

# COMPARATIVE ETHOLOGY OF THE CICONIIDAE. PART 6. THE BLACKNECKED, SADDLEBILL, AND JABIRU STORKS (GENERA *XENORHYNCHUS*, *EPHIPPIORHYNCHUS*, AND *JABIRU*)

M. P. KAHL<sup>1</sup>

Department of Ornithology  
American Museum of Natural History  
New York, New York 10024

Studies of comparative behavior are particularly rewarding if all or most of the species in a group can be encompassed. The stork family (Ciconiidae) is well suited for such a study, for it contains only 17 living species (Peters 1931). In addition to elucidating the evolution of behavior patterns within the group, ethological data furnish clues to taxonomic relationships that may be obscure or ambiguous from morphological evidence alone.

This paper reports on field studies of the behavior of the Blacknecked Stork (*Xenorhynchus asiaticus*) in Asia, the Saddlebill Stork (*Ephippiorhynchus senegalensis*) in Africa, and the Jabiru Stork (*Jabiru mycteria*) in South America. It is the sixth contribution in this series of papers (Kahl 1966, 1972a,b,c, d), which have now covered all 17 species in the family. Other data on the breeding biology of *Xenorhynchus*, *Ephippiorhynchus*, and *Jabiru* were published in Kahl (1970, 1971a).

## STUDY AREAS AND METHODS

Field observations of *X. asiaticus* were made near Bharatpur, Rajasthan, India, in August–October 1966 and August–October 1967. A total of seven active nests were located (Kahl 1970) and two of these were kept under close observation for several weeks.

Studies of nonbreeding individuals and pairs of *E. senegalensis* were made in various parts of Kenya and Uganda (mostly at Kisumu, Kenya, and Murchinson Falls Park, Uganda). Nesting observations were made at a breeding site near Kisumu, Kenya, in May–July 1966 and April–July 1967.

Six nests of *J. mycteria* were found in Corrientes Province, Argentina, in August–September 1969 (Kahl 1971a). Two of these were observed closely for several weeks at the start of the breeding season, before eggs were laid.

Nesting studies were made from blinds or elevated platforms erected within 30 m of active nests with 7× binoculars and a 15–30–60× telescope; observations were recorded in the field on a portable tape recorder and later transcribed. Both still (35 mm) and motion pictures (16 mm) were used to quantify and confirm behavioral descriptions. In the following account I have attempted to follow the general format of other papers in this series. Under each behavioral category are descriptions and comparisons of the patterns observed in each of the three

species. The names of ritualized displays (i.e., behavior patterns that show evolutionary specialization for social communication) are capitalized. The scientific nomenclature used in this paper is that of Peters (1931); suggestions and reasons for some changes in this classification are presented in the discussion.

## DESCRIPTION

Both *X. asiaticus* (figs. 1a and 1b) and *E. senegalensis* (figs. 2a and 2b) are similar in general appearance. They are the tallest of the storks, standing approximately 1.5 m high, and have a slim stature. They are predominantly black and white, with glossy black plumage on the head, neck, scapulars, wing coverts, and tail; and white plumage on the back, breast, abdomen, undertail coverts, and leading edge and flight feathers of the wing. The undertail coverts are not fluffy and plume-like as in some other storks (e.g., *Mycteria*, *Ibis*, *Leptoptilos*). Both species have long, thin, and slightly recurved bills. They are the only storks with pronounced sexual dimorphism; males have dark-brown irises (figs. 1a and 2a) and females, yellow ones (figs. 1b and 2b). The two species differ most in coloration of the legs, bill, and facial lappets. *X. asiaticus* has an all black bill, no facial lappets, and coral-red legs and feet (figs. 1a and 1b). *E. senegalensis* has a bill that is deep red in the distal third, black in the central third, and covered in the basal third with a deep red lappet that extends back to the eye. The red lappet is topped by a bright yellow lappet in the shape of a saddle, and there are two yellow, lobe-like flaps of skin hanging down 15–35 mm on either side where the rami of the lower mandible join the feathered area of the neck (figs. 2a and 2b). The legs of *E. senegalensis* are grayish-green, with fleshy-pink areas around the intertarsal joints and on the toes. *E. senegalensis* has a small, round, or oval patch of bare, deep red skin, about 40–50 mm in diameter, in the center of the breast, visible only when the bird stands erect. It was difficult to be certain, but it appeared that this bare breast-spot grew larger in diameter (an

<sup>1</sup> Present address: 661 Rudder Road, Naples, Florida 33940.



FIGURE 1. (a) Male *X. asiaticus* on nest, showing dark eye; (b) female *X. asiaticus* performing the Anxiety Stretch in response to a disturbance under the nest; note pale (yellow) iris. Bharatpur, India, October 1967.

FIGURE 2. (a) Male *E. senegalensis*, showing facial lappets and dark eye; (b) female *E. senegalensis*, showing pale (yellow) iris. Kisumu, Kenya, May 1967.

expandable air sac?) during periods of excitement.

*J. mycteria* was described in detail earlier (Kahl 1971a). In general, it is more robust than either of the other two species and is not quite as tall because of a somewhat shorter neck. It is the only stork having an all-white plumage. The variable color (deep pink to brilliant scarlet) of the lower neck is probably caused by changes in vascularization associated with excitement or display, and is often subdued after the excitement is passed. The neck contains an inflatable air sac that is often blown up, giving the bird a thick-necked appearance.

Other details of the external morphology of all three species can be seen in Kahl (1971c), where all of the storks are illustrated in color.

## BEHAVIOR OF ADULTS

### LOCOMOTION

All three species usually walk slowly and sedately on the ground or in shallow water, taking about 0.7–1.0 step/sec. The strides are long, each covering 0.8–1.2 m. When the bird is pursuing active prey in shallow water, or displaying to its mate, this gait occasionally changes to a rapid, loose-jointed run, often with wings spread and flapped slowly (see feeding behavior and Flap-Dash display, below).

Birds take flight from the ground after two or three running jumps. Launching from nests, trees, or other elevated perches consists of one upward and forward leap. The intention movements of flight include standing erect, lifting the bill slightly, sleeking the plumage, leaning forward with the neck held low and partially retracted, opening the wings, cocking the tail, and launching.

Once airborne, the wings are flapped rather slowly (Kahl 1971b), and several flaps are followed by short glides. Soaring on thermal air currents is common; the birds often ride thermals up to several hundred meters (Schomburgk 1922–23:121; Wetmore 1926:60) and then glide off to distant feeding areas. All three species fly with their necks fully extended; in *J. mycteria* the loose skin of the inflatable throat sac hangs down below the line of the neck in flight, giving the impression that the neck is partially retracted (Roosevelt 1914:91).

### FEEDING BEHAVIOR

Typically, *X. asiaticus* and *E. senegalensis* forage by walking slowly and probing vertically in the water and submerged vegetation

of shallow water marshes. The bill is held open about 50–70 mm at the tip and is raised about 200 mm above the water between probes. Aquatic vertebrates are a dominant feature of the diet (Jackson 1938:76; Ali and Ripley 1968:105). When prey is contacted, the bill is snapped shut, the head is raised, and the item is swallowed with a backward toss of the head. The birds occasionally run a few steps in pursuit of active prey (Dharmakumar-sinhji 1955:94), but most location of food appears to be by probing rather than by active pursuit. Both *X. asiaticus* and *E. senegalensis* usually forage singly or in loose pairs, with the male and female hunting independently within 30–100 m of each other. Once, in southern Uganda in December 1963, I saw as many as seven individuals of *E. senegalensis* feeding in a loose flock, but highly gregarious or cooperative feeding was never observed as it sometimes was in other storks.

*J. mycteria* commonly forages in the same manner as described above for the other two species. However, I have also seen them wading quickly through a pond teeming with small fish and feeding more actively by probing the water rapidly (ca. two times per second) with the bill held down and forward 45° in front of the vertical. In this situation, location of prey appeared to be more by tactile than visual means. Although most often seen feeding singly or in pairs, *J. mycteria* does sometimes feed in rather large, loose flocks. On 8 August 1969, I observed over 50 individuals foraging within a few hundred meters of each other in an extensive marsh in northeastern Argentina (Kahl 1971a). Other authors (Naumburg 1930; Hudson 1951) have also reported large feeding flocks in areas where food was abundant.

All three species drink by bending down, and placing the open bill in the water pointing forward. This is followed by a forward and upward scooping motion, and the raising of the bill above the horizontal to swallow. This is often repeated several times; I once saw a *X. asiaticus* drink 21 times in succession. In addition to quenching their own thirst, adults also ingest water and carry it back to the nest. I observed all three species regurgitating quantities of water (up to 1–2 liters at a time) onto the floor of the nest before or after the eggs were laid; water is also brought to the young (see Behavior of Young).

### COMFORT MOVEMENTS

The three species discussed here generally resemble the Marabou Stork (*Leptoptilos crumeniferus*) of Africa (Kahl 1966) and other

storks in most of the behavior patterns having to do with maintenance activities, i.e., preening, scratching, stretching, and thermoregulation. Spread-wing sunning postures were not observed, and excreting on the legs when overheated (Kahl 1963) was seen only rarely.

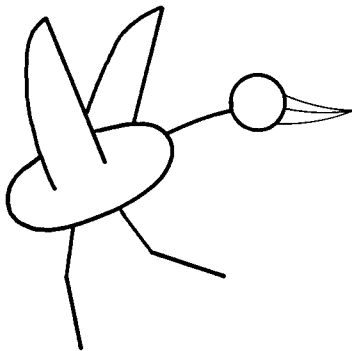
One comfort movement, rubbing the crown and side of the head with a rolling motion on the bend ("wrist") of a partially lifted wing, was commonly seen in *X. asiaticus* and *E. senegalensis*. This movement was seen only occasionally in *J. mycteria* as is the case in other storks.

#### SOCIAL DISPLAYS AWAY FROM NEST

As noted previously, the three species considered here are most often found singly or in pairs (von Heuglin 1873:1112; Ali and Ripley 1968:104; Haverschmidt 1968:28); only occasionally did I see them in groups of more than two and then the birds were rather widely spaced in loose flocks. Consequently, the aggressive and defensive social displays at natural feeding areas, observed in most other species of storks, were not seen. However, I did see a captive immature *E. senegalensis*, about one year of age, threaten a group of Yellowbilled Storks (*Ibis ibis*) in a feeding pond. The Saddlebill stood erect, opened its wings fully, lifted its bill to about 20° below the horizontal, and clattered its bill slowly (2-3 times/sec) about eight times as it advanced toward the retreating smaller birds. This display showed similarities to the Nestling Defense Display, given by young *E. senegalensis* to intruders near the nest (p. 25), and the Up-Down "greeting" display, given by adult *X. asiaticus* (p. 21).

The only social interactions noted away from the nest were between apparently mated individuals that were foraging near each other.

In such situations a similar action was observed in all three species, as follows:



Flap-Dash.

1) While walking on dry land or wading in shallow water, one member of a pair

—most often the male—suddenly stands erect;

2) Runs through water with long, loping strides and flapping wings;

3) Dashes away from mate, then turns and dashes back to within a meter or two of mate, and stands there a few seconds with wings widely spread.

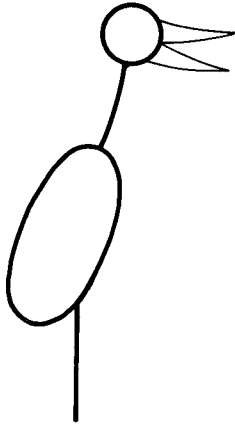
At first, I assumed this action represented the pursuit of active prey that was attempting to escape. However, I eventually came to believe that it is mainly a social signal, probably related to maintenance of the pair bond, although it may well have originated as a foraging maneuver. My reasons for this belief are as follows: (1) sometimes birds made a grab in the water at the end of a run but usually obtaining only vegetation or nothing; (2) the performance was most often seen when both members of the pair were foraging near each other (Stark and Sclater 1906:44) and frequently ended with the active member running up to the other and holding the opening position for a few seconds; and (3) the action was observed in a similar form and context in all three species.

It is significant that the Flap-Dash was noted only in *X. asiaticus*, *E. senegalensis*, and *J. mycteria*—the only species of storks with large areas of white in the flight feathers of the wing. These flashing wing patterns were conspicuously displayed during the performance.

#### SOCIAL DISPLAYS AT THE NEST

All three species are solitary nesters, building massive nest-platforms that are used repeatedly in successive seasons. Unlike many other storks, these species are often seen in pairs in the nonbreeding season suggesting a lifelong pair bond.

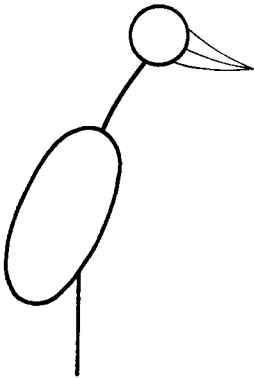
Because pair formation probably does not occur anew each season, pairs were generally rather undemonstrative at the nest, unlike the colonial storks which have a prolonged and often bizarre period of courtship and pair formation at the start of each nesting season. Pairs of these three species commonly arrived at their nests together and began nest repairs and copulation activities with little or no preliminary display. Thus, the repertoire of ritualized social behavior that I observed was less complex than in the other storks (Kahl 1966; 1972a,b,c,d). It is possible that displays additional to those described here exist, and that they are most likely to be discovered by observation of a newly formed pair during their initial breeding season.



Erect-Gape.

- 1) Bird stands very erect, with neck extended almost vertically upward and plumage compressed;
- 2) Bill held slightly below the horizontal agape about 50–75 mm at the tip.

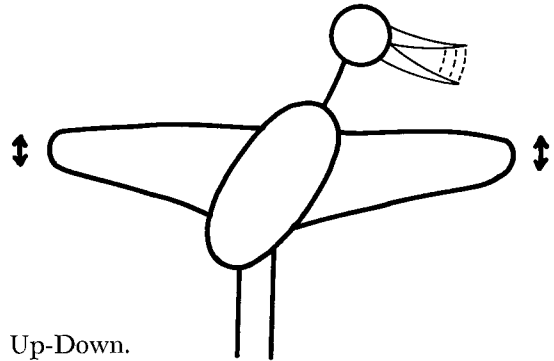
This was of similar form in all three species and, except that no vocalizations were given, appeared identical with the same display in *Leptoptilos crumeniferus* (Kahl 1966:91). It was most often performed when the bird seemed “undecided” about what to do next, as when preparing to take flight or to approach the nest from a nearby perch.



Anxiety Stretch.

- 1) Bird stands very erect with neck extended upward and forward about 45° in front of vertical;
- 2) Plumage compressed; bird peers intently at disturbing object; intermittently gives single, loud snap of the bill or short series of bill-rattles.

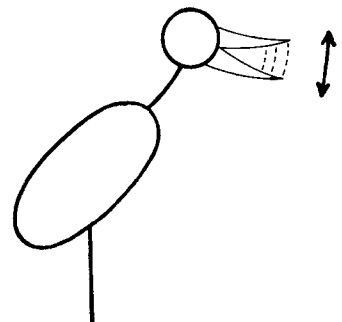
This display is similar in all three species, and is characteristic of birds on nests that are being approached by some disturbing animal (e.g., human, dog, etc.) on the ground below. Snapping of the bill usually occurs when the intruder is near (Lloyd 1895; Bent 1926:68), and often the performing bird takes flight shortly thereafter.



Up-Down.

In *X. asiaticus* (fig. 3):

- 1) Mates stand in nest facing each other; bodies held upright and crown feathers erect with necks extended vertically upward;
- 2) Wings fully open and fluttered rapidly (4–8 times/sec), with wing tips describing an arc of ca. 150–250 mm;
- 3) Bill held in approximately normal position, ca. 30–45° below the horizontal, and clattered loudly 8–10 times/sec.



Up-Down.

In *J. mycteria* (fig. 4):

- 1) Mates face each other in the nest, either standing or sitting on tarsi; bodies held erect with necks extended vertically upward;
- 2) Bill held in approximately normal position and clattered loudly 8–10 times/sec;
- 3) Head and neck swayed slowly from side to side several times, ca. 20–35° to either side of the vertical; bill raised and lowered from about 15° above horizontal to 45° below horizontal; bill of male usually passes over bill of female as both birds sway from side to side.

The Up-Down is given as a greeting display

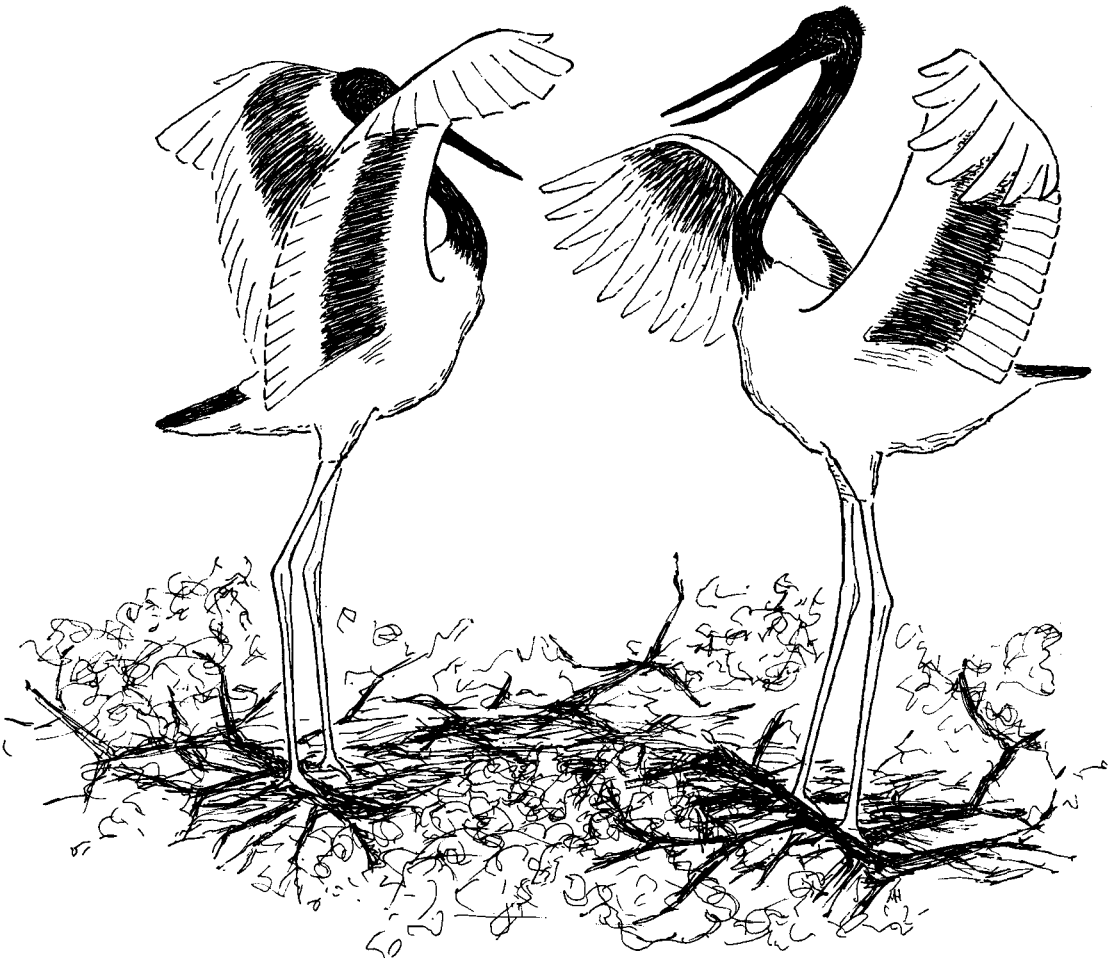


FIGURE 3. The Up-Down display as performed by *X. asiaticus* on the nest; male on right. Drawn from a 16 mm motion-picture frame by Mrs. David O. Hill.

when one member of the pair returns to the nest after an absence. Usually both birds give the display concurrently. The Up-Downs I witnessed lasted 5–10 sec in *X. asiaticus* and 8–14 sec in *J. mycteria*.

I observed and filmed the complete form of the Up-Down several times at one *X. asiaticus* nest at Bharatpur, India, but not at other nests of the same species, even though they were observed for many hours. The display was previously described by Hume and Oates (1890:266), who saw it given away from the nest at a feeding area. I also saw several displays in *X. asiaticus* that appeared to be incomplete, low-intensity forms of the Up-Down. Sometimes the birds stood erect in the nest and gave a slow bill-clatter (ca. 3–4 times/sec) without opening their wings; at other times they faced each other with their wings held open for several seconds without fluttering their wings or clattering their bills.

No Up-Downs were seen at the nests of *E. senegalensis* during approximately 146 hr of

observation during two seasons in western Kenya. Unfortunately, in both seasons I was not present to witness the first few weeks of the nesting cycle (arrival, nest repair, copulation, egg-laying); this is the period during which most storks are most demonstrative and the time when Up-Downs are most likely to occur. Thus, *E. senegalensis* is the only species of stork in the world for which the Up-Down has not been described. In view of the close similarities in morphology and behavior of *X. asiaticus* and *E. senegalensis*, I predict that the Up-Down displays of the two are similar.

Up-Downs were observed only two times in *J. mycteria*. On one occasion both birds remained standing during the display; in the other the female had been lying down on the nest before the male arrived and rose only to her tarsi to give the Up-Down. The Up-Down in *J. mycteria* showed similarities with that in *X. asiaticus*, except that the wings were not opened and fluttered and head and neck movements were more pronounced.

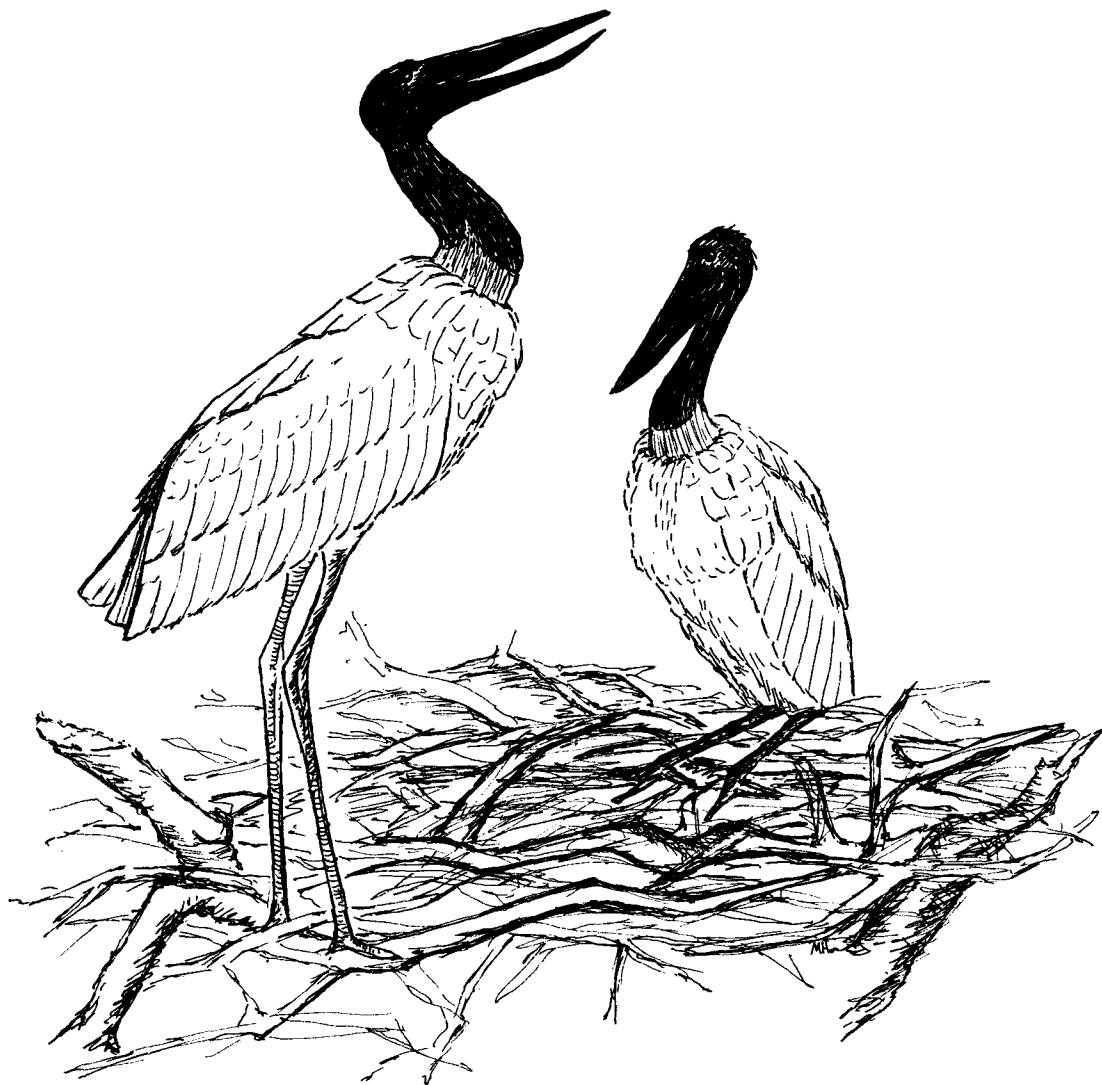
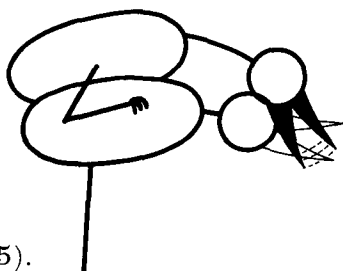


FIGURE 4. The Up-Down display as performed by *J. mycteria* on the nest. Here the female is sitting on her tarsi; at other times both birds stand during the display. Drawn from a 16 mm motion-picture frame by Mrs. David O. Hill.



Copulation  
Clattering (fig. 5).

1) Male steps slowly and sedately onto female's back from one side, hooks toes over her shoulders, and bends legs to lower himself into position for cloacal contact;

2) Female holds wings partially or fully open; male flaps wings slowly (2-2½ flaps/sec) for balance;

3) Male shakes head erratically and clat-

ters bill loudly and rather slowly (3-6 times/sec) alongside female's bill throughout the copulation.

Copulations were observed in *X. asiaticus* and *J. mycteria* but not in *E. senegalensis*. Four timed copulations in *X. asiaticus* averaged 23.8 sec (range 15-32) and eight copulations in *J. mycteria* averaged 15.4 sec (range 13-19). Usually copulations began with no apparent preliminaries, but sometimes the female appeared to solicit the male to mount her by standing with the body axis horizontal and pressing against his body.

The displays appeared and sounded quite similar in those two species, except that *X. asiaticus* females often held their wings fully spread throughout the copulation, whereas *J.*





FIGURE 5. The start of a copulation in *J. mycteria*. The male has mounted the female and is starting to bend his legs and lower his body; the female has partially closed her wings. Note sexual difference in bill size and shape. Corrientes, Argentina, September 1969.

*mycteria* females usually opened their wings fully at first and then closed them partially after the male was in position (fig. 5). During some copulations of *J. mycteria* a series of four or five gasping coughs was uttered by one of the birds.

The Copulation Clattering of both species most closely resembled that of the Marabou Stork (Kahl 1966:93), but it was performed more slowly and deliberately—as I commented in my field notes: “like an elderly couple.”

Several times I saw a female *J. mycteria* attempt (unsuccessfully) to copulate with a male that was sitting down on its tarsi in the nest. In such reverse mountings, the female performed bill-clattering and head-shaking movements that appeared identical with those given by males during normal Copulation Clattering. Reverse mountings have also been reported in the White Stork (*Ciconia ciconia*) by Schüz (1943).

#### BEHAVIOR OF YOUNG

I observed only the young of *E. senegalensis*, as my studies of the other two species were



FIGURE 6. Three nestlings of *E. senegalensis* approximately 90 days old; nestling on the left is exercising its wings, but the young were not yet able to fly. Kisumu, Kenya, July 1966.

conducted during earlier stages of the nesting cycle. When I first found the *E. senegalensis* nest, the three young were about 30 days old; I last observed them when they were approximately 90 days old. They were then nearly as tall as their parents (fig. 6) and were able to leap high into the air above the nest while exercising their wings. However, they were not yet ready to fly and I estimate that young of this species do not fledge until at least 100–115 days of age; this is considerably longer than the estimate of Pitman (1965).

The nestlings were fed by regurgitation onto the floor of the nest by both parents. The major food items (at Kisumu, Kenya, in May–July 1966) were fish, principally lung-fish (*Protopterus aethiopicus*) and catfish (*Clarias* sp.) about 150–300 mm in length.

On several occasions, particularly during the warmest part of the day, parents were seen regurgitating water to the nestlings. This behavior has been noted in several other species of storks and, like the action of excreting on the legs when overheated, shown by all storks (Kahl 1963), probably has a thermoregulatory function. During the transfer of water, the parent held its head high and re-



gurgitated the water over the begging nestlings and into their upward-pointing bills. Since the parents did not usually regurgitate water directly into the bills of the young, as did parents of Marabou Storks (Kahl 1966:97), much of the water was spilled.

Preening, stretching, scratching, and other comfort movements of the nestlings of *E. senegalensis* differed little from those of *Leptoptilos crumeniferus* (Kahl 1966).

I saw only three types of ritualized social displays given by *E. senegalensis* nestlings. When a parent arrived at the nest, the young immediately performed the Begging Display:

- 1) Nestling usually drops to tarsi, but may remain standing;
- 2) Bends forward with body axis nearly horizontal, wings slightly lifted and spread to wrist, tail cocked ca. 20° above line of the back;
- 3) Gives rhythmic "yes" nods of head with bill gaped open; weak vocalizations accompany upward movement of head.

The movements and vocalizations during the Begging Display of young *E. senegalensis* were generally similar to those of other storks, but the vocalizations were not as loud as those given by the colonial species. Perhaps it is more advantageous for the young of a solitary species to have a weak voice: the location of the nest is less likely to be disclosed to potential predators, and a loud voice is not needed to drown out other nearby young.

*E. senegalensis* nestlings often gave a bill-clattering display to their parents, usually just after the arrival of the adult at the nest (Pitman 1965). This display, which may represent an early ontogenetic stage of the Up-Down, was performed as follows:

- 1) Nestling stands erect with neck extended vertically upward;
- 2) Head and neck feathers erected; wings held loosely away from sides (but open only to the wrist);
- 3) Bill oriented toward head of adult (thus, nestling's bill was often held 20–60° above the horizontal); bill clattered rapidly (6–8 times/sec) several times.

When the nestlings were left alone as was often the case during the period of my observations when they were between 30 and 90 days of age, they reacted strongly whenever other large birds came near their nest. On various occasions, when their nest was approached by a Fish Eagle (*Haliaeetus vocifer*), a Harrier Hawk (*Polyboroides typus*), or even an army helicopter, the nestlings oriented to

face the intruder and adopted the Nestling Defense Display:

- 1) Body erect, neck extended vertically upward, bill lifted nearly to the horizontal;
- 2) Feathers of head, neck, and upper back strongly erected; wings opened to wrist and lifted up and away from sides;
- 3) Bill clattered rather slowly (2–5 times/sec) for several seconds at peak of display.

The display ceased as soon as the intruder left. It was similar to the bill-clattering display given to the parents (above), except that the feathers were more strongly erected and the wings held farther out from the body.

In both 1966 and 1967, the *E. senegalensis* nest at Kisumu, Kenya, was surrounded by a colony of Black-headed Weavers (*Ploceus cucullatus*). The ages of the respective nests indicated that the weaver colony was established after the storks had occupied the site each year. In Paraguay, parakeets are often said to nest in close association with *J. mycteria* (Naumburg 1930:90). Undoubtedly these smaller birds gain some protection by nesting close to storks (Dupond 1942; Collias and Collias 1964:149). On one occasion a Harrier Hawk landed in the tree near the nest of *E. senegalensis*—probably with the intention of raiding the weaver colony. It was driven away by threats from the nestling storks (cf. Moreau 1942:256).

## DISCUSSION

The three species treated here are the least social of the storks. Since they spend much of their time either alone or in the company of a familiar mate (they probably remain paired for life), social displays are not common.

Of the ritualized social displays that were seen, most appear to be homologous with displays previously described in other storks. Some forms of the Anxiety Stretch, Up-Down, and Copulation Clattering are shown by all storks. The Erect-Gape described in this paper is similar to a posture also shown by the three species of *Leptoptilos* (Kahl 1966, 1972a).

Of the displays thus far described in *Xenorhynchus*, *Ephippiorhynchus*, and *Jabiru*, only the Flap-Dash is unique to the group. This display was probably derived from movements used in the pursuit of active prey during foraging and was seen in a similar form and context in all three species. In established pairs it probably serves to strengthen and maintain the pair-bond, and it may also function as a courtship display in the initial formation of new pairs. The presence of large white areas

in the wings of all three species makes this display particularly striking.

*X. asiaticus* and *E. senegalensis* resemble each other closely in many aspects of behavior and morphology (cf. Dekeyser 1962:1229), and they are the only two storks with a sexual dimorphism in iris color. I see little justification for maintaining these two species in monotypic genera and suggest that they be combined under one genus, *Ephippiorhynchus*.

As was pointed out in a previous paper (Kahl 1971a), *Jabiru* shares a number of traits with the genus *Ephippiorhynchus* (including *Xenorhynchus*) and also with the genus *Leptoptilos*. The Up-Down of *Jabiru* shows obvious affinities with that of *Ephippiorhynchus* [= *Xenorhynchus*] *asiaticus* in the position of the head and body during clattering, but the wings remain closed. *Jabiru* also resembles *Ephippiorhynchus* in flying with the neck outstretched, in nesting solitarily, in feeding behavior, and in the Flap-Dash. However, in various morphological characters (e.g., massive bill, inflatable throat sac, unfeathered head and neck, iris color), *Jabiru* more closely resembles *Leptoptilos*. Because *Jabiru* shares a number of characters with both *Ephippiorhynchus* and *Leptoptilos*, yet is distinct from each of those genera, I recommend that it be retained as a monotypic genus.

Due largely to the "link" provided by *Jabiru*, the genera *Ephippiorhynchus* (including *Xenorhynchus*), *Jabiru*, and *Leptoptilos* are grouped together in a tribe, Leptoptilini (Kahl 1971c).

## SUMMARY

This paper, the sixth in a series covering all the stork species in the world, describes behavior observed in wild populations of the Black-necked Stork (*Xenorhynchus asiaticus*) in Asia, the Saddlebill Stork (*Ephippiorhynchus senegalensis*) in Africa, and the Jabiru Stork (*Jabiru mycteria*) in South America.

Ritualized and nonritualized behavior patterns are described and compared. Since the three species treated here nest solitarily and probably remain paired with the same mate in successive seasons, social displays are uncommon. Ritualized displays include the Flap-Dash, a display given at feeding areas, and the Erect-Gape, Anxiety Stretch, Up-Down, and Copulation Clattering—all performed at the nest.

On the basis of the behavior described here, in addition to morphological characters, I suggest combining *Xenorhynchus asiaticus* and *Ephippiorhynchus senegalensis* into one genus, *Ephippiorhynchus*, and retaining *Jabiru myc-*

*teria* in a monotypic genus. Those three species, along with the three species in the genus *Leptoptilos*, comprise the tribe Leptoptilini.

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