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## BREEDING BIOLOGY, MOULT AND SURVIVAL OF LESSER SHEATHBILLS *CHIONIS MINOR* AT MARION ISLAND

A. E. BURGER

FitzPatrick Institute, University of Cape Town,  
Rondebosch 7700, South Africa

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### 1. INTRODUCTION

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

The sheathbills are a monogeneric family (Chi-

onididae) of two species. The Wattled Sheathbill *Chionis alba* breeds on the Antarctic Peninsula and island of the Scotia Arc and occurs as a non-breeding migrant at the Falkland Islands, Tierra del Fuego and the Patagonian coast (Murphy 1936, Jones 1963). The Lesser Sheathbill *Chionis minor* (Fig. 1) has non-migratory populations at four island groups in the southern Indian Ocean: the Prince Edward Islands, the Crozet Islands, Kerguelen and Heard Island (Watson 1975). The populations of Lesser Sheathbills appear to be genetically isolated at present and are sometimes treated subspecifically (Peters 1934). No sheathbills occur at Bouvet Island which lies midway between the present ranges of the two species.

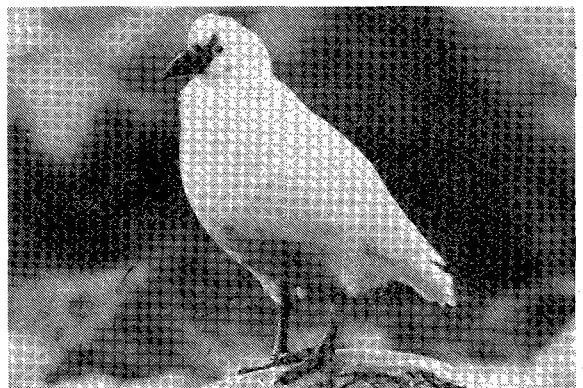


Fig. 1. An adult Lesser Sheathbill.

This paper reports on aspects of the breeding biology, moult and survival of Lesser Sheathbills

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

## 2. STUDY AREA AND METHODS

Marion Island lies 2° latitude north of the Antarctic Convergence, and the climate and biota are typically sub-Antarctic (Van Zinderen Bakker *et al.* 1971). Field work totalling 25 months was done between 1974 and 1978 and covered all months of the year. Observations were concentrated in a 100 ha study area, including 5 km of coastline, on the north-eastern side of the island. There were on average 197 Lesser Sheathbills within this area. About 3000 pairs of King Penguins *Aptenodytes patagonicus*, 2100 pairs of Macaroni Penguins *Eudyptes chrysolophus*, 1400 pairs of Rockhopper Penguins *E. chrysocome*, and 250 pairs of Gentoo Penguins *Pygoscelis papua* bred within the study area.

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

Estimates of survival, local movements and the age of first breeding were obtained from 480 Lesser Sheathbills which were ringed. Most birds were also individually colour-ringed. The survival of colour-marked breeding adults was monitored from season to season since they returned to breed in the same territories (Burger in prep.). Immature and non-breeding adults were less regular in their habits and an intensive search for

ringed birds was made in 1976. It was possible to read ring numbers with binoculars, without capturing the birds. Birds resighted in 1976 had been ringed one or two years previously, but in each case the mean annual survival was calculated. Differences between the percentage survival of two groups were tested for statistical significance using formulae and tables by Cass (1973: 72).

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

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

## 3. BREEDING BIOLOGY

### 3.1. THE BREEDING SEASON

Lesser Sheathbills at Marion Island and elsewhere (Hall 1900, Downes *et al.* 1959, Despin *et al.* 1972) breed annually during the austral summer. At Marion Island nest building was first seen on 4 October and by 10 November all nests had fresh material in them. Copulation was seen between 21 October and 30 December.

The earliest egg was laid on 4 December and 95% of all eggs had been laid by 31 December (n = 94 eggs from the 1974/75 and 1976/77 seasons). The modal date of laying of first eggs was 11–17 December. The latest clutch was laid in the period 16–19 January but these eggs were not incubated. Hatching occurred in January and

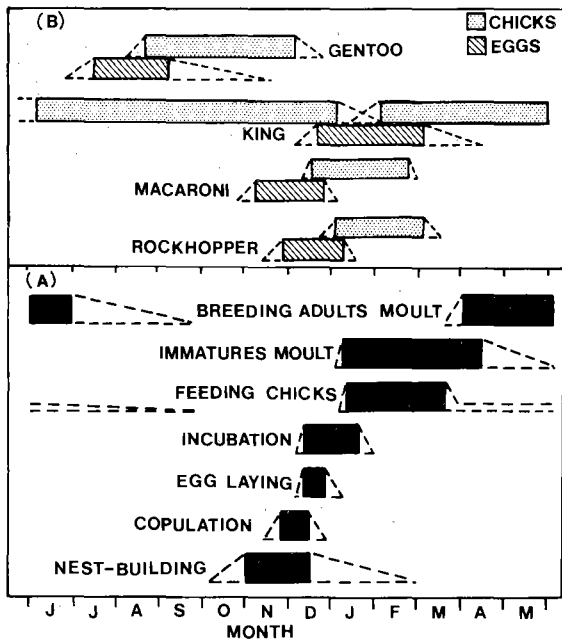


Fig. 2. The timing and duration of breeding and moult of Lesser Sheathbills at Marion Island (A) compared to the breeding activities of the four penguin species at the island (B). The periods of peak activity are shown as solid bars and the known extremes as dashed lines.

chicks were independent in the third week in March. Lesser Sheathbills at Marion Island bred at the same time as the three common penguin species (King, Macaroni and Rockhopper penguins) from which the sheathbills obtained most of their food (Fig. 2).

### 3.2. AGE OF FIRST BREEDING

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

During the breeding season there were always small numbers of adults present which did not attempt breeding, probably because they had not

established territories. Four adults were recorded as non-breeders for three successive seasons.

### 3.3. TERRITORIES AND NEST SITES

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

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

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

### 3.4. EGGS AND INCUBATION

Clutches ranged between one and four eggs and two and three eggs were most common, as with the Wattled Sheathbill (Table 1). Nest building but not relaying was observed following the loss of a clutch. The laying interval between

first (A) and second (B) eggs averaged 3.6 days and between B and third (C) eggs 4.0 days (Table 2). The mean length, breadth and mass of A, B and C eggs did not differ significantly (Paired *t*-test,  $P > 0.05$  in each case, Table 3). The mean size of all Lesser Sheathbill eggs was  $54.7 \times 37.2$  mm (41.7g).

The nest was continuously occupied by one of the parents from the day the first egg was laid, except for brief periods during nest relief or during disturbances (by skuas, etc.) near the nest.

Table 1. Clutch size of *Chionis minor* and *C. alba*

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

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

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

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

Table 3. Linear dimensions and masses of Lesser Sheathbill eggs at Marion Island

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

<sup>1</sup> Calculated from length and breadth

Both sexes had two elongated lateral brood patches, each about 19 cm<sup>2</sup>, which were unfeathered from the time of laying until the chicks were 50—60 days old. These brood patches appeared to be large enough to heat four eggs comfortably, two on either side.

Males had longer diurnal incubation shifts than females. The mean for males was 172 min (range 124—243 min,  $n = 9$ ) and for females 90 min (61—158 min,  $n = 7$ ). Females perhaps needed to forage more than males at this time, to replace energy reserves used during ovogenesis. The off-duty bird foraged for most of the time, chased intruders from the territory, or preened while standing outside the nest entrance. No data are available on nocturnal incubation behaviour but both parents were found inside nest cavities at night.

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

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

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

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

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

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

### 3.5. CHICKS

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

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

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

Lesser Sheathbills very seldom foraged outside penguin colonies when breeding. Food was carried in their beaks to the chicks and not regurgitated. During observations at three nests in Rockhopper Penguin colonies the sheathbill par-

ents obtained 97% of the meals ( $n = 2362$ ) delivered to chicks during the first 50 days after hatching, from within penguin colonies and the remaining 3% comprised terrestrial invertebrates taken from bordering vegetated areas. During a seven-hour watch at these three nests, 139 meals out of 176 delivered to the chicks, could be identified. These meals consisted of crustaceans stolen from Rockhopper Penguins (91%), flesh from penguin carcasses (7%) and fresh penguin excreta (2%). The adult diet appeared to be similar. Lesser Sheathbills breeding in King and Macaroni penguin colonies also fed their chicks almost entirely on food taken from penguins. Those at King Penguins colonies seemed to feed proportionately more carcass flesh to their chicks than those at Rockhopper Penguin colonies.

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

The growth of 13 chicks which fledged from nine nests was measured in 1977. These included seven, two and four chicks from first (A), second (B) and third laid (C) eggs respectively. The tarsus had the most rapid initial growth of the appendages measured and had reached adult size by the 30th day (Fig. 4). This coincided with the time when the chicks began to wander a few metres from the nest. The culmen grew gradually during the first 40 days and very little thereafter.



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

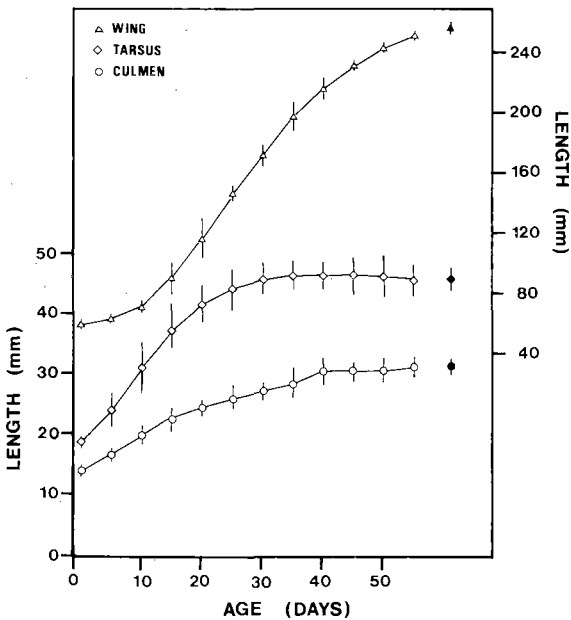


Fig. 4. Growth of the tarsus, culmen and wing (chord) in Lesser Sheathbill chicks. The mean  $\pm$  S. D. is shown at five day intervals. Adult dimensions are given as shaded symbols.

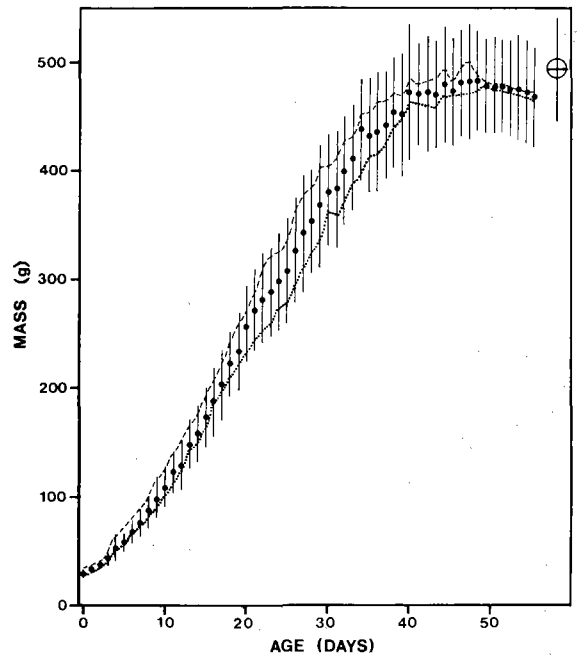


Fig. 5. Growth in mass of Lesser Sheathbill chicks. The mean  $\pm$  S. D. of all chicks is given at daily intervals. The mean mass of chicks reared singly (dashed line) is compared to that of chicks reared in broods of two chicks (dotted line). The mean mass ( $\pm$  S. D.) of breeding adults is indicated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

The wing (manus and primary feathers) grew rapidly from the 10th day and was almost adult size at fledging (55 days). Chick weight had a typical sigmoid growth curve (Fig. 5) to reach a mean asymptote of 483 g, equivalent to 98% of the mean weight of breeding adults, on the 48th day. The mean weight at fledging was slightly less than the asymptote.

The masses of chicks from A, B and C eggs, measured within 24 hours of hatching, did not differ significantly (paired t-test,  $P > 0.05$  in each case, Table 6). The A chicks were 0–2 days old when the B chicks hatched but the differences in mass at that stage were not significant ( $P > 0.05$ , Table 6). By the time the C chicks hatched, however, both the A and B chicks had grown to be significantly heavier than the newly hatched C chicks ( $P < 0.01$ , Table 6). The A chicks were then heavier than the B chicks but these differences were not significant ( $P > 0.05$ ). The A chicks were heavier than sibling B and C chicks throughout the nestling period at most nests and for the first 35 days at all the nests observed (Fig. 6). Similarly B chicks were generally heavier than sibling C chicks. Chicks reared singly were on average heavier than those reared with siblings, but had similar masses at fledging (Fig. 5).

Survival of chicks prior to fledging averaged 56% (Table 5). Starvation, predation and accidents seemed to be the main causes of chick

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

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

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

Most chick mortality occurred within the first

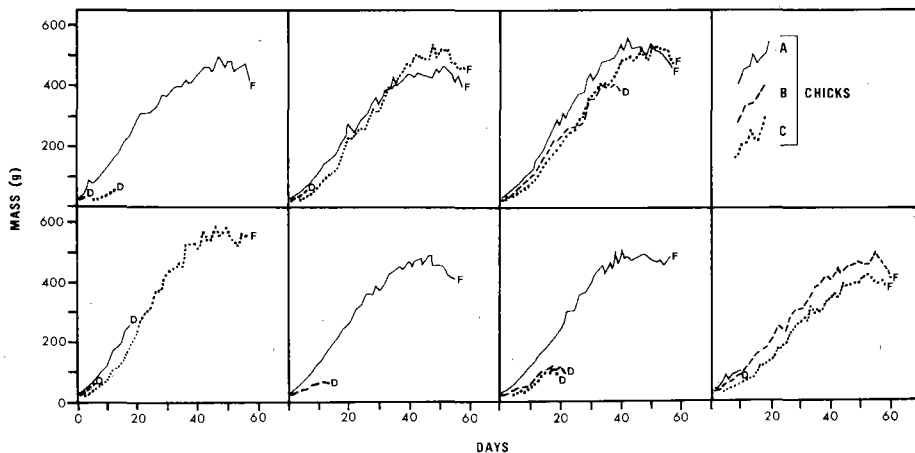


Fig. 6. Comparisons of the growth of chicks from A, B and C eggs in seven broods of Lesser Sheathbills. The time scale is dated from the hatching of the A chicks in each brood. Chicks which died (D) or fledged (F) are indicated.

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

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

three weeks of hatching (Table 7). Mortality was correlated with hatching sequence: all A chicks and some B chicks apparently died from predation or accidents but all D and C chicks and most B chicks from starvation. The youngest chick in any brood was always the first to die of starvation. No overt sibling aggression was seen but chicks were seen to take food from the beaks of siblings. Starvation of the youngest chick has also been reported for Wattled Sheathbills (Jones 1963).

The proportion of A chicks which fledged was significantly higher than that of B chicks ( $\chi^2$  test,  $P < 0.05$ , Table 5) but the differences between A and C and between B and C chicks were not significant ( $P > 0.05$ ). The relatively high proportion of C chicks which fledged was unexpected, since when they hatched they were lighter than

their older siblings. The result was, however, partially an artefact of the small sample of C chicks. Of the five C chicks which fledged, four were from nests where one or both siblings were lost (apparently from predation or accidents since they were not underweight when they disappeared) and one was from a nest in which all three chicks fledged.

### 3.6. BREEDING SUCCESS

Of the 42 pairs studied, none reared four chicks to fledging, 5% reared three, 26% two, 40% one and 29% no chicks per season (Table 8). Of these pairs, clutch sizes were known in 26 cases. A pair with a clutch of four fledged two chicks, 12 pairs with clutches of three fledged an average of 1.17 chicks per pair, 12 pairs with

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

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

<sup>1</sup> From unpublished British Antarctic Survey Reports, courtesy of J. P. Croxall



clutches of two averaged 0.67 fledglings per pair and one pair with a single egg clutch fledged no chicks.

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

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

#### 4. MOULT

Lesser Sheathbills moulted all their plumage once annually. Adults which had bred began moulting in the second half of March, once their

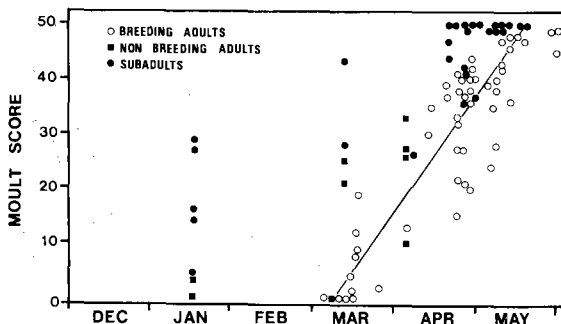


Fig. 7. Primary moult score in breeding adult, non-breeding adult and subadult Lesser Sheathbills. A line was fitted by eye to show the approximate duration of primary moult in a breeding adult.

chicks were independent. Their brood patches began to re-feather at this time. Immatures and non-breeding adults began moulting in January during the breeding season. Juveniles moulted for the first time at the end of their first year.

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

#### 5. LOCAL MOVEMENTS

Lesser Sheathbills are non-migratory residents at all the islands in their range (Barré *et al.* 1976, Watson 1975). None of the 448 birds ringed at Marion Island between 1951 and 1977 has been reported elsewhere, not even on Prince Edward Island, 22 km distant. Adults, including those not recorded to have bred, very seldom moved more than 1 km from the places where they had been ringed (Table 9). Over 700 sightings of 60 colour ringed breeding adults were made in 1976/77 and these birds were always seen within 1 km, and usually within 500 m, of their breeding territories. Immature birds were more inclined to wander than adults and almost half the subadults and a

Table 9. Percentages of ringed Lesser Sheathbills which were resighted (or recovered) at various distances along the coast from the initial ringing site

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

<sup>1</sup> Including non-breeding adults

Table 10. Percentage annual resightings of colour-ringed adult Lesser Sheathbills breeding at Marion Island. The numbers ringed at the start of each period are given in parentheses

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

third of the juveniles were seen 1 km or more from the places where they had been ringed (Table 9).

## 6. SURVIVAL AND PREDATION

### 6.1. RESIGHTINGS OF RINGED BIRDS

On average, 88% of breeding adults returned to their nesting sites in each season (Table 10) and since these birds attempted breeding in each year at the same territories, this was an accurate measure of their mean annual survival. The mean percentage survival of adults breeding in King Penguin colonies did not differ significantly from that of adults breeding in Rockhopper Penguin colonies ( $P > 0.05$ , Table 10). The samples from Macaroni Penguin colonies were too small for comparison. The survival of adult Wattled Sheathbills breeding at Signy Island was similarly high, being 90% (73 birds ringed) and 86% (116 birds ringed) in two successive years (Jones 1963, Topliffe 1963).

Significantly fewer non-breeding adults, sub-adults and juveniles were resighted than breeding adults ( $P < 0.001$  for birds of all areas combined, Tables 10 and 11). These differences were attributed to higher mortality (proportionately more

fresh carcass remains were found) and greater mobility (Table 10) of non-breeding adults and immatures. Comparisons of resightings of non-breeding adults and immatures from different areas of Marion Island are not valid since, unlike breeding adults, these birds showed little fidelity to any particular area.

### 6.2. CAUSES OF MORTALITY

The fresh remains of only 22 full-grown Lesser Sheathbills were found during the 25 months of the study. These included four adults, 16 immatures and two birds of indeterminate age. Seven had been partially eaten by predators or scavengers. Sixteen birds were found after exceptionally cold spells, with snow at sea level, during winter (June-September inclusive). Uneaten dead birds were generally very thin. Their mean mass was  $304 \pm 55$  g ( $n = 11$ ), considerably lower than the mean mass of living birds ( $492 \pm 48$  g for adults,  $454 \pm 51$  g for sub-adults and  $410 \pm 60$  g for juveniles, Burger in prep.). The apparent causes of mortality were thus the combined effects of starvation and inclement weather and, to a lesser extent, predation.

Sub-Antarctic Skuas and feral cats *Felis catus* are known to kill Lesser Sheathbills at Marion Island but sheathbills were unimportant in the diets of both predators. Only seven (0.5%) out of 1558 prey remains which were attributed to cats or skuas were sheathbills, no sheathbills were found in 125 cat stomachs and only one (0.2%) out of 442 prey items at skua nests was a sheathbill (Van Aarde 1977).

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

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

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

Table 12. Responses of groups of Lesser Sheathbills foraging on inland vegetated areas to the approach of a flying Sub-Antarctic Skua

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

depleted the numbers of Lesser Sheathbills (Derenne *et al.* 1976).

Lesser Sheathbills were always wary of Sub-Antarctic Skuas at Marion Island. These predators were seen to catch and kill sheathbills on three occasions and often swooped towards individuals or groups of sheathbills. When foraging farther than 20 m from the shore, groups of sheathbills almost always took flight towards the shore at the approach of a skua (Table 12). The sheathbills appeared to be less vulnerable when foraging amongst the boulders on the shore or in penguin colonies. Here they seldom flew off at the approach of a skua but sometimes adopted alert postures. Downes *et al.* (1959) mentioned that Lesser Sheathbills at Heard Island were reluctant to leave rocky areas to forage on open sandy beaches where they were apparently more vulnerable to skua predation.

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

## 7. DISCUSSION

### 7.1. ASSOCIATION WITH PENGUINS WHILE BREEDING

Lesser Sheathbills at Marion Island bred in close association with Rockhopper, Macaroni and King penguins. Gentoo Penguins which were uncommon and which bred during late winter and spring, were relatively unimportant to breeding Lesser Sheathbills. Penguins supplied most of

the food eaten by breeding adults and their chicks and no Lesser Sheathbills attempted breeding without access to breeding penguins. Elsewhere, breeding sheathbills of both species have similar close associations with penguins (Paulian 1953, Downes *et al.* 1959, Jones 1963, Derenne *et al.* 1976) or at a few localities with breeding cormorants (Paulian 1953, Parmelee *et al.* 1977).

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

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

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

Not all penguin colonies at Marion Island were suitable for the establishment of Lesser Sheathbill breeding territories. Fewer than 20 pairs of Lesser Sheathbills attempted breeding at two very large colonies at Kildalkey Bay and Bullard Beach which contained between them over 400,000 pairs of Macaroni Penguins and 80,000 pairs of King Penguins. These colonies are both situated on smoothed, glaciated grey lava, in

contrast to the more broken, younger black lavas most common on the coastal plain. The penguins bred at maximum density on these even surfaces which was perhaps too dense to permit freedom of movement by Lesser Sheathbills between the penguins. Nest sites for Lesser Sheathbills were restricted to the very few areas of broken lava at the perimeters of these colonies.

## 7.2. BREEDING ADAPTATIONS

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

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

Most pairs of Lesser Sheathbills fledged fewer chicks than the number of eggs laid. Starvation of chicks from D, C and to a lesser extent B eggs was the single most common cause of mortality. Lesser Sheathbills, in common with many species of birds (Lack 1954, Ricklefs 1968, O'Connor 1978) can evidently rear as many chicks as the average clutch size when conditions are favourable, but have adaptations for eliminating "excess" chicks when there is insufficient food to

rear the full complement. In Lesser Sheathbills brood reduction is facilitated by hatching asynchrony. Sufficient eggs are also laid to provide some insurance against unpredictable losses of eggs and chicks by predation and accidents.

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

## 7.3. POPULATION LIMITATION

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

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## 9. SUMMARY

Lesser Sheathbills *Chionis minor* were studied at Marion Island in the sub-Antarctic. All breeding adults held territories in penguin colonies; virtually all food eaten by these adults and their chicks was obtained from penguins, mostly by kleptoparasitism; and, the sheathbills bred when food from penguins was most freely available. The minimum age of first breeding was three years and there was a surplus of potential breeding adults. Clutches were one (3%), two (47%), three (47%) or four eggs (3%) and the average laying interval between successive eggs was four days. Eggs within a clutch were similar in size and in hatching success. Growth and survival of chicks, however, differed within broods (first-hatched chicks fared better) and this was related to hatching asynchrony. The adaptive significance of brood reduction is discussed. The mean reproductive output was 1.07 fledglings per pair per year. The advantages of nidicolous chicks and cavity nests are discussed in relation to the sheathbills' close association with penguins, the inclement weather and the presence of predators. Breeding adults moulted immediately after the breeding season and other, non-breeding birds moulted earlier. Breeding adults had a mean annual survival of 88%, non-breeding adults and subadults (combined) 49% and juveniles 37%. Apparent causes of mortality were starvation, inclement weather and predation by Sub-Antarctic Skuas *Catharacta antarctica* and feral cats *Felis catus*. The population on the island appears to be close to its carrying capacity and limited by the number of territories which can be established in penguin colonies.

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## 11. SAMENVATTING

### Broedbiologie, rui en overleving van de Kleine Zuidpoolkip op Marion Eiland

Temidden van de talrijke antarctische en subantarctische vogelsoorten vormen de zuidpoolkippen van het genus *Chionis* (Charadriiformes) een merkwaardige uitzondering doordat zij de enige zijn die geen zwemvliezen bezitten en bovendien niet zwemmen of duiken, maar met rhythmische kopknikjes als kippen op rotsige stranden of in moerassige venen rondlopen. Bovendien hebben zij geen zeil- of zweefvleugels, maar kleine, korte vleugels waarmee zij zich als duiven in snelle vleugelslag over land en zee voortbewegen. Over het leven van deze vogels, waarvan twee soorten worden onderscheiden, is naar verhouding niet veel geschreven.

In dit artikel wordt het broedleven beschreven van de Kleine Zuidpoolkip *Chionis minor* op het subantarctische Marion Eiland in de Indische Oceaan. De volgende details werden vastgesteld. Alle volwassen broedvogels bezetten een territorium binnen een pinguin-kolonie. Vrijwel al het voedsel voor zichzelf en hun jongen werd uit de pinguin-kolonie verkregen, meestal door middel van wat genoemd wordt "kleptoparasitisme", in dit geval het stelen van voedsel waarmee een pinguin-ouder zijn jong voedt. Het broedseizoen viel samen met de tijd dat voedsel door de pinguïns geleverd het gemakkelijkst beschikbaar was. De vogels broedden voor het eerst op een leeftijd van drie jaar; er was een overmaat aan potentiële broedvogels. Legselgrootte werd vastgesteld op één ei (3%), twee eieren (47%), drie eieren (47%) en vier eieren (3%). Gemiddelde tijd tussen het leggen van opeenvolgende eieren was vier dagen (Tabel 1 en 2). Binnen een legsel waren eigrootte en resultaat van uitkomen gelijk (Tabel 3 en 4). Binnen één legsel werden evenwel wel verschillen gevonden in groeisnelheid en overleving van de jongen (de eerst uitgekomen jongen maakten het het best; Tabel 5, Fig. 6); deze verschillen hingen samen met het op verschillende tijd uitkomen van de eieren. De adaptieve betekenis van de hierdoor ontstane vermindering van de effectieve legselgrootte wordt besproken. Het gemiddelde voortplantingssucces werd berekend op 1.07 uitgevlogen jong per jaar per jaar (Tabel 8). De voordelen van het broeden in nestholten en van nestblijvende (nidicole) jongen worden besproken in samenhang met de nauwe relatie van zuidpoolkippen met pinguïns, het slechte weer en de aanwezigheid van predatoren. Volwassen vogels ruiden onmiddellijk na afloop van de broedtijd; andere, niet-broedende vogels ruiden eerder. Volwassen broedvogels hadden een gemiddelde jaarlijkse overlevingskans van 88% (Tabel 10), niet-broedende volwassen en half-volwassen vogels haalden samen 59% en jongen 37% (Tabel 11). Als doodsoorzaken werden vastgesteld: verhongering, slecht weer en predatie door Subantarctische Grote Jagers *Catharacta antarctica* en verwilderde katten *Felis catus*. De totale populatie bleek dicht bij de oecologische draagkracht van het eiland te liggen en werd beperkt door het aantal territoria dat binnen pinguin-kolonies kon worden gevestigd. K.H.V.