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TIME BUDGETS, ENERGY NEEDS AND KLEPTOPARASITISM IN BREEDING LESSER SHEATHBILLS (*CHIONIS MINOR*)

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ABSTRACT.—Lesser Sheathbills (*Chionis minor*) were studied at Marion Island in the sub-Antarctic. Activity-time budgets of parents rearing chicks were converted into energy budgets and added to estimates of the food delivered to the chicks at the nest, in order to estimate the total energy costs of rearing chicks. Most of the food was obtained by stealing it from breeding penguins and it is improbable that Lesser Sheathbills could rear their chicks in the present manner without access to penguins, or possibly other colonial seabirds. Kleptoparasitism probably had little effect on the breeding success of the host Rockhopper Penguins (*Eudyptes chrysocome*), since a pair of sheathbills removed less than 1% of the food that the penguins brought into their territory. Investments of time, energy and risk of injury while rearing chicks were very similar for both sheathbill parents. The need to brood young chicks, owing to the harsh climate, restricted food delivery and caused chicks sometimes to starve.

Kleptoparasitism, the stealing of food by one individual from another, occurs amongst many bird species but is seldom a basis for specialization (Brockmann and Barnard 1979). Sheathbills (*Chionis* spp.), which live in the Antarctic and sub-Antarctic, obtain a significant portion of their diets by stealing food from penguins, and occasionally from cormorants and albatrosses (Jones 1963, Burger 1979, in press a). Pairs of breeding sheathbills maintain foraging and nesting territories centered on colonies of breeding seabirds, usually penguins, and they obtain virtually all their food from these colonies.

Reproduction in birds usually requires considerable investment of time and energy above the costs of normal maintenance (King 1973, Ricklefs 1974). Lesser Sheathbills (*Chionis minor*) apparently need to have access to a colony of penguins, or perhaps cormorants or albatrosses, in order to meet the costs of breeding (Burger 1979). In this paper I report time and energy demands of adult Lesser Sheathbills while they are rearing chicks, discuss whether breeding is theoretically possible if the birds have no access to penguins, and estimate the effects of kleptoparasitism on the breeding penguins. The division of labor between the sexes of breeding pairs is also examined.

The chick-rearing period was selected as being the most demanding phase of breeding, as it is in most nidicolous bird species (Ricklefs 1974). Lesser Sheathbills' nests are merely heaps of debris requiring little effort to make, their eggs are not large in relation to the size of the adult female and the clutch is small, averaging two or three eggs (Burger 1979). Both sexes incubate and the cost of incubation is likely to be far less than the cost of feeding chicks (King 1973, Ricklefs 1974, Drent 1975).

MATERIALS AND METHODS

Lesser Sheathbills are resident on four island groups in the southern Indian Ocean (Watson 1975). I studied the birds at Marion Island (46°54′S, 37°45′E) in the Prince Edward Islands. Observations in the austral summer of 1976/1977 concentrated on three pairs (A, B and C) which bred in adjacent colonies of Rockhopper Penguins (*Eudyptes chrysocome*). All six parents had been sexed (Burger 1980a) and color-banded 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 were determined at roughly weekly intervals from the time the chicks hatched (mid-January) until they left the nests to follow their parents (mid-March), making observations impracticable. I watched the birds from a blind 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 (see below) was assigned to part or the whole of each interval. The weekly observations were made on successive days to cover the periods dawn (±05:00) to noon and noon to dark (±20:20). Adults roosted throughout the night within their territories, and the dawn-dark observations were thus sufficient to construct 24-h activity-time budgets. Bad weather severely restricted observations in the last week and where necessary in this case, the data from 385 min of observations were extrapolated to cover the 870 min of daylight.

I estimated the mass of meals fed to chicks by placing 'chokers' around the chicks' necks to prevent swallowing, and by netting adults carrying food to the chicks. These samples were taken from territories in Rockhopper Penguin colonies bordering those used for activity-time observations. The energy contents of representative samples of food, dried to constant mass at 60–70°C in a convection oven, were determined with a Gallenkamp ballistic bomb calorimeter.

The diurnal behavior of Lesser Sheathbill parents was classified into eight activities, as follows:

Foraging. This included search effort (walking and looking for penguins who were feeding 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 behavior. This comprised sedentary activities, mainly preening but also stretching and scratching with rare spells of vigorous bathing.

Brooding. Adults brooded their chicks within nest cavities and their behavior there was 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 defense. Eviction of conspecific intruders from territories involved vigorous chasing: running, flapping, flying and, rarely, fighting.

Antipredator aggression. This involved mock attacks and running about, calling loudly, when Brown Skuas (*Catharacta lonnbergi*) and Kelp Gulls (*Larus dominicanus*), both potential predators of Sheathbill chicks, were near nests.

Pair displays. Most displays by Lesser Sheathbills lasted only a few seconds. Hence, only the more prolonged Bob-Call and Run-and-Call displays performed by members of mated pairs (Burger 1980b) were consistently recorded in these observations. These displays involved vigorous bowing of the body, walking, and running.

Daily energy expenses were calculated from activity-time budgets using estimates of the metabolic costs of each activity. All such estimates for birds suffer from the paucity of empirical measurements of metabolic costs (reviews by King 1974 and Kendeigh et al. 1977). The following empirical data were used as guides: the cost of flight averages 10–12 × Basal Metabolic Rate (BMR) (King 1974); swimming in ducks averages 4 × BMR (Prange and Schmidt-Nielsen 1970); hopping in passerines costs about 5 × BMR (Holmes et al. 1979); and running at various speeds in the Greater Rhea (*Rhea americana*) costs 3.5–14 × BMR (Taylor et al. 1971).

Resting and brooding by Lesser Sheathbills were estimated to cost 1.5 × BMR by day or night, which falls within the range of published 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 behavior was estimated to cost 2 × BMR. While engaged in foraging, nest building, antipredator aggression and pair displays, sheathbills were almost constantly walking or running and occasionally standing or flying; these activities were each estimated to cost 4 × BMR. The active spells of territorial defense were estimated to cost as much as flight, 12 × BMR. The BMR, calculated from equation 5.5 of Kendeigh et al. (1977), was 8.87 kJ h^{-1} (1 kJ = 0.239 kCal) for an adult male (mean summer mass 508 g, Burger 1980a), and 8.11 kJ h^{-1} for an adult female (450 g).

The costs of thermoregulation were added to the metabolic costs of activity. The Standard Metabolic Rate (SMR), which is BMR + costs of thermoregulation, was estimated to be 16.0 and 14.9 kJ h^{-1} for males and females respectively, at 0°C (Kendeigh et al. 1977, equation 5.15). The lower critical temperature, where SMR = BMR was estimated to be 15.3°C for males and 15.6°C for females (Kendeigh et al. 1977, equation 5.12). By interpolation (Wiens and Innis 1974:746) the SMR at 7.6°C, the mean temperature at the study site during the study period, was 12.4 and 11.7 kJ h^{-1} for males and females respectively. Hence the estimated costs of thermoregulation (SMR − BMR) at 7.6°C were 3.5 and 3.6 kJ h^{-1} for males and females respectively.

RESULTS

Lesser Sheathbills stole food from penguins in the following manner. A penguin in the act of regurgitating food (crustaceans, squid or fish) to its chick was jarred or startled by a sheathbill leaping or flying against it (Burger 1979). The sheathbill attacked just as a bolus of food was being passed from the adult penguin to its chick. In about a quarter of such instances some food was spilled by the penguin and was snatched off the ground by the sheathbill. Sheathbills occasionally hit large Rockhopper Penguin chicks with sufficient force to knock them over. Generally sheathbills attacked singly, but occasionally a mated pair combined to attack one penguin. Penguins threatened and sometimes chased sheathbills that were trying to rob them but at other times they tended to ignore them. Sheathbills were attracted by the importuning calls of a penguin chick on the arrival of its parent from the sea.

Other food taken by sheathbills from penguin colonies comprised eggs, small chicks, carcass flesh, excreta, ectoparasites and free-living invertebrates. Breeding pairs of Lesser Sheathbills foraged in territories within penguin colonies, and on bordering vegetated areas. Territories were 100–300 m^2 and generally included the nest cavity. Parents therefore seldom foraged more than 15 m from the nest. In the study area each pair of sheathbills had access to an average of 180 pairs of successful Rockhopper Penguins (N = 13 sheathbill pairs).

During the chick-rearing period, both parents performed all eight diurnal activities (Fig. 1). On any single day the activity-time budget of a male and a female might differ (e.g., Fig. 1, first week), but overall the mean time allocated to each activity by each sex did not differ significantly (*t*-test, $P > 0.05$ in each week when two or three pairs were sampled). Foraging (average 64% of time), brooding (19%) and comfort behavior (12%) were the major diurnal activities of each bird. Some of the time used for preening and resting also constituted sedentary food-searching behavior, since

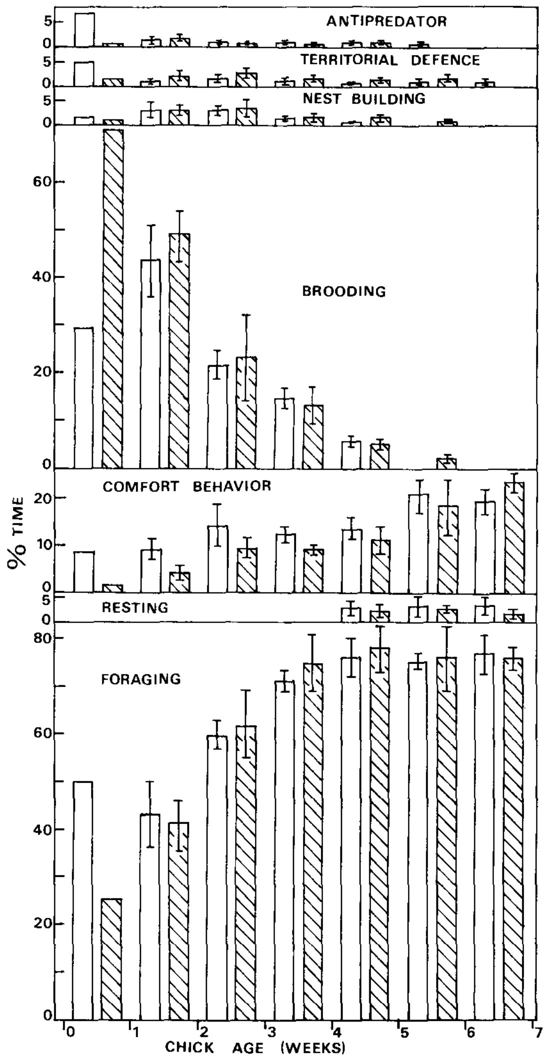

FIGURE 1. Activity-time budgets (percentage daylight hours) of male (open bars) and female (hatched bars) Lesser Sheathbills while rearing chicks. The mean (±SE) times of three pairs are given for each week except the first (one pair only) and last (two pairs) weeks.

Lesser Sheathbills abruptly ended these behaviors to forage if they spotted a penguin feeding its chick.

Chicks were brooded for 94% (SD = 7%) of the daytime, and probably all night during the first two weeks after hatching. Thereafter brooding time decreased and averaged 45 ± 16%, 28 ± 10%, 11 ± 4%, 1 ± 1% and 0% of the daytime in the third to seventh weeks respectively. Decreased brooding coincided with plumage changes in the chicks. Their brown natal down was replaced by thick grey (mesoptile) down by the 14th day, contour feathers covered most of the body by the 35th day and feather growth was virtually complete by the 50th day. These changes and increased body size should have improved the chicks' thermoregulatory abilities, making brooding less essential. The mean duration of brood bouts by both parents did not differ significantly (Burger 1979).

TABLE 1. Mean (±SD) daily energy expenditure (kJ) by adult male and female Lesser Sheathbills while rearing chicks. N = 18 bird-days for each sex.

Activity	Male	Female
Foraging	351 ± 67	320 ± 86
Resting	2 ± 4	1 ± 2
Comfort behavior	37 ± 16	27 ± 19
Brooding	33 ± 34	37 ± 43
Territorial defense	20 ± 20	25 ± 20
Pair display	0.4 ± 0.7	0.4 ± 0.6
Nest building	6 ± 9	8 ± 10
Antipredator	7 ± 10	4 ± 5
Roosting (night)	116 ± 16	105 ± 8
Total activity	573 ± 39	527 ± 52
Thermoregulation	84	86
Total	657 ± 42	613 ± 53

Sheathbill parents spent considerable time grooming themselves, mainly preening, particularly after diurnal brooding had decreased (Fig. 1). Penguin colonies were wet and muddy places, and frequent preening and bathing were required for sheathbills to keep their plumage clean and so retain insulation against the cold, wet and windy conditions. Resting was rare and recorded only in the second half of the chick-rearing period.

The three pairs of sheathbills maintained almost exclusive use of the food resources within their territories at very little cost. They spent only 2% of the daylight time (Fig. 1), and about 4% of the estimated daily energy output (Table 1) in overt territorial defense. This economical maintenance of territories is attributable to several factors (Burger 1980b): territories were re-occupied and boundaries established several weeks before breeding commenced; territories in colonies of Rockhopper Penguins were usually separated by undefended areas of rock or vegetation; adults preened and rested on conspicuous raised vantage points which constituted sedentary territorial advertisement; and, since adult survival was high and surviving adults retained the same mates and territories each season (Burger 1979) individuals might have been habituated to existing territorial boundaries.

The 24-h energy expenditure of each bird was calculated from activity-time data for each day of observation. Parental metabolism (activity + thermoregulation) was equivalent to 3.1 × BMR in either sex during this period (Table 1).

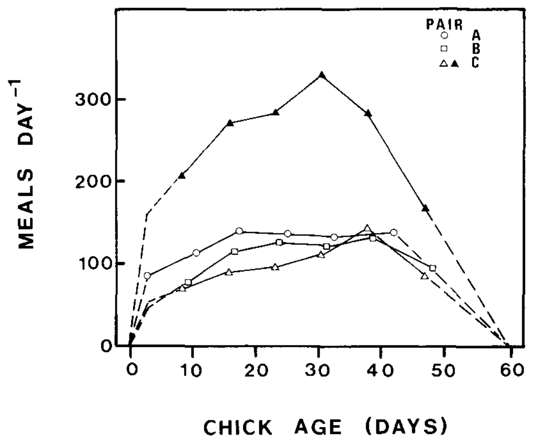

FIGURE 2. The numbers of meals fed daily to chicks by three pairs of Lesser Sheathbills. The numbers delivered per chick are shown in open symbols and the numbers per brood (pair C only) in solid symbols.

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 three pairs (Fig. 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 (Burger 1979). This suggests that the maximum energy needs of the chicks occurred quite early in their development, in common with other semi-precocial species of birds (Ricklefs 1974). From the age of 45 days the chicks began to pick up small food items from the ground near their nests. When 55–60 days old most chicks were feeding independently but often remained in the company of their parents. No newly fledged juveniles stole food.

During 83.8 h of observation, the total number of meals delivered to nests by males (1,405) and females (1,323) did not differ significantly ($P > 0.05$, χ^2-test). Similarly, the mean rate of meal delivery during parental foraging time by males (8.74 h^{-1}, SD = 3.23), and females (7.96 h^{-1}, SD = 4.29) did not differ significantly ($P > 0.05$, paired t-test, N = 18 bird-days for each sex).

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 g (SD = 0.55 g, range 0.14–1.98 g). Crustaceans (amphipods, euphausids and copepods) stolen from penguins were the most common meals delivered to the chicks, supplemented by flesh from carcasses, fresh penguin excreta and terrestrial invertebrates, mainly caterpillars and earthworms (Table 2). The mean energy content of the food was 6.6 kJ g^{-1} (Table 2) 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 6,290 (29,563 kJ), 5,550 (26,085 kJ) and 4,880 (22,936 kJ) meals per chick respectively during the 60-day period. On average, a chick received 26,195 kJ of food from its parents.

Energy ingested to meet the costs of parental metabolism plus energy delivered as food to the chicks gave the total daily requirements of the six birds (Fig. 3). The energy ingested for parental metabolism was assumed to be 1.25 × the calculated energy expenditure (80% efficiency) to account for energy 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 1,170 (5.5 × BMR) and 1,050 (5.4 × BMR) kJ $bird^{-1}$ day^{-1} respectively, and in pair C, 1,505 (7.1 × BMR) and 1,500 (7.7 × BMR), respectively.

TABLE 2. Percentage occurrence and energy value (mean ± SD) and percent energy contribution of food types delivered to chicks by Lesser Sheathbills breeding in colonies of Rockhopper Penguins.

Food type	% occurrence of meals[a]	Energy content (kJ g^{-1} fresh mass)	% energy contribution
Crustaceans[b]	89	6.76 ± 0.15 (N = 3)	91
Penguin carcass	6	8.08 ± 3.89 (N = 4)	7
Penguin excreta	2	2.14 ± 0.43 (N = 4)	1
Terrestrial invertebrates	3	3.04 ± 1.05 (N = 57)	1
Weighted mean	—	6.63	—

[a] From Burger (1979).
[b] Amphipods, euphausids and copepods stolen from Rockhopper Penguins.

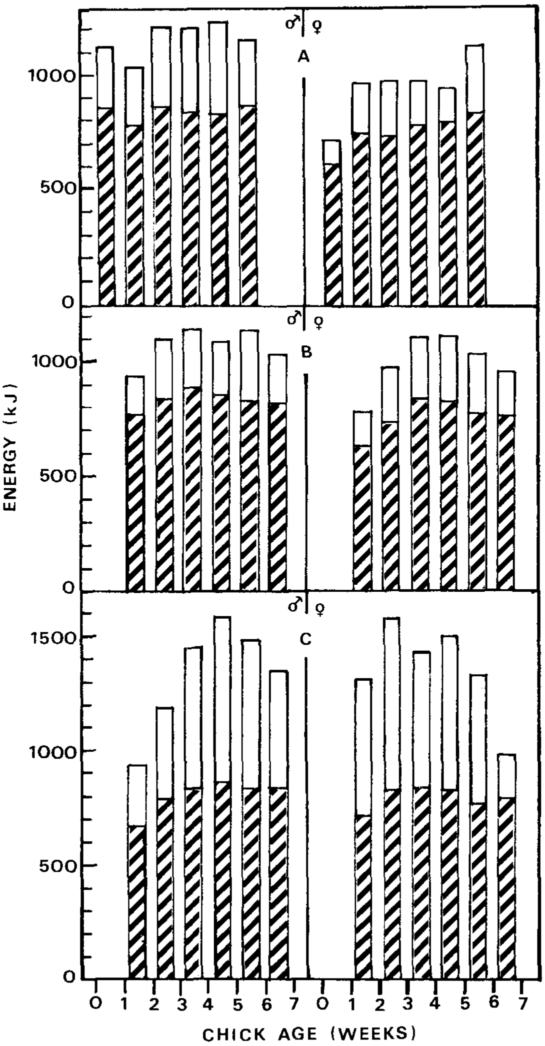

FIGURE 3. Estimated daily energy needs for parental activity and thermoregulation (hatched portions) and for food fed to the chicks (open portions) of Lesser Sheathbills. The energy needs of the males (left side) and females (right side) are given for pairs A and B, which fed one chick, and pair C, which fed three chicks for five weeks and then two chicks to fledging.

DISCUSSION

The daily commitments of time and energy by male and female sheathbills while rearing chicks were very similar. Both sexes also risked injury by harassing potential predators, chasing out conspecific intruders and kleptoparasitizing penguins. Earlier in the breeding season both sexes shared nest building and incubation activities (Burger 1979). Lesser Sheathbills appeared to be strictly monogamous and to have life-long pair bonds. Males did not compete directly with each other for females or mating sites (Burger 1979, 1980b). The key to breeding success was the acquisition of a territory that provided suitable food; both sexes defended these territories. The breeding season of sheathbills was relatively short and within the population at Marion Island was synchronized with the brief period of maximum food availability while the penguins were breeding in summer. Consequently, investment of time, energy and risk by both parents was adaptive in minimizing breeding time and maximizing food delivery to the chicks. The practice of brooding and feeding nidicolous chicks concurrently also favored a breeding habit involving parental care by both parents.

Penguin colonies supplied virtually all the food needed by breeding Lesser Sheathbills at Marion Island and probably on all the Indian Ocean islands where they occur (Paulian 1953, Downes et al. 1959, Derenne et al. 1976, Burger 1979, in press a), but other foods were extensively used by non-breeding birds. Apart from the food stolen from penguins, terrestrial invertebrates (earthworms, insects, spiders and snails) were the most frequently used food at Marion Island (Burger, in press a) 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 the sheathbills satisfy their energy requirements for rearing chicks without having access to penguins?

Sheathbills who were foraging intensively for terrestrial invertebrates in winter had a mean ingestion rate of 5.1 organisms per minute of foraging time (N = 75 birds watched for an average of 16 minutes each; Burger, unpubl. data). These organisms had a mean energy content of 0.18 kJ (Burger, in press b) so that the birds had a mean ingestion rate of 55 kJ per hour of foraging. At this rate, male and female sheathbills would require 21.3 and 19.1 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 were unevenly scattered, this increment would be considerable.

It seems improbable that Lesser Sheathbills feeding on terrestrial invertebrates alone could have sufficient time in the 16 h of summer daylight to feed themselves and one chick and to perform other essential activities such as brooding, comfort behavior and anti-predator vigilance. The rate of capture of invertebrates might be faster in summer than in winter but the availability and size of the prey items were similar in summer and winter (Burger, in press b).

Terrestrial invertebrates and other food sources were important during winter, and sometimes as supplementary food during breeding, but the Lesser Sheathbills at Marion Island, and probably on other islands, seemed to need access to breeding penguins or, less commonly, cormorants to get sufficient food to breed. The food available from penguins was spatially and temporally concentrated as well as rich in energy and protein (Burger, in press a). The sheathbills appeared to be obligate commensals with penguins, or possibly other colonial seabirds, in order to breed in their present manner.

The data permit an estimate of the effects of kleptoparasitism by sheathbills on the Rockhopper Penguins. A pair of sheathbills required 121,445 kJ to rear one chick over a 60-day period: 95,250 kJ for parental metabolism (Table 1) if 80% of the ingested energy was available, and 26,195 kJ for food delivered to the chick. Since 91% of the energy needs were met by crustaceans stolen from the penguins, this amounted to 16.4 kg (fresh mass) of crustaceans (Table 2). Each successful pair of penguins delivered 14.7 kg (fresh mass) of food to its chick prior to fledging (A. J. Williams, unpubl.), and each pair of sheathbills had access to an average of 180 pairs of successful penguins. Thus, a pair of sheathbills who fledged one chick would have used about 0.6% of the food brought into its territory by penguins. Similar calculations show that pairs who fledged two or three chicks would have used 0.8% and 0.9% of the incoming food respectively. Although these estimates are fairly crude, it is clear that breeding sheathbills removed a negligible portion of the food brought in by the host penguins.

Quantitative estimates of the effects of other kleptoparasite species on their host populations are few. In the great majority of species that are known to rob other birds, kleptoparasitism is a rare, unimportant feeding method (Brockmann and Barnard 1979) and unlikely to adversely affect hosts. Even amongst species in which the behavior is common, such as frigatebirds (Nelson 1975), jaegers (Arnason and Grant 1978), gulls (Hatch 1970, Fuchs 1977) and terns (Hopkins and Wiley 1972), being robbed does not seem to impair the survival or breeding success of host populations. Nettleship (1972), however, showed that the breeding success of Common Puffins (*Fratercula arctica*) in certain habitats was lowered through robbing by gulls.

Lesser Sheathbills laid clutches averaging two or three eggs, but most pairs reared only one chick per season. Chick survival between hatching and fledging averaged 56% and starvation within three weeks of hatching was the primary cause of mortality (Burger 1979). Why were sheathbills apparently unable to steal more than 0.6–0.9% of the penguins' food and so reduce starvation of the chicks? Rockhopper Penguins generally arrived ashore in groups to feed their chicks and, during the day, periods of intensive feeding activity alternated with periods when few or no penguins were feeding chicks. The sheathbills could not attempt to rob every penguin feeding a chick within its territory.

Starvation of sheathbill chicks occurred when the penguin chicks were less than three weeks old, when the latter were receiving little food and were still brooded by adults, making it difficult for sheathbills to rob them. At the same time, the sheathbills' chicks were being brooded almost continuously, leaving only one of the pair free to forage. Brooding was probably essential for the survival of sheathbill chicks in their first two weeks. Gales, frequent rain, and mean temperatures well below 10°C were usual at Marion Island 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 (Ricklefs 1974). The reduced heat loss from sheathbill chicks might have been sufficient to offset the loss of feeding time when they were young and their food intake small, as was found with Rock Ptarmigan (*Lagopus mutus*) chicks (Theberge and West 1973) but during temporary food shortages the non-brooding adult sheathbill might have had insufficient time to meet its own food needs plus those of the chicks.

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