N.S.	N.S.	N.S.	N.S.

[1] Not significant ($P > 0,05$)

of each pair were then used to compare pairs and to relate changes in parental activity to the ages of their chicks (Figure 1).

Foraging occupied most of the daytime of all six birds. In addition, some of the time allocated to preening and resting could constitute search time since Lesser Sheathbills frequently ceased these activities to forage if they detected a penguin feeding its chick. For the first four weeks after the chicks hatched, the percentage time spent foraging increased; thereafter it remained relatively constant (Figure 1).

Resting was a rare activity and was recorded only in the second half of the chick-rearing period. The parents did, however, spend considerable time in comfort behaviour, mainly preening, throughout the study and particularly once diurnal brooding had decreased (Figure 1). The penguin colonies frequented by Lesser Sheathbills were wet and muddy, and frequent preening and bathing were required to keep their plumage clean and so retain insulation against the cold, wet and windy conditions. Males performed comfort behaviours for greater portions of the day than females (Table 2) but the reasons for this are not known.

Brooding occupied much of the time of both sexes. Mean brood bouts by males and females were 54 ± 46 (SD) minutes (range 8 - 263 min., n = 37) and 56 ± 78 minutes (8 - 485 min., n = 43) respectively, which did not differ significantly (Students t-test $P > 0.05$). Chicks were brooded almost continuously for their first two weeks but after that the percentage time spent brooding by the parents decreased rapidly (Figure 1) as the chicks grew and underwent plumage changes. Their natal down was replaced by thick mesoptile down by the 14th day and contour feathers grew from the 12th to the 50th day. These changes and their larger body size probably improved the chicks' thermoregulatory abilities, making brooding less essential.

All other activities of the parent Lesser Sheathbills occupied very little time, although each activity was probably important for breeding success.

The 24-hour energy budgets of each bird were calculated for each day of the observations by applying the energy equivalents (Table 1) to activity-time budgets. Mean energy budgets for each bird are given in Table 3.

FOOD DELIVERED TO THE CHICKS

Food was carried in the parents' beaks to the chicks at the nest and was not regurgitated. Pair C which fed a brood of three and later two, delivered considerably more meals per day to the nest than pairs A and B which fed one chick each, but the daily number of meals supplied *per chick* was similar for all

TABLE 3. Mean (±SD) 24-hour activity energy budgets (kJ day^{-1}) of Lesser Sheathbills rearing chicks.

	Activity									
Birds	Sleep (Night)	Forage	Rest	Comfort behaviour	Brood	Territorial defense	Pair-bond display	Nest build	Antipredator aggression	Total
Males										
A	116±9	344±45	2±4	24±12	41±31	36±27	0.3±1	5±5	15±12	583±25
B	116±9	356±57	1±1	52±11	22±26	20±14	0.6±1	11±15	1±1	580±31
C	116±9	352±100	4±5	36±13	36±45	5±5	0.3±1	2±4	6±7	557±56
Mean males	116±9	351±67	2±4	37±16	33±34	20±20	0.4±0.7	6±9	7±10	573±39
Females										
A	105±8	291±99	1±2	14±9	58±51	29±17	0.3±1	5±5	6±7	509±61
B	105±8	302±78	1±1	39±24	33±44	34±27	0.6±1	16±13	1±1	532±59
C	105±8	368±74	2±3	29±15	20±29	11±9	0.3±1	2±2	5±8	542±37
Mean Females	105±8	320±86	1±2	27±19	37±43	25±20	0.4±0.6	8±10	4±5	527±52

three pairs (Figure 2). The daily feeding rate increased very little after the chicks were 16 - 18 days old, at which age the chicks were about 45% of the mean adult mass and were growing rapidly (Part one). This suggests that the maximum energy needs of the chicks occurred quite early in their development, in common with other precocial and semi-precocial species of birds (Ricklefs 1974). From the age of 45 days the chicks began to forage for themselves near the entrances of their nests. When 55 - 60 days old most chicks were feeding independently but were often still in the company of their parents.

At two of the three nests, one parent delivered significantly more food to the nest than its mate (Table 4). The male was the better provider at one nest and the female at the other. The pooled data from all three pairs, however, showed no significant differences between the sexes. The mean rate of delivery of meals per hour of parental foraging time differed significantly between the sexes at one nest, but the overall mean of the three nests did not differ significantly (Table 4).

Ten meals collected from Lesser Sheathbills breeding in colonies of Rockhopper Penguins when the chicks were 21 - 38 days old had a mean fresh mass of 0.71 ± 0.55 g (range 0.14 - 1.98 g). Crustaceans (amphipods, euphasids and copepods) stolen from penguins by kleptoparasitism were the most common meals delivered to the chicks, supplemented by flesh from

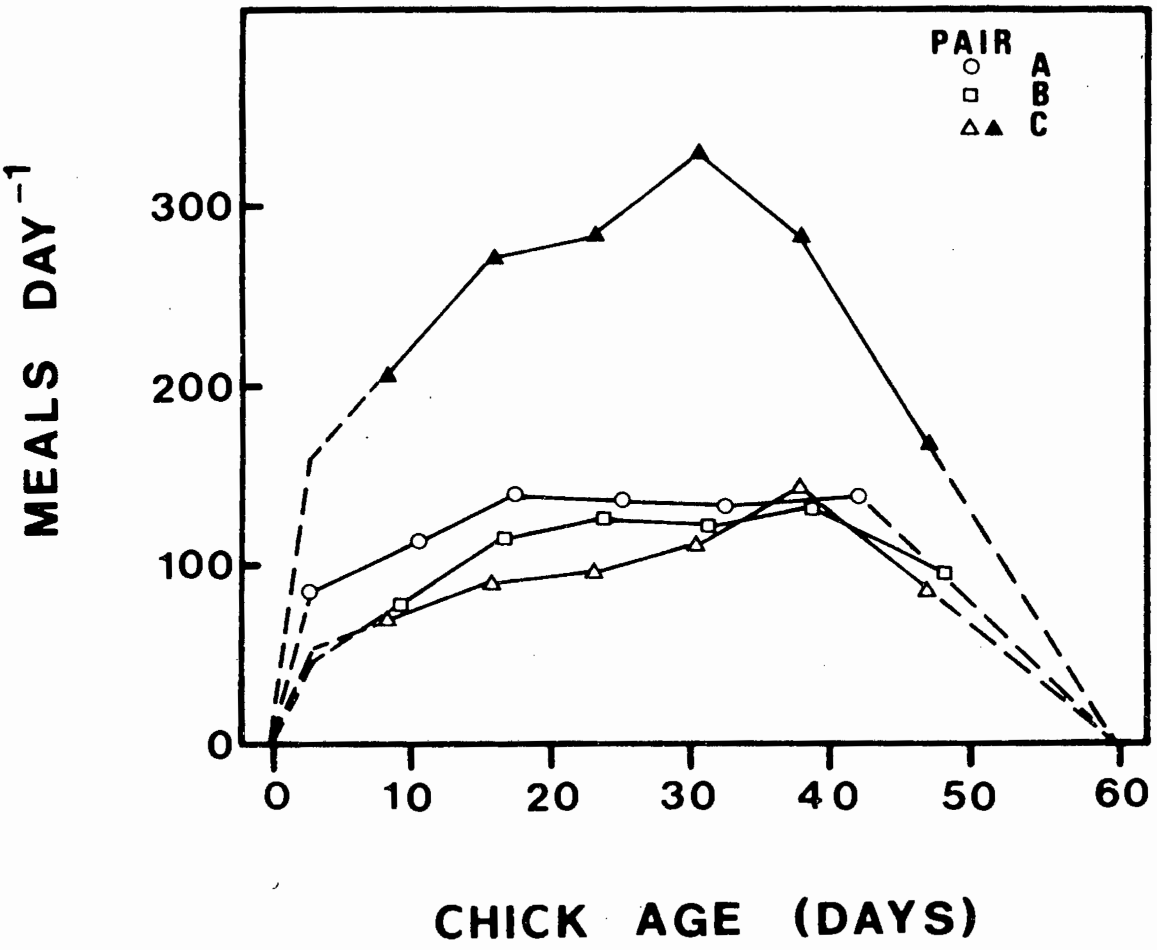

FIGURE 2. The numbers of meals fed daily to chicks by three pairs of Lesser Sheathbills. The numbers delivered per chick are shown in open symbols and the numbers per brood (pair C only) in solid symbols.

carcasses, fresh penguin excreta and terrestrial invertebrates, mainly caterpillars and earthworms (Table 5). The mean energy content of the food was 6.6 kJ g^{-1} (Table 5) and 4.7 kJ per meal. The total number of meals delivered to the chicks was estimated from the areas under the curves in Figure 2. Pairs A, B and C delivered 6290 (29563 kJ), 5550 (26085 kJ) and 4880 (22936 kJ) meals per chick respectively during the 60 day period. On average, a chick received 26195 kJ from its parents.

TOTAL DAILY ENERGY REQUIREMENTS

Energy ingested to meet the costs of parental metabolism added to the energy delivered as food to the chicks gave the total daily energy requirements of the six birds while rearing chicks (Figure 3). It was assumed that the energy available for parental metabolism, which was calculated from the metabolic costs of activities and the activity-time budgets, was 80% of the ingested energy. This was done to account for energy which was ingested but not assimilated, lost by excretion or used for specific dynamic action (Ricklefs 1974 : 167).

The greatest difference between the energy needs of the three pairs was the additional amount needed to feed the extra chick or chicks by pair C. The daily costs of parental activities were very similar in all three pairs. Peak energy requirements of males and females in pairs A and B averaged 1060 (5.0 x BMR) and 944 (4.9 x BMR) kJ $bird^{-1}$ day^{-1} respectively,

TABLE 5. Percentage occurrence and energy value (mean ± one standard deviation) of food types delivered to chicks by Lesser Sheathbills breeding in colonies of Rockhopper Penguins.

Food type	% occurrence of meals[1]	Energy content (kJ g^{-1} fresh mass)
Crustaceans[2]	89	6.76 ± 0.15 (N = 3)
Penguin carcass	6	8.08 ± 3.89 (N = 4)
Penguin excreta	2	2.14 ± 0.43 (N = 4)
Terrestrial invertebrates	3	3.04 ± 1.05 (N = 57)
Weighted mean	-	6.63

[1] N = 2362 meals (Burger in press, a)

[2] Amphipods, euphasids and copepods stolen from Rockhopper Penguins.

and in pair C, 1400 (6.6 x BMR) and 1390 (7.1 x BMR) respectively.

DISCUSSION

THE ROLE OF BROODING

Brooding by Lesser Sheathbills is probably essential for the maintenance of high body temperatures in chicks less than two weeks old. Gales and rain are usual at Marion Island and the grass-level temperatures average 3°C in summer (Schulze 1971). The chicks of most birds, even charadriiform and galliform species with precocial chicks, are unable to maintain high body temperatures at ambient temperatures below 10°C until they are one to three weeks old (literature reviewed by Ricklefs 1974). The reduced heat loss from brooded chicks may be sufficient to offset the loss of feeding time when the chicks are young and their food intake small (Theberge and West 1973) but if the foraging efforts of a single Lesser Sheathbill parent did not meet the food demands of a multiple-chick brood, this was to the detriment of the youngest sibling. Lesser Sheathbill chicks which died of starvation during the first two or three weeks after hatching were invariably the youngest chicks in broods of more than one chick (Part one).

By the time a Lesser Sheathbill chick was no longer continuously brooded, at three weeks old, its mass was almost ten times the hatching mass and it had a dense plumage of mesoptile down and the first contour feathers were growing (Part one). By the time the chick left the shelter of the nest cavity to follow the parents for long periods, it was almost fully feathered and nearly adult weight.

THE COSTS OF TERRITORIAL DEFENCE

The three pairs of Lesser Sheathbills maintained almost exclusive use of the food resources within their territories at very little cost. They spent only 2% of their daylight time and about 5% of their daily energy output in overt territorial defence. This economical maintenance of territories might be due to several factors.

Territorial adults rested and preened on raised vantage points from which they could see most of their territories and, perhaps equally important, be seen by potential intruders which might then have been deterred. Adults advertised their presence by their conspicuousness with no additional use of time or energy above the cost of normal maintenance. The increased risk of predation from conspicuousness was probably small since the only important predator on adult Lesser Sheathbills at Marion Island was the Sub-Antarctic Skua which was very seldom seen to attack Lesser Sheathbills in penguin colonies.

The territories of the three pairs were, like most territories centred on Rockhopper Penguins, separated from each other by areas of undefended vegetation and rock. These territorial pairs seldom encountered one another whilst foraging and most of the observed territorial defence was directed against intruding non-territorial birds seeking food. At colonies of King Penguins *Aptenodytes patagonicus*, however, Lesser Sheathbill territories were small and abutted on several other territories. Consequently, pairs living in these colonies spent more time in displaying to neighbouring territorial birds in addition to evicting the non-territorial intruders.

Lesser Sheathbills retained the same mates and territories from season to season and the annual mortality of adults was only 12% (Part one). Neighbouring pairs of territorial adults could thus probably recognise each other and might have been less likely to intrude into each other's territories.

PARENTAL INVESTMENT BY THE SEXES

The daily commitments of time, energy and risk from predation by male and female Lesser Sheathbills while rearing chicks were very similar. The sexes also played similar roles in nest building and incubation earlier in the breeding season (Part one). Lesser Sheathbills appear to be strictly monogamous, have life-long pair-bonds and males do not compete directly with each other for females or mating sites (Parts one and six). The key to breeding success is the acquisition of a territory which provides a suitable food supply and both sexes defend these territories. These characteristics are consistent with the predictions made by Trivers (1972) for species in which parental investment by males is similar to that of females. Since all breeding activities of Lesser Sheathbills occur within relatively small, well defended territories, opportunities for cuckoldry are rare and the chicks on which a male invests considerable time and energy are very unlikely to be the progeny of another male.

DEPENDENCE ON PENGUINS WHILE BREEDING

Food from penguin colonies supplied virtually all the energy needed by breeding Lesser Sheathbills at Marion Island (Part one) and probably also elsewhere (Paulian 1953, Downes *et al.* 1959, Derenne *et al.* 1976), but other food resources were extensively used by non-breeding birds. Apart from penguins, terrestrial invertebrates were the most frequently used food at Marion Island and the most probable alternative food for breeding birds if penguins were not available. Carcasses and placentae of seals, algae and intertidal invertebrates were also eaten. Could Lesser Sheathbills meet the energy requirements for rearing chicks without having access to penguins?

Lesser Sheathbills which were foraging intensively for terrestrial invertebrates in winter had a mean ingestion rate of 5.1 organisms per minute of foraging time (data from 75 birds watched for an average of 16 minutes each (Part six). These organisms had a mean energy content of 0.18 kJ (Appendix two) so that the birds had a mean ingestion rate of 55 kJ per hour of foraging. At this rate, male and female Lesser Sheathbills would require 19.3 and 17.2 hours respectively to meet their peak energy demands while rearing one chick. A larger brood would demand more time. Additional time would be required to carry the food to the nest and since the invertebrates had a very scattered, patchy distribution this would be considerable.

It seems improbable that Lesser Sheathbills feeding on terrestrial invertebrates could have sufficient time in the 16 hours of summer daylight to feed themselves and one chick and perform other essential activities such as brooding, comfort behaviour and anti-predator vigilance. The rate of ingestion of invertebrates might be faster in summer than in winter but the densities and the biomasses of the prey items were similar in summer and winter (Appendix two).

Terrestrial invertebrates and other food sources are important during winter and sometimes as supplementary food for chicks but the Lesser Sheathbills at Marion Island, and probably on other islands, seem to need access to breeding penguins to get sufficient food to breed. The food available from penguins is spatially and temporally concentrated and relatively rich in energy and protein (Part two).

Lesser Sheathbills appear to be obligate commensals with penguins in order to breed in their present manner.

THE EFFECTS OF KLEPTOPARASITISM ON THE PENGUINS

A pair of Lesser Sheathbills required 108 695 kJ to rear one chick over a 60 day period : 82500 kJ for parental activities (Table 3) if 80% of the ingested energy was available, and 26195 kJ for food delivered to the chick. If 89% of the energy needs were met by crustaceans stolen from the penguins, this amounted to 14.3 kg (fresh mass) of crustaceans (Table 5). Each successful pair of Rockhopper Penguins delivered 14.7 kg (fresh mass) of food to its chick prior to fledging (Williams in prep.), and each pair of Lesser Sheathbills had access to an average of 180 pairs of successful Rockhopper Penguins (personal observations, n = 13 pairs). Thus, a pair of Lesser Sheathbills which fledged one chick would use about 0.5% of the food brought into its territory by Rockhopper Penguins. Similar calculations show that pairs which fledged two or three chicks would use 0.7 and 0.8% of the incoming food respectively.

The margins of error in these calculations are unavoidably wide, but are very unlikely to be greater than one order of magnitude. The conclusion that breeding Lesser Sheathbills remove a negligible portion of the food brought in by the host penguins seems well founded. The Rockhopper Penguins threatened and sometimes chased Lesser Sheathbills which were attempting to rob them but at other times they ignored them.

SUMMARY

The energy required by Lesser Sheathbills *Chionis minor* to rear chicks was estimated from activity-time budgets plus the food delivered to the chicks at the nest. Peak energy requirements by males and females in two pairs feeding one chick each averaged 5.0 and 4.9 x Basal Metabolic Rate (BMR) respectively and in a pair feeding three (later two) chicks 6.6 and 7.1 x BMR respectively. The major difference in energy expenditure between these pairs was in food delivered to the chicks and not in extra parental activities. During daylight the parents spent their time in foraging (64%), brooding (20%), comfort behaviour (12%), territorial defence (2%), resting (1%), nest building (1%), antipredator aggression (1%) and pair displays (0.1%). The chicks were brooded almost continuously for their first two weeks but for progressively less time after that. The investments of time and energy in caring for the chicks were very similar in males and females. Crustaceans stolen from Rockhopper Penguins *Eudyptes chrysocome* were the major food item of breeding Sheathbills and the data suggest that the high energy demands while feeding chicks could only be met by pairs with access to penguins. Lesser Sheathbills are thus obligate commensals with penguins. Kleptoparasitism by the sheathbills probably had little effect on the breeding success of the penguins, since a pair of sheathbills feeding chicks removed

less than 1% of the food brought into its territory by the penguins.

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THESIS SYNTHESIS, SUMMARY AND ACKNOWLEDGEMENTS

SYNTHESIS

The Lesser Sheathbills' roles in the ecosystem

This study contributes to the construction of an energy model for the Marion Island ecosystem. The estimated annual energy intake by Lesser Sheathbills from various resources within the 100 ha study area is given in Table 1. The birds' impact on these resources cannot yet be fully ascertained since the standing crops and productivity of few resources have been estimated. Penguins deposit great quantities of energy on Marion Island in the form of excreta, eggs, carcasses of chicks and adults (Burger *et al.* in press, Siegfried *et. al.* in press, Williams *et. al.* in press) and the Lesser Sheathbills take appreciable quantities of the eggs and carcasses but not much excreta. Many tons of food are delivered annually by penguins to their chicks but Lesser Sheathbills' kleptoparasitise only 1% or less (Part seven). Overall, the predation of eggs and small chicks and kleptoparasitism by Lesser Sheathbills probably has little effect on the breeding success of penguins or other birds.

The removal of *Porphyra* algae by Lesser Sheathbills is probably a significant part in the energy flow in the littoral zone. Lesser Sheathbills within the 100 ha study area annually ingest 572 kg (dried mass) of terrestrial macro-invertebrates (estimated from the census data in Part two and the observed rates of intake in Part six), which is 3.4% of the standing crop (Appendix two). Within localised areas, intensive foraging causes significant depletions of the prey invertebrates

Table 1. Estimates of the energy taken annually by Lesser Sheathbills within the 100 ha study area (average population 197 birds) from various food resources.

	Nos. sheathbills		Energy (10^6 kJ)	
Food resource	% annual count[1]	Bird-days year^{-1}	DEM[2]	Gross intake[3]
Food from penguins				
King	23.5	16898	7.99	9.99
Macaroni	5.2	3739	1.77	2.21
Rockhopper	15.8	11361	5.37	6.72
Food from seals	2.1	1510	0.71	0.89
Intertidal organisms	16.7	12008	5.68	7.10
Kelp jetsam invertebrates	8.3	5968	2.82	3.53
Terrestrial invertebrates	27.5	19774	9.35	11.69
Kitchen scraps	0.9	647	0.31	0.38
Total	100.0	71905	34.00	42.51

[1] From Part two.

[2] Daily existance metabolism (473 kJ bird^{-1} day^{-1}; Part six).

[3] DEM X 1.25 (see Ricklefs 1974:167).

(Part six). In addition, by uprooting plants, Lesser Sheathbills retard the vegetation succession, particularly in mires (Huntley 1971, pers. obs.).

The input of energy from Lesser Sheathbills into the island's ecosystem is very small. Given the age structure and age-specific mortalities found within the study area, (Part one), fewer than 800 (23%) of the island's total population of 3 500 Lesser Sheathbills die annually. Since each carcass contains 2 887 kJ (unpublished data) of energy and a dried mass of 157 g, the total annual input from carcasses would be 2.3 X 10^6 kJ (0.13 t dried mass). This amount is negligible, relative to the contributions of the penguins, which produce 126 t (dried mass) of adult and chick carcasses annually, and whose chick carcasses alone contribute 1.57 X 10^9 kJ annually (Williams, Burger and Berruti in press). Similarly, Lesser Sheathbills contribute only 0.6% of the annual guano production at Marion Island (Burger, Lindeboom and Williams in press).

Foraging and social behaviour

The diet of Lesser Sheathbills at Marion Island includes a wide variety of food items taken from several habitats (Part two). Food from penguin colonies is of sufficiently high quality, spatially concentrated and available for sufficient time to support breeding in Lesser Sheathbills. Food from seals is of similar quality and concentration but is available for insufficient time to support breeding. Food from the intertidal, kelp jetsam and coastal plain zones, is available all year, has low food value, is spatially scattered and is seldom eaten by breeding birds but is important as winter food. The seasonal fluctuations in availability of the preferred food, low levels of interspecific competition for certain food resources and the short-term effects of the weather make a broad trophic niche adaptive to Lesser Sheathbills (Part two). It is postulated that the exploitation of a wide variety of different foods is facilitated by phenotypic variations in social behaviour to benefit the individual birds. The foraging of Lesser Sheathbills in flocks and territories is examined to test the hypothesis.

Lesser Sheathbills foraging for invertebrates on the coastal plain usually flock. The birds' success in exploiting these invertebrates is largely due to their astute selection of the vegetation types with high prey densities. Flocking and communal roosting appear to facilitate this selection process (Part six). Even within favourable areas, individuals improve their feeding success and might reduce their risks of predation by flocking. The advantages acrued by flocking are a major factor enabling Lesser Sheathbills to expand their trophic niche to include terrestrial invertebrates.

Territoriality is examined in two situations:during summer in colonies of Rockhopper Penguins while Lesser Sheathbills are breeding (Part seven), and during winter in a King Penguin colony, outside the Lesser Sheathbills' breeding season (Part five). In both situations the time and energy costs of overt territorial defence are low. The resources defended are foraging areas and not nest-sites, mates or mating-sites. Consequently, although a wide variety of displays is used to defend and advertise the territories, few displays are centred on nest-sites or used in copulation (Part three). In addition, testosterone, which appears to be important in mediating seasonal changes in sexual behaviour and physiology, is apparently unimportant in maintaining territorial aggression outside the breeding season (Part four).

The food available to Lesser Sheathbills in colonies of Rockhopper Penguins is almost exclusively used by the territorial pairs and their chicks (Part two). The supply of food to the nest is an important limiting factor for the survival of the nidicolous chicks (Part one) and the exclusive access to concentrated food resources within an area close to the nest site must be a strong selective force for territoriality, as postulated by Orians (1971). Territorial pairs within a King Penguin colony in winter are less successful at excluding conspecifics than those in the Rockhopper Penguin colonies in summer. Nevertheless, their fitness is improved by remaining territorial outside the breeding season in three ways:(Part five): the adults improve the rates and quality of food intake relative to non-territorial conspecifics eating the same resources; they improve their chances of retaining the same territories in forthcoming breeding seasons;and, by tolerating their juvenile offspring within their territories, the adults improve the chances of survivalof these offspring.

Territoriality is only adaptive if the resources in demand are 'economically defendable' (Brown 1964, Brown and Orians 1970). Territoriality by Lesser Sheathbills is restricted to penguin colonies during the period that food is being supplied by the penguins (Part three) and only in penguin colonies does the available food have sufficient quality, quantity and spatial comcentration to be economically defendable (Part two). A mathematical model by Pulliam (1976) gives a useful explanation of how the behaviour of a species might change from flocking to territoriality if the food resources changed. Pulliam predicted that under low levels of food abundance, the feeding success of dominants and subordinates should be similar, with little time available for aggression, and the feeding success of both would be greater than that of solitary birds. At higher food concentrations, however, the dominant bird reaches its maximum feeding rate and has time available to chase the subordinate birds, which consequently have reduced feeding success and might be more successful if they moved away from the area.

The interaction between food resources and social behaviour of Lesser Sheathbills fits Pulliam's (1976) model. On the coastal plain, ie. at low food abundances the birds tend to flock,which improves their feeding success; the birds spend most of the day foraging, leaving little time for other activities; aggression is rare and has negligible effect on feeding success ; and, the feeding success of dominants (adults) is not significantly higher than that of subordinates (subadults and juveniles)(Part six). At penguin colonies, ie.at high food abundances, the non-breeding Lesser Sheathbills appear to spend less time foraging than on the coastal plain; aggression occurs frequently and disrupts the foraging of subordinate birds more than that of the territorial adults; and the territorial birds have greater feeding success than the subordinate intruders (Part five). It is now evident why Lesser Sheathbills which are obliged to leave colonies of Rockhopper or Macaroni Penguins in winter do not all attempt to forage in the King Penguin colonies, where they would be subordinate to the territorial adults already established. Under these circumstances it is more adaptive for these birds to forage in flocks on the coastal plain, particularly if it were advantageous for them to remain near the territories they will use for breeding when the penguins return in summer.

The importance of penguins

A recurrent theme in this dissertation is the importance of penguins to Lesser Sheathbills. Penguins have the most productive source of animal material at Marion Island (Siegfried _et_ _al_. in press, Williams _et_ _al_. in press) and the food they supply to Lesser Sheathbills has higher energy, protein and fat contents than the alternative foods most commonly eaten. Seasonal variation in the foraging behaviour of Lesser Sheathbills is dictated largely by the availability of food from penguins (Part two).

It is suggested that Lesser Sheathbills could only breed if they have access to the food resources in penguin colonies (Part one). Evidence based on estimates of the time and energy demands of pairs of Lesser Sheathbills rearing chicks (Part seven), indicates that the birds can probably not breed successfully in their present manner if they were to rely entirely on terrestrial invertebrates, which are the most commonly used food items outside penguin colonies. It appears thus that Lesser Sheathbills are obligate commensals with penguins, or possibly also cormorants. Throughout their ranges, both species of sheathbills rely on penguins, or rarely cormorants, for food while breeding (Parts one & two). At Marion Island, the reproductive output, which is apparently the limiting factor for the population, is restricted by the number of territories which can be established in suitable penguin colonies (Part one).

One can only specualte 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 thatthis close association, coupled with the sheathbills' abilities to switch to other resources when necessary, outside the breeding season, has been fundamental to their success as land-based birds on very inhospitable islands.

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SUMMARY

1. The social behaviour, feeding ecology and breeding biology of the Lesser Sheathbill *Chionis minor* (Aves: Chionididae) were studied at Marion Island (46°54'S, 37°45'E) in the sub-Antarctic.

2. Pairs of Lesser Sheathbills bred only within territories centred on colonies of King Penguins *Aptenodytes patagonicus*, Macaroni Penguins *Eudyptes chrysolophus* or Rockhopper Penguins *E. chrysocome*. Breeding adults and chicks derived 97% of their food from penguins, mostly by kleptoparasitism. Nests, eggs, chick growth and survival, breeding success and moult are described. The Lesser Sheathbills' breeding season co-incided with the maximum availability of food from penguins. The mean reproductive output was 1.07 fledglings pair^{-1} year^{-1}.

3. The annual survival of adult Lesser Sheathbills was 88% butwas lower for subadults and juveniles. Causes of mortality were starvation during periods of inclement weather, and predation by Sub-Antarctic Skuas *Catharacta antarctica* and feral cats *Felis catus*. The population of Lesser Sheathbills appeared to be close to the carrying capacity of Marion Island and was limited by the number of territories available in suitable penguin colonies.

4. Food from penguin colonies had higher concentrationsof energy, protein and fat than intertidal algae and invertebrates, the most common food items eaten outside penguin colonies. The broad trophic niche of Lesser Sheathbills was related to

seasonal fluctuations in the availability of preferred food, a low level of interspecific competition, and short-term climatic fluctuations. The close association with penguins is fundamental to the successof Lesser Sheathbills as land-based birds on inhospitable islands.

5. The variations in social behaviour of Lesser Sheathbills, including territoriality, flocking and solitary foraging appeared to depend on the quality of the food resources and their temporal and spatial distributions.

6. Lesser Sheathbills' territories were maintained for defending food resources and were only occupied when food supplies were reliable within penguin colonies. The birds used a complex array of displays for defending and advertising territories but few displays were used in flocks, at nest sites or in copulation. Pair bonds were maintained only within territories.

7. Seasonal increases in plasma testosterone levels in adult male Lesser Sheathbills co-incided with increases in the mass of testes, the seasonal peak in mutual pair displays and the occurrence of nest-building and copulation. Territorial aggression outside the breeding season was not dependant on high testosterone levels.

8. During winter, outside the breeding season, adult Lesser Sheathbills remained territorial in colonies of King Penguins when other adults had abandoned territories. These territorial adults improved their fitness by: improving their feeding success relative to conspecifics taking the same

food resources; improving their chances of retaining the same territories for breeding in the forthcoming summer, and, improving the chances of survival of their juvenile offspring which were tolerated within territories.

9. In winter, many Lesser Sheathbills exploited terrestrial invertebrates, a food resource with small prey objects, spatially scattered and patchy. Birds eating these prey had precarious daily energy balances. Their foraging success and chances of avoiding predation were improved by flocking and by astute selection of foraging habitat. The preferred habitats were characterised by high prey densities, low vegetation canopy and had a mean locus close to the sea.

10. The energy required by three pairs of Lesser Sheathbills to rear chicks in Rockhopper Penguin colonies was estimated from activity-time budgets plus food fed to the chicks. Parental investments of time and energy by each sex were similar. The high energy demands could probably only be met by pairs with access to penguins; Lesser Sheathbills appear thus to be obligate commensals with penguins. Kletoparasitism by the sheathbills removed less than 1% of the food brought into the colonies by the Rockhopper Penguins.

11. Morphometric data and aging characters are given for adult, subadult and juvenile Lesser Sheathbills. Males were larger than females in all dimensions but were otherwise similar in external appearance.

12. The seasonal and spatial distribution, biomass, densities and energy contents of terrestrial macro-invertebrates are given for 19 vegetation types on the island's coastal plain. Lesser Sheathbills annually ingest an estimated 3.4% of the 16.86 t (dried mass) standing crop withinthe 100 ha study area.

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APPENDIX ONE

SEXUAL SIZE DIMORPHISM AND AGING CHARACTERS IN LESSER SHEATHBILLS

SEXUAL SIZE DIMORPHISM AND AGING CHARACTERS IN THE LESSER SHEATHBILL AT MARION ISLAND

ALAN E. BURGER

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SUMMARY

BURGER, A. E. 1980. Sexual size dimorphism and aging characters in the Lesser Sheathbill at Marion Island. *Ostrich* 51:39–43.

Mass and linear dimensions of adult, subadult and juvenile Lesser Sheathbills *Chionis minor* at Marion Island are given. Males were larger than females in all dimensions but were otherwise similar in external appearance. The larger size of males is attributed to selection favouring male dominance in aggressive territorial encounters. External features of the head and the voice could be used to differentiate adults, subadults and juveniles in the field.

INTRODUCTION

Lesser Sheathbills *Chionis minor* are endemic residents of four island groups in the southern Indian Ocean (Watson 1975). During a study of the species at Marion Island (46 57S; 37 45E), techniques for sexing and aging live birds in the field were developed and these are reported here. No previous attempts have been made to discriminate sex and age classes based on mensural data or external features in the Chionididae. Previous mensural data of Lesser Sheathbills from all four island groups were summarized by Despin *et al.* (1972) and Derenne *et al.* (1976) but there were then few data available from the Marion Island population.

Three age classes were recognized in this study: juveniles comprised all fledged birds in the first year of their lives, subadults were birds in their second and third years (*i.e.* one or two years old) and adults were birds three or more years old. Lesser Sheathbills first attempted breeding at the end of their third year at Marion Island (Burger in prep.), although many birds older than that did not attempt breeding.

METHODS

Lesser Sheathbills were captured using a hand net or baited walk-in traps. Pulli captured in nests provided data for birds of known age. All captured birds were ringed, most with colour rings. Measurements were taken from live birds or from those freshly killed. Body *masses* were obtained using Pesola spring balances, correct to 5 g. The following linear dimensions were taken: *culmen length; culmen depth* taken at the nostril just anterior to the sheath; *sheath depth* taken vertically from the highest point of the sheath to the under edge of the lower mandible; *culmen width* taken at the nostril; *tarsus length* taken from the intertarsal joint to the base of the last completed scute above the toes; and *wing length* taken flattened and straightened from non-moulting birds. A beak shape index:

$$\frac{\text{Culmen length} \times \text{Culmen width} \times \text{Sheath depth}}{10}$$

in mm (Warham 1972) was used to give a measure of gross beak size. Measurements were taken in all months.

SEXUAL SIZE DIMORPHISM

Thirty-nine adults which were known to have occupied breeding territories were sexed by dissection, by recording their role in copulation, or by having their mate so sexed. Males were significantly larger than females in all dimensions (Table 1). A larger sample of measurements from breeding adults, with equal proportions of both sexes, was obtained by assuming that the larger bird of each pair was the male (Table 2). The beak shape index provided a means of sexing adults when both members of a pair could not be measured. Within the sexed sample (Table 1) all females had beak shape indices less than 450 and 95% of males had indices greater than 450.

Adult males and females differed externally only in size; neither sex had external features which were not found in the other sex. When seen singly it was often impossible to sex birds visually, but when seen in pairs the larger size of the male was apparent.

TABLE 1

DIMENSIONS OF ADULT LESSER SHEATHBILLS WHICH WERE SEXED BY DISSECTION OR BY THEIR ROLE IN COPULATION. THE MEAN ± ONE STANDARD DEVIATION AND RANGE IN BRACKETS ARE GIVEN. ($P < 0{,}01$ FOR ALL VALUES OF t).

Dimension	Males	Females	t-value
Mass (g)	533 ± 37 (480 — 620)	457 ± 38 (405 — 525)	6,29
Culmen Length (mm)	32,1 ± 1,0 (30,0 — 33,6)	29,9 ± 0,9 (28,4 — 31,5)	7,11
Culmen Depth (mm)	13,6 ± 0,5 (13,0 — 14,6)	12,4 ± 0,4 (11,8 — 13,5)	8,09
Sheath Depth (mm)	16,8 ± 1,0 (15,2 — 18,9)	14,8 ± 0,7 (13,4 — 16,4)	7,02
Culmen Width (mm)	9,6 ± 0,4 (8,8 — 10,1)	8,8 ± 0,4 (8,2 — 9,2)	6,19
Tarsus (mm)	47,4 ± 1,3 (45,5 — 50,5)	44,1 ± 1,2 (41,8 — 46,2)	8,03
Wing (mm) (14 males 9 females)	222 ± 4 (214 — 230)	212 ± 3 (208 — 215)	6,41
Sample sizes	22	17	

TABLE 2

MASS AND LINEAR DIMENSIONS OF LESSER SHEATHBILLS OF KNOWN AGE AT MARION ISLAND. THE MEAN ± ONE STANDARD DEVIATION, RANGE AND SAMPLE SIZE (IN PARENTHESES) ARE GIVEN

Dimension	Young birds			Breeding adults		
	Juveniles	1-year olds	2-year olds	Both sexes	Males	Females
Mass (g)	410 ± 60 269 — 577 (89)	446 ± 57 365 — 530 (17)	472 ± 44 450 — 540 (7)	492 ± 48 397 — 635 (98)	523 ± 36 470 — 635 (50)	455 ± 34 397 — 555 (48)
Culmen length (mm)	31,6 ± 1,5 28,1 — 34,5 (54)	31,5 ± 1,1 30,0 — 33,9 (13)	31,4 ± 1,0 30,5 — 32,3 (4)	31,3 ± 1,5 28,4 — 34,5 (98)	32,1 ± 1,0 30,0 — 34,5 (50)	30,2 ± 0,8 28,4 — 31,4 (48)
Culmen depth (mm)	11,5 ± 0,6 10,4 — 12,4 (54)	12,1 ± 0,6 11,4 — 13,1 (13)	12,2 ± 0,7 12,0 — 13,6 (4)	13,0 ± 0,8 11,4 — 14,6 (98)	13,7 ± 0,5 12,8 — 14,6 (50)	12,3 ± 0,4 11,4 — 13,1 (48)
Sheath depth (mm)	12,4 ± 0,6 11,3 — 13,6 (54)	14,1 ± 1,2 12,7 — 15,9 (13)	15,1 ± 1,1 14,1 — 16,5 (4)	15,9 ± 1,5 13,2 — 19,7 (98)	17,1 ± 1,0 15,2 — 19,7 (50)	14,7 ± 0,7 13,2 — 16,4 (48)
Culmen width (mm)	8,8 ± 0,5 7,8 — 10,1 (54)	9,0 ± 0,4 8,3 — 9,5 (13)	9,1 ± 0,5 8,5 — 9,5 (4)	9,2 ± 0,5 8,2 — 10,7 (98)	9,6 ± 0,4 8,7 — 10,7 (50)	8,8 ± 0,4 8,2 — 9,8 (48)
Tarsus (mm)	45,0 ± 1,9 41,3 — 49,7 (54)	45,4 ± 1,5 43,3 — 48,3 (13)	46,2 ± 1,7 43,9 — 47,6 (4)	46,0 ± 2,0 40,6 — 50,4 (98)	47,3 ± 1,3 44,5 — 50,4 (50)	44,3 ± 1,3 40,6 — 46,0 (48)
Wing (mm)	214 ± 6 201 — 225 (54)	216 ± 4 211 — 222 (9)	no data	217 ± 7 199 — 230 (63)	221 ± 4 210 — 230 (36)	211 ± 4 199 — 216 (27)

Measurements given by Murphy (1936) and Holgersen (1957) for Wattled Sheathbills *Chionis alba* indicate that in that species too males are larger than females.

AGE CHARACTERS

Very little post-fledging growth was apparent in Lesser Sheathbills (Table 2). *Mass*, *culmen depth* and *sheath depth* were the only dimensions to increase appreciably with age. The increase in *mass* is attributed to increased fat reserves and probably also increased musculature in older birds The pectoral and leg muscles of most juveniles felt thinner than those of adults when held in the hand.

The greatest change of linear dimension with age was in *sheath depth* (Table 2). This was the result of growth in the sheath (see below) and an increase in the depth of the mandibles themselves (see *culmen depth* in Table 2). The *culmen length* appears to decrease with age but this is an artefact caused by the growth of facial caruncles covering the proximal part of the culmen.

Mass and linear dimensions cannot be used alone to age Lesser Sheathbills because of the considerable overlaps between dimensions of age classes. Leg colour was also an unreliable age character: a greater proportion of adults and subadults had pale legs than had juveniles (Table 3), but this was very variable.

TABLE 3

COLOUR OF THE LEGS OF LESSER SHEATHBILLS AT MARION ISLAND

Leg colour	Number of birds		
	Adults	Subadults	Juveniles
Pale purple or purple	74	16	15
Dark purple or black	17	6	14

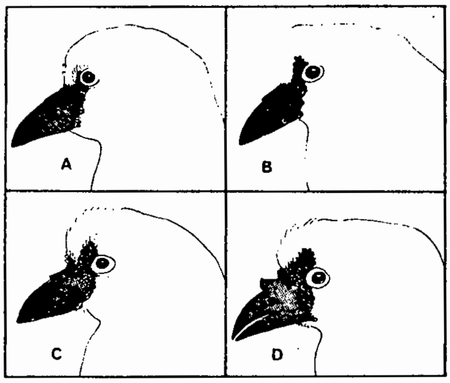

FIGURE 1

Facial features of Lesser Sheathbills at Marion Island, showing a four month old juvenile (A), a one year old subadult (B), a two year old subadult (C) and a four year old adult (D). (Drawn from close-up photographs.)

External features of the head (Fig. 1) and the voice were found to be most reliable in aging birds. These features, and others, were regularly noted in ringed birds of known age. The recognizable characteristics of each age class are summarized below.

a) Juveniles

At fledging the culmen sheath was not clearly separate from the culmen but began to grow and separate within the first year. Juveniles had little or no head crest; the caruncle around the eye was small or absent and made no lump at the proximal part of the culmen; the fleshy eye-ring was present but was small and very pale pink; the carpal spurs were small and barely protruded from the plumage; the primary feathers were more pointed than in older birds. Juveniles had feeble, high pitched cheeping calls.

b) Subadults

Lesser Sheathbills in their second and third years could be differentiated from juveniles on the following features: the culmen sheath was separate from the culmen although still small; the caruncles anterior to the eye were visible; the head crest was visible; the carpal spurs, though small, had grown. Subadults rarely vocalised and their voices were similar to those of adults.

Birds in their second year (*i.e.* one year olds) and some of those in their third year could be differentiated from adults on the following characters: the eye-ring was still pale; the facial caruncles were small and did not form a lump at the proximal part of the culmen; the sheath was smaller; the bill was smooth and not rough proximally. It was often impossible to differentiate between some two year olds and adult females on external features alone, although their behaviour often gave clear indications of their age and status.

c) *Adults*

At maturity Lesser Sheathbills had a large sheath, particularly males; the black facial caruncles covered a large part of the face anterior to the eye; the eye-ring was thickened and usually bright pink; the head crest was visible, although not larger than in subadults. The blunt black carpal spurs up to 10 mm long were prominent in adults when the wings were opened. Adult voices were strong and staccato and no difference could be discerned between sexes.

No apparent changes in appearance occurred in adults at the onset of breeding, although the eye-ring appeared to be brighter in colour in some birds at this time. Similarly, breeding adults could be distinguished from neighbouring non-breeding adults only on behavioural features.

TABLE 4

SEASONAL CHANGES IN BODY MASS (g) OF LESSER SHEATHBILLS AT MARION ISLAND. THE MEAN ± ONE STANDARD DEVIATION AND SAMPLE SIZE (IN PARENTHESES) ARE GIVEN.

Month	Juveniles	Subadults	Adult males	Adult females
December — January	—	435 ± 34 (7)	503 ± 26 (19)	442 ± 25 (16)
February — March	—	453 ± 53 (5)	513 ± 54 (16)	456 ± 65 (20)
April — May	437 ± 57 (65)	469 ± 51 (29)	521 ± 41 (28)	467 ± 33 (21)
June — July	427 ± 88 (9)	480 ± 70 (13)	564 ± 34 (18)	455 ± 50 (13)
August — September	404 ± 41 (12)	406 ± 49 (23)	523 ± 32 (19)	461 ± 32 (10)
October — November	392 ± 70 (11)	416 ± 55 (11)	509 ± 34 (14)	451 ± 24 (9)

SEASONAL CHANGES IN MASS

The sampling distribution of adult *masses* was approximately even throughout the year (Table 4). Mean *masses* of adult females did not change significantly during the year (analysis of variance, $P > 0{,}05$) but those of males did ($P < 0{,}01$), being highest in winter (April to September). The lower mean *mass* of males during the summer might be due to increased activity, and thus decreased fat reserves during the breeding season (October to March).

Most *masses* of juveniles were measured in April and May, after they had fledged (Table 4) Their mean *mass* decreased during late winter and spring but these changes were not significant ($P > 0{,}05$). Subadults were sampled relatively evenly throughout the year and their mean *mass* changed significantly ($P < 0{,}01$) decreasing sharply in late winter. The most severe, cold weather during the sampling period occurred in August when several subadults and juveniles were found starved.

DISCUSSION

Sexual size dimorphism is apparently an adaptation for alleviating intersexual competition for food in some bird species (Selander 1966). This does not seem probable in Lesser Sheathbills, however, as the foraging habits and food items of both sexes were similar and the sexes played equal roles in feeding the chicks (Burger in prep.). Sexual size dimorphism has also been shown to facilitate recognition of sexes, which permits rapid pair formation in certain species having very short breeding seasons (Jehl 1970). This does not apply to Lesser Sheathbills since breeding adults re-mate at every fourth year on average, pairs use the same breeding sites every season and re-occupy these sites at least five weeks before laying.

Breeding males were involved in significantly more agonistic territorial behaviour than females (Table 5), particularly in fighting and in ritualized boundary disputes, when fighting was probable. The larger size of males is attributed to selection favouring male dominance in aggressive territorial encounters.

The most noticeable differences between adult and immature Lesser Sheathbills were in facial features and voice. Similarly, adult Wattled Sheathbills had larger sheaths, greater areas of facial caruncles (pink in this species) and deeper, harsher voices than juveniles (Jones 1963).

TABLE 5

THE RELATIVE FREQUENCY WITH WHICH INDIVIDUALLY MARKED LESSER SHEATHBILLS PERFORMED AGONISTIC DISPLAYS IN THEIR TERRITORIES. ($P < 0{,}01$ FOR ALL VALUES OF χ^2).

Display	No. of displays by		χ^2-values
	Males	Females	
Threat posture	56	19	18,25
Chasing intruders	117	73	10,19
Ritualized boundary disputes	94	7	74,94
Fighting	33	1	30,12
All displays	300	100	100,00

The black bill, culmen sheath and facial caruncles and pink eye-rings of adult Lesser Sheathbills contrast with the pure white plumage. These features appear to be adaptations to facilitate intraspecific visual communication, since agonistic and sexual displays of Lesser Sheathbills all involve ritualized movements or postures of the head (Burger in prep.). The less conspicuous facial features of immature birds might elicit fewer aggressive responses from conspecifics. The cheeping calls of juveniles, given when in appeasement postures or when soliciting food, are believed to differ from the harsh, staccato adult calls for the same reasons. In this species, features which are useful to ornithologists to classify age classes appear to be those used by the birds themselves for social communication.

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APPENDIX TWO

TERRESTRIAL INVERTEBRATES AT MARION ISLAND; DENSITY, BIOMASS AND DISTRIBUTION

INTRODUCTION

This Appendix reports on the density, biomass and energy content of selected terrestrial invertebrates, those which were eaten by Lesser Sheathbills *Chionis minor*, in a study area on the eastern coastal plain of Marion Island. Terrestrial invertebrates which were studied are earthworms (*Microscolex kerguelarum* (Grube)), flightless lepidopterans (*Pringleaphaga marioni* Viette and *Embryonopsis halticella* Eaton), coleopteran weevils (Curculionidae, mostly *Ectemnorrhinus 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 at 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). Lesser Sheathbills 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 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 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 x 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^3 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 programmes 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 % 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. The list does not include all possible vegetation types at 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.

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 scheucherioides* bog, (4% of the study area), which has a sparse plant cover of *Juncus scheucherioides* 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%).

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

4) *Clasmatocolea humilis* - *Agrostis magellanica* mire (6%), 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%), which occurs in less waterlogged areas and has a well developed herb layer.

6) Mixed species mire (17%), 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%). Eroded and sparsely vegetated, peaty bogs with *Agrostis magellanica* and occasionally *Ranunculus biternatus* present.

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

Slope communities

Due to the hummocky nature of the coastal lowlands at 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%). A densely vegetated community of ferns, equivalent to Huntley's (1971) type nine.

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

11) *Agrostis bergiana* grass community (2%), 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 of sparse.

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

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

14) *Azorello selago* - mixed species community (5%), 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%), which occurs on revegetated seal wallows and other highly manured sites. *Poa cookii* grass is usually present.

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

17) *Clasmatocolea vermicularis* - *Marchantia berteroana* mire

(3%), 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%), 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 fjaeldmark community

19) Lowland Azorello selago - Andraea spp. fjaeldmark community (1%), 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% of all the organisms and 86,8% of the dried biomass (Table 1). Earthworm cocoons were common but contributed only 2,2% 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

Table 1

Mean annual density (no. m^{-2}), dried biomass (g m^{-2}) 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[1] (%)	% of total numbers	Weighted mean	Max.	CV[1] (%)	% 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	

[1] Co-efficient of Variation (100 x standard deviation/mean)

halticella but these probably contribute very little to the biomass. Although Lepidoptera adults were seldom found, the larvae contributed 3,7% 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 numbers of adults relative to the larvae were not entirely unexpected however, since Pringleaphaga kerguelensis at Kerguelen, which may be conspecific with P. marioni (Vari, 1971), has a larval stage lasting several years while 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 at 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 1980 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 1980 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 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

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	1
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

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^{-2})			Biomass (g m^{-2})		
		Mean	S.D.[1]	C.V.	Mean	S.D.[1]	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
Slopes	9	347	418	121	2,86	3,47	121
	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
Weighted mean		1980	–	–	16,86	–	–

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[1] Standard deviation

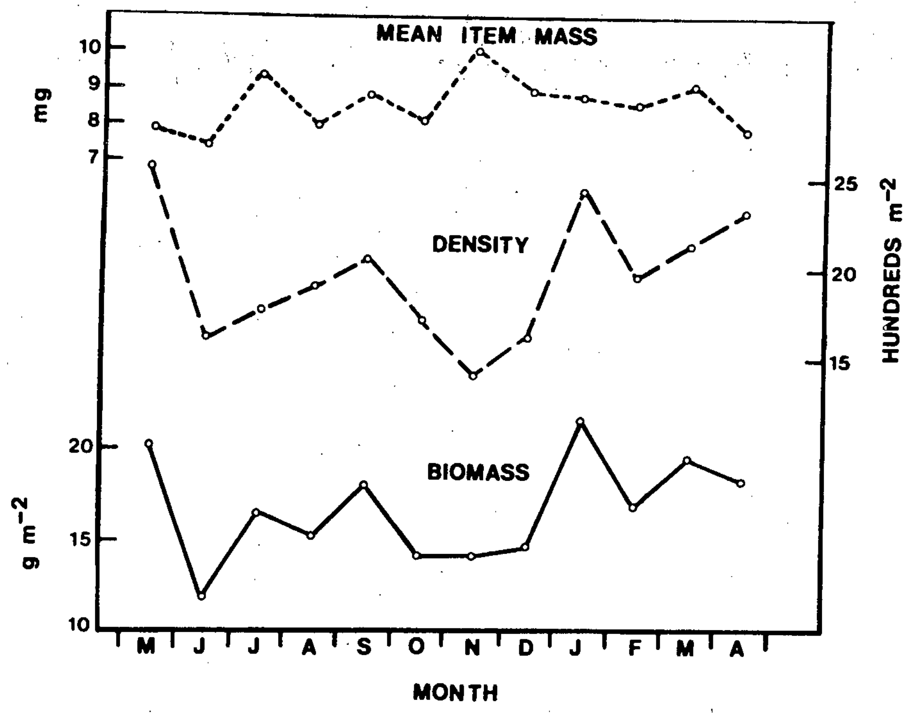

Fig. 1. Weighted monthly means of total biomass, density and mean item mass of terrestrial macro-invertebrates in 19 vegetation types at Marion Island.

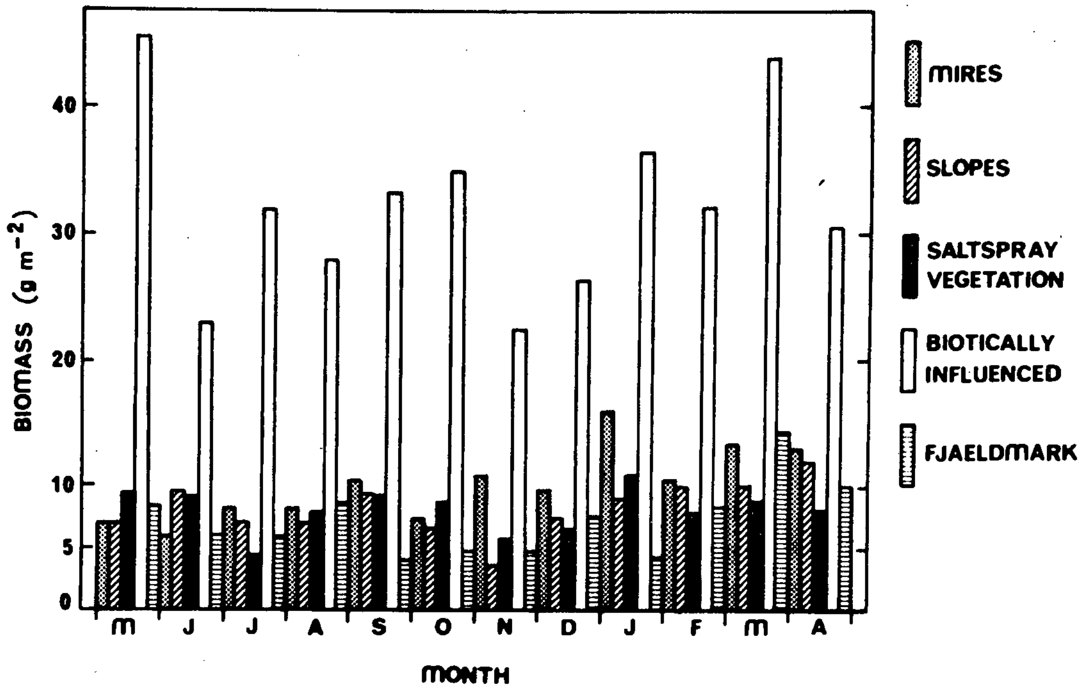

Fig. 2. Monthly values of mean invertebrate biomass in each vegetation-type complex at Marion Island.

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 micro-habitats 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 Tilleae 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,) 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 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 too few to indicate spatial distribution.

Table 4

Annual mean biomass (dried g m^{-2}) 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
Mires									
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
Slopes									
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
Saltspray									
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
Biotic									
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
Fjaeldmark									
19	6,12	0,06	0,18	0	0,50	0,14	0,01	0,24	0
Weighted mean	14,63	0,37	0,62	0,02	0,42	0,12	0,14	0,32	0,22

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 dikei* - *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 co-efficient of variation (CV = 100 x 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 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 earthworms 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) (students t-test $p < 0,05$ but $P > 0,01$) but other energy contents of earthworms were not significantly different ($p > 0,05$).

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 at 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 at Marion Island

Table 5

Mean (± SD) energy contents of terrestrial invertebrates (including ash) at Marion Island.

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

was 16,86 g m^{-2} (dried mass) or about 101 g m^{-2} (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^{-2} (fresh mass), even in the most favourable areas (Holdgate, 1967). At a moorland site in Britain, the total live biomass of invertebrates, including micro-invertebrates, was about 260 g m^{-2} (Cragg, 1961). At grassland and meadow sites in Britain the live biomass of soil and litter invertebrates was about 190 g m^{-2} (Macfadyen, 1963).

The dominance of earthworms in the soil and litter fauna at 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 6). The abundance of earthworms supports Smith's (1977) statement that plant products at Marion Island are primarily used via a detritus, rather than a grazing, food chain.

Table 6

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

abitat and region	Density (No. m^{-2})	Fresh biomass (g m^{-2})	Reference
oastal plain, Marion Island	1354	91[1]	This study
3 Habitat types, Britain and Europe	0,01 - 848	0,9 - 287	Satchell (1967)
halk grassland, Britain	103	23	Chappell _et_ _al_. (1971)
ontane soils, Australia	7 - 135	1 - 82	Wood (1974)
orest and grassland, Britain	524	152	Satchell (1967)
astures, Southern Australia	260 - 740	39 - 152	Barley (1959)
astures, Southern Australia	357	80	Noble _et_ _al_. (1970)
astures, New Zealand	650 - 1400	140 - 320	Waters (1955)

[1] Fresh mass at Marion Island was 6,2 times dried mass.

The density, biomass, mean organism mass and species' composition of terrestrial invertebrates at Marion Island varied from month to month but there were no clear seasonal trends. At 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 at 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. At 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 at 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 at 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.

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SUMMARY

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 1980 organisms m^{-2} and 16,86 g m^{-2} respectively (weighted in proportion to the % area of each vegetation type). Earthworms comprised 86,8% of the biomass, earthworm cocoons 2,2%, Lepidoptera larvae 3,7%, Lepidoptera adults and pupae 0,1%, weevil larvae and pupae 2,5%, weevil adults 0,7%, spiders 0,8%, snails 1,9%, and slugs 1,3%. 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. The standing crop of macro-invertebrates in the 100 ha study area was about 16,86 t (dried mass).

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