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WINTER TERRITORIALITY IN LESSER SHEATHBILLS ON BREEDING GROUNDS AT MARION ISLAND

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There is an expanding literature on the adaptiveness of social behavior outside the breeding season, particularly in shorebirds. Most studies have dealt with birds foraging solitarily or in flocks (e.g., Evans 1976, Silliman et al. 1977, Sutherland and Koene 1982) or in territories on wintering grounds (e.g., Myers et al. 1979a,b; 1981). There is less known about birds defending breeding territories outside the breeding season. Territoriality is generally viewed as an adaptation facilitating the use of certain limiting resources to improve the individual's fitness (Brown 1964, Brown and Orians 1970, Davies 1978). Since territorial behavior usually incurs some cost, there should be evidence that territoriality outside the breeding season enhances the survival of an individual or its close relatives and/or enhances subsequent breeding opportunities. In this study, I have examined ways in which territoriality during the winter non-breeding season might benefit Lesser Sheathbills (*Chionis minor*) on sub-Antarctic Marion Island (46°54'S, 37°45'E) in the Indian Ocean.

Sheathbills are opportunistic predators and scavengers found in parts of the Antarctic and sub-Antarctic (Watson 1975). At Marion Island, the birds ate a wide range of food in several habitats, but were primarily dependent on food from penguin colonies during the breeding season (Burger 1981a, b). Breeding adults maintained territories centered on penguin colonies during the summer breeding season (November–mid-March), in which they foraged and nested (Burger 1979, 1980a; Burger and Millar 1980). Territories within colonies of Rockhopper (*Eudyptes chrysocome*) and Macaroni (*E. chrysolophus*) penguins were abandoned during the austral winter (April through October), when these penguins deserted the island. The sheathbills then foraged solitarily or in flocks on the shoreline or the vegetated coastal plain and some moved to colonies of King Penguins (*Aptenodytes patagonicus*) (Burger 1981a, 1982). King Penguins were present at the island throughout the year and the carcasses of chicks and adults provided food for sheathbills all winter (Williams et al. 1978). Sheathbills also kleptoparasitized those King Penguins which continued to feed chicks during the winter.

About 48% of the 3500 sheathbills at Marion Island foraged in King Penguin colonies in winter (Burger 1981a). Sheathbill pairs which bred in these colonies in summer remained territorial all year. Territorial defense, involving both sexes, appeared to be equally vigorous in winter

and summer (Burger 1980a, Burger and Millar 1980). Breeding adults retained the same mates and territories from season to season and had an annual survival of 88% (Burger 1979) and so the adults defending winter territories probably bred there the following summer. I compared the time budgets and diets of territorial and non-territorial sheathbills wintering in a King Penguin colony to determine the effects of territoriality.

METHODS

Observations were made at a colony of King Penguins at Archway Bay, Marion Island in early winter (21 April–10 May 1978). These observations were supplemented with others from a larger study at the same site, from 1974–1978 (Burger 1979; 1980a,b; 1981a; Burger and Millar 1980). The colony contained 1000 adult penguins and 1200 chicks as well as 40–50 sheathbills. The sheathbills' territorial boundaries were known and most of the resident birds were color-banded.

Three categories of sheathbills were recognized: territorial adults, intruders, and juveniles. There were 12 pairs of territorial adults; all of those observed were color-banded, paired, and known to have bred in their territories. There were variable numbers (10–20) of intruders, mostly subadults (Burger 1980b) in their second or third winters, but also including non-territorial adults. These birds visited the colony to forage in undefended fringe areas and by intruding into the territories. Juveniles were 3–4 months old and independent of their parents. They were tolerated within their parents' territories where they did most of their foraging. All the juveniles and all but two intruders observed were either color-banded or marked with small dabs of picric acid solution. Since parents and juveniles were all marked, family relationships were accurately determined.

Focal animal observations (Altmann 1974) were made of sheathbills actively foraging in the penguin colony and the adjacent beach. Sheathbills were unafraid of people and were studied with the aid of binoculars and a tape recorder while I sat quietly at 20–60 m range. Temperatures varied from −2–5°C and there were occasional ice squalls. Each focal observation lasted 30 min. Three males, three females, two intruders, and two juveniles were each watched for two periods, all other birds once. The duration and frequency of behaviors were measured from recorded commentary using stopwatches and tally-counters. Handling and eating time (Schoener 1971), hereafter referred to as "eating," included time to swallow, pull bits off carcasses, extract invertebrates from the substrate, and wait next to penguins for opportunities to kleptoparasitize them. "Walking" included searching and movements between food sources. The rate of swallowing was used as a rough means of comparing the intake of similar foods between birds.

Instantaneous-scan observations (Altmann 1974) were used to provide estimates of time spent foraging (eating, walking and other activities while seeking food), resting, preening, and displaying from dawn to dusk (06:00–17:20) on 21 April 1978. Observations were made from a raised vantage point and scans made every 5 min. It was not possible to record the sex, age or status of birds at each scan.

Body weights and annual survival rates were analyzed to determine whether juveniles living in the King Penguin colony fared better than those living elsewhere. Body weights of live birds were measured between 1974–1978, as described by Burger (1980b). Annual survival was estimated from recaptures and sightings of banded birds, between 1974–1976 (see Burger 1979 for methods).

Standard deviations are given with means. Non-parametric Mann-Whitney *U*-tests were

used to analyze the focal-animal data. Student's *t*-tests were used to analyze the duration of feeding bouts at carcasses, where the sample sizes were large.

RESULTS

Agonistic encounters between sheathbills at the King Penguin colony consisted mostly of chases (Burger 1980a, Burger and Millar 1980). These ranged from low intensity encounters where one bird supplanted another at a food source, to vigorous chases of 10–20 m involving rapid running and often flapping flight as a territorial adult evicted an intruder from its territory. Although chasing and being chased used little of the foraging time (Table 1), these activities disrupted the birds' foraging; at a rate of once every 5 min for territorial adults and juveniles, and every 2 min for intruders (Table 2). Territorial males and females were rarely chased by other birds, and they spent significantly more time chasing and less being chased, than either intruders or juveniles (Tables 1 and 2). Although the juveniles were subordinate to the intruders, which were older birds, the juveniles were chased for significantly less time (Table 1) and far less frequently (Table 2) than intruders, with fewer disruptions to their foraging. Juveniles reduced agonistic encounters by foraging within their parents' territories. Those that strayed outside their parents' territories were regularly chased by neighboring territorial adults, intruders and other juveniles. Adults quite frequently chased their own offspring, but these chases were brief, usually supplantings, and the offspring were not driven out of territories at this time.

Sheathbills ate four recognizable food types in the King Penguin colony. Food kleptoparasitized from the penguins (hereafter referred to as "penguin food") and flesh from carcasses were food of high quality. Penguin food consisted of fish, squid, and marine crustaceans stolen from penguins as they regurgitated to their chicks (Burger 1979). Penguin food had an energy content of 4.5–6.8 kJ g^{-1} (fresh weight) and a protein content of 14–18% of fresh weight (Burger 1981a). When a sheathbill was successful at robbing a penguin, the mass of food ingested per peck appeared to be about 10× that of other food.

The colony was littered with numerous carcasses of penguins, virtually all within sheathbills' territories. All that remained of most carcasses was skin and bones. Sheathbills generally gained access to a carcass only after the skin had been ripped off and most of the flesh eaten by Southern Giant-Petrels (*Macronectes giganteus*), Northern Giant-Petrels (*M. halli*) and Brown Skuas (*Catharacta lonnbergi*). Sheathbills picked off small pieces of meat, skin and blubber, which had energy contents of 4.9–11.6 kJ g^{-1} and protein contents of 13–19% of fresh weight (Burger 1981a).

Invertebrates taken from the Penguin colony represented food of in-

TABLE 1

MEAN (± SD) PERCENTAGE OF TIME SPENT BY LESSER SHEATHBILLS IN VARIOUS ACTIVITIES WHILE FORAGING IN A KING PENGUIN COLONY

Activity	Territorial males (M) (N = 10)	Territorial females (F) (N = 10)	Intruders (I) (N = 14)	Juveniles (J) (N = 10)	Significant differences[a]
Eating	45 ± 13	52 ± 18	29 ± 15	49 ± 17	M > I (U = 108), F > I (U = 122), J > I (U = 112)
Walking	44 ± 12	34 ± 18	57 ± 13	40 ± 17	I > M (U = 109), I > F (U = 119), I > J (U = 111)
Looking around	8 ± 12	11 ± 7	11 ± 6	8 ± 5	No differences
Chasing	2.1 ± 1.5	1.4 ± 1.2	0.4 ± 0.6	0.4 ± 0.7	M > I (U = 133), F > I (U = 104), M > J (U = 80), F > J (U = 76)
Fleeing	0.0	0.1	3.3 ± 2.0	0.8 ± 0.7	I > M (U = 140), J > M (U = 80), I > F (U = 14), J > F (U = 95), I > J (U = 133)
Threatening	0.6 ± 1.9	0.2 ± 0.2	0.3 ± 0.6	0.0	Not tested
Pair display	0.3 ± 0.3	1.4 ± 1.2	0.0	0.0	Not tested
Preening	0.7 ± 1.1	0.8 ± 0.8	0.9 ± 1.1	0.3 ± 0.4	No differences
Soliciting food	0.0	0.0	0.0	3.2 ± 2.5	Not tested
Mean observation time (min)	30 ± 1	28 ± 3	25 ± 5	28 ± 4	

[a] Mann-Whitney U-test, $P < 0.05$.

TABLE 2

MEAN (± SD) RATE OF AGONISTIC EVENTS (PER H) BY SHEATHBILLS IN A KING PENGUIN COLONY

Behavior	Territorial males (M) (N = 10)	Territorial females (F) (N = 10)	Intruders (I) (N = 14)	Juveniles (J) (N = 10)	Significant differences[b]
Chasing	15.6 ± 8.4 (99)[a]	13.4 ± 11.5 (69)	3.9 ± 4.8 (25)	3.0 ± 5.4 (22)	M > I (U = 127), M > J (U = 92), F > I (U = 104), F > J (U = 78)
Being chased	0 (0)	0.2–0.8 (3)	28.2–10.3 (184)	10.2–9.6 (89)	I > M (U = 140), I > F (U = 140), J > M (U = 80), J > F (U = 80)
Both combined	15.6 ± 8.4 (99)	13.6 ± 11.7 (72)	32.0 ± 12.9 (209)	13.2 ± 9.8 (111)	I > M (U = 120.5), I > F (U = 120), I > J (U = 127)

[a] Figures in parentheses show the numbers of encounters observed.
[b] Mann-Whitney U-test, $P < 0.05$.

termediate quality, averaging 3.0 kJ g^{-1} and 11% protein (Burger 1981a). Small flies (Diptera), Collembola and mites (Acarina) were widely distributed across the colony. Larger kelp flies (*Paractora* sp. and *Apetenus* sp.), their larvae and pupae and small oligochaetes occurred within rotting kelp on the beach and colony floor and were quite abundant in patches. Use of invertebrates by sheathbills involved considerable search time spent walking, but negligible handling time.

Freshly voided excreta from penguins represented low quality food, averaging 2.1 kJ g^{-1} and 3% protein (Burger 1981a). The sheathbills did not appear to seek this food actively but ate it opportunistically as they walked about the colony. In addition to the above food types, the sheathbills also ate unidentified small items, which were probably tiny arthropods, excreta and the fragments of blood-sheaths shed from the feathers of molting penguins.

The instantaneous-scan observations revealed that the sheathbills spent 69% of the day foraging, 21% resting, 9% preening, and displaying ($N = 45 \pm 4$ birds per scan). Ninety percent of the foraging birds were located among the penguins, 8% on piles of rotting kelp jetsam, and 2% on small patches of vegetation within and bordering the colony. The sheathbills' territories covered most of the penguin colony and the adjacent beach. Non-territorial birds moved away from these areas to rest and preen and almost all agonistic encounters involved foraging birds.

Focal-animal observations revealed that foraging birds performed several activities, but eating, walking and looking around made up 97% of the foraging time of each class of sheathbill (Table 1). Of these major activities, intruders spent significantly less time eating, but more walking, than the territorial adults and juveniles but there were no other significant differences (Table 1). Since the rates of food intake by intruders were not higher than the other birds (see below), but their eating time was less, these data suggest that the intruders had to spend more of the day foraging than other birds. Sheathbills frequently raised their heads to look about. This probably had at least two functions: to look for new feeding opportunities and to watch for skuas which foraged in the penguin colony and occasionally attacked sheathbills (Burger 1979). Agonistic behavior, pair displays and brief intervals of preening took little of the foraging time (Table 1). Juveniles spent 3% of their foraging time soliciting food from their parents, an activity which yielded negligible amounts of food. This behavior was also an appeasement signal (Burger 1980a).

The percentage of foraging time spent eating each food type (Table 3) and the rates of swallowing (Table 4) were used to indicate the sheathbills' access to the food types and a rough measure of food intake. With the exception of penguin food, all bird classes ate all food types and most individuals included all types of food in their diets.

TABLE 3

MEAN (± SD) PERCENTAGE OF FORAGING TIME SPENT EATING VARIOUS FOOD TYPES[a]

Food type	Territorial males (M)[b]	Territorial females (F)	Intruders (I)	Juveniles (J)	Significant differences[c]
Penguin food	12 ± 15 (30)	10 ± 17 (30)	4 ± 12 (7)	0	Not tested (see text)
Carcass	20 ± 22 (90)	39 ± 26 (100)	18 ± 18 (93)	31 ± 22 (100)	F > I ($U = 112$)
Invertebrates	10 ± 21 (80)	1 ± 1 (70)	2 ± 2 (86)	2 ± 5 (80)	No differences
Excreta	2 ± 2 (90)	1 ± 2 (70)	2 ± 1 (93)	4 ± 4 (80)	No differences
Unidentified objects	1 ± 1 (100)	1 ± 1 (100)	3 ± 2 (100)	12 ± 15 (100)	I > M ($U = 110$), I > F ($U = 126$), J > M ($U = 75$), J > F ($U = 85$)
Total eating	45 ± 13	52 ± 18	29 ± 15	49 ± 17	

[a] Sample sizes as in table 1.
[b] Figures in parentheses show the percentages of birds eating the foods.
[c] Mann-Whitney U-test, $P < 0.05$.

TABLE 4

MEAN (± SD) RATES OF SWALLOWING FOOD (SWALLOWS/MIN OF FORAGING TIME) BY SHEATHBILLS

Food type	Territorial males (M) (N = 10)	Territorial females (F) (N = 10)	Intruders (I) (N = 14)	Juveniles (J) (N = 10)	Significant differences[a]
Penguin food	0.2 ± 0.5	0.2 ± 0.5	0.1 ± 0.3	0	Not tested (see text)
Carcass	11.2 ± 14.5	25.4 ± 26.3	7.4 ± 7.3	16.2 ± 15.0	F > I ($U = 110$)
Invertebrates	1.1 ± 2.2	0.3 ± 0.6	0.6 ± 0.7	0.6 ± 1.2	I > F ($U = 109$)
Excreta	0.7 ± 0.6	0.4 ± 0.6	0.8 ± 0.6	1.3 ± 1.1	J > F ($U = 77$)
Unidentified objects	0.8 ± 0.3	0.6 ± 0.4	1.9 ± 1.0	3.7 ± 3.6	I > M ($U = 120$), I > F ($U = 125$), J > M ($U = 79$), J > F ($U = 82$)

[a] Mann-Whitney U test, $P < 0.05$.

Territorial males and females appeared to spend more time attempting to rob penguins, and were seemingly more successful at this activity than were the intruders. Sample sizes were too small for statistical testing (Tables 3 and 4). During 20 observation periods involving territorial adults, four males and four females (40% of the adults) actually leapt against the penguins to disrupt their feeding of chicks, and three males and three females (30%) obtained food in this manner. By contrast, only two intruders (14% of 14 records), both non-territorial adults, leapt against the penguins but only one (7%) was successful in obtaining food. The only sheathbills which obtained appreciable amounts of food by kleptoparasitism (10 swallows or more per 30 min focal-watch) were those which devoted 30% or more of their foraging time to this task. Successful sheathbills regularly had to spend long periods (>1 min) watching for the right moment to disrupt a penguin as it delivered food to its chick. Territorial adults, which could stand for long periods without being chased by conspecifics, had an advantage in getting penguin food over intruders, which were frequently chased. No juveniles attempted to rob penguins.

The sheathbills spent most of their eating time and obtained most of their food at carcasses. Territorial females spent significantly more time and had higher rates of swallowing at carcasses than intruders, but there were no other significant differences between other sheathbill classes (Tables 3 and 4). The swallowing rate by males at carcasses was higher than intruders but not significantly so. This was partially due to the fact that in 5 of the 10 observations, the males appeared to concentrate on getting penguin food or large invertebrates, rather than food from carcasses.

Territorial adults were dominant at all carcasses within their territories and tended to feed on fresher carcasses, which yielded larger portions per peck, than those normally accessible to intruders. Territorial males were never chased during feeding bouts at carcasses (N = 65 bouts) and territorial females were chased in only 2% of feeding bouts (N = 109). Subordinate birds were frequently chased from carcasses; intruders and juveniles ended 38% (N = 65) and 47% (N = 85), respectively, of their feeding bouts at carcasses by being chased. Consequently, the mean durations of these feeding bouts at carcasses for territorial males (54 ± 80 sec, N = 65) and females (62 ± 63 sec, N = 109) were each significantly longer than those of intruders (37 ± 44 sec, N = 98) ($t = 1.74$, df = 161 and $t = 3.27$, df = 205, respectively, $P < 0.05$ in each case). The mean bout duration by juveniles (41 ± 46 sec, N = 131) was significantly less than that of females ($t = 2.98$, df = 238, $P < 0.05$), but was not significantly different from those of males ($t = 1.44$, df = 194, $P > 0.05$) or intruders ($t = 0.66$, df = 227, $P > 0.05$).

Most sheathbills swallowed few invertebrates and spent little time eating

them (Tables 3 and 4). The only significant differences here were that territorial females had lower swallowing rates than intruders. Although most territorial males ate few invertebrates, their mean eating time and intake of this food was boosted by two records in which males spent 79% and 95% of the eating time ingesting large kelp fly larvae taken from particularly productive patches of rotting kelp.

Most sheathbills ate some excreta, but generally only small amounts. Juveniles had higher rates of swallowing excreta than territorial females but there were no significant differences between other classes (Tables 3 and 4). Intruders and juveniles spent significantly more time eating and had higher rates of swallowing unidentified objects than territorial males and females (Tables 2 and 3). These unidentified objects were all very small and probably of low nutritional value.

The mean weight of juveniles trapped in King Penguin colonies during the winter (April through September) was 446 ± 74 g (N = 14), which was significantly higher (two-tailed *t*-test, $t = 1.90$, $df = 67$, $P = 0.05$) than the mean weight of juveniles trapped elsewhere in the same period (414 ± 50 g, N = 55). The minimum annual survival of juveniles banded in King Penguin colonies and those banded elsewhere was 0.55 (N = 14) and 0.33 (N = 59), respectively, over a two year period, 1974–1976. These data are presented tentatively since the disappearance of banded juveniles was due to death and also to movements to other parts of the island (Burger 1979).

DISCUSSION

The costs of territorial defense by sheathbills wintering in the King Penguin colony appeared to be low. Territorial adults spent less than 2% of their foraging time and similar low proportions of their overall daily time budget in overt chasing and threatening. There was also little risk of injury from fighting. Fighting occurred rarely, only between neighboring territorial adults and was seldom damaging (Burger 1980a, Burger and Millar 1980). The economical defense of territories was facilitated by conspicuous visual and vocal advertising (Burger 1980a), but there was no evidence that this conspicuousness might have increased the risk of predation by skuas. The sheathbills maintained the same territories with relatively stable boundaries from year to year (Burger 1980a), which probably facilitated their defense, as was found for some other species (Southern and Lowe 1968, Davies 1976).

Sheathbills appeared to benefit from winter territoriality in at least two ways, and possibly a third. Firstly, the territorial adults had greater access to high quality food than intruders. Very few non-territorial birds had the freedom from interference needed to stand waiting for opportunities

to kleptoparasitize penguins. Territorial adults were immediately dominant at penguin carcasses within their territories. They had longer feeding bouts at carcasses, with fewer interruptions, than the intruders did. Territorial females had significantly higher rates of swallowing carcass flesh than the intruders did. Territorial adults were undoubtedly very familiar with the food resources in their territories, which they crosssed many times a day. They spent more time eating and less walking in search of food than intruders.

The overall impression was that territorial adults had little difficulty in getting sufficient food, whereas the intruders had to spend more time and effort and quite frequently resorted to eating small items of low quality food. Despite this, many intruders appeared well fed, the King Penguin colonies attracted many non-territorial birds (Burger 1981a) and several banded individuals foraged as intruders all winter (Burger, unpubl. data 1974–1977).

Secondly, a territorial pair probably enhanced its inclusive fitness by permitting its offspring to overwinter in the territory. Juveniles were lighter than other birds (Burger 1980b), had higher rates of mortality than adults and were more commonly found dead and underweight following inclement weather (Burger 1979). Juveniles which foraged in King Penguin colonies were heavier in winter and appeared to have higher chances of survival than those elsewhere. Within their parents' territories they avoided much of the interference competition for food in these colonies. Juveniles were subjected to less chasing than intruders, although subordinate to those birds. Consequently, juveniles spent more time eating, with fewer interruptions, and less time walking than intruders.

Finally, adults which were territorial all winter were probably more likely to have retained their territories in King Penguin colonies at the onset of breeding than if they had abandoned them. I was unable to determine how many of the birds observed in 1978 subsequently bred in their territories but observations of color-banded birds in other years (1974–1977) showed that survivors always retained their territories in spring (Burger 1980a). At Marion Island, only the sheathbills with territories in penguin colonies bred, and some adults failed to obtain territories (Burger 1979), suggesting that there was competition for territories. Since King Penguin colonies generally attracted many sheathbills, it seems likely that the costs of re-establishing an abandoned territory there might exceed the cost of maintaining the territory all winter. Similar ideas have been suggested for other bird species (Fretwell and Lucas 1970, Pyke 1979). Snow (1956) showed that European Blackbirds which remained in their territories outside the breeding season were more likely to retain the territories.

Sheathbills which bred in Rockhopper Penguin colonies abandoned their territories in winter, but survivors always regained these territories, and their survival rates and breeding success were similar to those of adults from King Penguin colonies (Burger 1979, 1980a). Unlike King Penguin colonies, the Rockhopper Penguin colonies provided little food and attracted few sheathbills during winter (Burger 1981a). Nevertheless, adults began to re-occupy former territories there for several hours a day, several weeks before the Rockhopper Penguins arrived in the last week of October and there was once again a reliable food supply. By contrast, sheathbills in a King Penguin colony could maintain territories at this time while still getting sufficient food there.

It appeared that the cost of territorial behavior was low relative to the benefits which acrued to the territorial adults and their offspring. In general, territories are only economically defendable if the resources are predictable and spatially concentrated (Brown 1964, Brown and Orians 1970). During winter at Marion Island, only the King Penguin colonies met these requirements. Sheathbills foraging in other parts of the island in winter adopted other strategies, such as flocking (Burger 1982).

SUMMARY

Lesser Sheathbills (*Chionis minor*) were studied at Marion Island in the sub-Antarctic. During the winter non-breeding season, pairs defended their breeding territories in King Penguin colonies against adult and subadult intruders, but they permitted their juvenile offspring to forage within the territories. Adults defended the territories at apparently little cost and gained immediate benefits by having greater access to the high quality food than intruders. Their offspring also benefitted by avoiding much of the aggressive competition for food, and this probably enhanced their survival. Adults remaining in their territories might also have improved their chances of retaining the territories in the following breeding season, but this was not directly confirmed. Although intruders were chased frequently and had less access to superior food, the King Penguin colonies remained attractive foraging sites in winter for many sheathbills. Only at these colonies was the food supply predictable and concentrated to allow territoriality in winter.

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