

Behavioural patterns in the Southern Bald Ibis (*Geronticus calvus*) at breeding sites

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The Southern Bald Ibis behavioural patterns and their daily and seasonal frequency of performance were analysed in a breeding colony in the eastern Free State, South Africa. This species behaviour is characterised by varied and often performed breeding displays and comfort movements. The breeding displays were performed more often by non-breeding pairs than by breeding birds. Much higher copulation rates among non-breeding than among breeding pairs and low frequency of extra-pair copulation has been noted. On general, displays were performed more often in the early breeding season, and on daily basis, mainly in the morning and in late afternoon. All comfort movements are of universal occurrence and basically have the same form and context as in other bird species, with preening movements being most often performed and most complex in function.

Key words: *Geronticus calvus*, behaviour, breeding displays, Free State, South Africa.

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1. Introduction

The Southern Bald Ibis *Geronticus calvus* is a close relative of the Palearctic Northern Southern Bald Ibis *Geronticus eremita*. At present, the latter species is one of the most endangered bird species in the world (BRINDLEY et al. 1995), while the current situation of the Southern Bald Ibis is apparently stable (DEL HOYO et al. 1992). However, due to extreme difficulties in field work virtually nothing is known about the behaviour of the species. To ensure its survival, movements and displays of the Southern Bald Ibis were studied in a breeding colony in the eastern part of the Free State, South Africa, in an area regarded as the main stronghold of the species (KOPIJ 1998).

2. Study site

The main study was carried out at a colony situated in a gorge, 7 km north of Clarens in the eastern Free State (28°30'S, 28°20'E), South Africa. The gorge is narrow (c. 10–20 m), but deep (c. 80 m) and a small stream is flowing through it. Since the gorge is closed from three sides the stream is flowing into it forming a narrow waterfall. There was a small (c. 30 m²) but quite deep (2 m) water body at the point where the gorge was broadened. Further on, the gorge was much broader forming a valley covered with trees and thorns (main plants: *Leucosidea sericea*, *Salix babylonica*, *Populus tremula*, *Grewia occidentalis*). The gorge was bordered with montane grassy highveld utilised as pastures for sheep on one side, and with cultivated field with maize as a main cultivated plant on the other side. A dam was situated 3 km north of the gorge.

A mean annual precipitation 800–900 with 80% rainfall in summer (October–March) indicates clearly sub-humid zone of the area. Winters are extremely cold and snowfall is not uncommon. During the main study period (July–October, 1994) the total precipitation was exceptionally low (50 mm) and days with strong wind and very low temperature occurred more often than normal.

The colony was occupied by 23 breeding and seven non-breeding pairs, later in the breeding season (after 5 September), seven immatures stayed in the colony. Five other nests were located out of the gorge 100, 200, 400 and 500 m away. All nests were located on sandy rock ledges.

Few additional observations on the Southern Bald Ibis's behaviour were also made in two other breeding colonies in the Bethlehem district, namely at Bramleyshoek (28 27 S; 28 30 E) and Vaalbank (28 25 S, 28 20 E).

3. Methods

Studies on the behaviour of the Southern Bald Ibis were conducted at the Welgelegen colony during the breeding season from 2 July till 31 October 1994. Two nests were under detailed week-to-week observations. The first one was occupied by one breeding pair, the second by a non-breeding pair. Observations were aided by 10x50 binocular and video camera Panasonic TTL 200 mm, from a shelter built on a rocky outcrop on the opposite wall in a distance 15 m from the first and 20 m from the second nest. The shelter was entered without any disturbance of the bird behaviour.

Observations of the two nests were standardized and were carried out on weekly basis since 21 July 1994 till 4 October 1994. Since 21 July to 25 August studies were conducted throughout the whole day (i.e. 6h00–18h00) whereas later first part of observations in the mornings (6h00–12h00) and the second one afternoon (12h00–18h00) on the consecutive day.

The nest of the breeding pair which was under detailed study was already occupied on the first day of the study. The first egg was laid on 4 August, the second one on 8 August and the third on 10 August. The nestlings hatched on 1 September. The youngest chick died being 5 day old and the next one at an age of 12 days, the oldest being 35 days old was killed by a Black Eagle *Aquila verreauxii*.

Notes were kept in the form of time-scores grouped into 15 minutes. On 4, 11 and 18 August both nests were under detailed observation. From 30 August the nest of the non-breeding pair was occupied by birds only occasionally, so observations were suspended. Some movements were also noted in four other nests visible from the hide throughout the breeding season.

There is no sexual dimorphism in the Southern Bald Ibis. Individuals were distinguished in the nests by characters such as signs on their foreheads or cheeks.

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4. Results

4. 1. Maintenance behaviour

4. 1. 1. Flight

The flight of the Southern Bald Ibis is more graceful and buoyant than that of other ibis species. Gliding with outstretched wings is often performed and usually follows 'diving' into the wind with the wings bent at the carpal joints. This flight resembles that of the White Stork *Ciconia ciconia*. When the ibises depart from their breeding colonies for feeding purposes, they normally follow the valley contour, flying just above the tree-tops. After a few hundred metres they begin to soar upwards and fly directly towards their feeding places. On arrival at the colony the so-called 'towering' is usually performed: the birds soar upwards and then 'dive' into the colony with wings bent at the carpal joints. Some birds would land first on ledges not occupied by nests before continuing to their own nests. During the later stages of breeding, when many pairs have lost their broods, arriving birds often land on rocky outcrops some distance from the colony. After having rested for several minutes they would fly to the colony with a slow, buoyant and deep wing-flapping, a flight pattern resembling that of crows. The same flight pattern was observed when birds passed from one place to another in the colony. Some arriving or departing birds would circle a number of times in the sky (average number of circles = 7, range 3–9; n = 22) before landing or departure. This often involved afternoon departures (81%; n = 85) or late morning or afternoon arrivals (72%; n = 60).

4. 1. 2. Resting

Southern Bald Ibises usually rest in a standing position, often on one leg. In general, non-breeding birds spent much more time resting in a standing position (70% of the entire time spent in nest) than breeding birds (30%). Breeding males spent almost twice as much time standing than their mates ($\chi^2 = 8.06$; $p = 0.01$). Among non-breeders, however, females were recorded standing more often than the males (Fig. 1).

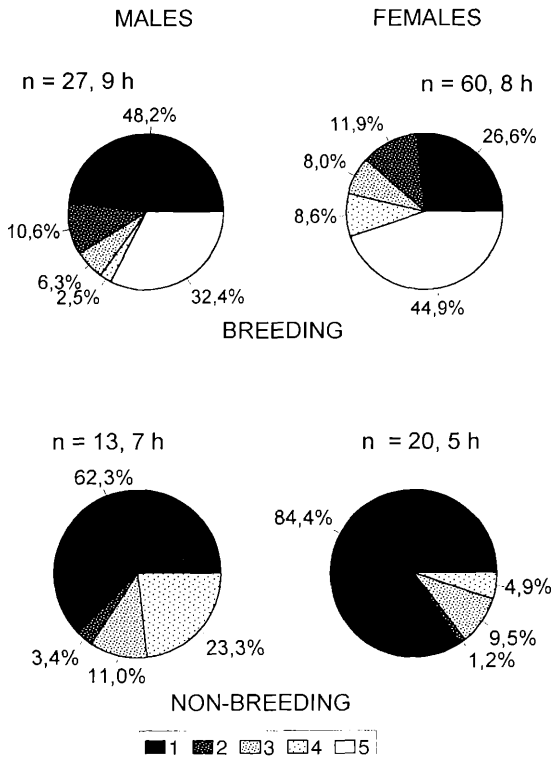


Fig. 1: Southern Bald Ibis continuing activity time budget at the Welgelegen breeding colony (1 – standing; 2 – sitting, 3 – sleeping, 4 – preening, 5 – nest-building).

Abb. 1: Zeitbudget einzelner Aktivitäten beim Glattackerrapp (Brutkolonie Welgelegen). (1 – Stehen, 2 – Sitzen, 3 – Schlafen, 4 – Gefiederpflege, 5 – Nestbau).

Ibises were occasionally seen leaving the colony to rest on rocky outcrops situated nearby. This occurred most often just before sunset. Similar behaviour was observed when the birds returned from the feeding grounds during the late nestling phase, or when birds were disturbed by potential predators in the breeding colony.

4. 1. 3. Sleeping

Although Kahl (1983) classified sleeping as a display, it should rather be considered as a maintenance activity. The Southern Bald Ibis usually sleeps in a standing position, often on one leg, with eyes closed and with its head turned back and tucked beneath its upper wing covers. However, during the incubation period both male and female sleep in a sitting position. Overall, breeding birds spend less time sleeping during the day than their non-breeding counterparts (Fig. 1). Sleeping individuals frequently wake for short preening bouts, mutual billing or allopreening. Whereas males sleep more often in the afternoons, females do so mainly in the mornings. Overall, both sexes spent similar time sleeping (Fig. 1).

4. 1. 4. Defecation

The ibises defecate in the colony as well as in the field. Being in the nest, the adult bird drops excrements always outside. Small chicks drop excrements, in a form of faecal sacs, into the nest but these are immediately eaten by parents. Older chicks, like adults, drop excrements usually outside the nest, but sometimes on its edges; nests, therefore, often became quite dirty towards the end of the breeding season. Birds defecated most often in the morning. While on the nest during the incubation and early nestling phases, adults defecate on average six times a day compared to only 1–3 times a day during the prelaying and late nestling phase.

4.2. Feeding techniques

4. 2. 1. Searching for prey

The Southern Bald Ibis forages only on the ground. The most universal feeding technique of Ciconiiformes, that of standing (HANCOCK et al. 1992), was not recorded during this study. Likewise, preying by running or walking slowly were not observed either, as the only technique recorded was walking quickly. Hadedá Ibises *Bostrychia hagedash* were often seen foraging alongside the Southern Bald Ibises when in harvested corn fields. They, however, used the slow walking feeding technique, which is less effective in foraging in this habitat, thereby reducing feeding competition and enabling the coexistence of the two species.

The birds forage by head swinging (swiping the bill from side to side). On average nine swings per minute were recorded ($n = 1\ 752$ swings) during which time they covered a distance of c. 50 m. They swing more quickly on burnt grass ($\bar{\chi} = 14/$ min.; $n = 70$) than on harvested maize fields ($\bar{\chi} = 9/$ min.; $n = 1\ 112$ swings) and short grass ($\bar{\chi} = 10/$ min.; $n = 570$). On average every 15 swings ($n = 1\ 094$ swings) resulted in food being obtained. While foraging by head swinging the ibises quickly peck at potential prey items on the ground or probe small holes with the tip of their bills either in the ground or on the maize stalks trampled by cattle.

4. 2. 2. Catching and handling prey

As a tactile forager the Southern Bald Ibis apparently does not use sight while feeding. Their bill tips are highly innervated, thereby registering contact with potential prey items (DEL HOYO et al. 1992). Catching prey is by means of bill snapping which involves the rapid closing of the bill as a reflex reaction to the tactile stimulus generated by contact with the prey by pushing the head.

Forward to engulf prey items, which have been temporarily released, all prey is swallowed immediately after capture. Softening, stubbing or strangling prey were not recorded, not even in respect to such relatively large prey as the Striped Mouse *Rhodomys pumilio*.

4. 3. Comfort movements

4. 3. 1. Body shake

This behaviour involves the ruffling of the contour feathers, vigorous movements of the wings (in and out) a short distance from the body and tail wag, but without head movement. Body shake was often seen when incubating birds changed position and it usually preceded preening and nest-building and was followed by resting and preening (Table 1). The body shake was also recorded in the African Spoonbill *Platalea alba*, mainly during bouts of allopreening (Kahl 1983) and probably helps to rearrange the feathers. It is performed throughout the breeding season, although only occasionally in the July prelaying phase (Fig. 2). After an early morning peak in this activity, the body shake shows a progressive decline during the rest of the day (Fig. 2). Probably due to their greater involvement in breeding activities, this behaviour is performed more often by females (67% of all records) than by males (33%; $n = 73$).

4. 3. 2. Tail wag

This movement involves the tail being shaken rapidly from side to side several times and was often seen when an incubating bird changed position. As shown in Table 1, tail wag was associated mostly with nest-building and, to a lesser extent with preening. This behaviour has not been recorded in the African Spoonbill (KAHL 1983). It probably serves to rearrange misplaced rectrices. This behaviour was performed throughout the breeding season except during the July prelaying phase (Fig. 2). The activity shows a progressive increase during the day, reaching a peak in the late afternoon (Fig. 2). It occurs commonly in breeding birds and is performed mostly by the female of both breeding and non-breeding pairs (Table. 2).

4. 3. 3. Wing-and-leg stretch

In the wing-and-leg stretch, the wing and leg on the same side are extended outwards in a posterior and ventral direction. KAHL (1983) also recorded this movement in the African Spoonbill but its function is not clear. It is, however, plausible that it can lead to improved blood circulation as suggested by MCKINNEY (1965). The wing-and-leg stretch was more often observed in the prelaying (July) and nestling phases (October), usually in the early morning and late afternoon (Fig. 2). This movement was performed more often by females than males, usually in association with nest-building or preening activities (Table 1). No such comfort movement was recorded for non-breeding birds at the colony.

4. 3. 4. Both wings stretch

During this comfort movement both wings are bent at the carpal joints and raised upwards until the scapulars touch above the back, while the head and neck are stretched forward and downwards. This behaviour was seen when incubating birds changed position in the nest. KAHL (1983) did not record this behaviour in the African Spoonbill, although he pointed out that it 'may occur'. It is related to the yawn of mammals and probably serves to improve respiration and blood circulation (MCKINNEY 1983). The behaviour peaked in the beginning of August (early incubation phase) and decreased rapidly during the later parts of the month (Fig. 2). During the day, this wing stretch was performed mostly in the morning, with a conspicuous peak between 10h00 and 11h00 (Fig. 2). This movement was performed more often by males than females, and was not recorded for non-breeding pairs (Table 2), probably because it is strictly associated with incubation.

4. 3. 5. Jaw stretch

During the jaw stretch the bird raises its head and opens its bill wide for a few seconds. No physiological evidence of its function is known but the movement is often associated with resting and preening (Table 1). The jaw stretch was also observed in the African Spoonbill (KAHL 1983). The behaviour showed a pronounced increase during the early stage of the breeding season but declined rapidly during the nestling phase (late September/early October). It was usually recorded during the early mornings (Fig. 2). Although the jaw stretch occurred commonly in both breeding and non-breeding birds, it was observed more often in males (67% of all records) than females (33%).

4. 3. 6. Scratching

When scratching the head, the neck is stretched forward while one foot is directed to the head and moves rapidly up and down on the head in a fixed arc. In the African Spoonbill, it is usually associated with the jaw stretch and with preening in males and with sleeping or allopreening in females (KAHL 1983). It probably serves to relieve a local irritation (caused, for example, by lice) which the bird is unable to reach with its bill; the bird may remove an object from the feathers which was atta-

Table 1: Context of comfort behaviour (percentages) in the Southern Bald Ibis (numbers in brackets indicate number of observation).

Tab. 1: Bewegungsweisen des Komfortverhaltens (in Prozent) beim Glattnackentrapp (Zahlen in Klammern entsprechen Anzahl an Beobachtungen).

Comfort movement		Nest building	Preening	Resting	Sleeping	Others
Body shake	Before (33)	21	30	18	–	31
	After (22)	–	23	64	–	13
Tail wag	Before (41)	34	17	10	10	29
	After (17)	53	18	6	–	23
Wing-and-leg stretch	Before (20)	30	25	25	–	20
	After (7)	29	42	29	–	–
Both wings stretch	Before (3)	–	33	33	33	–
	After (1)	–	100	–	–	–
Jaw stretch	Before (55)	9	20	55	7	11
	After (54)	2	20	59	2	17
Scratching	Before (69)	15	15	42	–	28
	After (27)	7	11	48	15	19
Preening	Before (403)	2	–	62	1	35
	After (324)	21	–	46	19	14

Table 2: Comfort behaviour of breeding and non-breeding Southern Bald Ibises.

Tab. 2: Komfortverhalten brütender und nichtbrütender Glattnackentrappe.

Comfort movement	Breeding birds				Non-breeding			
	male	female	$\bar{\chi}$	p	male	female	$\bar{\chi}$	p
Body shake	24	49	7.89	**	5	3	0.13	–
Tail wag	41	57	2.30	–	4	9	1.23	–
Wing-and-leg stretch	7	12	0.84	–	–	–	–	–
Both wing stretch	7	5	0.08	–	–	–	–	–
Jaw stretch	84	51	7.59	**	43	13	15.04	**
Scratching	49	45	0.10	–	6	6	–	–
Preening	182	291	24.66	**	135	77	15.33	**
Total	394	510			193	108		

ched during feeding or roosting. This behaviour was performed with similar frequency throughout the day (Fig. 2) and with similar intensity by both males and females, but only occasionally by non-breeding birds (Table 2).

4. 3. 7. Preening

Preening involves contact of the bird's bill with the feathers as rubbing or combing in the form of several bill movements. Some stereotypic movements have been recognised in preening, namely preening behind the wing (the bill is moved over the neck or upper part of body), dorsal preening (the bill is moved over the neck or upper part of back) preening the back behind the wings (the bill is moved upwards over the inside of the wings and lower part of back) and ventral preening (the bill is moved over the breast and upper part of the bell). Some of the movements were also distinguished in the Northern Bald Ibis (SAHIN 1983b). This movement enables a bird to keep its feathers clean and in order and to release irritation caused by ectoparasites; it is thus complementary to

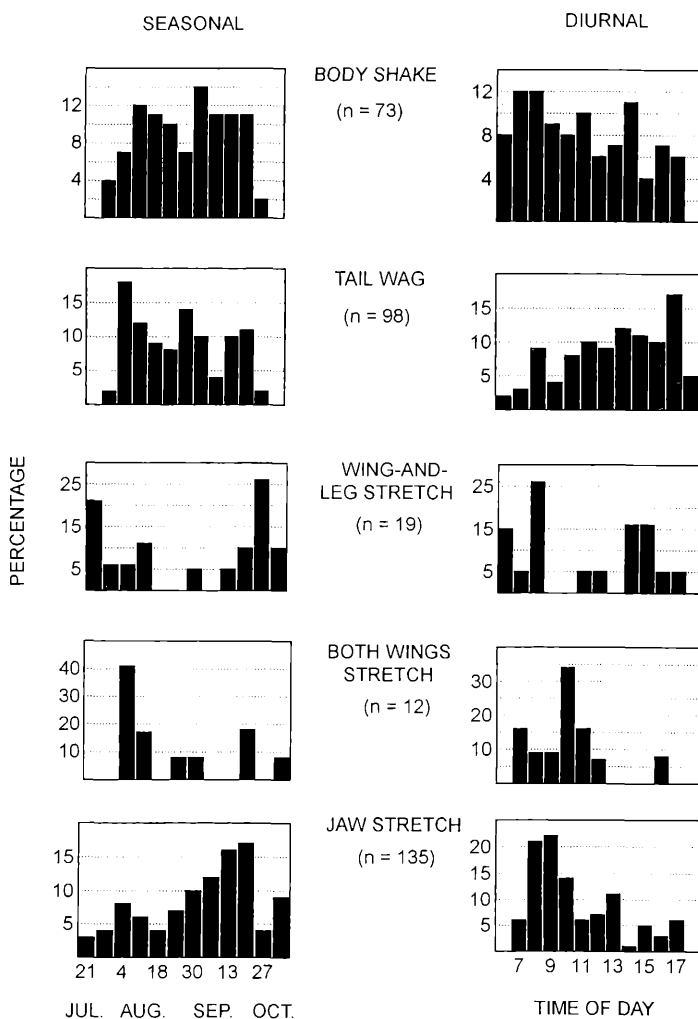


Fig. 2: Temporal variation in comfort behaviour of the Southern Bald Ibis at the Welgelegen breeding colony.

Abb. 2: Zeitliche Variation im Komfortverhalten beim Glattnackennapp (Brutkolonie Welgelegen).

scratching. It was performed often, usually in association with resting, and was followed mainly by resting, nest-building and sleeping (Table 1). Preening was performed mainly in the early morning and late afternoon (Fig. 3).

4. 3. 8. Oil preening

Oil preening consists of a continuous sequence of bill movements near the oil gland on the rump during which the secretion is collected from the gland and distributed over the plumage. This serves to redistribute the secretions from the oil glands all over the body except for the head region. Oil preening was most frequently performed by the breeding female but reverse proportion was noted for non-breeding birds (Table 2).

4. 3. 9. Head rubbing

During head rubbing the head is rubbed against the back; it might therefore be complementary to oil preening and serves to redistribute oil gland secretion to the head. Head rubbing peaked in the early incubation phase (Fig. 3), but it was not recorded in July (prelaying phase). This movement was usually performed in the morning or late afternoon (Fig. 3), more often by males than females. Head rubbing was performed with a frequency 15 times lower than oil preening.

4. 3. 10. Bathing

During bathing, the birds stand in shallow water and rapidly plunge their heads, necks and other body parts under water; several wing-thrashing movements may follow. Washing was seen on a few occasions only during October, on the shore of a farm dam and near a small waterfall at the Welgelegen colony. On one occasion in August an individual was seen wagging its wings three times like a duck during bathing, but this movement was never recorded again. VINCENT (1948) reported that the ibises 'certainly do not enter water at all'. KAHL (1983) also did not record this activity in the African Spoonbill. DEL HOYO et al. (1992), however, do document this behaviour together with a photograph.

4. 3. 11. Sun bathing

During sun bathing the bird stands in the sun in an upright position with its wings spread laterally and slightly forwards, much like a cormorant during sun bathing. Also the Northern Bald Ibis performs similar posture while bathing in sun (SAHIN 1983b). It was recorded on a few occasions only. KAHL (1983) did not record sun bathing in the African Spoonbill. Sun bathing was more often observed in the Northern Bald Ibises probably because their breeding colony was situated in close proximity to the Euphrates River (SAHIN 1983b).

4. 3. 12. Gular fluttering

During gular fluttering the throat flutters for a period of several seconds to several minutes at a time; the bill is usually closed. This behaviour was seen slightly more often in males than females, mainly in the morning from the late incubation phase onwards. Gular fluttering was not recorded in the African Spoonbill (KAHL 1983).

4. 3. 13. Development of comfort movements in nestlings

The jaw stretch was the first comfort movement to be recorded in Southern Bald Ibis chicks, even while still inside the egg-shell (seen through a small opening). This was the only comfort movement that chicks performed within the first two weeks after hatching (Table 3). Compared to its occurrence in adults, the jaw stretch is uncommon in chicks.

At an age of 21 days, chicks were seen preening, scratching and stretching their wings and legs for the first time (Table 3). Although most of these movements became more frequent as the chicks grew older, the both wings stretch was not recorded again. The tail wag was first seen in a 27-day old chick, while the body shake and allopreening were not recorded for Southern Bald Ibis chicks at all. Northern Bald Ibis's chicks are also known to take care of their body (SAHIN 1983b).

At the age of 28 days a chick was seen rearranging material in the nest for the first time. A week later many chicks were doing this quite often. Chicks were also able to sleep in a standing position from the age of 35 days onwards.

During the first three weeks after hatching, chicks defecated in their nests, whereupon the faecal sacs would be eaten immediately by the brooding parent. As they grew older, the chicks usually defecated over the nest rim and the faeces were no longer eaten by the adults. Northern Bald Ibis's chicks are also known to maintain nest-sanitation (SAHIN 1983b).

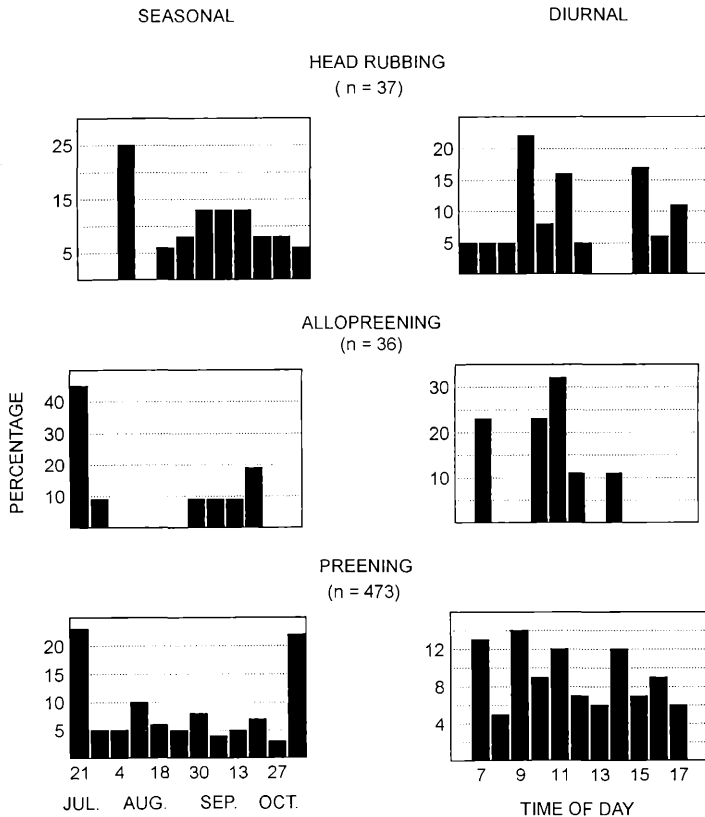


Fig. 3: Temporal variation in preening behaviour of the Southern Bald Ibis at the Welgelegen breeding colony.

Abb. 3: Zeitliche Variation im Verhaltenskomplex Gefieder-Pflege beim Glattnackensrapp (Brutkolonie Welgelegen).

4. 4. Anti-predator behaviour

In reaction to potential predators (e.g. Black Eagle, Tawny Eagle *Aquila rapax*, Spotted Eagle Owl *Bubo africanus* and human), all birds present in a colony would fly away and circle in a flock above the colony, uttering alarm calls. This would often be interrupted by birds perching for a while on rocky outcrops in the vicinity. In cases where the predator flew in close proximity of the colony, the flock of ibises mobbed the raptor from a distance of c. 10–20 m uttering the same alarm call. No raptor attack was ever recorded under such circumstances. In other situations, however, actual predation on Southern Bald Ibis nestlings was occasionally witnessed (KOPIJ 1995). Nestlings appeared quite defenceless during such attacks. In one instance a 34-day old chick only crouched silently and motionless against the cliff prior to the attack. Even during the attack it did not utter any calls, nor did it attempt to defend itself (KOPIJ 1995). No alarm response was recorded when a Gymnogone *Polyboroides typus*, Rock Kestrel *Falco tinnunculus*, Rock Pigeon *Columba guinea* or Egyptian Goose *Alopochen aegyptiacus* made its appearance at the colony or in its immediate vicinity. In general, the Southern Bald Ibis appears to be more timid in the field than either the closely rela-

ted Hadeda Ibis or Sacred Ibis *Threskiornis aethiopicus*. It proved difficult to approach feeding flocks closer than distances of 50 m, although on a few occasions they were seen foraging close to human settlements and even in parklands of towns.

4. 5. Agonistic displays

Serious fights occur only sporadically in Southern Bald Ibis's colonies. Likewise in the Northern Bald Ibis (SAHIN 1983a) most of the fights are ritualised into so called forward display and crouching display.

4. 5. 1. Forward display

In the forward display, the head and neck position, which is a product of a combination of fear and aggression, provides an accurate clue regarding the context of this behaviour pattern. The display appears similar to that of the African Spoonbill (KAHL 1983) and the Sacred Ibis (URBAN 1974). When an intruder approaches within an individual distance, the defender usually reacts with the forward display, causing the intruder to flee. However, the intruder sometimes remained at this distance for a comparatively longer time, and the defender did not react aggressively. Two variations in the forward display can be distinguished:

A) *Agitation*. In this variation the neck is straightened and directed forward, with the bill more or less square with the neck and body in a slightly upright position compared to the neck being slightly bent backwards and the bill more or less parallel to the neck while the bird is resting. Sometimes the bird performed this display with outstretched wings. This position is performed when a bird is agitated or when an intruder approaches within an individual distance (0.5–2 m from a nest). SAHIN (1983) illustrated Northern Bald Ibises in similar agitation postures (vide Fig. 3 in opus cit.).

B) *Alarm*. In this variation the neck is straightened and directed forward, with the body in a upright position while the bird utters an alarm call. It was usually performed in response to an alarm call from other birds and flight often followed. The so-called 'flight intention movement' recorded in the African Spoonbill (KAHL 1983) is an integral part of this posture.

4. 5. 2. Crouching display

The crouching display involves a sudden body withdrawal with flexed head, usually directed downwards. When an intruder flies to a nest occupied by other birds (this was recorded on a few occasions only), the nest owner usually reacted aggressively by pecking at the intruder. This caused the trespassing bird, if a male to flee, or, if it was an unmated female, to remain in the nest, performing the crouching display. A younger chick being pecked by an older sibling behaves in the same manner. The crouching display was also performed by an individual in a defensive position during the back-biting display. Under similar condition the Northern Bald Ibis performs similar crouching display (cf. Fig 2 in SAHIN 1983a). KAHL (1983) noted crouching displays performed frequently by female African Spoonbills when they confront aggressive males during pair formation.

4. 6. Breeding displays

4. 6. 1. Mutual billing

During mutual billing birds seize each other's bills and shake them vigorously with movements of their heads. Preening and other displays (mainly allopreening) often preceded or followed this behaviour (Table 4). WACKERNAGEL (1964) recorded the mutual billing as a component of the greeting ceremony. The display is probably homologous to the head shaking of the African Spoonbill (KAHL 1983). The Hadeda Ibis performs mutual billing under similar circumstances throughout the year

Table 3: Ontogeny of comfort movements in Southern Bald Ibis nestlings.

Tab. 3: Ontogenie der Komfortbewegungen bei Nestlingen des Glattackennacktrapp.

Comfort movement	Age in days			
	14	21	28	35
Body shake	–	–	–	–
Tail wag	–	–	1	3
Wing-and-leg stretch	–	2	5	11
Both wings stretch	–	1	–	–
Jaw-stretch	1	3	2	3
Scratching	–	1	1	6
Preening	–	1	15	9
Total	1	8	24	32

(SKEAD 1951). The mutual billing or the twinning together of the neck and bill of the Sacred Ibis (URBAN 1974) can be regarded as a kind of appeasement behaviour. In Southern Bald Ibises this display was observed usually in the late morning and late afternoon. Non-breeding pairs performed mutual billing more often than breeding pairs as it is the main mechanism to maintain pair bonds in non-breeding birds. Mutual billing was also recorded from immature birds roosting in the colony during the late nestling phase.

4. 6. 2. Twig shake

During the twig shake a bird grasps a twig in its beak and shakes it vigorously for few seconds. The grasping is directed downwards, sometimes in front of the bird but never upwards. Southern Bald Ibises often perform this display with a leaf of *Scilla natalensis* instead of a twig. The grasped material was often array from the nest.

This display is preceded most often by arrival of the male with nest material or by other displays (usually allopreening or mutual billing), and was usually followed by resting and other displays (Table 4). It is a characteristic display for both non-breeding and breeding pairs during the prelaying and early incubation phases. This display was recorded slightly more often during mornings than during afternoons (Fig. 4).

The twig shake could have developed from the head movements of chicks while begging for food and probably functions to maintain the pair bond. According to SAHIN (1990) the twig shake in the Northern Bald Ibis can motivate a partner to fly away. However, in this study the twig shake was not recorded in such context. Head shaking recorded by SAHIN (1990) for the Northern Bald Ibis can be considered a variation of the twig shake, as the latter was often interspersed with head shaking. These movements are also similarly performed, except for the involvement of twigs and leaves.

Ritualised manipulation of nest material was found to be strictly linked with the twig shake. It occurred at the start of the breeding season only, being performed mainly in the morning by non-breeding birds, usually by males. Ritualised manipulation of nest material was also recorded in the African Spoonbill and was also followed by preening or allopreening (KAHL 1983). URBAN (1974), however, did not observe such a ritualised display in the Sacred Ibis.

4. 6. 3. Allopreening

Allopreening is a common behaviour in both breeding and non-breeding pairs, especially during the prelaying phase. When one bird starts preening the other, it often becomes mutual with both birds being preened simultaneously on different parts of the body, usually the neck. Quite often, espe-

cially in the late afternoon, the behaviour may be interrupted with mutual billing or allopreening. Both sexes may initiate the allopreening, but the female does so more often than the male. This behaviour was never seen away from the nest. Allopreening of the young by the parent was often seen, especially in the early days of the chicks' life. Allopreening was performed more often by non-breeding than by breeding birds and the occurrence of the behaviour peaked in the early breeding phase, usually in the late morning (Fig. 3).

Allopreening was often witnessed in the Northern Bald Ibis (C. BOWDEN, pers. info.) and in the African Spoonbill (KAHL 1983; WHITELAW 1968), but was not recorded in the Sacred Ibis (URBAN 1974). It can probably be considered as an outlet for aggression. ASLO HARRISON (1964) suggested agonistic function of the allopreening. Although it also serves to keep the feathers clean (MCKINNEY 1965), its primary function is to facilitate social behaviour, hence it should be regarded as a display rather than a comfort movement.

4. 6. 4. Back-biting

In back-biting, one member of a pair, usually the male, pushes up against its mate and runs its closed bill with head shake movements to-and-fro over its mate's back and sometimes through its wing-, neck- and head feathers. This display is often accompanied by preening and calling and is included in a simplified and shortened form as a part of the greeting ceremony.

Within the nest of a breeding pair this display can occasionally be transformed into an overt attack by the male on its mate. On a few occasions, a male was seen biting its mate's feet, probably forcing her to crouch. This may be regarded as a modified back-biting display.

This display ('Schnäbeln') is regarded by WACKERNAGEL (1964) as a precopulatory behaviour in the Northern Bald Ibis. Sparring in the African Spoonbill (KAHL 1983) is probably homologous to the back-biting display of the Southern Bald Ibis. The so-called bill popping and head quivering commonly observed in the African Spoonbill (KAHL 1983) were not recorded in the Southern Bald Ibis.

4. 6. 5. Greeting ceremony

The greeting ceremony consists of a complex of displays following in rapid alternation and performed by both the male and female on their arrival at the nest. It is more intense, more prolonged and accompanied by vocalizations after longer separation of the partners, while being more simplified, of shorter duration and often silent after a brief separation. Typically, a sitting or standing bird seeing its mate approaching, utters a greeting call (recorded in 52% of 48 observations) with its head pointed upwards. The incoming bird lands beside its mate and starts the rapid alternation of displays. Back-biting by the arriving individual and twig shaking by the sitting bird are the most common displays performed. WACKERNAGEL (1964) distinguished similar elements in the Northern Bald Ibis's greeting ceremony. The greeting ceremony of the Southern Bald Ibis resembles the up-and-down display of storks (CREUTZ 1988) but it is different from that of the African Spoonbill (KAHL 1983).

The greeting ceremony was usually performed by paired birds. On average 45% of all arrivals at the nest ($n = 93$) were accompanied by this display in breeding pairs, while only 17% of arrivals ($n = 65$) prompted this display in non-breeding pairs. The greeting ceremony was recorded more often during the prelaying and early incubation phase than during later stages of breeding, and usually occurred in the early morning.

4. 7. Copulation

During copulation the male steps onto his mate's back and the female responds by crouching. While mounting the male grasps the female's beak and shakes it rhythmically. During that time the male lowers his tail while the female bends her tail to one side to achieve cloacal contact. The male re-

Table 4: Context of breeding displays (percentages) in the Southern Bald Ibis. Numbers in brackets indicate number of observation.

Tab. 4: Verhaltensweisen der Balz (in Prozent) beim Glattackerrapp. Zahlen in Klammern entsprechen Anzahl an Beobachtungen.

Breeding display		Arrival	Nest- building	Preen- ing	Rest- ing	Sleep- ing	Other displays	Other behaviour
Mutual billing	Before (91)	13	1	27	3	9	44	3
	After (79)	–	6	14	34	3	43	–
Allopreening	Before (78)	–	–	25	7	–	54	14
	After (74)	–	–	30	5	–	62	3
Twig shake	Before (15)	60	–	–	13	–	27	–
	After (15)	7	13	–	27	–	43	10
Copulation	Before (49)	41	4	4	14	–	30	7
	After (44)	24	6	21	6	–	44	3
Copulation attempt	Before (17)	6	–	18	12	–	42	22
	After (20)	–	–	5	15	–	55	25

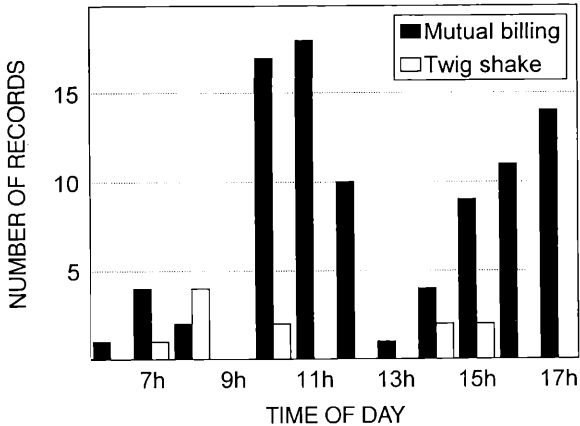


Fig. 4: Diurnal activity of mutual billing and twig shake in the Southern Bald Ibis at the Welgelegen breeding colony.

Abb. 4: Tageszeitliche Aktivität zweier Balzbewegungen („gegenseitiger Schnabelkontakt“ und „Zweigeschütteln“) beim Glattackerrapp (Brutkolonie Welgelegen).

tains balance with delicate flapping movements of his wings. Copulation persisted for 19 seconds on average (range 8–52 sec.) with most (88%) lasting for 15 to 25 seconds ($n = 43$). In three cases, after an interval of 1–2 minutes, another copulation took place. While mounted, the female starts calling after 1–6 seconds. Only in cases where copulations were not fully performed, the female remain silent. SAHIN (1982) gives very similar description of the copulation in the Northern Bald Ibis. Copulation normally took place within the nest. On seven occasions, however, birds were seen copulating outside their nests, four times within the colony and three times on a rocky outcrop located c. 200 m from the colony. Copulations often took place just after the arrival of one of the partners at the nest or after mutual billing (Table 4). Immediately after copulation the male usually lea-

ves the nest or both partners either participate in preening or they perform some displays (usually allopreening or mutual billing; Table 4). The male was never seen grasping the female by the neck as was recorded for the African Spoonbill (WHITELAW 1968); otherwise copulation of the Spoonbill (KAHL 1983) appears similar to that of the Southern Bald Ibis.

Both breeding and non-breeding birds copulate. Four copulations only were recorded in the nest of breeding pairs (ten days of observation throughout the breeding season), whereas in the nests of non-breeding pairs (four days of observation), 35 copulations were witnessed, mainly in the early morning and between 10h00 and 11h00 (Fig. 5). Sixteen copulation attempts were also recorded in the nests of non-breeding pairs during the morning (70%) and afternoon (30%). This gives, on average, five copulations per non-breeding pair per day (range 1–11) as against only 0,3 copulations per breeding pair per day. In a case where the last surviving chick died eight days previously, six copulations took place within one day.

Copulation took place throughout the breeding season with a peak in August (Fig. 5). Among breeding pairs, copulation normally ceased when the first egg was laid, but on one occasion it was observed when all eggs were already being incubated. In another instance copulation was performed again when the pair lost their young.

5. Discussion

Since the Southern Bald Ibis is a highly gregarious species, complexity in its displays can be expected. Some of these displays could have developed from comfort movements, especially those displays which were often performed during conflict situations, or when these displays were performed in alternation. Preening movements clearly have two functions in birds: they serve to keep the feathers and body clean and also strengthen the pair bond. Preening can also be a prelude to displays such as mutual billing, twig shaking and copulation.

Aggressive behaviour in the Southern Bald Ibis does not tend to be frequent, which is characteristic for other ibis species as well (DEL HOYO et al. 1994; SAHIN 1983a). In members of the Threskiornithidae, it is more common for an individual to simply touch another with the tip of the bill or to perform a threat display rather than to engage in territorial fights. Hierarchy among breeding Southern Bald Ibises may be well established for a long time in some colonies, especially the larger ones. Many sites in those colonies might be reoccupied year after year by the same birds. As they know their place within such colonies, most conflicts over breeding sites in prelaying season are avoided.

Breeding displays have been studied in a few ibis species only (BROWN et al. 1982; DEL HOYO et al. 1994; HANCOCK et al. 1992; URBAN 1974; WACKERNAGEL 1964). In the Southern Bald Ibis, breeding displays are performed more often by non-breeding pairs than by breeding birds, mainly in the prelaying season. These probably serve to strengthen the pair bond, but some displays (for example allopreening and mutual billing) may play an important role in the development of sexual and social behaviour patterns and thus serve as stimuli for other birds in the colony, synchronising their breeding activity.

Several authors have suggested that copulation is an important behaviour in the formation and maintenance of pair bonds (e.g. AGUILERA & ALVAREZ 1989; BIRKHEAD et al. 1987). Although this idea is difficult to test because it makes no clear predictions (BIRKHEAD et al. 1987), my observations seem to support it. This study shows a much higher copulation rate among non-breeding than breeding pairs. This suggests that the function of copulation is also to maintain a bond among non-breeding pairs. Since the Southern Bald Ibis is a species which forages at considerable distances from the breeding sites, and in which one member of the pair must guard the nest prior to egg laying, a relatively high frequency of copulation between members of a pair was noted as this is positively correlated with the risk of cuckoldry (BIRKHEAD et al. 1987). The low frequency of extra-pair copulations recorded at the Welgelegen colony does not support a hypothesis about the optimal use

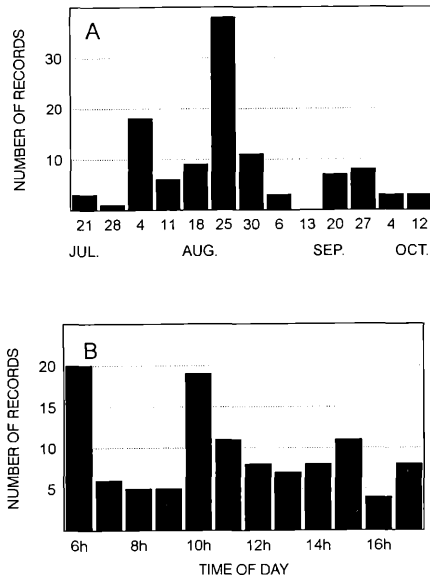


Fig. 5: Seasonal (A) and diurnal (B) occurrence of copulations in the Southern Bald Ibis at the Welgelegen breeding colony.

Abb. 5: Jahres- (A) und tageszeitliches (B) Auftreten von Kopulationen beim Glattnackentrapp (Brutkolonie Welgelegen).

of sperm production by paired males, developed for the European Spoonbill *Platalea leucorodia* in Donana National Park (AGUILERA & ALVAREZ 1989)

All comfort movements of the Southern Bald Ibis are of universal occurrence and basically have the same form, function and context as in other bird species. Variation in the comfort postures of the Southern Bald Ibis can be accounted for by only body size, morphological features (especially the long, decurved bill) and as a result of an adaptation to non-aquatic habits. Some comfort movements were not recorded for the Northern Bald Ibis (e.g. body shake, wing-and-leg-stretch, both wings stretch), but since in the Southern Bald Ibis these movements were recorded mainly in the nest during the incubation phase, these could have been overlooked in the Northern Bald Ibis if not intensive observation were made during that period.

Comfort behaviour in the Southern Bald Ibis is quite similar to that of other members of the family (HANCOCK et al. 1992; SAHIN 1983b; URBAN 1974) and even to other members of the order (DEL HOYO et al. 1994; MCKILLINGAM 1975). The rate of comfort movements is very high both in the Southern (this study) and the Northern Bald Ibis (WACKERNAGEL 1964). As a colonial species the Southern Bald Ibis is heavily infested by lice Phthiraptera (pers. observ.), the same can be true for the Northern Bald Ibis. These lice may caused local irritation, which can be released by preening. Both ibis species are regarded as highly monogamous (HANCOCK et al. 1992; SAHIN 1982), autopreening may therefore facilitate allopreening and this display can play an important role in maintaing the pair-bond. It has been suggested that the high rate of comfort movements in the ibises may also contribute to the long life of these species (SAHIN 1983b).

No clear seasonal peak in the occurrence could be distinguished for most behavioural patterns of the Southern Bald Ibis. In general, however, displays were performed more often in the early breeding season, and on a daily basis, mainly in the morning and in the late afternoon. This supports

data from the literature (e.g. DEL HOYO et al. 1994). Although all displays seems to have only slightly different diurnal rhythms, they are not all shown simultaneously. Each activity is to be seen rather at somewhat irregular intervals. These intervals can be determined both by internal factors and by changing external stimuli. In fact, each activity tends to occur in bursts, each of which is repeated several times, separated by intervals in which each occurs only sporadically.

Anti-predator behaviour of the Southern Bald Ibis is submissive. The survival value of attacking predators such as the Black Eagle or eagle owls may be doubtful; mobbing performed in such situations by the ibises may anticipate attack. In fact, no case of predation on adults has ever been recorded, in spite of high levels of predation on chicks.

6. Zusammenfassung

In einer südafrikanischen Brutkolonie des Glattackensrapps wurde das gesamte Verhaltensinventar dieser Art sowie die tages- und jahreszeitliche Häufigkeitsverteilung einzelner Verhaltensweisen erfaßt. Das Verhalten der Art zeichnet sich durch ein reichhaltiges Repertoire vielfältiger und häufig dargebotener Balz- und Komfort-handlungen aus. Balzhandlungen und Kopulationsraten nichtbrütender Paare waren beträchtlich höher als die entsprechenden Aktivitäten bei Brutpaaren. „Extra-pair copulations“ wurden durchweg in nur geringer Anzahl festgestellt. Balzhandlungen fanden generell zu Beginn der Brutsaison am häufigsten und im Tagesverlauf vornehmlich in den Morgenstunden und am späten Nachmittag statt. Verhaltensweisen aus dem Komplex Komfortverhalten entsprechen in Form und Funktion denen anderer Vogelarten. Verschiedene Bewegungsabläufe des „preening“ (Gefiederpflege mit dem Schnabel) wurden am häufigsten beobachtet und waren zugleich diejenigen mit der größten funktionellen Bandbreite.

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