Oecologia (Berl) (1982) 52:236–245

Oecologia


# Foraging Behaviour of Lesser Sheathbills *Chionis minor* Exploiting Invertebrates on a Sub-Antarctic Island

Alan E. Burger
FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa*

**Summary.** During winter (May through 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 for invertebrates on the island's coastal plain. The study describes factors affecting feeding success, time budgets and predation risk of the sheathbills which exploited these small, patchily dispersed prey. The birds appeared to select prey $\geqq 1$ mm in diameter, and ignore smaller, common invertebrates.

Sheathbills were highly selective of foraging habitat. During 17 censuses made through the winter, 97% of the 1,504 bird-sightings were at only eight of the 19 available vegetation types. Multiple regression analysis revealed that prey density was the most important criterion in habitat preference, followed by plant canopy height and distance of the habitat from the sea. These variables accounted for 78% of the variance of habitat use. Focal-animal observations in a sample of habitats showed that feeding success was correlated with prey density and distance from the sea. Tall vegetation impeded the locomotion and foraging of sheathbills. The sheathbills reduced predation risk from skuas *Catharacta lonnbergi* and travelling time by foraging near the shore. The spatial distribution of prey within vegetation types was apparently unimportant in habitat selection.

During winter 83% of the sheathbills in the study foraged communally and 98% roosted communally. Flocks occurred only on good quality habitat and flocking probably facilitated habitat selection. Feeding success increased initially with increasing flock size but decreased in flocks greater than 15 birds, which was attributed to localized prey depletions. The sheathbills spent 88% of the daytime foraging; and feeding, looking around and walking comprised 99% of foraging time. Feeding time increased with increasing flock size, looking around decreased but walking was unaffected. Aggression was rare, was unaffected by flock size and did not significantly affect feeding. A probability model showed that sheathbills could greatly reduce predation risk by flocking but the benefits would not improve much in flocks greater than eight birds.

The habitat selection, time budgets and feeding success of adults, subadults and juveniles were very similar.

The exploitation of terrestrial invertebrates by sheathbills was interpreted as an expansion of the population's trophic niche to tap an underexploited resource on a species-poor island.

* Present address: Department of Biology, Memorial University of Newfoundland, Corner Brook, Newfoundland A2H 6P9, Canada

## Introduction

The behavioural adaptations for island life have seldom been studied in birds outside temperate or tropical regions. In the Antarctic and sub-Antarctic, land-based birds appear to have acute problems in meeting food requirements throughout the year. The diversity of food types is low and there are sharp seasonal variations in food availability: seals and seabirds provide food for predators and scavengers in summer but very little is available in winter. Sheathbills (Charadriiformes: Chionididae) are among the very few land-based birds to have overcome the problems of living on Antarctic and sub-Antarctic islands (Watson 1975). Their success is attributed to an ability to exploit food resources provided by penguins, other seabirds and seals, their flexible foraging behaviour and broad trophic niche (Jones 1963, Burger 1979a, 1981a, b).

At Marion Island (46° 54′ S, 37° 45′ E) in the sub-Antarctic Indian Ocean, 90% of the Lesser Sheathbills *Chionis minor*, including all breeding pairs foraged in penguin colonies during summer (Burger 1981a). During winter, however, following the exodus of most of the penguins, many sheathbills were forced to use other food resources. Some ate intertidal organisms, but 80% of those forced to leave the penguin colonies foraged on the vegetated areas of the island's coastal plain where they ate invertebrates (earthworms, insects, spiders and land-molluscs). Flocks of sheathbills on the vegetated areas comprised birds of all ages and included adults which had maintained summer territories in penguin colonies (Burger 1980a, 1981a). Sheathbills foraging on the coastal plain encountered problems which were different from those in penguin colonies (Burger 1978, 1979a, 1981a). Unlike food in penguin colonies which was spatially and temporally concentrated, usually rich in energy and protein and readily located, the invertebrates on the coastal plain were small prey objects, patchily dispersed, fossorial and cryptic. Heavy snow cover or frozen ground occasionally curtailed access to the invertebrates by sheathbills which sometimes resulted in starvation. Lesser Sheathbills on the coastal plain were more vulnerable to harassment by predatory Sub-Antarctic Skuas *Catharacta lonnbergi* than those on the shore or in penguin colonies (Burger 1979a). No birds at Marion Island fed exclusively on terrestrial invertebrates. Small numbers of Kelp Gulls *Larus dominicanus* and Kerguelen Terns *Sterna virgata* used this food, but interspecific competition was unlikely to have been a limiting factor.

This paper is an attempt to analyze foraging strategies used

0029-8549/82/0052/0236/$02.00

by Lesser Sheathbills to successfully exploit terrestrial invertebrates at Marion Island. The results illustrate how a resident on a species-poor island expanded its trophic niche by seasonal modifications of foraging and social behaviour.

## Materials and Methods

### *Study Area*

Marion Island lies 2° north of the Antarctic Convergence and has a typical climate of the sub-Antarctic: cool to cold temperatures (annual mean 5° C), usually overcast skies, very windy with frequent precipitation (Schulze 1971). The tundra-like vegetation is largely restricted to the coastal regions, below 500 m a.s.l., and comprises a mosaic of fairly distinct communities, dominated by grasses, bryophytes, ferns and low perennial angiosperms (Huntley 1971).

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 which supported, on average, 197 Lesser Sheathbills. A meteorological station was situated within the study area.

### *Definitions*

The period May to October inclusive, when terrestrial invertebrates were most commonly eaten, 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 localized searching and eating activities of foraging birds i.e., 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 average time spent foraging by sheathbills within a 6 ha area was determined, using instantaneous scans (Altmann 1974) at 5 min intervals from first light until darkness.

Secondly time budgets of foraging birds were determined from focal-animal observations (Altmann 1974) with the aid of binoculars and a tape recorder. Lesser Sheathbills were not afraid of man and it was possible to sit quietly within 15 m of foraging birds without causing noticeable changes in behaviour. Observations lasted 9–23 min bird$^{-1}$. The mean temperature and windspeed during each focal watch were recorded.

Thirdly, the age, foraging habitat and flock size of each sheathbill in the study area were recorded during 17 censuses made at roughly 10-day intervals from May through October 1976. The censuses were made on foot, between 8.00 h and 14.00 h on days without gales or heavy rain. Age was classified as *juvenile* (0–12 months), *subadult* (13–24 months) or *adult* (> 2 years old) based on criteria given by Burger (1980b). Foraging habitat was recorded as one of 19 vegetation types, classified according to plant species dominance and physiognomy. The mean densities, biomass and spatial distribution of prey, and physiognomic characteristics of samples of each vegetation type were determined at monthly intervals throughout the study period as described elsewhere (Burger 1978). Similarly, the area of each vegetation type and its mean locus relative to the sea were known from strip transects (Burger 1978). The average plant canopy height was estimated on an arbitrary scale: 0 = no vegetation: 1 = between 1–5 cm; 2 = 6–10 cm; 3 = 11–15 cm; 4 = 16–20 cm; and 5 > 20 cm.

The typical flock size (TFS) was calculated as follows (from Jarman 1974):

$$\mathrm{TFS} = \frac{n_1^2 + n_2^2 + n_3^2 \ldots n_i^2}{N}$$

where $n_1$, $n_2$, $n_3$, etc. are the numbers in each flock and $N$ is the total sample population for the particular census. The TFS is the flock size in which the "average" individual occurs and gives 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 dependent variables were the percentage of foraging time spent by the focal-birds on each activity (*PCFEED, PCLOOK, PCWALK*, etc.) and their rates of feeding success *(RFS)*. Independent variables included the mean prey densities 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 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 angiosperms *(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 did not show clear seasonal fluctuations (Burger 1978). 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. Sheathbills stripped away the vegetation to reveal the fossorial prey

**Table 1.** Linear correlation co-efficients between the occurrence and mass of terrestrial invertebrate types in the gut contents of 13 Lesser Sheathbills (Burger 1981a) and their density, biomass and mass per animal in the substrate (Burger 1978)

| Invertebrates in gut contents | Invertebrates in the substrate | | |
|---|---|---|---|
| | Density | Biomass | Mean animal mass |
| % occurrence | 0.80* | 0.82* | 0.14 |
| % mass | 0.46 | 0.53 | 0.09 |

* $p<0.05$, df=8

or, less commonly, probed with their bills into the substrate or 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 was about 12 s per object (see below).

Since search time greatly exceeded handling-and-eating time the optimal set of prey types was expected to be broad (see review by Krebs 1978). This appeared to be true. Sheathbills ate the nine prey types roughly in proportion to their densities and biomass in the substrate but within the size range taken the selection of prey types did not correlate with their mean size (Table 1). In other words, all prey greater than about 1 mm in diameter appeared to be taken when encountered, regardless of their size. Micro-arthropods smaller than about 1 mm in diameter, including mites, Collembolla and staphylinid beetles were evidently unprofitable prey for sheathbills. They were not found in stomach contents and were very rarely seen to be eaten by Lesser Sheathbills although they were often very common in the substrate (Burger 1979b).

Areas where sheathbills had fed intensively were recognizeable, having a "ploughed" appearance as a result of plants being uprooted. Samples from these areas had densities and biomasses of prey significantly lower than in neighbouring unexploited areas of the same vegetation type (Table 2).

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

| Prey item[a] | Prey density (organisms $m^{-2}$) | | Prey biomass ($g\ m^{-2}$ dried mass) | |
|---|---|---|---|---|
| | Un-exploited areas | Exploited areas | Un-exploited areas | Exploited areas |
| Earthworms | 810±887 | 318±334[b] | 9.05±8.63 | 3.20±4.13[b] |
| Earthworm cocoons | 94±197 | 40±153 | 0.09±0.20 | 0.04±0.15[b] |
| Lepidoptera larvae | 40± 82 | 0 | 0.19±0.40 | 0 |
| Coleoptera larvae | 304±249 | 106±147[b] | 1.43±1.34 | 0.41±0.58[b] |
| Total | 1,248±997 | 464±342[b] | 10.76±8.44 | 3.65±4.12[b] |
| No. samples[c] | 15 | 15 | 15 | 15 |

[a] Coleoptera and Lepidoptera adults, spiders, snails, and slugs were absent from these samples
[b] Significantly less than unexploited ($p<0.05$, $t$-test)
[c] Each sample was a core of area 50 $cm^2$ (Burger 1978)

## *Habitat Selection: The Use of Vegetation Types*

Lesser Sheathbills encountered 19 vegetation types (Burger 1978) in which the plant species composition, physical and physiog-

**Table 3.** The occurrence of adult, subadult, and juvenile Lesser Sheathbills in 19 vegetation types during censuses, made in winter (May to October) and the mean values of certain characteristics of the vegetation types in the same period. See text for explanation of abbreviations. Descriptions of the vegetation types and their areas are given in Burger (1978)

| Vegetation tapes | % birds per vegetation type: All ages | Adults | Subadults | Juveniles | Bird $ha^{-1}$: FORALL | FORAD | FORSUB | FORJUV | HERB (%) | BRYO (%) | VEGHT (0-5) | DENSITY ($m^{-2}$) | CV1 (%) | BIOMASS ($g\ m^{-2}$) | CV2 (%) | PATCHY | ITEMASS (mg) | VEGDSEA (m) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.4 | 0.5 | 0.3 | 0.0 | 1.50 | 1.25 | 0.25 | 0 | 35 | 5 | 1 | 1,027 | 92 | 7.75 | 109 | 1.67 | 7.5 | 130 |
| 2 | 6.2 | 6.6 | 4.5 | 6.6 | 23.25 | 16.25 | 3.50 | 3.50 | 28 | 88 | 1 | 1,613 | 78 | 14.62 | 78 | 1.50 | 9.1 | 90 |
| 3 | 0.2 | 0.1 | 0.0 | 0.9 | 0.60 | 0.20 | 0 | 0.40 | 37 | 82 | 1 | 120 | 121 | 0.32 | 139 | 0.78 | 2.7 | 130 |
| 4 | 7.2 | 5.9 | 10.6 | 8.5 | 18.67 | 10.17 | 5.50 | 3.00 | 31 | 92 | 1 | 1,060 | 83 | 8.45 | 92 | 1.52 | 8.0 | 130 |
| 5 | 0.1 | 0.0 | 0.0 | 0.5 | 0.33 | 0 | 0 | 0.33 | 34 | 89 | 2 | 307 | 99 | 1.28 | 126 | 1.35 | 4.2 | 140 |
| 6 | 12.4 | 10.4 | 18.6 | 12.8 | 11.00 | 6.00 | 3.41 | 1.59 | 54 | 38 | 2 | 1,727 | 78 | 15.67 | 86 | 1.50 | 9.1 | 130 |
| 7 | 0.1 | 0.0 | 0.0 | 0.5 | 0.50 | 0 | 0 | 0.50 | 19 | 1 | 1 | 333 | 153 | 2.16 | 198 | 2.88 | 6.5 | 90 |
| 8 | 0.4 | 0.3 | 0.0 | 1.4 | 0.54 | 0.27 | 0 | 0.27 | 55 | 78 | 2 | 1,327 | 60 | 12.01 | 63 | 1.21 | 9.1 | 140 |
| 9 | 0.1 | 0.0 | 0.0 | 0.9 | 0.29 | 0 | 0 | 0.29 | 97 | 4 | 3 | 493 | 108 | 3.59 | 114 | 1.80 | 7.3 | 140 |
| 10 | 0.0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0 | 75 | 72 | 3 | 1,073 | 79 | 10.15 | 78 | 1.45 | 9.5 | 50 |
| 11 | 0.1 | 0.0 | 0.3 | 0.0 | 0.50 | 0 | 0.50 | 0 | 95 | 31 | 4 | 1,140 | 69 | 9.70 | 78 | 1.31 | 8.5 | 20 |
| 12 | 1.9 | 2.1 | 1.0 | 1.9 | 28.00 | 21.00 | 3.00 | 4.00 | 92 | 2 | 1 | 600 | 80 | 3.48 | 81 | 1.31 | 5.8 | 10 |
| 13 | 4.0 | 4.1 | 1.9 | 6.6 | 30.00 | 20.00 | 3.00 | 7.00 | 95 | 2 | 1 | 1,740 | 46 | 10.71 | 58 | 1.09 | 6.2 | 10 |
| 14 | 9.0 | 8.7 | 7.1 | 13.3 | 27.00 | 17.00 | 4.40 | 5.60 | 71 | 2 | 2 | 1,607 | 106 | 9.71 | 111 | 2.05 | 6.0 | 30 |
| 15 | 4.9 | 4.7 | 4.5 | 6.6 | 24.67 | 15.33 | 4.67 | 4.67 | 98 | 1 | 1 | 3,680 | 95 | 27.63 | 90 | 1.86 | 7.5 | 50 |
| 16 | 0.2 | 0.2 | 0.0 | 0.5 | 0.33 | 0.22 | 0 | 0.11 | 96 | 15 | 5 | 2,833 | 59 | 26.27 | 69 | 1.28 | 9.3 | 80 |
| 17 | 5.5 | 3.4 | 10.9 | 7.1 | 27.33 | 11.00 | 11.33 | 5.00 | 42 | 71 | 1 | 3,127 | 71 | 24.67 | 91 | 1.45 | 7.9 | 100 |
| 18 | 47.4 | 53.1 | 40.2 | 31.8 | 79.22 | 57.89 | 13.89 | 7.44 | 92 | 1 | 2 | 6,760 | 113 | 53.93 | 146 | 2.31 | 8.0 | 40 |
| 19 | 0.0 | 0.0 | 0.0 | 0.0 | 0 | 0 | 0 | 0 | 46 | 9 | 2 | 740 | 84 | 6.23 | 86 | 1.45 | 8.4 | 100 |

**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 $r \geqq 0.56$ or ($p<0.05$)* if $r \geqq 0.44$

| | *FORAD* | *FORSUB* | *FORJUV* | *HERB* | *BRYO* | *VEGHT* | *DENSITY* | *CV1* | *BIOMASS* | *CV2* | *PATCHY* | *ITEMASS* | *VEGDSEA* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *FORALL* | 0.99** | 0.89** | 0.90** | 0.30 | −0.25 | −0.30 | 0.81** | 0.03 | 0.75** | 0.08 | 0.31 | 0.02 | −0.05 |
| *FORAD* | – | 0.83** | 0.86** | 0.34 | −0.29 | −0.26 | 0.79** | 0.06 | 0.74** | 0.11 | 0.32 | 0.01 | −0.04 |
| *FORSUB* | | – | 0.81** | 0.12 | −0.05 | −0.30 | 0.81** | 0.01 | 0.78** | 0.08 | 0.28 | 0.19 | 0.02 |
| *FORJUV* | | | – | 0.30 | −0.25 | −0.42 | 0.64** | −0.10 | 0.56** | −0.06 | 0.20 | −0.09 | −0.18 |
| *HERB* | | | | – | −0.55* | 0.51* | 0.41 | −0.34 | 0.39 | −0.39 | −0.08 | 0.17 | 0.01 |
| *BRYO* | | | | | – | −0.16 | −0.25 | −0.18 | −0.21 | −0.16 | −0.48* | −0.02 | −0.06 |
| *VEGHT* | | | | | | – | 0.07 | −0.27 | 0.15 | −0.26 | −0.13 | 0.41 | 0.36 |
| *DENSITY* | | | | | | | – | −0.09 | 0.99** | −0.01 | 0.30 | 0.33 | 0.22 |
| *CV1* | | | | | | | | – | −0.12 | 0.95** | 0.67** | 0.48* | −0.22 |
| *BIOMASS* | | | | | | | | | – | −0.05 | 0.27 | 0.42 | 0.30 |
| *CV2* | | | | | | | | | | – | 0.68** | −0.49* | −0.23 |
| *PATCHY* | | | | | | | | | | | – | 0.12 | 0.35 |
| *ITEMASS* | | | | | | | | | | | | – | 0.93** |

**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 $R^2$ |
|---|---|---|---|
| *FORALL* | 1) *DENSITY* (+)[a] | 0.649 | 0.649 |
| | 2) *VEGHT* (−) | 0.778 | 0.129 |
| | 3) *VEGDSEA* (−) | 0.845 | 0.067 |
| *FORAD* | 1) *DENSITY* (+) | 0.628 | 0.628 |
| | 2) *VEGHT* (−) | 0.727 | 0.099 |
| | 3) *VEGDSEA* (−) | 0.803 | 0.076 |
| *FORSUB* | 1) *DENSITY* (+) | 0.650 | 0.650 |
| | 2) *VEGHT* (−) | 0.779 | 0.129 |
| *FORJUV* | 1) *DENSITY* (+) | 0.414 | 0.414 |
| | 2) *VEGHT* (−) | 0.635 | 0.221 |
| | 3) *VEGDSEA* (−) | 0.800 | 0.165 |

[a] Nature of the relationship (+ve or −ve)

nomic properties, prey abundance and prey distribution differed (Table 3). Ninety-seven percent of 1,504 sightings of foraging birds were made in only eight vegetation types, which comprised 49% of the study area. The densities of birds per vegetation type *(FORALL, FORAD, FORSUB, FORJUV)* correlated significantly with mean prey *DENSITY* and *(BIOMASS)* (Table 4). Stepwise multiple regression analysis showed that bird densities were related to prey *DENSITY*, vegetation height *(VEGHT)* and the mean distance of vegetation types to the sea *(VEGDSEA)* (Table 5). These variables accounted for 78% or more of the variance in the selection of habitat by adults, subadults, juveniles and all birds combined ($R^2 \geqq 0.78$, Table 5). Prey *BIOMASS* which was intercorrelated significantly with *DENSITY* was not included in the multiple regression. Log. transformations of the dependent and independent variables did not produce higher linear or multiple correlation co-efficients.

Although sheathbills had strong preference for habitats with high prey densities they did not select habitats where the spatial distribution of prey (CV1, CV2, or PATCHY) was least variable

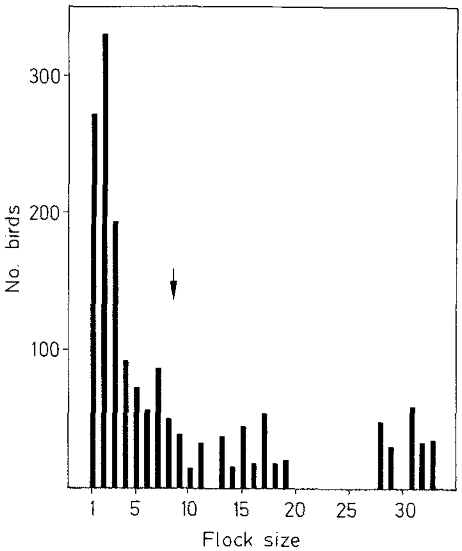


**Fig. 1.** Flock sizes of Lesser Sheathbills foraging for terrestrial invertebrates in winter (May to October). Data from 1,641 sightings during 17 censuses made a ten-day intervals. The typical flock size (TFS) is shown by an arrow

(Tables 3 and 4). This was probably because the spatial distribution of prey was clumped in all habitats, and differences between vegetation types were very slight, unlike the very large differences in prey densities and biomass.

### *Social Arrangement of Foraging and Roosting Birds*

During winter, sheathbills exploiting terrestrial invertebrates foraged and roosted communally. At foraging areas, 83% of sightings during censuses were birds in flocks of 2–33 (Fig. 1). The typical flock size (TFS) was 8.3 birds and the modal size was two. Flocks included birds of all ages, and adults, subadults and juveniles occurred in flocks of similar size (Burger 1981a).

Sheathbills which foraged inland on the coastal plain roosted at night near the shore, on lava platforms or rocky beaches. Between May and October 1976, 17 censuses were made at 10 day intervals after dark at 13 roost sites in part of the study

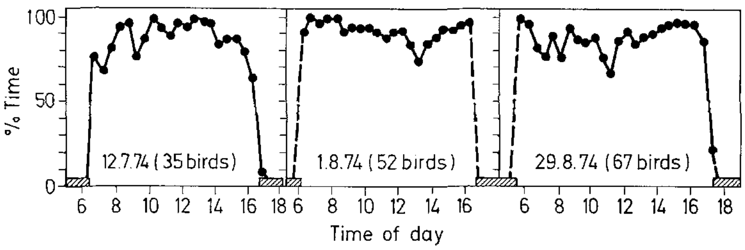


**Fig. 2.** Percentage of Lesser Sheathbills recorded as foraging during five-min scans from first-light to darkness on three days. The data are given in 1/2 h intervals and the mean number of birds visible per scan are given. Hatched areas delineate darkness

**Table 6.** Mean ($\pm$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 | $90.1\pm5.2$ | $83.8\pm14.9$* | $88.4\pm4.3$ | $88.9\pm7.3$ |
| Looking around | $5.5\pm3.2$ | $7.9\pm6.6$ | $6.1\pm3.2$ | $6.0\pm3.8$ |
| Walking | $3.0\pm2.0$ | $7.8\pm9.4$* | $4.9\pm2.8$* | $4.1\pm4.2$ |
| Preening | $1.4\pm3.7$ | $0.1\pm0.3$ | $0.3\pm0.8$ | $1.0\pm3.1$ |
| Chasing conspecifics | $0.2\pm0.5$ | $0.1\pm0.1$ | $0.1\pm0.4$ | $0.2\pm0.4$ |
| Fleeing conspecifics | 0 | $0.5\pm1.0$* | $0.1\pm0.3$ | $0.1\pm0.4$ |
| Display | $0.1\pm0.4$ | 0 | 0 | $0.1\pm0.3$ |
| No. birds | 50 | 10 | 15 | 75 |
| Mean observation time (min bird$^{-1}$) | $15.9\pm3.7$ | $13.5\pm3.0$ | $17.0\pm2.9$ | $15.8\pm3.6$ |

* Significantly different from adults ($t$-test, $p<0.05$)

area. The average number of birds per census was $38\pm9$ (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 Budgets*

Lesser Sheathbills spent, on average, 88.3% (9.45 h) 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 inland rocky outcrops or reacting to the passage of predators. Movement between the coastal roosts and foraging grounds, which were usually less than 200 m inland, took only a few minutes a 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).

*Feeding Success and the Factors Affecting It*

Lesser Sheathbills ingested an average of $5.11\pm1.57$ (S.D.) prey-objects min$^{-1}$ while on the foraging grounds ($N=75$ focal-birds). The successes of adults ($5.12\pm1.73$, $N=50$), subadults ($4.90\pm1.25$, $N=10$) and juveniles ($5.17\pm1.67$, $N=15$) did not differ significantly ($p<0.05$, $t$-tests). It is not known whether the prey types or prey sizes taken by various age classes of sheathbills differed.

The focal-animal data were inadequate for rigorous analysis of the effects of habitat on feeding success, since the focal observations were all from the frequently used habitats, which tended to have moderate or high prey densities. Even within this sample, however, feeding success (RFS) was significantly and positively correlated with prey density (Table 7). Foraging success was also significantly but negatively correlated with the distance of the bird from the sea *(BIRDSEA)*. The linear correlation analysis and a multiple regression analysis showed no additional significant relationships, at the 95% confidence level, between RFS and other variables (Table 8).

Sheathbills preferred habitats with low vegetation (Tables 3,

**Table 7.** Correlation matrix of variables considered in the analysis of Lesser Sheathbill focal-animal observations. Correlations were significant ($p<0.01$)** if $r\geq0.29$ or ($p<0.05$)* if $r\geq0.22$

| | *RFS* | *PCFEED* | *PCLOOK* | *PLWALK* | *VEGHT* | *DENSITY* | *FLOCK* | *DNNEIGH* | *BIRDSEA* | *DATE* | *TIME* | *TEMP* | *WIND* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *RFS* | – | 0.11 | 0.03 | −0.06 | 0.20 | 0.25* | 0.01 | −0.02 | −0.27* | 0.19 | 0.19 | −0.05 | 0.04 |
| *PCFEED* | | – | −0.75** | −0.78** | −0.09 | −0.30** | 0.28* | −0.07 | 0.06 | 0.24* | 0.50** | 0.13 | 0.29** |
| *PCLOOK* | | | – | 0.42** | 0.14 | 0.38** | −0.43** | 0.35** | −0.15 | −0.21 | −0.34** | −0.11 | −0.28* |
| *PCWALK* | | | | – | 0.12 | 0.22* | −0.05 | −0.13 | 0.02 | −0.18 | −0.36** | −0.13 | −0.24* |
| *VEGHT* | | | | | – | 0.50** | 0.00 | 0.10 | −0.42** | 0.07 | 0.19 | −0.45** | −0.18 |
| *DENSITY* | | | | | | – | −0.26* | −0.07 | −0.27* | −0.08 | −0.07 | −0.35** | −0.32** |
| *FLOCK* | | | | | | | – | −0.42** | 0.38** | −0.14 | 0.07 | 0.09 | 0.40** |
| *DNNEIGH* | | | | | | | | – | −0.04 | 0.01 | 0.08 | 0.01 | −0.20 |
| *BIRDSEA* | | | | | | | | | – | −0.20 | −0.26* | 0.16 | 0.18 |
| *DATE* | | | | | | | | | | – | 0.31** | −0.08 | 0.03 |
| *TIME* | | | | | | | | | | | – | −0.10 | 0.15 |
| *TEMP* | | | | | | | | | | | | – | 0.10 |
| *WIND* | | | | | | | | | | | | | – |

Table 8. 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 determination ($R^2$) | Change in $R^2$ |
|---|---|---|---|---|
| *RFS* | 1) *BIRDSEA* | (−)[a] | 0.071 | 0.071 |
| *PCFEED* | 1) *TIME* | (+) | 0.253 | 0.253 |
| | 2) *DENSITY* | (−) | 0.324 | 0.071 |
| *PCLOOK* | 1) *FLOCK* | (−) | 0.182 | 0.182 |
| | 2) *TIME* | (−) | 0.280 | 0.098 |
| | 3) *DENSITY* | (+) | 0.348 | 0.068 |
| | 4) *DNNEIGH* | (+) | 0.405 | 0.057 |
| *PCWALK* | 1) *TIME* | (−) | 0.131 | 0.131 |

[a] Nature of the relationship (+ve or −ve)

4, and 5) but the effects of vegetation height on feeding success were not adequately tested, since all the focal birds were in vegetation with average canopy height of less than 15 cm. Qualitative observations indicated that taller plants tended to restrict the birds' locomotion and feeding.

Climatic factors, date and time of day did not apparently affect feeding success (Table 7), but during strong gales (wind exceeding 35 km $h^{-1}$), when no focal-observations were made, the sheathbills' abilities to walk, fly or feed appeared to be impeded.

Lesser Sheathbills could improve their daily food intake by increasing the time spent feeding and reducing time spent walking or looking around. Other behaviours took negligible portions of foraging time (Table 6). *PCFEED, PCWALK* and *PCLOOK* were each significantly correlated with several variables, which were, however, intercorrelated (Table 7). Stepwise multiple regression analysis, which partially corrected for intercorrelations, provided the results in Table 8. Sheathbills spent more time feeding and less looking around or walking in the late afternoon. This is interpreted as behaviour aimed at ensuring that birds leaving for nocturnal roosts had full stomachs. Sheathbills spent less time feeding and more time looking around when prey densities were higher. A possible interpretation for this is that with high prey densities the birds could achieve optimal feeding rates and still have time left for other behaviour. The time budgets were influenced significantly by flock size and by the mean distance to the nearest neighbour. These factors are examined in detail below.

### *Flocking and Feeding Success*

The correlation and multiple regression analyses of focal data suggested that the sheathbills' feeding success was not affected by flock size (Tables 7 and 8). These analyses used linear correlations, but the relationship between the two variables was actually more complex (Fig. 3). Despite the broad scatter of data points, there was a trend for feeding success to increase as flock size increased up to 11–15 birds, but decrease again in flocks of 16–30 birds. This trend was not merely due to the effect of prey density, since a similar trend was evident if samples from areas of high prey densities were excluded (Fig. 3). The typical flock size of the sheathbills in winter falls within the range of flock sizes in which feeding success was high.

The time budgets of foraging sheathbills were affected by flock size. As flock size increased, the time spent feeding in-

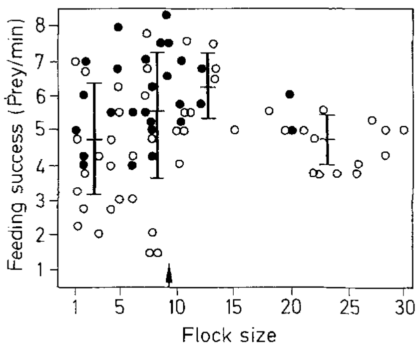


Fig. 3. Relationship between feeding success and flock size in Lesser Sheathbills eating terrestrial invertebrates. Each point is the result of focal-animal observations on an individual bird; birds at vegetation types with high mean prey densities (2,650–5,540, prey $m^{-2}$) are shown as dots, those at vegetation types with moderate prey densities (1,140–1,920 $m^{-2}$) 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

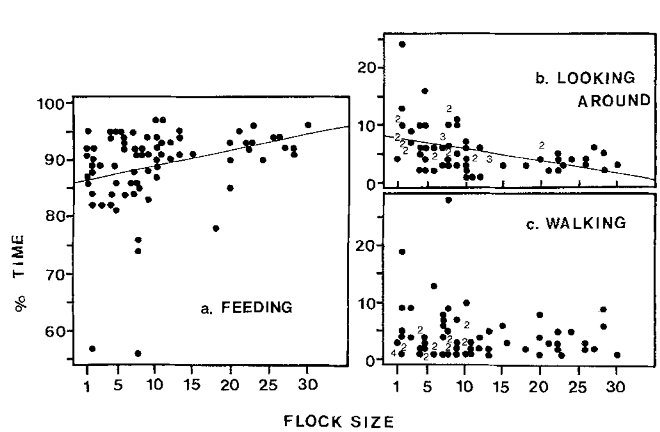


Fig. 4A–C. The relationships between flock size and the percentage time spent feeding (A), looking around (B) and walking (C) by Lesser Sheathbills during focal-animal observations. Feeding and looking around were significantly correlated with flock size and the regression lines are given ($p<0.02$ in each case), but walking was not ($p>0.05$)

creased, looking around decreased but walking was unaffected (Fig. 4).

The census data were used to examine the relationship between flock size and habitat quality. Prey density was used as an index of habitat quality, since it appeared to be the most critical factor affecting the birds' selection of foraging areas (Table 5), and was shown to affect feeding success (Table 7). The typical flock size from each vegetation type was weakly correlated with prey density (Fig. 5). Large flocks formed only in vegetation types with moderate to high prey densities, but the largest flocks did not necessarily occur on the richest habitats. In each vegetation type in which >10 birds were sighted (a very conservative measure of habitat preference) the great majority of sheathbills were in flocks and the TFS was greater than two (Fig. 5). Thus in areas where numbers of sheathbills forage, they tend to flock and flocks occur only on good quality habitat.

### *Aggression Among Foraging Birds*

Overt aggressive encounters among foraging sheathbills on the coastal plain were rare; the mean frequency was 2.5 ± 5.6 $bird^{-1}$

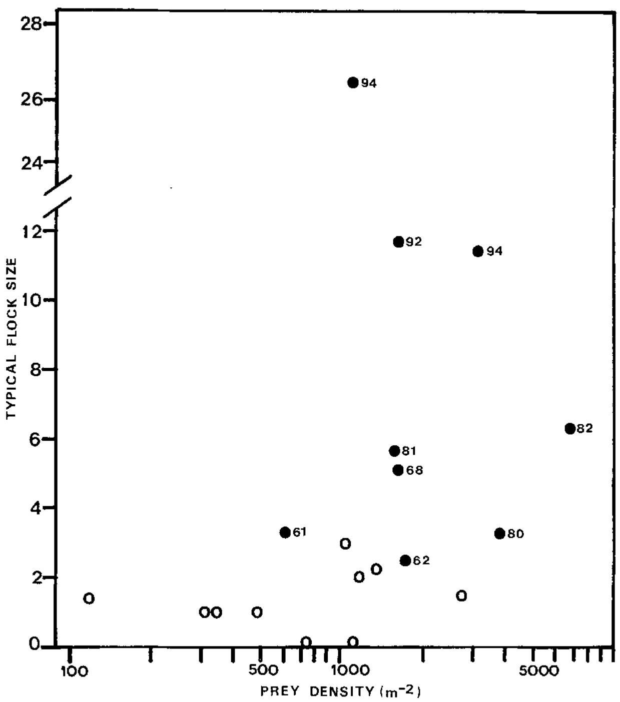


**Fig. 5.** Relationships between typical flock sizes of foraging Lesser Sheathbills and the mean prey densities (log. scale) at 19 vegetation types in winter. The correlation was not statistically significant ($r=0.17$, $n=19$, $p>0.05$) and was not significant after logarithmic transformations of either variable. Vegetation types in which $<10$ birds were sighted, out of 1,504 sightings, are shown as open circles, those with $\geq 10$ sightings as solid dots with the percentages of birds in flocks ($\geq$ two birds) given

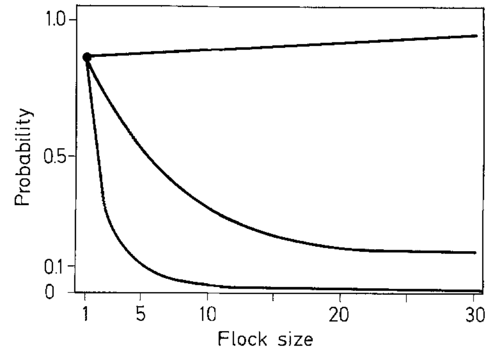


**Fig. 6.** The effect of flock size on the vulnerability of Lesser Sheathbills to attack from Sub-Antarctic Skuas.Line 1 shows the mean percentage time spent feeding by individuals (from Fig. 4). Line 2 is the theoretical vulnerability of the flock assuming each individual was behaving independently and had the same % feeding time as in line 1 (see text). 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

hour$^{-1}$ ($N=75$ focal birds). Aggressive encounters averaged only 2.9 s in duration (range 1–10 s, $N=51$ incidents), were usually supplantings at feeding sites and involved very few displays. Chasing and being chased amounted to an average of only 0.3% of the foraging time (Table 6). The percentage time and frequency of aggressions did not increase with increasing flock size ($r \leqq 0.10$, $p>0.05$, $N=75$). Lesser Sheathbills seldom foraged within 1 m of each other and the mean interbird distance in flocks of 3–30 birds was $4.3 \pm 4.7$ m ($N=63$ focal-birds).

### *Predation and Flock Size*

Sub-antarctic Skuas seldom killed Lesser Sheathbills but frequently attacked them on the coastal plain (Burger 1979a). Skuas attacked from the air, in rapid, powerful flight (Sinclair 1980). No empirical data are available on the effects of flocking on the probability of predation of sheathbills, but a model was constructed from probability theory, in a similar manner to Pulliam (1973).

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 (VI) of an individual was taken to proportional to the foraging time that was *not* spent feeding. Each bird was assumed to organize its vigilance independently of surrounding conspecifics: amongst undisturbed sheathbills, as with some other birds (Pulliam 1973; Bertram 1980), there appeared to be no correlation between the time at which one bird looked around and the time at which a neighbour looked around. The minimal flock vigilance was taken to be the probability that at least one bird was vigilant. A whole flock of sheathbills was instantly alerted by calls and/or sudden flight or running by any member which had detected an approaching predator.

Given a mean vigilance $VI_{\bar{n}}$ per bird of flock size n, and assuming that each bird's vigilance is an independent event, then group vigilance $VI_{gr}$ can be calculated as follows (Parzen 1960:92):

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

With 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 ($VU=1-VI$) 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.

The theoretical vulnerability of the flock and of the individual decreased sharply as flock size increased while the flocks were relatively small but levelled off rapidly with larger flocks (Fig. 6), as with Pulliam's (1973) model. Individual vulnerabilty improved very little in flocks greater the 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 adaptations for foraging. These were non-breeding birds foraging outside their summer breeding grounds and the ultimate factors which affected an individual's fitness at that time were its abilities to meet its daily food requirements, to maintain sufficient reserves to meet unpredictable future food shortages, and to avoid being predated.

In order to increase its daily food intake a bird could spend more hours per day feeding, increase the instantaneous rate of food intake while feeding or do both. Sheathbills were unlikely to have spent more time foraging, since this already comprised 88% of the daytime, leaving little time for essential maintenance and to allow for disturbances by predators. 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. Sheathbills foraging in other habitats and at other times of the year also spent 10% or more of the daylight preening (Burger 1981b and unpublished data). In addition, increased foraging time would incur increased predation risk, since sheathbills on the coastal vegetation were more frequently harassed by skuas than those in penguin colonies or on the shore (Burger 1979a, 1981a).

Proximate objectives of the sheathbill's foraging strategy were thus to minimize the time spent on the foraging grounds, to maximize the net rate of food intake while foraging and to adopt behaviour which reduced the risk of being depredated. These objectives 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*

The impression from many hours of observations plus analysis of a fairly small sample of gut contents suggested that the Lesser Sheathbills did select invertebrate prey according to size. They appeared to eat all prey types larger than 1 mm which were available, in proportion to their abundance, but ignored smaller invertebrates even when these were common. Since the handling time of larger prey was still very small, relative to search time, and large invertebrates were evidently sufficiently abundant to sustain the birds' requirements, this selective behaviour was tentatively assessed as a successful strategy.

### *Selection of Foraging Periods*

Lesser Sheathbills had very little chance to vary their foraging periods since they foraged for 88% of the daytime. 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 was thus similar throughout the day unless the ground was frozen or snowcovered. The feeding success of the focal-animal birds was not related to the time of day. The risk of predation to sheathbills also seemed similar throughout the day, since skua attacks occurred at any time. These sheathbills therefore had little opportunity nor apparent need to feed only at certain times of the day. The percentage time spent foraging by the birds was in fact similar throughout the day. Foraging by night was precluded since prey were usually detected by sight.

### *Selection of Foraging Habitat*

Lesser Sheathbills were highly selective of habitat and concentrated their foraging on a few vegetation types. These were characterized by high prey densities, low vegetation height and were close to the sea. These three factors all influenced the feeding success and/or predation risk of the sheathbills.

The advantages of selecting areas with high prey densities were intuitively obvious, particularly since prey densities varied 60-fold between vegetation types but the mean sizes of prey and their spatial distributions varied little. Even within the focal-animal samples, which were all birds on areas of moderate to high prey densities, feeding success was positively correlated with prey density. Given that the birds, having selected high prey densities, still spent 88% of the daytime foraging, then it was unlikely that they could survive the winter by foraging on the large areas with low prey densities. The astute selection of suitable habitat was thus central to this species' ability to exploit these terrestrial invertebrates. There was no reason why predation risk should have been any higher for sheathbills in vegetation types with high prey densities.

Lesser Sheathbills avoided vegetation with a plant canopy at breast height or higher (15 cm) despite the high prey densities found at some of these habitats, for example in the *Poa cookii* tussock-grass community (type 16 in Table 3). 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.

Vegetation types near the sea were used more frequently than those inland because they were the first areas to be encountered by sheathbills leaving the penguin colonies at the end of summer, or when moving inland from the nocturnal roosts on the coast in winter. By foraging close to the shore the sheathbills were less troubled by skuas (Burger 1979a) and also reduced the commuting time to and from roost sites.

One vegetation type, dominated by *Cotula plumosa* plants (No. 18 in Table 3) provided all the requisites for sheathbills, and almost 50% of the total winter sightings were on this habitat. Here the prey density was almost double that of any other vegetation type, the canopy was low, and this vegetation type was almost always close to the sea and to the penguin colonies where the sheathbills foraged in summer. *Cotula plumosa* communities were associated with the borders of penguin colonies and seal wallows, where the manuring by the animals stimulated plant growth and a vigorous detritus food web (Huntley 1971; Burger 1978).

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 birds did not sample a wide variety of sites each day but tended to move directly to foraging areas in the morning and unless disturbed by a skua, each individual's foraging range was only about 0.1 ha. Visual cues, such as differences in plant physiognomy, might have been used to locate high prey densities. However, most of the mires and bogs (types 1–8) were very similar in appearance although their prey densities varied greatly (Table 3). The "ploughed" appearance of intensively foraged areas might have indicated profitable food sources in the vicinity but the disturbed areas themselves often had depleted prey densities. A likely possibility was that high prey densities were located by "local enhancement" whereby birds are guided to favourable areas by the behaviour of other birds feeding there. This possibility is discussed below.

### *Selection of Foraging Group Size*

Lesser Sheathbills usually foraged in flocks when exploiting terrestrial invertebrates. These flocks did not have a purely social function, such as for the establishment of pair bonds or dominance hierarchies. All breeding, pair formation and territorial behaviour by sheathbills at Marion Island was confined to penguin colonies (Burger 1979a, 1980a), and social interactions were rare in flocks on the coastal vegetation. The benefits associated with group living in most free-living animals are: enhanced feeding success, decreased risk of predation or both (Bertram 1978; Rubenstein 1978).

Do sheathbill flocks function to improve feeding success? This might be achieved by "local enhancement", whereby birds optimize choice of prey items or foraging habitat by observing successful conspecifics in the flock (Murton 1971; Krebs 1974; Krebs et al. 1972) or use the information obtained by members of the flock to facilitate the location of good foraging areas (Ward and Zahavi 1973; Krebs 1974). This study did not attempt to determine whether sheathbills improved their feeding success by watching nearby conspecifics in the flocks, but the fact that individuals occasionally supplanted other conspecifics at feeding sites suggested that this might have been so.

There was circumstantial evidence that communal foraging and roosting by sheathbills was a means of locating profitable foraging areas. Large flocks formed only on vegetation types with higher than average prey densities. Sheathbills usually commuted in groups between foraging areas and communal nocturnal roosts. Lesser Sheathbills have pure white plumage and a flock was very conspicuous against the dark substrate of the foraging grounds and roost sites. These are all factors believed to facilitate the exploitation of profitable foraging areas by "local enhancement" (Siegfried 1971; Ward and Zahavi 1973). Flocking can also result in a more profitable time budget, by reducing the need for anti-predator vigilance. In several species of birds, individuals were found to reduce the time spent looking around when feeding in flocks thereby increasing the time available for feeding (Drent and Swierstra 1977; Inglis and Isaacson 1978; Bertram 1980). The focal-animal observations showed that this was also true for sheathbills.

Flock size did appear to affect feeding success, the rate of prey capture while foraging, in the focal-animal sample of Lesser Sheathbills. Feeding success increased with increasing flock size up to flocks of 11–15 birds, but was lower in larger flocks. The initial increase in feeding success was at least partially due to increased feeding time as flock size increased, and might also have been due to birds optimizing their prey and micro-habitat selection by watching nearby conspecifics. Notice that the variance of feeding success was much greater for birds foraging singly or in small flocks than for those in larger flocks (Fig. 3). The decreased feeding success of sheathbills in flocks greater than 15 was attributed to localized prey depletions, which were observed following intensive foraging by sheathbills. The increased aggression and interference competition sometimes found in large flocks of some species can adversely affect feeding rates (eg. Silliman et al. 1977), but this was not true for sheathbills. Aggression in flocks of sheathbills was rare, demanded negligible time and did not increase with increasing flock size.

Do sheathbill flocks function to reduce predation risk? 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 prey conspecifics in the group (Hamilton 1971; Bertram 1978). The model shown in Fig. 6 showed that these advantages should acrue to sheathbills. The sheathbill's vulnerability should not have changed significantly 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. This applies to sheathbills, which had conspicuous white plumages and foraged in open areas.

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 optimize their foraging behaviour. A better approach is to test whether the observed grouping enhances fitness in the criteria thought to be most crucial.

Are flocks of Lesser Sheathbills of optimal size? An individual could improve its daily food intake and reduce the risk of predation by foraging communally on the coastal plain. The observed feeding success was greatest in flocks of 11–15 birds. The expected predation risk was least in large flocks, but changed little in flocks greater than eight birds. The flock sizes in which most sheathbills foraged were within the range in which feeding success was high and some reduction of predation risk could be expected. One factor which also influenced flock size was the sedentary nature of Lesser Sheathbills, particularly adults (Burger 1979a). During winter the birds tended to remain close to their summer foraging areas in penguin colonies. In many parts of the study area, the penguin colonies were small, supporting few sheathbills in summer. Large flocks did not form in these areas during winter.

## Conclusions

Terrestrial invertebrates were not important prey for most populations of sheathbills (see references in Burger 1981a); the birds at most localities depended on food from seabird and seal colonies and, in winter, from the shoreline. At Marion Island sheathbills ate terrestrial invertebrates only when other, preferred food was not available in penguin or seal colonies (Burger 1981a). The invertebrates were nevertheless an important food resource and sustained large numbers of sheathbills through the winter. This exploitation appeared to be an example of trophic niche expansion on a species-poor island. Although some gulls and terns also took the invertebrates, the sheathbills were tapping an underexploited resource (Burger 1978).

Niche shifts by island birds are believed to occur most readily through phenotypic behavioural adaptations, particularly with regard to habitat expansion (MacArthur and Wilson 1967; Diamond 1970) and this appeared to be true for Lesser Sheathbills. Successful exploitation of terrestrial invertebrates was dependent on behavioural adaptations, particularly critical habitat discrimination and flocking. Since the sheathbills which ate invertebrates also ate many other food types and relied on food from penguins when breeding (Burger 1979a, c) genetic change purely to facilitate the exploitation of invertebrates was not adaptive.

*Acknowledgements.* I thank Dr. Tony Williams for field assistance, Valerie Burger, Diana Gianakouros and Lindsay Scott for help in preparing the manuscript and Prof. W.R. Siegried, Dr. G. Puttick and Dr. J.M. Juritz for advice. The financial and logistic support of the South African Department of Transport, the South African Scientific Committee for Antarctic Research and the University of Cape Town is gratefully acknowledged.

## References

Allen J (1973) STEPREG 1: Stepwise multiple regression analysis. University of Wisconsin, Madison

Altmann J (1974) Observational study of behaviour: sampling methods. Behaviour 49:227–267

Bertram BCR (1978) Living in groups: predators and prey. In: Krebs,

JR, Davies NB (eds) Behavioural ecology, an evolutionary approach. Blackwell, Oxford, pp 64–96
Bertram BCR (1980) Vigilance and group size in ostriches. Anim Behav 28:278–286
Burger AE (1978) Terrestrial invertebrates: a food resource for birds at Marion Island. S Afr J Antarct Res 8:87–99
Burger AE (1979a) Breeding biology, moult and survival of Lesser Sheathbills *Chionis minor* at Marion Island. Ardea 67:1–14
Burger AE (1979b) Sampling of terrestrial invertebrates using sticky-traps at Marion Island. Polar Record 19:618–620
Burger AE (1980a) An analysis of the displays of Lesser Sheathbills *Chionis minor*. Z Tierpsychol 52:381–396
Burger AE (1980b) Sexual size dimorphism and aging characters of Lesser Sheathbills at Marion Island. Ostrich 51:39–43
Burger AE (1981a) Food and foraging behaviour of Lesser Sheathbills at Marion Island. Ardea 69:167–180
Burger AE (1981b) Time budgets, energy needs and kleptoparasitism in breeding Lesser Sheathbills (*Chionis minor*). Condor 83:106–112
Diamond JM (1970) Ecological consequences of island colonization by south west Pacific birds: I types of niche shifts. Proc Nat Acad Sci 67:529–536
Drent R, Swierstra R (1977) Goose flocks and food finding: field experiments with Barnacle Geese in winter. Wildfowl 28:15–20
Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311
Huntley BJ (1971) Vegetation. In: Zinderen Baker EM van, Winterbottom JM, Dyer RA (eds) Marion and Prince Edward Islands. A.A. Balkema, Cape Town, pp 98–160
Inglis IR, Isaacson AJ (1978) The response of Dark-bellied Brent Geese to models of geese in various postures. Anim Behav 26:953–958
Jarman PJ (1974) The social organization of antelope in relation to their ecology. Behaviour 48:215–267
Jones NV (1963) The Sheathbill, *Chionis alba* (Gmelin) at Signy Island, South Orkney Islands. Brit Antarct Surv Bull 2:53–71
Kenward RE (1978) Hawks and doves: attack success and selection in goshawk flights at wood pigeons. J Anim Ecol 47:449–460
Krebs JR (1974) Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour 51:99–134
Krebs JR (1978) Optimal foraging: decision rules for predators. In: Krebs JR, Davies NB (eds) Behavioural ecology, an evolutionary approach. Blackwell, Oxford, pp 23–63
Krebs JR, Cowie RJ (1976) Foraging strategies in birds, Ardea 64:98–116
Krebs JR, MacRoberts MH, Cullen JM (1972) Flocking and feeding in the Great Tit *Parus major* – an experimental study. Ibis 114:507–530
Lazarus J (1972) Natural selection and the functions of flocking in birds: a reply to Murton. Ibis 114:556–558
Lloyd M (1967) Mean crowding. J Anim Ecol 36:1–30
McArthur RH, Wilson EO (1967) The theory of island biogeography. University Press, Princeton
Murton RK (1971) Why do some species of birds feed in flocks? Ibis 113:534–536
Parzen E (1960) Modern probability theory and its applications. Wiley, New York
Pielou EC (1974) Population and community ecology: principles and methods. Gordon and Breach, New York
Powell GVN (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim Behav 22:501–505
Pulliam HR (1973) On the advantages of flocking. J Theor Biol 38:419–422
Rubenstein DI (1978) On predation, competition and the advantages of group living. In: Bateson PPG, Klopfer PH (eds), vol 3 Perspectives in ethology. Plenum, New York, pp 205–231
Schoener TW (1971) Theory of feeding strategies. Ann Rev Ecol Syst 2:369–404
Schulze BR (1971) The climate of Marion Island. In: Zinderen Bakker EM van, Winterbottom JM, Dyer RA (eds) Marion and Prince Edward Islands. A.A. Balkema, Cape Town, pp 16–31
Sepkoski JJ, Rex MA (1974) Distribution of freshwater mussels: coastal rivers as biogeographic islands. Syst Zool 23:165–188
Siegried WR (1971) Communal roosting of the cattle egret. Trans Roy Soc S Afr 39:419–443
Siegried WR, Underhill LG (1975) Flocking as an antipredator strategy in doves. Anim Behav 23:504–508
Silliman J, Mills GS, Alden S (1974) Effect of flock size on foraging activity in wintering Sanderlings. Wilson Bull 89:434–438
Sinclair JC (1980) Subantarctic Skua *Catharacta antarctica* predation techniques on land and sea. Cormorant 8:3–6
Sokal RR, Rohlf FJ (1969) Biometry. W.H. Freeman, San Francisco
Treisman M (1975) Predation and the evolution of gregariousness II: An economic model for predator-prey interaction. Anim Behav 23:801–825
Ward P, Zahavi A (1973) The importance of certain assemblages of birds as "information centres" for food finding. Ibis 115:517–534
Watson GE (1975) Birds of the Antarctic and Subantarctic. American Geophysical Union, Washington, D.C.

Received June 1, 1981