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An Analysis of the Displays of Lesser Sheathbills *Chionis minor*

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With 6 figures

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Abstract

Lesser Sheathbills were observed and filmed at Marion Island in the Sub-Antarctic. Displays and sequences of displays used by the birds are described. The use of certain displays by colour-marked birds of known age and sex in sexual or agonistic encounters is quantified. Territorial behaviour and pair bonds are described. Where possible the behaviour of the Lesser Sheathbill is compared with that of the Wattled Sheathbill *Chionis alba*.

Introduction

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

Study Area and Methods

This report is part of an investigation into the foraging and social behaviour of Lesser Sheathbills at Marion Island (46° 54′ S, 37° 45′ E) in the Southern Indian Ocean. Field work totalled 25 months and covered all seasons twice, between 1974 and 1978. Notes were kept on the descriptions, contexts and apparent stimuli of displays, and supplemented by still and 8 mm movie photography. Data on the behaviour of birds of known sex, age and social status were obtained from observations of 210 individuals which had been colour-marked with rings. These birds were aged and sexed using criteria described by Burger (1980).

Social Organization

Lesser Sheathbills defended territories of 100—300 m² within colonies of breeding penguins. Neighbouring territories frequently abutted but appeared to overlap very little. Territories were maintained only by pairs of adults. Juveniles were tolerated within their parents' territories. The principal objective of territorial defence by Lesser Sheathbills was to maintain exclusive use of the reliable and relatively abundant food resources supplied by the penguins, and territories were maintained only while the penguins were present: throughout the year within some colonies of King Penguins *Aptenodytes patagonicus* but only between November and the end of April in colonies of Rockhopper Penguins *Eudyptes chrysocome* (Fig. 1).

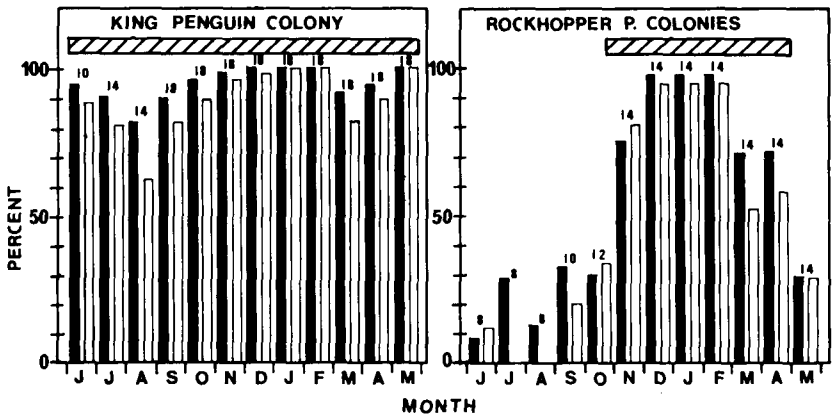


Fig. 1: Mean monthly percentages of colour-marked adult Lesser Sheathbills seen within their territories (black bars) and in the presence of their mates (open bars). The birds observed were all known to have bred or attempted breeding in a colony of King Penguins (left) or in colonies of Rockhopper Penguins (right). The presence of the penguins within the colonies is indicated by the horizontal hatched bar. The mean number of sheathbills, observed every 10 days, is given for each month

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

Lesser Sheathbills retained the same mates and territories from season to season and pair-bonds were terminated by the loss of a mate. This was noted for the colour-marked pairs living in 15 territories over four years. During this time 6 males and 5 females re-mated, one female twice, on the death or disappearance of their mates. With one exception, re-mating involved the acceptance of a new partner into the established territory, without noticeable changes in its boundaries. New partners had frequented the area,

sometimes for years, as non-territorial adults. The one exception was when two neighbouring birds mated after their respective mates had disappeared and the new pair then defended both former territories. The displacement of an established pair by another pair was not recorded. The members of a pair did not necessarily forage together when outside their territory (Fig. 1).

Lesser Sheathbills nest in cavities and the nest and attendant parent were usually invisible from outside. Nests were usually within the foraging territory but a few pairs (about 5 %, N = 52 pairs) used nest sites separated from the foraging territories by 10—50 m. Nestbuilding and nocturnal roosting within cavities commenced 6 weeks prior to laying and several pairs started nests in more than one cavity within their territory but used only one to breed in. Breeding pairs spent little time together within nest cavities.

Displays

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

Bill-wiping

Description: The bird wipes its bill on the ground in front of it several times. Most movements were identical to autochthonous bill cleaning, which occurs repeatedly following feeding in non-agonistic situations, but in others the bird merely brushed its bill across the substrate.

Context: Bill-wiping was seen in conjunction with other displays (see below) in agonistic situations. It was usually performed by territorial adults when intruders or neighbours were at the boundaries of the territory. Bill-wiping was also reported to occur as an agonistic display in *C. alba* (JONES 1963).

The Forward display

Description: The bird lowers its head with the bill pointing forward, usually facing another sheathbill (Fig. 2). In this posture the bird may swing its head in a narrow arc to look about. The display is frequently, but not invariably, accompanied by a series of harsh, sharp calls, "kék, kék, kék, . . .". The tail pumps up and down slightly as the bird calls. The posture is held for several seconds and repeated several times within 10 to 60 s. Bill-wiping very frequently accompanies this display.

Context: This display was commonly used by territorial adults of either sex but more frequently by the male (Table 1). It was given from within a territory, often from a raised rock where the bird was resting or preening and was elicited by the approach or intrusion into the territory by a conspecific and also when neighbouring pairs were calling. The display evidently communicated aggressive threat to an intruder or potential intruder which was at a distance. The threat posture of *C. alba* has been described as a "forward-oblique" pose which is usually accompanied by Bill-wiping and calling (JONES 1963).

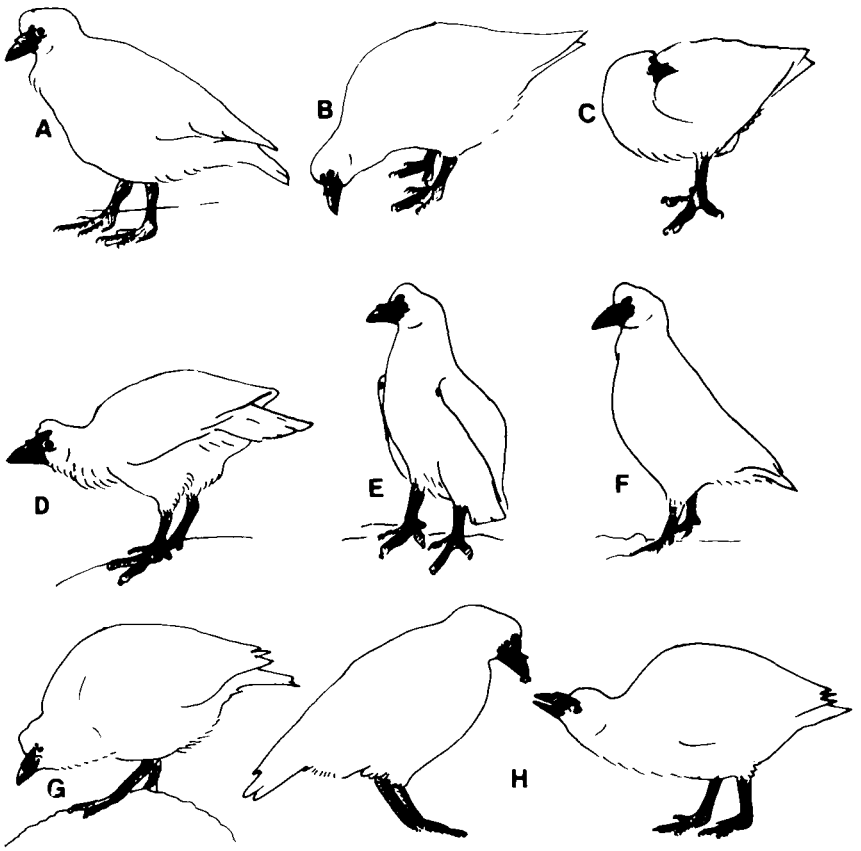


Fig. 2: Normal and display postures of Lesser Sheathbills, including: the normal standing posture (A); foraging (B); roosting (C); the Forward display (D); Aggressive Upright (E); Anxiety Upright (F); the Hunched display (G); an the Hunched display while soliciting food in a juvenile (H). (Drawn from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

The Hunched display

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

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

Table 1: The relative frequency with which individually-marked territorial male and female Lesser Sheathbills performed various displays. Observations were made in King and Rockhopper Penguin colonies

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

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

Facing Away

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

Context: This display was brief and rare and usually occurred when a bird in a non-territorial foraging group approached another. Detailed notes on only 12 performances were made. These involved non-territorial adults and immatures. In 8 encounters one bird attacked the other; this followed Facing Away by both birds involved (three times), by the attacking bird (three times) or by the attacked bird (twice). The display was also sometimes performed by females following copulation (see below).

The Upright display

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

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

Chasing

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

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

Table 2: Birds chased by male, female and unidentified territorial Lesser Sheathbills. Observations were made at a King Penguin colony and involved 10 marked territorial pairs

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

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

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

Very brief supplanting Chases occurred frequently (2.5 chases/bird/h during 20 h of focal-animal watching) in foraging groups of non-territorial Lesser Sheathbills. These usually involved one bird running 1 m or 2 to chase another from the spot where it was feeding and the chaser then resumed foraging at that spot.

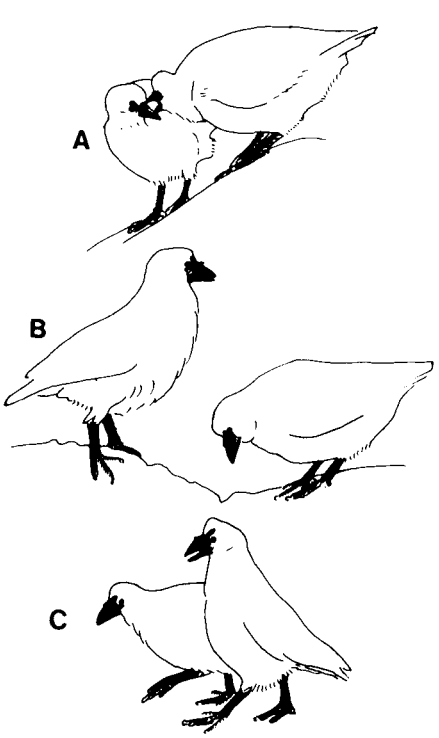
Bob Call

Description: The display is performed by two birds of opposite sex standing next to each other. Both birds bow the head and neck rapidly up and down, while uttering a long series of staccato calls, "kék-kék-kék . . ." (Figs. 3, 4). A mean frequency of two bows per s was obtained from an analysis of movie film of 8 displays.

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

The display is initiated by one of the pair beginning to bob and call, followed by the other. Occasionally (39 % of 103 displays) the bird initiating the display pecks at the bill of the other before both display (Fig. 3). The body movements of the two birds are not synchronised with each other and neither are the calls synchronised with the movements. Frequently one bird performs more vigorously than the other. Bill-wiping and Run-and-Call displays (see below) were sometimes seen during or after bouts of Bob Call displays.

Context: This is essentially a display by mated pairs within territories but on rare occasions (< 1 %) it was performed by two marked adults which were known to have other mates. 94 % of Bob Call displays occurred within the territories of the birds involved (N = 103). The display was initiated equally by either sex (Table 3, $p > 0.05$, Chi-quare test) and when bill-biting was involved, this was also performed equally by either sex (18 times by males, 20 by females, $p > 0.05$).



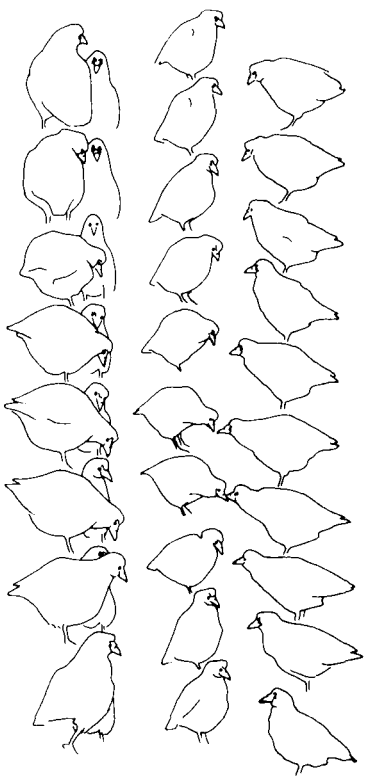


Fig. 3 (left): Bill-biting prior to a Bob Call display (A); the Bob Call display (B) showing birds in the head up and head down postures; and, the Run-and-Call display (C). (Drawn from photographs and field sketches)

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

Table 3: Analysis of 103 Bob Call displays performed by colour-marked, territorial Lesser Sheathbills of known sex

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

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

A homologous pair display, called the "bowing ceremony" by JONES (1963) is the most conspicuous display reported for Wattled Sheathbills and its function is apparently to maintain the pair bond.

Run-and-Call

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

Context: The display was seen to be performed only by the members of mated pairs within or adjacent to their territories. In 39 out of 46 displays observed in detail, the paired birds displayed while moving slowly behind an intraspecific intruder as it left their territory. Intruders most commonly evicted in this manner were non-territorial adults. In this context Run-and-Call displays functioned as low-intensity defence. The display also occurred when neighbouring pairs gave a similar display or the Bob Call display (4 of the 46 obs.) or for no apparent reason. On rare occasions two pairs displayed simultaneously while moving along their common territorial boundary.

Fly-and-Call

Description: The members of a pair take flight simultaneously and fly, separately, in low circles to land near to where they started. The flight appears

to be slower than in normal flight and while in the air one or both birds give loud staccato calls. The flight is often preceded or followed by the Bob Call display.

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

Fighting

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

Context: Fighting occurred between neighbouring territorial adults and almost invariably involved two males (Table 1). These fights were included in sequences of displays including Bill-wiping, Crouch-and-Jab (see below) and Bob Call displays. Brief exchanges of a few pecks also occurred in non-territorial situations when sheathbills were crowded around a rich food source, such as a seal carcass.

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

Crouch-and-Jab

Description: Two birds, facing directly at each other, crouch low with their bodies parallel to the ground, tarsometatarsi touching the ground and wings partially opened (Fig. 5). The birds jab with their bills towards each other, sometimes jabbing at stones

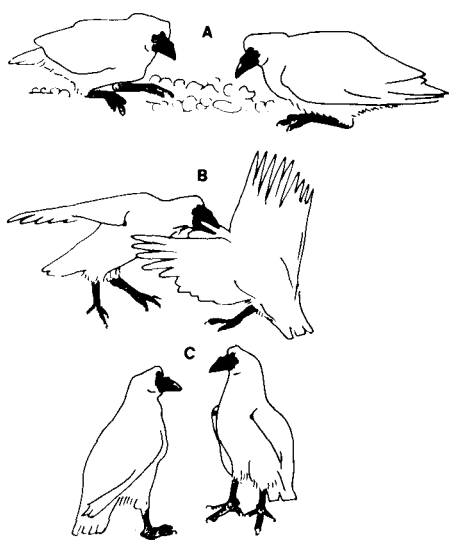


Fig. 5: Display seen in boundary disputes, including the Crouch-and-Jab display (A); Fighting (B); and, Aggressive Upright postures (C). (Drawn from photographs)

or debris in front of them or merely jabbing the air. The birds remain crouched in one spot for many seconds but may also shuffle sideways or towards each other. Birds occasionally peck viciously and pull at pieces of kelp debris or feathers in what appears to be redirected aggression.

Context: The display was seen to be performed only by territorial adults at the boundaries of their territories in high intensity boundary disputes (see below). Lesser Sheathbills probing amongst small pebbles for oligochaete worms and insect larvae crouched and probed with the bill in a manner quite similar to the ritualized Crouch-and-Jab display.

Prancing

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

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

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

Copulation

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

Copulation ends when the female moves away and dislodges the male. Post-copulatory behaviour was very variable. Out of 10 observations of mount-

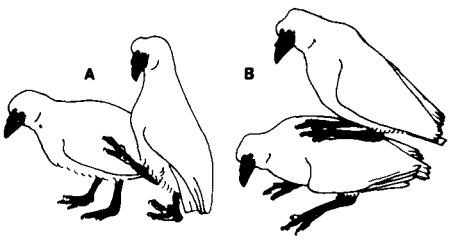


Fig. 6: Pre-copulatory behaviour (A) showing the male Prancing and scratching the flanks of the female and the female in a receptive semi-crouched posture; and, Copulation (B). (Drawn from movie film and field sketches)

ing, the female gave: a brief Facing-away movement, while standing very erect, in three cases; a Forward threat facing away from the male on one occasion; a Bob Call display with mutual bill-biting on one occasion; and in all other cases, the pair wandered apart to preen.

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

Vocalizations

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

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

Boundary Disputes

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

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

Boundary disputes led to Fighting, followed by Aggressive Upright postures in 29 % of encounters (N = 68) and Fighting occurred in 44 % of

Table 4: The occurrence (and percentage occurrence in parentheses) of certain postures and displays during boundary disputes between neighbouring territorial Lesser Sheathbills

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

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

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

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

Comfort Behaviour

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

Discussion

Morphological Adaptations for Display

Movements of the head were prominent in many displays by Lesser Sheathbills. In distance-increasing displays (TINBERGEN 1959), such as the Forward and Crouch-and-Jab, the bill and face are thrust forwards, whereas

in distance-reducing displays such as Facing Away and the Hunched, the bill and face are turned away from other birds. The black facial caruncles and culmen sheath which are present in both sexes contrast with the white plumage, apparently enhancing agonistic signals in a similar manner to the black faces of *Larus ridibundus* and other "masked" gulls (TINBERGEN and MOYNIHAN 1952; TINBERGEN 1964). Facial features are poorly developed in immature Lesser Sheathbills (BURGER 1980) and these birds do not hold territories, seldom use the Forward threat display and never participate in boundary disputes. In Wattled Sheathbills the caruncles are pink and the culmen sheath is greenish (JONES 1963) but these features could still enhance the signalling effects of ritualized head movements.

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

Male Lesser Sheathbills performed agonistic displays more frequently than females, and boundary disputes and Fighting, which involved prolonged physical proximity and contact, were almost exclusively performed by males. Males are significantly larger than females and this has been attributed to selection favouring male dominance in territorial agonistic encounters (BURGER 1980).

Displays within the Territorial Context

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

Territorial defence usually occupied less than 5 % of the daily time and energy budgets of breeding adult Lesser Sheathbills (BURGER in prep.), but involved a wide range of behaviour (Table 5). Territorial adults usually rested

Table 5: Behaviour used by Lesser Sheathbills to advertise and defend territories

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

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

Lesser Sheathbills did not compete directly for mates, nests or mating sites, but for the acquisition of foraging territories which were the key to successful breeding (BURGER 1979). The birds had no displays which might have functioned purely to attract mates or to advertise nest sites, such as Choking in gulls (TINBERGEN 1959). The acceptance of a new partner into an established territory occurred infrequently and the behaviour involved is not adequately known. The Bob Call display, which was seen on rare occasions to be performed by birds which were not mated, is probably involved. A new partner had usually frequented the area of the territory as a non-territorial bird and individual recognition between the territory holder and the prospective mate probably facilitated the establishment of a pair-bond.

Pair-bonds did form outside territories and existing pair-bonds were relevant only within territories. Adults which were temporarily non-territorial in winter tended to ignore their mates. Mutual pair displays were almost always performed within territories, usually in agonistic situations and probably promoted mutual tolerance within the territory. The Bob Call display is possibly comprised of alternating elements of aggression (Aggressive Upright and Bill-biting) and appeasement (Hunched) in a similar manner to the ambivalent Bowing displays in pigeons (MURTON and WESTWOOD 1977; 106). Bob Call displays could thus serve to inhibit attack by the mate while demonstrating a measure of territorial aggression.

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

Taxonomic Implications of Displays

The displays of the two species of sheathbills are superficially very similar in form and function, although those of the Wattled Sheathbill are poorly

known. It is not known, for instance, whether the frequency of use of the various displays is similar in both species in similar ecological contexts.

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

Summary

Agonistic and sexual displays, sequences of displays and comfort behaviour of Lesser Sheathbills *Chionis minor* living in the sub-Antarctic are described. Pairs of adults maintained territories within penguin colonies with the principal objective of defending food resources. Territorial birds of both sexes used a complex array of displays to: (a) advertise their presence; (b) threaten intruding conspecifics; (c) evict non-territorial intruders; and (d) maintain territorial boundaries, re-inforced by Fighting neighbouring territorial adults. Both members of a pair defended their territory but males did so more frequently. Pair-bonds were formed and maintained only within territories, and mutual pair displays probably promoted mutual tolerance of the mate within the territory. Copulatory behaviour appeared to be used for insemination only. Intraspecific behaviour among non-territorial sheathbills was largely restricted to very brief agonistic interactions over ephemeral food items and involved few and simple displays. The black facial caruncles and culmen sheath apparently serve to emphasize ritualized movements of the head. Vocalizations accompanied many displays and were usually audible above the noise of the penguin colonies. A comprehensive study of the behaviour of both species of sheathbills could provide valuable information on the evolution of displays in the Charadriiformes.

Zusammenfassung

Scheidenschnäbel, *Chionis minor*, wurden im subantarktischen Raum beobachtet. Adulte Paare besetzten Nahrungsreviere in Pinguinkolonien. Territoriale Vögel beiderlei Geschlechts benutzten vielerlei Signal-Verhaltensweisen um a) ihre Gegenwart anzuzeigen, b) artgleichen Eindringlingen zu drohen, c) nicht-territoriale Eindringlinge zu vertreiben, und d) die Reviergrenze beizubehalten (dazu dienen auch Kämpfe mit benachbarten territorialen Vögeln). Beide Paarpartner verteidigen ihr Revier, männliche häufiger als weibliche. Paarbindungen bildeten sich nur innerhalb der Territorien und wurden nur dort unterhalten. Paar-Rituale förderten wahrscheinlich die gegenseitige Duldung des Partners im Revier. Die Begattung dient offenbar lediglich der

Besamung. Intraspezifisches Verhalten zwischen nicht-territorialen Scheidenschnäbeln beschränkt sich auf kurze Auseinandersetzungen an Nahrungsbrokken und umfaßt wenige einfache Imponierbewegungen. Die schwarzen Kehl-Lappen und die Culmenscheide unterstreichen die ritualisierten Bewegungen des Kopfes. Häufig werden Imponierbewegungen von Lauten begleitet, die den Lärm der Pinguinkolonie übertönen. Aus einem Verhaltensvergleich beider Scheidenschnäbelarten sind wichtige Hinweise auf die Evolution von Imponierbewegungen der Charadriiformes zu erwarten.

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