AN ETHOLOGICAL COMPARISON OF THREE STORKS: CICONIA BOYCIANA, C. CICONIA, AND C. MAGUARI

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CHAPTER I

INTRODUCTION

Taxonomic relationships of the three storks addressed in this study have not been unequivocally established. Ciconia maguari, which has been considered historically to be in the monotypic genus Euxenura (e.g. Peters 1931), was placed in Ciconia by Delacour and Mayr (1945) and Kahl (1971a, 1972a, b). However, some authorities have continued to treat the Maguari Stork separately (e.g. Blaker 1977; Hanagarth and Riberia 1985; de Schauensee and Phelps 1978).

Three geographically isolated populations of Ciconia ciconia are usually recognized and treated as sub-species: C. c. ciconia, C. c. asiatica and C. c. boyciana (Kahl 1972a). Little is known of C. c. asiatica but it seems to be similar to the nominate species, at least superficially. Though the boyciana and ciconia populations are indisputably congeneric, their status as conspecifics is more questionable (Kahl 1972b; King 1981; Luthin 1987). Some authorities have remarked on the close morphological similarities between C. maguari and the boyciana population (e.g. Heinroth and Heinroth 1924-1931; Kahl 1972a; Schrenk 1860), and some authorities have suggested that closer affinities may lie between *C. maguari* and the *boyciana* population of *Ciconia* than between *ciconia* and *boyciana* (W. Grummt, C. Luthin, B. Schmitt pers. comms.).

The *boyciana* population is considered endangered (King 1981), thus its taxonomic treatment may have political repercussions; conservation priorities are likely to be higher for a full species. Additionally, conservation efforts based on data collected from the *ciconia* population could be ineffective and even detrimental if important differences exist.

Comparative behavioral studies, when considered in view of ecological constraints, could be effective in defining important interpopulation differences and associated management considerations: comparative studies of phylogenetically closely related species have natural "control" of many variables, and rely only on relative, rather than absolute, measurements (Mock 1980a). In-depth comparative behavioral study to determine subtle taxonomic relationships is particularly appropriate for the Ciconiidae, because much of the taxonomic work to date has been based in this approach (Kahl 1972a, 1972b; Wood 1983, 1984).

Objectives of the present study are threefold: to describe selected behavioral displays in terms of quantifiable elements, 2) to compare behaviors of captive birds with data available for wild populations, and 3) to identify morphological and behavioral differences among the three species in relation to their ecology and taxonomic treatment. Results from the study not only provide discrete data in motor patterns which are directly applicable in phylogenetic analysis, but are also heuristic, suggesting areas that warrant further study in natural populations.

Henceforth the following denotations will be used in this paper: *C. boyciana*, *C. ciconia* and *C. maguari*, in accordance with the classification scheme used by the International Council for Bird Preservation/Waterfowl Research Bureau Specialist Group on Storks, Ibises and Spoonbills (Luthin 1987). *Ciconia ciconia* represents the most western population of *C. ciconia*, as information on *C. c. asiatica* is limited.

CHAPTER II

LITERATURE REVIEW

General Description

Ciconia boyciana, *C. ciconia*, and *C. maguari* are similar in appearance; all have red legs and feet, a white body plumage and primarily black flight feathers. Facial characteristics are illustrated in Fig. 1. As in all storks (Kahl 1978), males tend to be somewhat larger in both body and bill size (Table 1). Some interspecific size variation occurs: *C. boyciana* is the largest of the three, and *C. ciconia* the smallest (Table 1). Both *C. boyciana* and *C. maguari* have a proportionally longer bill than *C. ciconia* (Fig 1). Morphological characteristics of these storks throughout ontogeny are provided in Table 2.

Distribution and Status

The three species are found in association with wetlands throughout their range, though migratory habits and climatic zones differ (Table 3). *Ciconia boyciana*, the Oriental White Stork, is restricted to the Far East, migrating from breeding areas in the U.S.S.R. and China that are along the Amur and Ussuri Rivers and their tributaries, to winter along the Yangtze river and its surrounding lakes in southeastern China (Luthin 1987). Sedentary populations were once found in Japan and the Koreas, where the bird was considered common (Austin 1948; Campbell 1892; Sakomoto 1966). Recently C. boyciana has been extirpated from Japan and South Korea, its status in North Korea is not known (King 1981; Luthin 1987).

Ciconia ciconia, the European White Stork, is a primarily palearctic migrant of wide distribution. Though most breeding occurs on the Eurasian continent (north to Denmark and Leningrad, U.S.S.R., west to the Netherlands and east to Asiatic Turkey, Iraq and Iran), breeding also occurs in northern and southern Africa. Most winter in Africa, though some winter in the Middle East and on the Indian subcontinent (Haverschmidt 1949; Lack 1966; Kahl 1978). A drastic decline of C. ciconia throughout western Europe has been well documented, however populations in eastern Europe are more stable (Lack 1966; Luthin 1987; Schüz 1973).

Ciconia maguari, the Maguari Stork, is found throughout northern and south-central South America in low lying, seasonally flooding wetlands; primary range includes the Chaco and northern Argentina (Luthin 1987; Thomas 1985). Breeding populations in Venezuela are declining (Luthin 1987). Population trends have not been monitored in south-central South America, but they are still highly visible there (F. Elize, F. Hayes, C. Luthin pers. comms.).

Natural History

Feeding Ecology and Social Behavior

All three species feed visually, opportunistically foraging on almost all invertebrates and vertebrates of suitable size, however some difference in types of prey taken does occur. *Ciconia boyciana* feeds almost exclusively on aquatic animals, *C. ciconia* primarily relies on terrestrial prey, particularly insects, and *C. maguari* mainly feeds on aquatic items, but also takes terrestrial prey where these are abundant (*C. boyciana*: Austin 1948; Rosylakov 1977; Winter 1982, *C. ciconia*: Cramp 1977; Haverschmidt 1949; Lack 1966, *C. maguari*: Hudson 1920; Kahl 1971b; Thomas 1985). During the non-breeding season all three species tend to forage in flocks, but maintain some distance between individuals. Family groups are not maintained during this period, and flock size generally depends on food availability. During the reproductive season non-breeding birds of each species also form small groups. (*C. Ciconia*: Cramp 1977; Rockingham-Gill and Mundy 1985, *C. boyciana*: Dymin and Pankin 1975; Rosylakov 1977, *C. maguari*: Hudson 1920; Thomas 1985).

Reproduction

All three species display nest site fidelity, and at least in *C. ciconia* and *C. maguari*, it has been shown that birds tend to return to their natal area (*C. boyciana*: Austin 1948; Fei et al. 1983; Won 1973, *C. ciconia*: Zink 1963, 1967, *C. maguari*: Thomas 1986). Generally, breeding partners in *Ciconia* are determined by nest site selection, and courting takes place at the nest (Kahl 1971a). *Ciconia maguari* may be the exception to this rule; there is evidence that courting takes place in assemblies in breeding areas prior to removal to breeding sites (Thomas 1986, pers comm.).

Courtship of unfamiliar storks at the nest can involve agonistic encounters that become quite violent. Typically, the male arrives at the nest first, and defends it against all conspecifics. An approaching female is repeatedly attacked and repulsed by the male, only becoming accepted if she persists in her efforts long enough for the male's hostility to abate. Some males are sporadically aggressive to the female for a short period following initial acceptance. Social displays of high frequency and intensity are performed throughout these first stages of pair formation (Kahl 1971a, 1972a).

Some characteristics of reproduction of the three species addressed here are compared in Table 3. Both sexes participate in nest building, incubation and parental duties in the Ciconiidae (Kahl 1971a, 1972a). Nests of *C. boyciana* and *C. ciconia* are built on elevated structures. The nests are similar in construction (Table 3), but those of C. boyciana are generally larger (Winter 1982), in accordance with the larger size of the bird.

Nests of C. maguari are built in trees or shrubs in the northern extremities of its range (Kahl 1971b; Thomas 1986, Zahl 1950). Nesting on elevated sites is probably opportunistic in this species; C. maguari is the only stork that typically nests on the ground. Ground nests fabricated from piles of aquatic vegetation by this stork throughout most its range are quite unlike nests of other storks, more closely resembling nests of Anhimidae (Screamers) or Gruidae (cranes) (Kahl 1971b).

Average clutch size is three to four eggs for all three storks. Eggs are laid at two to five day intervals, and the young hatch asynchronously (C. boyciana: Rosylakov 1977; Winter 1982, C. Ciconia: Haverschmidt 1949; Jovetic 1961, C. maguari: Hudson 1920; Thomas 1986). Incubation time may be slightly shorter for C. maguari than C. ciconia and C. boyciana (Table 3).

Storks feed their young by regurgitating boluses of whole food items in the floor of the nest. Parents brood or shade, and sometimes even water, the young until they can thermoregulate well on their own (Kahl 1978). A behavior that has been frequently observed in C. ciconia is "Kronism"; in which parents typically suddenly become aggressive to an offspring, kill it, and consume it if the carcass is small enough. Multiple offspring may be killed, but usually not simultaneously. There is a large size difference in the nestlings, and killing of offspring may be a form of brood reduction when food supplies are inadequate (Haverschmidt 1949; Jovetic 1961; Lack 1966; Schüz 1984).

Development of the Young

Some behavioral characteristics of the three species during the nestling stage are related in Table 4, and morphological characteristics in Table 2. The most apparent disparity in appearance between *C. maguari* and the other two species is the black plumage and primarily black soft part coloration of the former during most of the nestling stage (Thomas 1984). Other nestling storks are typically white in plumage.

Length of dependency on the parents appears to be different between species (Table 4), and is longest for *C. maguari*. Not much data is available on juvenile and subadult behavior, but immature *C. ciconia* are known to wander in flocks in Africa during the breeding and non-breeding season. Subadults also sometimes appear in breeding areas on the Eurasian continent during the breeding season, occasionally attempting to build nests (Haverschmidt 1949; Jovetic 1961; Schüz 1973; Zink 1963).

CHAPTER III

METHODS

Study Sites and Animals

Thirty-nine storks in four zoological institutions were studied between 1985 and 1987 (Table 5). Observation periods, sites, times, and an inventory of study subjects, including ages and number of each species observed are reported in Table 5. Observations of juveniles and adults were usually made from blinds or public viewing areas. Most observations were at distances of less than 30 m; observations at longer distances were made using 7 X 50 binoculars. Hand-reared nestlings were observed from distances of 0.5 to 10 m without using a blind. Efforts were made to sample each group during all daylight hours on a regular basis, and some night observations were made.

Some _C_. _maguari_ (N = 10) were observed in more than one setting and/or with different enclosure mates. Excluding attempts to introduce groups of unfamiliar individuals, this species was kept in groups of two. Six groups of two Maguari Storks were observed in four monospecific enclosures ranging in size from 71 X 40 m to 25 X 9 m. Five groups of two individuals were observed in three mixed mammal and bird species enclosures that were 36 X 23 m, 78 X 18 m, and 57 X 21 m in size.

Adult and juvenile C. ciconia were confined together in a 33 X 32 m enclosure shared by a variety of anseriform birds. Adult C. boyciana were in 14 X 4 X 4 m monospecific enclosures, housed individually, but adjacent to conspecifics. One male and one female C. boyciana were housed together in a 14 X 8 X 4 m enclosure. Hand-reared nestling C. ciconia, and C. boyciana were kept with siblings in nests until 51-60 days of age, at which time they were placed in 14 X 3.4 X 2.3 m enclosures.

All C. maguari observed were imported from Argentina and Paraguay in 1971 and 1972 (C. Chase pers. comm.). Zoo records indicate that most of these individuals were adults on arrival, one was a sub-adult. Adult C. boyciana were removed from nests before fledging in the Lower Amur River area of the USSR in 1977, 1980 and 1981, and were reared thereafter with siblings or other same aged conspecifics in captivity (S. Smirenskii pers. comm. to K. Archibald; Wennrich 1982). During the present study two C. boyciana were parent-reared to 5 and 18 days, at which times they were removed for hand-rearing. Another two from the same clutch were hand-reared from hatching.

Adult C. ciconia were caught as adults in West Germany, and the juveniles were produced in 1986 by the same pair that raised two young during the study (H. Zink pers. comm.). The two C. ciconia nestlings hand-reared during this study were siblings donated at two and four days of age from a reintroduction project in West Germany.

Excluding nestling C. ciconia, all C. ciconia and C. maguari studied were rendered flightless, either by pinioning or wing-clipping. Nestlings and adult groups of C. boyciana were physically unaltered, but flight in their covered pens was restricted to landing on and flying from high perches through spatial limitations. Alteration of locomotor patterns would be expected to affect other aspects of behavior in captive storks, including ability to perform some social displays, particularly those involving aerial movements. Social displays of Ciconia that are normally executed on the ground (Kahl 1972a) and/or involve only intention movements of locomotor patterns (Daanje 1950) would not necessarily be affected.

Data Recording and Analysis

Time budget information was gathered by recording the activities of individuals observed at 2 min intervals (C. maguari and C. boyciana) and 5 min intervals (C. ciconia) on prepared data sheets. An ethogram of 27 activity categories was used (Appendix A). Groups ranging from 2-11 individuals were scanned from left to right immediately following a signal emitted from a preset West Bend electric timer. Each bird's location within the enclosure and its posture (standing, sitting on the tarsi, sitting directly on the substratum, or lying on the substratum) were concurrently recorded. Amount of time spent perching was noted for C. boyciana.

Social interactions, reproductive activities and some maintenance patterns were recorded as they occurred in notes or on magnetic tape, and these records provided data on frequency of occurrence. Video tapes of the same activities were made using a National NV-M1 Cam-Corder when possible to permit analyses and quantification of components of behavior patterns. The video tapes were condensed from the original 101 hours to 18 hours of footage that were analyzed for this particular study.

Display postures were examined using slow and stop actions on a Panasonic PV-1642 Video Cassette Recorder. Amplitude extremes of movements were measured on three planes with a protractor (Fig 2). An Advance quartz stop watch was employed to analyze duration of behavior sequences in 1/100 s increments. Vocalizations and mechanical sounds documented on video tapes were transferred to recording tape at 19 cm/s via a Sony reel-to-reel tape recorder and then analyzed on a Multigon Uniscan Sound Analyzer.

Typical performances of social displays and contexts in which they are performed were determined, and variations in postures, amplitude of movements and vocalizations identified. Individual and sexual variations were analyzed statistically using standard deviations and comparisons of sample means.

Terminology and Assumptions

Reproductive Activities

Mate (vs. enclosure mate) - a conspecific with whom courtship activities (minimally) were engaged. Two male C. maguari participated in such activities together, and were thus considered a "same-sex" pair.

Breeding Pair - a pair of conspecifics (male-female) that produced and incubated eggs that did not necessarily hatch.

Courtship Activities - includes nest building, exchange of plant material, copulation activities, and adult allopreening.

Reproductive Activities were divided into the following categories: 1) courtship phase - courtship activities performed, 2) incubation/chick rearing phase, 3) post-reproductive phase - courtship activities were reinitiated following the incubation/chick-rearing phase.

Social Signals

A social signal is "any behavior pattern which often and effectively conveys information from one individual to another, even if it has another function" (Moynihan 1970).

Social signals described here are primarily in the form of ritualized behaviors, behaviors that have specialized through phylogeny to permit or facilitate communication; i.e. "displays" (Morris 1957; Moynihan 1970). Terminology used in discussion of social signals is after Smith (1965, 1968, 1969):

Message - that which is encoded in the signal sent by the communicator, the message is in some way descriptive of the communicator's central nervous system state (the semantic level of communication).

Meaning - the recipient's interpretation of the signal, this is peculiar to the recipient, and is dependent on context (the pragmatic level of communication).

Context - a term for anything that accompanies the signal; the immediate context is the other sensory stimuli that the recipient simultaneously is receiving along with the signal. Historical context refers to the genetic program of the individual.

Displays for Ciconiidae have been described by Kahl (1966, 1971a, 1972a, b, c, d, e, 1973), whose comparative behavioral study is the definitive work on this family (Parkes 1978). His suggestions for taxonomic treatment of Ciconiids are the most widely used (e.g. A.O.U. 1987; Clements 1981; Howard and Moore 1980; Mayr and Cottrell 1979; Soothill and Soothill 1982; Walters 1980).

Kahl's terminology is used wherever possible in this paper to avoid duplication of effort and to provide consistency. Furthermore, comparison of results here with Kahl's work offers an opportunity to assess effect of captivity on behavior of study subjects. Alternative terms proposed herein are based on physical appearance during display performance for some behaviors, in conformity with current ethological practices.

Several behaviors not described by Kahl appear to have signal function and are described below. Criteria for such treatment included stereotypy or exaggeration of behavior patterns (Moynihan 1970) coupled with multiple performances in similar contexts (Lewis and Gower 1980; Smith 1965). Presence of components common in displays, e.g. generalized or specialized feather erection (Morris 1955), or presentation of "weapons" in agonistic displays, also aid in identification of displays (Marler 1968). Almost all vocalizations are displays (Moynihan 1970).

CHAPTER IV

RESULTS

Social Signals

Basal Neck Feather Erection

Essential Elements. Basal neck feathers are erected.

This behavior was observed in all three species. Although mentioned by Kahl as a component of displays performed by Ciconiidae (Kahl op. cit.) it has not been described as a separate display.

Variations. Posturing during, and duration of this display are highly variable.

Contexts. Erection of the basal neck feathers may be performed in response to various disturbances and interactions, including those involving zoo visitors and personnel, other species and conspecifics.

Comments. The neck feathers of the three species addressed here have a reduced number of barbs that are spaced more widely on the rachis than those of contour feathers. Barbs on the neck feathers are devoid of interlocking barbules, thereby creating a filmy net effect which is particularly noticeable in _C_. _maguari_. Feathers in the basal neck area are quite long; some taken from _C_. _maguari_ measured more than 18 cm.

Basal neck feather erection is an integral part of many of the displays described here. Erection of these feathers is also commonly observed in resting _Ciconia_ (Kahl 1972a). Basal neck feathers are sometimes erected in other contexts; this may be an autonomically controlled behavior with no signal function in some situations. Ritualized erection of basal neck feathers possibly has a generalized function, e.g. to signal awareness of a situation or to draw attention to the performer. Alternatively, message content may vary with context.

Basal neck feather erection was observed to be of singular importance in social behaviors of _C_. _maguari_ in this study. Significance of this signal in social interactions of this species is in agreement with Thomas's (1986) observations concerning _C_ _maguari_ in Venezuela, wherein several references to erection of the neck feathers are made.

Forward (Forward threat, Kahl 1972a)

Essential _Elements._ The back is arched (Fig. 2), the neck is retracted, and the bill positioned below the horizontal. Wings are folded, and the tail held in the normal position (Fig. 2). The back, basal neck, and head feathers are erected. The stork thus approaches its opponent with a "jerky, stalking gait" (Kahl 1972a).

Forwards were observed here in C. ciconia (Fig. 3), and C. maguari but not C. boyciana. These were similar to descriptions provided for Ciconia by Kahl (1972a).

Variations. Bill position ranged from 15-55° below the horizontal in five Forwards of C. maguari analyzed. Erection of back, head and basal neck feathers varied, ranging from slightly to fully erect. There was little variation in neck retraction (ca. 20-35° behind the vertical axis) or body posture (ca. 15-35° above the horizontal axis) in Forwards of this species.

Forwards of C. ciconia sometimes involved a stronger retraction of the neck (to 45° behind the vertical) and arching of the back (to ca. 65° above the horizontal) so that these were contiguous. An adult male was observed gaping his bill ca. 25° three times during a 16.4 s performance.

Contexts. Ciconia maguari primarily performed Forwards during introductions of unfamiliar conspecifics. During four introductions observed, a single bird or pair (male-male and male-female) frequently directed Forwards to the less aggressive individuals. Possibly because of the receivers' inability to entirely escape the situations, threats would often develop into chases. Two males also directed this display toward King Vultures (Sarcoramphus papa).

Adult C. ciconia (both sexes) performed 98% of the 45 Forwards recorded for this species. Some Forwards (21%) were directed towards Lilford's Cranes, Grus grus lilfordi and Canada Geese, Branta canadensis. Juveniles were recipients in 57% of 30 intraspecific Forwards executed. Forwards were directed at birds of the same or other species at feeding stations (6%), that approached defended nest sites (45%), or that engaged in play or agonistic interactions (20%) near the performer. No obvious stimuli were apparent in 27% of the Forwards performed. One Forward, executed by an adult on a nearby nest, was directed towards two juveniles that were nest building on a recently abandoned nest.

Comments. Kahl (1972a) noted that the Forward differs from overt aggression in its deliberate movements and in the rarity of actual attack. The signal provided by the display was apparent to the receiver from distances of up to 10 m in this study, as efforts were made to avoid the performer in this range. Forwards typically resulted in the departure of the receiver; even in the C. maguari introductions physical contact was seldom involved when this display was given.

The Forward appears to be an adult display; it was not observed in nestlings up to 72 days of age, and only once in one-year old juveniles. No Forwards were performed by _C. boyciana_ housed together or separately. Because the Forward is a display that may be homologous throughout the Ciconiidae (Kahl 1966, 1972a, c, d, e, 1973) it is assumed that its absence in _C. boyciana_ studied here was due to the small number of birds capable of physical contact.

Wing Flash

Essential Elements. The neck is retracted, the back arched, and wings held upwardly extended. Head, back and basal neck feathers are strongly erected. The stork rapidly (walking quickly, running or hopping) approaches its opponent in this posture (Fig. 4).

Wing Flashing was observed in all three species here, but was not described by Kahl (1966, 1972a, c, d, e, 1973) for any member of the Ciconiidae.

Variations. Mean duration of this display was 3.5 s (SD = 2.2 s, range = 0.6-10.3 s) in 60 displays of Maguari Storks timed. The neck was always held above the horizontal axis in this species. Bill position ranged from above to below the horizontal, with 88% (N = 51) being below. The back was strongly arched in some performances, tipping the body forward. Tail position ranged from ca. 55° below the horizontal axis to 20° above, and was spread in some displays (generally those involving running or hopping). Wings were held more than 50° above the horizontal axis, measured from the point of attachment of the humerus to the body, in 89% (N = 65) of the C. maguari displays analyzed, and ranged from ca. 30-70°.

Mean duration of six Wing Flashes by C. ciconia was 2.7 s (S.D. = 1.8). Wing Flashing of C. ciconia differed from that of C. maguari in wing and neck positioning and presence of an auditory element. Wings were generally held lower in displays of C. ciconia; mean angle of wing position above the horizontal was 15° in six performances analyzed (range = 6-32°, S.D. = 10). A form of the Wing Flash in which the neck was lowered below the horizontal and the bill pointed downwards was observed only in C. ciconia. This form was recorded four times, and was performed by three males and one female.

Performances by adults and juveniles generally included a hissing vocalization that was audible in 12 of 17 displays. Snapping of the bill was recorded in three Wing Flashes performed by three nestling C. ciconia ca. 60 days of age. A vocalization similar to that of C. ciconia was heard in two of eight encounters involving adult C. boyciana.

Wing Flashes were sometimes accompanied by jabs (forceful thrusts of the bill, initiated with neck retracted). Jabs were associated with 53% of 81 Wing Flashes by C. maguari analyzed; 51% of the 43 jabs resulted in physical contact. One pair of C. maguari performed 77% of the jabs and 95% of the physical contact during interspecific nest defense. Wing Flashes were accompanied by jabs in 25% of 20 performances by C. ciconia, and 36% of 14 by C. boyciana recorded. Physical contact was rare in C. ciconia. Jabs of C. boyciana were made through chain-linked fencing, thus physical contact was prohibited.

Contexts. Wing Flashes were executed during intra- and interspecific encounters, and were performed by all age groups. One male C. maguari habitually executed a Wing Flash when approaching the feeding station in a multispecific enclosure, effectively dispersing the avifauna present, including his conspecific female enclosure mate. This behavior was also exhibited by the other five Maguari Storks kept in multispecific enclosures, but was not recorded in the other two species.

Wing Flashes of C. ciconia and C. boyciana were executed by the opponents simultaneously in 5 of 15 and 6 of 8 encounters respectively. The hissing often heard, lack of physical contact and stereotypy of the movements distinguished these encounters from other non-display agonistic behaviors in which wings were opened.

Comments. Although performed in much the same contexts in all species, the Wing Flash had a much more prominent role in the display repertoire of Maguari Storks. This species tended to perform Wing Flashes in contexts that *C. ciconia* would execute a Forward. Wing Flashes were primarily restricted to close situations, as the display was usually initiated within 5 m of the receiver(s). This contrasts with Forwards, which were often performed at longer distances. The message incorporated in the Wing Flash consistently appeared to be "Leave!". This display commonly resulted in relocation of the receiver; if it did not, actual attack almost invariably followed.

More data are needed to determine whether bill snapping in nestling *C. ciconia* Wing Flashes observed in this study serves the function of, and is replaced during ontogeny by, the whistling vocalization typical of adult and juvenile *C. ciconia* and perhaps *C. boyciana*.

Arch-Gape

Essential Elements. The stork arches its back, and retracts the neck while holding the bill slightly open and below the horizontal. Simultaneously, the wings are slightly raised. Strong erection of the head feathers begins when the neck is retracted to the extreme back position, and is maintained through the remainder of the display. Basal neck feathers are strongly erected throughout the entire performance (Fig. 5).

Arch-Gapes were recorded in all three species observed here. The Arch-Gape was not described by Kahl (1966, 1972a, c, d, e, 1973) for any member of the Ciconiidae.

Variations. Duration of this display ranged from 0.6 to 2.8 s (mean = 1.9 s, SD = .96, N =11) in Maguari Storks. Extent of the bill gape varied from 12° to 27°, and retraction of the neck did not extend more than 30° behind the vertical axis. Tail was variable, ranging from ca. 25° above the horizontal axis to 65° below. Slight spreading of the tail was observed in some performances. The Arch-Gapes observed in the other two species fell within these variable ranges. The wings were usually only slightly raised during this display, while still in the folded position; rarely they were fully opened and upwardly outstretched.

Contexts. This display was almost invariably directed towards conspecifics that rapidly approached the performer, or passed closely by (within 3 m) while moving quickly. Maguari Storks directed Arch-Gapes to gulls or pigeons flying within 1 m above the performer on three occasions. Arch-Gapes were recorded 37 times (performed by 8 of 10 individuals) during observations of Maguari Storks and once each during observation of C. ciconia and C. boyciana. The Arch-Gape recorded in C. boyciana was performed by a nestling 65 days of age when rapidly approached by a sibling. Arch-Gapes of Maguaris were sometimes directed towards conspecifics with whom a pair bond had been established.

Comments. The term "Arch-Gape" was chosen for this display because it highlights the two most prominent elements: gaping of the bill and the retracted posture. Two other gaping displays, Gaping and Erect Gape, have been described by Kahl (1966, 1972c) for other genera of the Ciconiidae, but appear to be unrelated to the Arch-Gape.

Gaping has been interpreted by others as a threat (Harrison 1965; Lewis and Gower 1980; Moynihan 1955a). Marler (1968) noted that threat signals in which the bill is opened and angled at the opponent and the head held low are prevalent in birds. Moynihan (1955a) suggested that gaping is a strong indication of pecking, which in a hostile situation is probably an intention movement of attack. Arch-Gape displays presumably contain the message "keep your distance", based on contexts in which they are observed, posturing (erected head and neck feathers, gaping, arched back), and pre-attack movements involved (retraction of the neck, lifting of the wings). It was often difficult to ascertain whether the behavior of the recipient was altered when a Arch-Gape was directed to it. Immediate social contact between the performer and recipient rarely succeeded performance of an Arch-Gape; this might be interpreted as successful message transmission.

Based on the Arch-Gapes observed in this study, this display may have a more prominent role in behavior of Maguari Storks than in the other two species.

Bill Duel

Essential Elements. Two storks face each other, standing less than 0.5 m apart. Both birds are erect, with the mantle angled ca. 50° below the horizontal axis and the neck straight, just behind the vertical axis. Feather erection is limited to slight, intermittent erection of the front neck feathers. Bills are horizontal, and contact between the bills is made in the form of light blows with little force as the birds alternately extend and retract their necks (one bird extends the neck while the other one retracts it). Sometimes one individual grabs, or attempts to grab, the bill of the opponent rather than striking at it. Some blows do not result in contact, though the bills are parallel or adjacent in position (Fig. 6).

Bill Duels were performed by all three species, but were not described by Kahl for any of the Ciconiidae (Kahl 1966, 1972a, c, d, e, 1973).

Variations. Two Bill Duels performed by *C. maguari* were 1.3 s and 1.9 s in duration. Mutual blows were dealt two and four times during these incidences, and the wings were folded. Bill Duels executed by adult *C. boyciana* were similar, but Bill Duels observed in juvenile *C ciconia* and nestling *C. boyciana* were sometimes performed with the wings extended. These performances were more prolonged in duration; one by *C. ciconia* was 13.1 s, and three between *C. boyciana* nestlings were 4.0, 4.1, and 6.5 s. More "blows" were delivered in these longer performances.

Contexts. Bill Duels in Maguari Storks were observed seven times and involved three pairs of enclosure mates (male-male and male-female). One male Maguari Stork also engaged in Bill Duelling on two occasions with an American Wood Stork (*Mycteria americana*) housed in the same enclosure. All but one Bill Duel involving *C. maguari* occurred during feeding sessions. Bill Duels between juvenile *C. ciconia* were observed twice, and between nestling *C. boyciana* (49-57 days of age) three times; these occurred in conjunction with play behaviors. Two *C. boyciana*, a male and a female housed next to each other, Bill Duelled three times through the mesh of a chain-linked fence.

Comments. Although form of physical contact (blows or such intention movements) involved in Bill Duels signify an agonistic behavior, vertical posturing, limited erection of feathers and weakness of blows dealt indicate a lack of serious hostility. Performances resulted in displacement of one bird on one occasion; generally following Bill Duelling both storks reinitiated the activities engaged in prior to the Bill Duel, or both moved away simultaneously.

Thomas (1986) witnessed a Bill Duel between two _C_. _maguari_ that were foraging in Venezuela. Bill Duels between captive _C_. _ciconia_ and also _C_. _boyciana_ have been observed by others (Archibald and Schmitt in press; K. Vos pers. comm.). Displays similar to Bill Duels have been reported in two other free ranging Ciconiiformes; Ardeidae (Blaker 1969; Mock 1976), and Threskiornithidae (Brouwer and van Wieringen 1986). This suggests that Bill Duels observed here were not just aberrant agonistic encounters, rather they constitute performances of a display that is probably present in wild populations of the species addressed.

The signal function of Bill Duelling is not clear. It is possible that this display provides a means for evaluating the opponent, though performers were usually quite familiar with their partners. It seems more likely that, at least in adult performances, Bill Duels allow individuals to dissipate agonistic tendencies in a non-disruptive manner. The preponderance of Bill Duels during feeding encounters supports this conclusion.

Upright Display (Kahl 1972a)

Essential Elements. The neck is held ca. 15° behind the vertical axis, and the back is not arched. The bill is positioned below the horizontal axis and wings are folded.

Body, head and upper neck feathers are compressed, and basal neck feathers variably erected. The performer moves its body away from the opponent in this posture, maintaining an orientation of the bill toward, or lateral to, the opponent throughout (Fig. 7).

Upright Displays were observed in C. ciconia and C. maguari but not C. boyciana. The Upright Displays observed in this study resembled Kahl's (1972a) description of the Upright Display for Ciconia in the following elements: erect stance, body plumage compressed, body turned away from attacker, and taking of quick evasive steps to the side or away. Bill positioning observed here was less horizontal than in Kahl's description.

Variations. Duration of Upright Displays ranged from 1.5-5.5 s in 10 Maguari displays timed. Three forms of the Upright were observed in Maguari Storks studied here, termed Type 1, 2, and 3. The bill was held vertically, close to the erected neck, in Type 1 Uprights. Feathers on the head and back of the neck were compressed, and frontal and lateral neck feathers intermittently erected. Posturing was slightly vertical, with the mantle angled ca. 30° below the horizontal axis and the tail visible beneath folded wings.

The other forms of the Upright involved more extreme vertical posturing of the body, with the mantle at an angle ca. 50-75° below the horizontal and the tail lowered beyond the vertical axis. The bill was positioned below the horizontal, away from the erect neck. Feathers on the head, body, and back of the neck were tightly compressed. Neck feathers on the front and sides were concurrently erected, giving the head and neck region a triangular appearance. The orange brood patch was clearly visible on the breast.

Folded wings were held tightly against the body in Type 2 Uprights, and in some performances two to five soft bill claps were emitted at the end of the display. The wings were extended upward in Type 3 Uprights (greater than 50° above the horizontal axis), and one slow (more than 1 s) snap of the bill, resembling a gape, was made as the bird moved away from its opponent.

Type 1 Upright Displays were similar in C. maguari and C. ciconia. Type 2 Uprights in C. ciconia differed from those of C. maguari in that the tail was held just below the horizontal, and the wings slightly raised while still in the folded position. The brood patch was not visible on the breast, nor were bill claps emitted.

Contexts. The Type 1 Upright Display was the most common form of this behavior performed by both C. maguari and C. ciconia in response to keeper activities, and during both intra- and interspecific encounters. Not all of these encounters were obviously hostile. For example, four C. maguari (two separate pairs) consistently fled a location, sometimes performing a Type 1 Upright, at the approach of a Common Trumpeter (Psophia crepitans). This behavior was puzzling, as the much smaller Trumpeter was never observed to act aggressively towards the storks, nor did zoo personnel ever document such activity.

Type 2 Uprights were performed during introductions and also in agonistic encounters between exhibit mates. During one introduction a female C. maguari occasionally executed Type 2 Uprights up to five days after the initial introduction when her new enclosure mate approached, even if he displayed no obvious aggression. Type 2 Uprights were performed by 4 of 10 C. maguari, totaling less than 15 performances (excluding introductions). Type 2 displays recorded in C. ciconia were performed by a 62 day old individual during introduction to the group enclosure, in response to the approach of three juveniles.

Type 3 displays, restricted to Maguari Storks, were infrequently observed. Four displays of this form were performed by one female in response to aggression from her male enclosure mate.

Comments. Upright Displays observed by Kahl were shown by a subordinate stork in a hostile encounter; if the aggressor continued to advance after performance of the Upright by the subordinate bird, the subordinate bird usually took flight. This was generally true in conspecific agonistic encounters observed here. Storks directing

Upright Displays towards other species or keepers almost always changed locations.

Upright Displays observed in this study were more variable than Kahl's (1972a) description of the Upright Display for Ciconia. Uprights of C. maguari were more diverse than those of C. ciconia. Lack of performance of Uprights by C. boyciana observed here is attributed to limited opportunities for physical contact, as this display may also be homologous throughout the Ciconiidae (Kahl 1966, 1972a, c, d, e, 1973).

Sleeking of the body feathers, vertical posturing and movement away from the source of stimulation are interpreted as signals conveying messages of appeasement in all forms of the Upright. Impossibility of total escape and close contact with species that the storks do not associate with in the wild may be responsible for performance of this display in contexts not observed under natural conditions (i.e. apparently non-hostile encounters).

Neck Weave (Mock Fighting, Kahl 1972a)

Essential Elements. The bird is stationary, standing with the tail slightly lowered (not beyond the vertical axis) and the back not arched. Feather erection is restricted to slight erection of the basal neck feathers. The neck varies from crooked to straight, and is woven so that the head orientation is alternately lateral and frontal. The bill is open at a gape of 30-35°, and is held above the horizontal axis. As the neck moves the bill is intermittently opened and snapped shut (Fig. 8).

Neck Weaving was performed by C. maguari and C. ciconia, but not C. .boyciana in this study. A similar behavior was observed in the Abdim's Stork, Ciconia abdimii, by Kahl (1972a), although that species movements appear to be more vigorous than those observed here. Bill rattling observed in C. abdimii and strong erection of neck, breast and rear head feathers were not noted in this study.

Variations. Mean duration of eight Neck Weaves performed by Maguari Storks was 9.0 s (range = 2.2-22.8 s, SD = 8.5). Neck movements were not highly stereotyped, and bill position varied from 0-135° above the horizontal. The wings were folded or held loosely out from the body, slightly bent at the carpal joint. Following this behavior the performer sometimes struck at nearby vegetation with its bill. This was observed in 16% of Neck Weaves (N = 37) recorded for C. maguari, and was also recorded in C. ciconia.

Contexts. Both sexes of C. maguari engaged in this behavior: five of six males performed 74% of the Neck Weaves, and two of four females performed the other 26%.

This activity was frequently associated with comfort movements, e.g. preening, yawning and scratching. The nine observed performances of Neck Weaves by *C. ciconia* were restricted to juvenile birds and nestlings of unknown sex, and were associated with striking at vegetation or vertical and lateral leaps into the air (see Play).

Comments. Kahl (1972a) reported that Neck Weaves of *C. abdimii* were generally performed by unmated or newly mated males, and were often alternated with bouts of the Head-Shaking Crouch at the approach of a female. Neck Weaves were not observed in this context in the present study, and reproductively active individuals performed only 21% of the 46 Neck Weaves recorded. The behaviors observed here appear to be homologs however, as Kahl too reported that the birds often bit vigorously at nesting material or vegetation at the end of this display, and sometimes made erratic flights following performance. Greater exaggeration in displays of *C abdimii* compared to other *Ciconia* was generally noted by Kahl; an observation that seems applicable here. Kahl commented that Neck Weaving resembled attempts to catch flying insects, though none were detected.

The association of Neck Weaves with comfort movements and play activities, and performance of this behavior by both sexes, as well as by both adults and juveniles, suggests that it may be a form of play or a comfort movement, rather than a predominantly male nest-related social display.

<u>Neck Stretch</u> (Anxiety Stretch, Kahl 1972a)

<u>Essential Elements.</u> Posture is erect, with the neck held straight and positioned forward relative to the vertical axis. The bill is held below the horizontal, the wings are folded, and the tail is in the normal position. Body plumage is compressed, and neck feathers sometimes slightly erected. The stork leans forward in this posture and stares fixedly at an object of interest (Fig. 9).

The Neck Stretches observed in this study were performed by all three species of all age groups and sexes. They resemble the description of the Anxiety Stretch provided by Kahl for <u>Ciconia</u>.

<u>Variations.</u> Slight variations in the angle of incline of the neck, degree of neck feather erection, bill position and vertical posture were observed.

<u>Contexts.</u> Performance occurred in response to various stimuli that constituted unusual events, e.g. approach of an animal or human not usually in close proximity to the birds.

<u>Comments.</u> The Neck Stretch is homologous throughout the Ciconiidae, but performance is more ritualized in some

of the other storks than in <u>Ciconia</u> (Kahl 1972a). Kahl (1972a, c) suggested that this display may signal potential danger to other conspecifics nesting nearby. Bill clapping appears to be present in extreme forms of this display in all three species addressed here, and may provide a means of grading signal message, or of transmitting the signal over farther ranges.

A single bill clap was produced during performance of a <u>C</u>. <u>ciconia</u> Neck Stretch observed by Kahl, and also in performances observed by Schüz (Kahl 1972a). Schmitt (1967) reported that alarmed captive <u>C</u>. <u>ciconia</u> extend the neck forward and bill clap in a manner discernible from claps used in other contexts; in alarm clapping a second softer clap immediately follows a first louder clap, resembling an involuntary rebounding of the mandibles. Performance of this alarm bill clapping prompts other adult <u>C</u>. <u>ciconia</u> to also bill clap, and nestlings to fall into a state of Akinesia. Thomas (1985) noted the same behaviors in free ranging <u>C</u>. <u>maguari</u>. Some bill claps produced by alarmed <u>C</u>. <u>boyciana</u> at the nest are also distinctive, and appear to communicate danger to neighboring birds and/or young (Winter 1982).

Kahl (1972a) considered the Neck Stretch to be a nest related display, but it was frequently observed in non-breeding birds on the ground in this study. This signal may also be employed by non-breeding birds in natural conditions. When approaching a flock of roosting C. ciconia, Cott (1947) found that some birds, possibly acting as sentinels, sounded an alarm by bill clapping. The clapping resulted in the immediate departure of the entire flock.

Aerial Clattering (Aerial Clattering Threat, Kahl 1972a)

Essential Elements. The attacker pursues an opponent in flight, maintaining a position slightly above and behind the opponent. Flight is slowed as the opponent is approached, the attacker lifts its head, holding the bill oriented towards the opponent, slightly above the horizontal, and clatters the bill loudly, up to 25 times.

This display, described by Kahl (1972a) for Ciconia was not observed in this study.

Comments. Performance of Aerial Clattering was not possible in this project due to flight restriction of the study subjects. Kahl (1972a) observed it in C. ciconia and C. maguari, but apparently not in C. boyciana. His observation of the latter stork was also limited to captive individuals.

Head-Shaking Crouch (Kahl 1972a)

Essential Elements. The stork crouches on the nest as if incubating eggs. Back and neck feathers are erected and the wings and tail raised slightly. The head is shaken vigorously 2-3 times/s. This description, based on performances by _C_. _ciconia_, _C_. _nigra_ and _C_. _episcopus_ (Kahl 1972a), resembled the one performance by a male _C_. _boyciana_ observed in this study (Fig. 10).

Variations. Duration of the performance recorded here was 12.1 s. The male _C_. _boyciana_ held his wings slightly out, and opened to the carpal joint, as he slowly lowered his body on to the nest. During the descent he paused twice, shaking his head three times. After he sat down the head was shaken eight times before he stood up to actively defend the nest.

Contexts. The Head-Shaking Crouch was directed towards personnel approaching the nest eight days prior to laying of the pair's first egg. When the personnel reached the nest a Nest Covering Display was performed, accompanied by jabbing.

Comments. Kahl (1972a) reported that Head-Shaking Crouches are directed towards conspecifics of the opposite sex, and are usually performed by unmated or newly mated males defending a nest. The display occurs during pair formation, and is extinguished by egg laying. Performance in the context observed here demonstrates that the message is not necessarily sexual in nature, but agrees with Kahl's interpretation: "No, you can't enter my nest".

Kahl (1972a) noted that movements of this display resemble those made by storks settling for incubation, and that the Head-Shaking Crouch also has similarities to the Begging Display. Wing posturing does resemble that in Begging Displays of older nestlings, and the Threat Up-Down of _C_. _ciconia_ described by Kahl (1972a) and Haverschmidt (1949), as well as the Threat Up-Down and Nest Covering Display of _C_. _boyciana_ observed here.

The Head-Shaking Crouch is probably specific to _Ciconia_, and has been observed in four species, but not in _C_. _maguari_ (Kahl 1972a). _Ciconia_ _maguari_ apparently forms breeding pairs in assemblies (Thomas 1986), rather than on the nest as do most storks (Kahl op. cit.). Thus, it is possible that the Head-Shaking Crouch is not part of the display repertoire of this species.

Nest _Covering_ _Display_ (Kahl 1972a)

Essential _Elements._ The stork stands on the nest depression, over the eggs or young if these are present, oriented towards the approaching receiver. The back is arched (Fig. 2), and the head, back and upper neck feathers are strongly erected. Basal neck feathers are variably erected (Fig. 11).

Nest Covering Displays were recorded here for _C_. _maguari_ and _C_. _boyciana_ but not _C_. _ciconia_. Kahl (1972a) observed this behavior only in _C_. _maguari_. Performances by

C. maguari in this study resembled Kahl/s description, though they were more variable in form. Kahl noted that the tail was often cocked during C. maguari performances, a posture not observed here.

Variations. Duration of this display depended on the length of time that an opponent was close enough to elicit the response. Duration of C. maguari performances ranged from 4.7 to 70.9 s (mean = 30.3 s, S.D. = 21.0, N = 18). Neck position of C. maguari varied from ca. 35° behind to 70° in front of the vertical axis, but was in the frontal position in 91% of 21 occurrences. Bill position, ranging from ca. 5° above to 55° below the horizontal axis, was more than 30° below the horizontal axis in 86% of these performances. The tail varied from horizontal to vertical in position and was sometimes spread. Wing position varied from folded to fully raised (ca. 70° above the horizontal axis).

When the opponent was at a distance greater than 2 m, C. maguari performing Nest Covering Displays generally stood with the wings slightly extended and dropped so that the tips of the outer primaries were within 5-15 cm of the ground. This posture gave the performer a "blocky" appearance when viewed from the front. The bill was clapped at a slow rate of sometimes less than 1 clap/s. Peak frequencies of claps ranged between 4.3 and 10.2 KHz

(N = 256). The performer tended to increase its clapping rate (to ca. 7-8 claps/s) as the opponent approached more closely. Two bill claps were often quite close together (0.02-0.14 s apart) and then separated from the next claps by a longer duration (Fig. 12); this paired clapping is possibly similar to the double clapping described by Schmitt (1967) for alarmed _C_. _ciconia_ (see Neck Stretch). Mean clapping rate of one male was 5.9 s, averaged over entire performances (N = 12). The performer also tended to extend the neck forward and lift the wings as the opponent advanced. Basal neck feathers were not erected when the neck was extended far forward, but were erected at other times.

Nest Covering Displays of _C_. _boyciana_ were less variable than those of _C_. _maguari_. During _C_. _boyciana_ performances the head was retracted and legs bent so that the bird squatted over the nest. Wings were held out slightly farther, but the tips were not dropped as low as in _C_. _maguari_; rather, these were held horizontally. The tail was strongly cocked, and all feathers highly erected. The performer had an almost spherical appearance when viewed from the front or above.

Bill clapping was infrequently observed during Nest Covering Displays of _C_. _boyciana_; paired claps (0.02-0.05 s apart) were interjected between series of three or more bisyllabic vocalizations (Fig. 12). Mean peak frequency of the pitch in 11 vocalizations was 3.9 KHz (S.D. = 0.41 KHz), and the base mean frequency was 2.5 KHz (S.D. = 0.76 KHz). Mean duration was 0.21 s (S.D. = 0.09). Nest Covering Displays were accompanied by jabs at the opponent in 32% of 22 displays analyzed for C. maguari, and also in the four displays recorded in C. boyciana.

Context. The Nest Covering Display is a predominantly male signal; 95% of 37 performances were by three male C. maguari and one male C. boyciana. Two males, one C. maguari and one C. boyciana, were observed replacing their mates on the nest before executing this display if the female was attending the nest. Females then either performed a Mock Rest display (below), Wing Flash, actual attack, or left the area. Two female Maguari Storks performed subdued Nest Covering Displays, including light clapping of the bill, on one occasion each.

Nest Covering Displays were directed toward humans and other species during nest defense, usually when receiver(s) approached within 5 m of the nest. Ciconia maguari in a multispecific enclosure directed 10 of 24 Nest Covering Displays toward South American Tapirs, Tapirus terrestris and 13 towards zoo personnel. Seven of nine other performances by C. maguari and C. boyciana were directed towards humans. No contact with other potential opponents was observed at the two sites where these occurred. All performances by C. boyciana were oriented towards humans.

Comments. The type of nest defense used is selective, at least in Maguari Storks. In a multispecific enclosure 96% of the Nest Covering Displays were directed at humans or tapirs. Wing Flashes were employed during nest defense in the same enclosure against other species, but never in response to humans. Common Rheas (Rhea americana) were the recipients of 71.1% of 38 nest defense Wing Flashes, while only 21.1% were directed at tapirs. Nest defense Wing Flashes were also directed toward three other species: Alpacas (Lama pacos), Patagonian Cavies (Dolichotis patagonum), and Chilean Flamingos (Phoenicopterus ruber chilensis). Thomas (1986) also found that Maguari Storks were selective in form of nest defense: individuals nesting in groups performed a mobbing behavior during a disturbance in the colony while singly nesting males used a passive defense strategy that Thomas (1986) called the "Lead Away" when the nest was approached by humans.

Flexibility of nest defense strategies toward different species by other C. maguari and the C. boyciana observed here could not be ascertained, as they were kept in monospecific enclosures. No conspecifics other than the nesting pair were housed in the enclosures, thus it is unclear whether this display would be used in intraspecific nest defense by these species. Kahl (1972a) observed Nest

Covering Displays when flying over the nests of C. maguari; the displays appeared to be given in response to the presence of the plane, although they were not directed aerially.

Ciconia ciconia did not perform the Nest Covering Displays in response to humans as did the other two species. It is possible that this is a result of the long term association the species has had with humans. A Nest Covering Display, directed toward conspecifics, has been described for C. ciconia (Cramp 1977; Haverschmidt 1949, and a photograph of the behavior is available in Haverschmidt 1949:25). These descriptions resemble that of performances by C. boyciana, though feather erection in the descriptions was not as extreme as that observed here.

Differences in stance (C. maguari's more erect posture), sounds made (bill clapping of C. maguari vs. mostly hissing of C. boyciana and possibly C. ciconia), as well as form of Nest Covering Displays may result from dissimilar natural threats to the nest. Nests of C. maguari that are typically placed on the ground in flooded savannahs would be accessible to many predators: Jaguars (Panthera onca) are found in marshes of the Pantanal (Crawshaw, 1977). Seven species of Felis are found in South America, including the Pampas Cat, F. colocolo (Walker 1964). Range and habitat of Maguari Storks overlap with four species of crocodilians (Zappalorti 1976); two of these, Caiman crocodilus and C. latirostrus, are known to opportunistically feed on birds (Diefenbach 1988; Schaller and Crawshaw 1982). Chrysocyon brachyurus, the Maned Wolf, also inhabits swamps in the same areas as C. maguari and feeds on birds (Walker 1964).

Records of predation on C. maguari by any of the above species have not been located, but given the paucity of information on foods of South American predators, absence of literature on predation of C. maguari does not preclude the existence of predation. Non-human predation on nests of the other two species appears to be rare; Prjevulsky (1870 in Vorbiev 1954) did, however, observe taking of C. boyciana nestlings by a Himalayan Bear, Selenarctos thibetanus on one occasion in the Soviet Union. Haverschmidt (1949) noted that invading conspecifics were really the only threat to C. ciconia nests and nestlings.

Intraspecific battles over nests of C. ciconia commonly occur throughout the reproductive season. These encounters sometimes result in injury, and even death of participants, or destruction of eggs and young (Haverschmidt 1949; Jovetic 1961; Veroman 1976). Hissing and growling are commonly heard in intraspecific battles at nests of this species (Haverschmidt 1949; Schmitt 1967, pers. comm.) Maguari Storks nesting in Venezuelan colonies also engage in intraspecific agonistic interactions, and bill clap during both intra- and interspecific agonistic interactions

(Thomas 1986), but frequency of intraspecific encounters may be reduced in ground breeding areas due to visual isolation at nest sites.

Differences in orientation of defensive displays, depending on the direction of approaching threats (aerial or ground), and nature of the threat (potential predator or conspecific attempting to appropriate a nest site) may have affected evolution of this display.

Mock Rest

Essential Elements. The performer stands motionless with the back strongly arched and the neck retracted so that it rests against the mantle. The bill is positioned well below the horizontal and the wings are folded. Head and basal neck feathers are strongly erected. Mock Resting resembles true resting, except head feathers are not erected in the former. This posture is assumed at the approach of the receiver to the nest, and is usually sustained until the receiver departs (Fig. 13).

Mock Resting was observed here only in *C. maguari*, and was not previously described by Kahl for this species, or any member of the Ciconiidae (Kahl 1966, 1972a, c, d, e, 1973).

Variations. The stork stood on or near the nest, or if sitting, remained so while performing the behavior. Little variation in posture, other than positioning of the bill (ranging from ca. 35-80° below the horizontal axis) has been observed.

Contexts. Two female and one male *C. maguari* performed this behavior when humans approached the nest. The male vacillated between Nest Covering Displays and Mock Resting during incidences in which when he engaged in the latter display. One female in a multispecific enclosure sometimes also engaged in Mock Resting when *Tapirus terrestris* approached the nest.

Mock Resting may be a primarily female behavior; 88% of observed performances (N = 17) were by the two breeding females. One breeding male engaged in the behavior twice, (only in conjunction with Nest Covering Displays) and the other breeding male not at all. The latter male executed Nest Covering Displays during all incidences in which his mate engaged in Mock Resting, and both sexes were present at the nest.

Comments. Mock Resting may well be restricted to Maguari Storks, as the context in which this display was frequently given, presence of a human near the nest, was also often observed in the other two species. Transitional movements of the Nest Covering Display of the two species observed here resemble this display; it is possible that one developed from the other.

The function of Mock Resting in *C. maguari* is unclear. The performance of this behavior and the Nest Covering Display only in response to species that could probably do the most damage to a nest may be relevant. Mock Resting could have evolved as an adaptation to nesting on the ground in dense vegetation, as the behavior might have concealing value. Posturing maintained in this display would be advantageous in this function: it is a position in which the storks normally stand motionless for long periods of time, and also has some pre-attack elements, i.e. retracted neck, arched back, and lowered bill.

That this strategy would be more likely to be employed by females is not surprising: in the three species observed here males were more often (and in some pairs exclusively) involved in active defense on the nest, though females were sometimes observed chasing conspecifics or heterospecifics away from the nest site. Jovetic (1961) and Schmitt (1967) reported that only male _C_. _ciconia_ engage in intraspecific battles over nests or mates, but Haverschmidt (1949) has observed nest defense by both sexes.

Up-Down (Kahl 1972a)

Essential _Elements._ The bird throws its head rearward and then forward; sound is emitted during performance.

This behavior is homologous throughout the Ciconiidae

(Kahl op. cit.) and has been described for members of Ciconia (Kahl 1972a). All species addressed here performed Up-Downs.

Variations. Maguari Up-Downs began with the back slightly arched and the wings held close to the body. Basal neck feathers were fully erected, and the head was usually positioned slightly forward with the bill held vertically, against the neck. Throughout the "Up" portion of the display the body became increasingly erect, the tail was lowered, the neck drawn rearward and the bill upward. During the initial phase of the "Up" the maroon distal portion of the bill, and the red caranculated area on the face below the eye were eclipsed by upward movement of the bill through the erected basal neck feather. As the rearward neck movement continued the bill was extended upward away from the neck (Fig. 14).

Hissing vocalizations resulting from deep intakes and exhalations of air were made during the "Up" phase. Mean rate of the hissing for four birds was 9.45/s (S.D. = 0.09, N = 14). Hisses were composed of three to five ca. 0.5 KHz concurrent bands of sound that jointly created a band of sound ranging from ca. 1.2 to 4.5 KHz (Figure 15). Head and bill movements were synchronized with the vocalizations. The tail was lowered to its most extreme position during exhalations; in 90% of 93 performances the tail was lowered 90-105° below the horizontal axis. The tail was raised 5-15° above the extreme lowered position, toward the horizontal, during inhalations. Upward bill movements were jerky as the vocalizations were made.

As the extreme rearward positioning of the neck and bill was reached, the body was held the most erectly, so that the mantle was angled ca. 50° below the horizontal axis (Fig. 2). This extreme position was held momentarily, then the bird began the forward movement of the neck. Head feathers were variously erected, creating a crest-like effect. Forward descent was more rapid than the rearward motion, and vocalizations ceased in the beginning of "down" phase. The bill was tucked against the neck again when the neck was about vertical, and then drawn through the erected basal neck feathers.

Final movements of _C_. _maguari_ Up-Downs took three forms; these can be considered variations of the same behavior pattern, but are distinguished here as "Types" for convenience. Type "A" terminated immediately after the performer drew its bill through the neck feathers. The bill was sometimes momentarily pressed against the basal neck feathers rather than drawn through them in this form, and only one or two hisses were audible. Extreme position of the bill during the apex of "A"s did not exceed the horizontal axis in 67% of 39 performances.

Up-Downs ending in the "B" form (Fig. 14) involved a continuing downward movement of the neck and bill after the bill was passed through the neck feathers, ceasing when the bill tip was about equal with the abdomen. The mantle was arched ca. 20° above the horizontal axis during the final stages of this form. Three to four hisses were given during type "B"s.

Type "C" was similar to Type "B" Up-Downs, but the downward movement of the neck and bill was continued until the bill contacted the substratum. Several grasping movements of the bill were usually made. If loose plant materials (e.g. grass, hay, leaves) were present the performer picked them up, and the movements resembled nest material manipulation.

One female and two male Maguari Storks displayed with nest material in their bills on twelve occasions. In these cases the head was not thrown back very far behind the vertical. Performances were terminated by several small shaking motions of the bill (holding the material), or the bill was lowered without the typical movements through the basal neck feathers.

Mean duration of Type "A" Up-Downs was 2.9 s (S.D. = 1.5, N = 45), Type "B" was 3.9 s (S.D. = 1.0, N = 30), and Type "C" 5.4 s (S.D. = 1.5, N = 65). Of 130 performances analyzed from video tapes 30% were Type "A", 21% were Type "B", and 49% were Type "C". Type "C" comprised 48% of 463 performances in which this variable was recorded; 51% of male and 41% of female performances were of this form. The three forms were interchangeably used in the same contexts.

Sexual differences were observed in amplitude of head and neck movements of C. maguari: males drew their bill behind the vertical axis in 44% of 70 performances analyzed, while females did so in only 3% of 60 performances.

Up-Downs of C. ciconia and C. boyciana were characterized by bill clapping. Claps had both a percussive component and reverberative component. Harmonics of the percussive component were consistent; apparently this component resulted from closing the bill sharply. Different bill sizes between the two species (Fig. 1) may be responsible for differences in peak frequencies of claps of the two species: the larger bill of C. boyciana produced peak frequencies of 1.0-4.0 KHz in 41%, 4.1-5.0 KHz in 41% and 5.1-10.5 KHz in 18% of claps (N = 2547), while peak frequencies of C. ciconia were 1.0-4.0 KHz in 7%, 4.1-5.0 KHz in 48%, and 5.1-10.5 KHz in 45% of claps (N = 443). Sonograms of bill clapping in Up-Down performances of both species are provided in Fig. 17.

The reverberative component of the clapping appeared to result from lowering of the hyoid apparatus into the base of the gular region, thus creating a sound chamber. The gular sac was highly visible during the Up-Down of these two species, unlike that of C. maguari. Bill claps reverberated on one to four frequency bands, perhaps varying with vertical movement of the sac during Up-Downs (Fig 17). Frequency bands of reverberation in claps of _C_. _ciconia_ were rather consistent within performances, and possibly within individuals: these occurred at ca. 0.4-1.0 KHz, 1.3-1.8 KHz, 2.0-2.8 KHz, and 2.8-3.5 KHz (17).

Magnitude of reverberation was greater in _C_. _boyciana_ than _C_. _ciconia_. Width and frequency of reverberative bands, particularly those at higher frequencies, were variable within many performances of Up-Downs of this species. Generally the bands were within frequency ranges of 0.3-1.2 KHz, 0.9-2.0 KHz, and 1.7-3.0 KHz. Changes in frequency were audible when the birds tilted their heads from side to side, a characteristic of a variation of the Up-Downs discussed below.

Typically, Up-Downs of _C_. _ciconia_ and _C_. _boyciana_ involved rearward movement of the neck, however some Up-Downs of these species involved only "forward" clapping, in which the neck was extended forward but not moved rearward or to either side. The body axis was held roughly in line with the outstretched neck; e.g. if the neck was roughly horizontal in position, the mantle was angled within ca. 20° of the horizontal axis, and if the neck was extended outwardly towards the ground the body was tipped forward. Wings were folded, with the tail in the normal position (Fig. 2) during this variation of Up-Down. Up-Downs consisting only of forward clapping comprised 7% of the Up-Downs of C. ciconia (N = 75) and 5% of the Up-Downs of C. boyciana (N = 266).

Feather erection was not a component of this, or any form of Up-Down performed by these species. During Up-Downs the performer often shifted the body weight from one leg to the other in a stepping motion. Birds sometimes performed Up-Downs when sitting or lying on the nest, or when standing on just one leg.

The forward clapping described above was a component of most Up-Downs performed by these species. Up-Downs involving rearward movement began with this form of forward clapping in 41% of performances by C. ciconia (N = 70), and in 8% of those performed by C. boyciana (N = 257). Up-Downs often terminated in forward clapping. Performances involving multiple bouts of Up-Down movements almost invariably had forward clapping interspersed between them.

A form of forward clapping, in which the head and body were swung as much as 90° to either side, was specific to adult C. boyciana. During the side-to-side movements the head was tilted in the direction of the movement; when the extreme side positions were reached the head might be tilted as much as 50°. The tilting of the head, and possibly also realignment of the neck position relative to the body, presumably caused the frequency changes of reverberations.

Though not present in all Up-Downs involving rearward neck movement of C. boyciana, side-to-side forward bill clapping comprised 62% of the overall time in such performances (N = 257). Performance of this variation of forward clapping did not preclude performance of the stationary form described above; both were often observed during a performance sequence. The side-to-side variation was performed by all males, but was not observed in three of five females. One of these females was not visible during many of the observation periods however.

Motor patterns of performers were similar in rearward Up-Downs performed by the two species: typically the wings were folded, the tail was in the normal position and feathers not erected. Position of the body axis was variable, but if rearward movement of the head and neck continued until the bill was lying below the horizontal axis against the birds back (Fig.16), the body was held erectly, such that the mantle was angled ca. 50° below the horizontal axis.

One variation of the typical posture was observed: in this the tail was cocked between 25-70°, and the wings held loosely away from the body, dropped slightly from the carpal joint. This variation, only performed at the nest, was sometimes performed by two male C. boyciana, and two male and one female C. ciconia. One of the male C. boyciana did not have a mate at that time, but did maintain a nest that he lined with fresh materials.

Multiple Up-Down movements (bouts) without intermissions comprised 14% of performances by _C_. _boyciana_ (N = 209) and 8% of those by _C_. _ciconia_ (N = 69). Number of bouts ranged between two and seven. Characteristics of these bouts often differed within a performance, therefore each bout was considered separately in analysis of variations in forms of Up-Downs.

Performance length was highly variable, depending on the number of bouts and amount of forward clapping involved. Mean Duration of Up-Down performances was 13.0 s (S.D. = 15.7 s, N = 215) for _C_. _boyciana_, and 8.7 s (S.D. = 8.1 s, N = 65) for _C_. _ciconia_. Performance time of _C_. _boyciana_ exceeded 10 s in 37% of the performances; 3% were over 1 min. Performances of _C_. _ciconia_ were longer than 10 s in 21%, but did not exceed 1 min.

Both _C_. _ciconia_ and _boyciana_ sometimes began Up-Downs by throwing the neck rearward (but not beyond the vertical axis), and then forward, before throwing the neck to the most extreme rearward position. This variation was observed in 7% of bouts of _C_. _boyciana_ (N = 257) and 17% of those by _C_. _ciconia_ (N = 70).

Up-Downs sometimes began with the performer throwing the head back so that the bill was positioned horizontally (beyond the vertical axis), and then forward, prior to throwing the neck to the most rearward position. Forward movement was either ca. 5-25° forward from the extreme position, or ca. 135° from this position (Fig. 16). Ciconia boyciana threw the head forward 5-25° in 12%, and 135° forward in 25% of bouts (N = 257). Ciconia ciconia performed each variation in 3% of rearward Up-Downs analyzed (N = 70).

Ciconia boyciana tended to throw the head further back during Up-Downs than did C. ciconia. Extreme rearward positioning of the bill during performances of this display is given in Table 6.

Both species characteristically flicked one or both wings during some performances of the Up-Down. Flicking could vary from being almost imperceptible to raising of the wing well above the body (Fig. 16). Only the latter variation was recorded for analysis of this behavior, as recognition of the former was largely dependent on position of the bird relative to the observer.

Wing flicking was infrequent in performances involving only forward clapping, and those performances that did not involve rearward bill movement further than 80° beyond the vertical axis (Table 6): flicking was absent in 76% of such bouts of C. boyciana (N = 80), and 77% of C. ciconia (N= 31). Conversely, it was present in 90% (N = 186), and 84% (N = 44), respectively, of bouts involving more extreme rearward bill movement.

Just one wing was flicked in 58% of C. boyciana bouts

(N = 177), and 76% of C. ciconia (N = 46) that included this component. Both wings were flicked one time in 41%, and 20% of bouts that involved wing flicking respectively. Both wings were flicked multiple times in 1% of bouts by C. boyciana and 4% by C. ciconia. Flicking of both wings usually occurred asynchronously; wings were flicked simultaneously in only 26% of C. boyciana bouts (N = 73) and 3% of C. ciconia bouts (N = 9) in which both wings were flicked.

No discernible patterns existed concerning which wing was flicked within one performance bout, however if more than one bout occurred within a performance, the wing flicked was almost invariably alternated. The left wing was flicked 52% of the time, and the right 48% in both species. Sexual differences were not observed, nor were differences relating to the variation of Up-Down performed.

Wings were usually flicked as the performer began the "Down" (forward) movement: 86% of wing flicks by C. boyciana (N = 249) and 77% of those by C. ciconia (N = 63) occurred during this phase. Flicking was observed during forward clapping in 2% and 13% of bouts respectively. Flicks occurred during rearward neck movement or in the extreme rearward position in 12% of C. boyciana bouts, and 10% of C. ciconia.

Though nest material arranging often followed Up-Downs of C. ciconia and C. boyciana, continuous downward movement of the bill to the substratum, and grabbing at plant materials (Arranging) was not routinely incorporated into this display. Arranging was not observed in any of the performances by C. ciconia (N = 75), but occurred in 20% of the performances by five male and two female C. boyciana, (N = 257). Arranging was included in 24% of 174 male bouts and 11% of 83 female bouts by C. boyciana. Touching of the ground sometimes terminated multiple bouts within a performance.

Although a few bill claps were made during rearward movements, most clapping in both species occurred when the performer was in the forward, or extreme rearward positions. Claps were also emitted during the forward descent; this was also true of the aforementioned variations in which forward movements were made prior to extreme rearward movement. Variation in clapping rate was audible in bouts of C. ciconia; rate was most rapid when the performer was in the most rearward position. Overall clapping rate of four birds was 7.7 claps/s (S.D. = 1.0, N = 46). Mean clapping rate of six C. boyciana was 12.1 claps/s, (S.D. = 1.7, N = 99); this was significantly more rapid than that of C. ciconia (Fisher's Exact Test: $P < 0.01$, 2-tailed).

Whistling vocalizations were sometimes heard during Up-Downs of both C. boyciana and C. ciconia. The vocalization was emitted during the "Up" phase of the display. Whistling was also sometimes audible between bouts in performances of C. boyciana. Whistles were produced by both males and females, but were not audible in most performances. The exception to this was performances by the one breeding male C. boyciana; whistles were present in 69% of 68 bouts analyzed for this individual.

Characteristics of the whistle appear to be different between the two species (Fig. 18), however more data is needed to confirm this. Four bisyllabic whistles, chevron in form, produced during one performance by C. ciconia were emitted at intervals of 0.25-3.0 s. Mean duration of these whistles was 0.17 s (S. D. = 0.03). A similar whistle form, but inverted, was produced by C. boyciana. Two to four of these whistles were rapidly produced, creating one continuous vocalization. Mean duration of 20 such vocalizations was 0.21 s (S.D. = 0.02).

Storks with a mate usually performed Up-Downs in close proximity to this individual, even if the mate did not also perform the display. Ciconia maguari executed 90% of Up-Downs (N = 98) within 1 m of mates. Distances of less than 0.3 m between mates were maintained during 59% (N = 36) of the single-bird, and 53% (N = 62) of the two-bird performances. Most (76%) performances by the breeding pair of C. boyciana involving one or both birds occurred when the birds were within 1 m of each other, 11% were performed at distances of less than 0.3 m (N = 46). Distances of <

0.3 m were maintained in 54% of 38 performances by breeding pairs of C. ciconia.

Pair members that spontaneously began displaying when not close together sometimes moved toward their mate to stand with a particular orientation to the other individual. Preferred orientations for performance seemed to be somewhat species specific. Orientations of breeding pairs performing Up-Downs (involving one or both birds) are provided in Table 7. Single C. boyciana often had visual access to conspecifics during Up-Down performances; in some but not all cases the direction of head position appeared to be oriented towards other individuals.

Up-Downs of nestling C. boyciana and C. ciconia contained an element of the Up-Down not observed in adults; during the "Up" phase nestlings lowered the hyoid apparatus, opened the bills ca. 30°, and emitted one to six monosyllabic grunting vocalizations. These were generally of decreasing peak frequency, (i.e. each vocalization was lower in frequency than the preceding one). Final grunts typically had sound extending into higher frequencies. The first grunt in sequences of C. ciconia vocalizations had peak frequencies of 3-5 KHz, while those of C. boyciana were at 5-7 KHz. The grunts consisted of broad bands of sound; mean duration of grunts was 0.28 s for C. ciconia (S.D. = 0.08, N = 21) and 0.27 s for C. boyciana (S.D. = 0.10, N = 18). A sonogram of an

Up-Down performed by a nestling C. boyciana is provided in Fig. 19.

Sometimes a series of grunts were emitted, but claps not produced. Posturing of the performer resembled that observed during the "Up" phase of completed Up-Downs, hence this behavior was considered to be incomplete performance of nestling Up-Downs. Mean number of grunts/complete performance throughout the nestling period was 3.4 for C. boyciana nestlings (N = 37, S.D. = 1.5), and 3.7 for C. ciconia nestlings (N = 21, S.D. 1.8). Grunts were sometimes omitted in performances by nestlings 35 days of age or older.

At the apex of the Up-Down, nestlings began clapping their bills. The clapping continued throughout the entire "Down" phase, and usually for a short time when the most forward position was reached at the end of the Up-Down. Bill clapping was almost inaudible when the birds were a few days old due to the softness of the mandibles. Though bill claps of nestlings did not have the carrying quality of adult claps, they did also include both a reverberative and percussive element.

Mean clapping rate of the four C. boyciana nestlings was 14.8 claps/s, (S.D. = 2.7, N = 39); this was significantly more rapid than that of adults (12.1 claps/s) (Fishers Exact Test: $P < 0.01$, 2-tailed). Mean clapping rate of the two C. ciconia nestlings was 9.4 claps/s

(S.D. = 2.0, N = 32). This may also be more rapid than that of adults (7.7 claps/s), but sample size was insufficient for testing this. Mean duration of nestling Up-Downs for C. ciconia was 3.3 s (S.D. = 1.2, N = 52), and 2.5 s for C. boyciana (S.D. = 0.76, N = 43).

Nestlings of either species 20 days of age or younger did not move their neck rearward more than 65° beyond the vertical axis in 94% of performances analyzed (N = 33), while those over 20 days of age moved the neck 90° or more past the vertical axis in 83% of 12 performances. Up-Downs of nestlings became more variable in form at ca. one month of age. At about this age nestlings of both species sometimes also terminated the display with wings partially extended to the carpal joints, similar to wing positioning in the Begging Display of older nestlings (Fig. 22).

Contexts. Storks performed Up-Downs both singly and with other individuals: Ciconia maguari performed the display alone in 33% of 310 recorded occurrences, and in pairs in 67% of occurrences. Ciconia ciconia performed 23% singly, 55% in pairs, 6% in groups of threes, and 16 % in groups of four to seven (N = 336). One male C. ciconia that fabricated and defended a nest without a mate performed 72% (N = 76) of the single-bird performances by this species. It was not always possible to determine how many C. boyciana were involved in display occurrences; one bird and sometimes possibly more performed 49% of the Up-

Downs, two or more birds performed 31%, three or more 11%, and groups of four to ten were involved in 9% of occurrences (N = 1506).

Up-Downs were sometimes associated with particular activities occurring in the vicinity of the performer(s), or with interactions involving the birds; these are given in Table 8 for breeding pairs of all three species. Up-Downs were also sometimes performed with no apparent stimulus, this was particularly true of single C. boyciana. Up-Down performance by one individual often prompted other conspecifics to display.

Frequency of Up-Down performances by breeding pairs varied throughout the reproductive season, being lowest during incubation and chick rearing stages. Occurrences involving one or both pair members are reported in Table 9. Single C. boyciana performed more Up-Downs than other groups: performances by one or more single birds occurred at a mean rate of 3.15/hr (N = 1386).

Nestlings first performed Up-Downs at one to two days of age. Frequency of Up-Downs decreased during the nestling period (Table 10). The frequency pattern of incomplete Up-Downs, in which only grunting was emitted, was slightly different from that of completed Up-Downs; frequency of completed Up-Downs was highest during the first 10 days of life, while that of incomplete Up-Downs was highest in days 11-20 (Table 10). Up-Downs were absent in the behavioral repertoire of juveniles observed.

Up-Downs of both hand- and parent-reared nestlings were most frequently performed during feeding sessions. Very young individuals, i.e. less than 15 days of age, performed Up-Downs in the presence of any large figure, be it their parents or a human. Parent-reared chicks of this age group performed Up-Downs immediately after the attending parent rose during brooding, and when one of the parents got on the nest and the nestlings were uncovered. Sporadic performances occurred throughout periods that the nestlings were not brooded.

Comments. The Up-Down display is the only social signal that persists the duration of the breeding season in a recognizably homologous form throughout the Ciconiidae (Kahl 1971a, 1972a). Consequently Kahl gave performance variations of this display within and among genera considerable weight in assessing phylogenetic relationships (Kahl op. cit.). Because of the prior importance that has been placed on the Up-Down, and because it is a major component in the behavioral repertoire of the storks, it was also emphasized in this study.

Contextual information that provides information in addition to that available from the structure of a display can be important in altering the message and meaning of signals (Beer 1975; Lewis and Gower 1980; Mock 1980; Smith

1965, 1969). The diversity of Up-Down structure forms, and contexts in which they are used, provide an almost unlimited source of subtle alterations in message and meanings of the display. The full range of uses of a display must usually be ascertained before the messages that it carries can be determined (Smith 1969). However, displays must be somewhat specific in message, or ineffective transmission would result (Moynihan 1970). Therefore, possible messages of displays and relevant considerations are addressed here.

Kahl reported that the Up-Down primarily serves as a greeting display between pair members (Kahl op. cit.). Yet, the display must also have a more general function: Up-Downs of wild _C_. _ciconia_ are performed almost any time a bird returns to the nest, even when the performer does not have a mate (Haverschmidt 1949). Performance of Up-Downs by solitary birds or pairs on the nest at the approach of another bird is commonly observed in _C_. _ciconia_ (Haverschmidt 1949; Jovetic 1961). Thomas (1986) noted that _C_. _maguari_ performed the display in assemblies, during nest exchanges, and at the approach of birds flying overhead. _Ciconia_ _maguari_ at nests also directed Up-Downs toward neighboring storks when the mate of the displaying bird was absent.

The association between nest exchanges and Up-Down performances documented in wild birds was not observed here: of 417 nest exchanges observed, only 5% were accompanied by Up-Down performances, and they were only observed in C. ciconia and C. maguari (Table 8). This deviation was not due to the captive situation alone: pairs of captive C. ciconia maintained in large groups almost invariably perform Up-Downs whenever the mate returns to the nest, even if its absence is short, and the pair remain in visual contact (M. Bloesch, B. Schmitt, and K. Vos pers. comms.).

Lack of social stimulation in a relatively unthreatening environment may be responsible for the rarity of Up-Downs observed during nest exchanges in this study: i.e. it was unlikely that another stork would appropriate the nest when the birds were kept in an enclosure with no other conspecifics, as was the situation in C. boyciana and C. maguari, or, as in C. ciconia, if housed with only a few other birds that had been sharing the same enclosure for several years. Kahl (1971a, 1978) found that storks that breed singly are not as demonstrative at the nest as group breeders, rarely engaging in Up-Down performances. This suggests that even when performed as a greeting, the Up-Down has an identification message (Smith 1969); i.e. either announcing to conspecifics that the nest is occupied, and/or unambiguously identifying the performer to its mate. Audible differences (even to humans) in acoustical properties of bill claps among individuals within a species occur (K. Archibald, B. Schmitt pers. comms.; pers. obs.)

Data from this study indicate that, at least in C. ciconia and C. boyciana, the Up-Down is in some contexts an "exemplary" display, i.e. performance by one individual provokes performance by nearby conspecifics (Moynihan 1955a). Kahl (1972a) noted that mutual Up-Down performance by pairing Ciconia seemed to sometimes defuse the male's aggressiveness; an observation also made in this study. Moynihan (1955a) suggested that performance of an exemplary display by a group of conspecifics might act to communally suppress overt fighting. Some Up-Downs performed by group nesting Ciconia may also have this function.

Frequency of performance of Up-Downs tends to decrease over the breeding season (Kahl 1978). This was also found among breeding pairs in this study during the incubation/chick rearing phase, though frequency increased immediately thereafter in post-reproductive stages, particularly for C. ciconia and C. boyciana (Table 9). Pair bonds had been established prior to observation in all cases; it is possible that newly paired birds would display more frequently. A higher performance rate than that observed in breeding birds was observed in unpaired C. boyciana, particularly following transfers of birds into enclosures adjacent to individuals that they had only had visual contact with at farther ranges previously.

Frequency of performance by these individuals did not perceptibly vary throughout the breeding season.

Kahl (1972a) noted that males tend to perform the Up-Down at a higher intensity, and more repeatedly than females. Male _C_. _maguari_ did tend to have more extreme rearward neck movements than females. No difference in repetitions (bouts) between sexes of _C_. _maguari_ was observed; this species rarely performed the display multiple times in succession. Number of bouts, amount of forward clapping, and amplitude of rearward neck movements of _C_. _ciconia_ and _C_. _boyciana_ seemed to vary with sex, individual, and also context; e.g. one male _C_. _boyciana_ that habitually performed long Up-Downs with multiple bouts and much forward side-to-side clapping began executing only short performances when moved into a pen next to a particular female. The female concurrently began to perform longer duration Up-Downs (with more bouts), and performed them more frequently than she had previously. Another male moved next to a female began performing Up-Downs of longer duration than he had typically performed previously, and the female did likewise. Frequency of performance by the female of the breeding pair of _C_. _boyciana_ declined more throughout reproduction than did that of the male.

Archibald and Schmitt (in press) discriminated between several types of Up-Downs, one of which, called "Female

Bill Clattering", has been observed in both C. ciconia and C. boyciana, and is believed to be restricted to females. Clapping that fits their description was infrequently observed in males during this study as well. In conclusion, though sexual bias may exist in performance of certain forms of the Up-Down, its existence is confounded by other variables.

Kahl (1972a) and Thomas (1986) both reported the presence of the bisyllabic vocalization that is characteristic of Up-Down performances of adult C. maguari. Kahl (1972a) rarely saw Up-Downs performed by adult C. maguari, but in those observed he reported that the bill was slowly clattered (4-6 clatters/s) six to ten times when the head was just behind or at the vertical axis. This clattering was conspicuously absent in performances of C. maguari studied here: it never occurred in the more than 562 performances by ten birds observed. Absence of bill clapping in Up-Downs performed during this study agrees with Thomas's observations of this species in the wild; she also found that bill clapping was restricted to agonistic encounters (pers. comm.), and was not part of the Up-Down.

Kahl noted that C. maguari sometimes began bill clapping with all the head and neck feathers erected as they aerially approached the nest. Bill clapping in this context may serve to identify the incoming bird to its mate and/or offspring. This does not preclude the possibility that the behavior also advertises to other Maguari Storks nesting in the area that the incoming bird has returned to the nest. Erection of all feathers was only observed during agonistic behaviors in this study; possibly the behavior observed by Kahl had a hostile message.

Although C. ciconia and C. boyciana sometimes emitted a hissing vocalization in addition to the bill clattering that is characteristic of Up-Downs of these storks, the vocalizations were different in frequency and duration from that of C. maguari. Hisses of all three had a chevron form, though that of C. maguari was less sharp than the others. Morton (1982) reported that chevron sounds with an average frequency intermediate to either endpoint (such as most of those here) code only arousal and interest, and symbolize neutral or adaptively indecisive motivation. Hisses in the same performance were not always of the same frequency; in-depth analysis of frequency relationships between hisses within a performance might provide motivational information (Morton 1982).

Posturing of Ciconia maguari was more erect during Up-Downs than in the other two species; the body was held more vertically, the wings were closely drawn in, the tail lowered, and the head feathers variably erected to form a crest. The phase typical of Up-Downs of C. boyciana and C. ciconia in which the neck was extended forward was entirely absent in C. maguari. Instead the head was kept conspicuously close to the body as the neck and bill were drawn up through the neck feathers. Basal neck feathers were not erected during Up-Down performances of C. ciconia and C. boyciana; yet, this was a prominent element in those of C. maguari.

Orientation to the mate during Up-Downs was also different, C. maguari tended to stand closer to the mate, oriented in a position that maximized both frontal and lateral viewing of the performer by the mate, while orientation of the other two species was rather variable (Table 7). Relatively more performances by C. maguari were associated with the mates joining together, on or off the nest (Table 8).

A large expanse of brightly colored, roughly textured, facial skin surrounding and extending below the eye, and the bi-colored bill of C. maguari (Fig. 1), may accent Up-Down movements. During Up-Down performances the light coloration of the upper bill is more conspicuous than the lower, darker portion (pers. obs). Special surfaces on structural elements such as facial warts and wattles may aid communication by reflection (Hailman 1977).

During Up-Downs of C. maguari the performer averts and conceals the bill, which is its chief weapon. The performer partially conceals the bare facial area, a prominent signal element, when the bill is drawn through the basal neck feathers. Hiding of weapons, avoidance of eye contact or "cutting off" contact, and minimization of prominent signal features are considered to be signals of "antithetical appeasement", the opposite of those given during threats (Darwin 1872, in Barlow 1977; Hailman 1977; Jouventin 1982).

Wing flicking during Up-Downs has not been reported for *C. ciconia*, but has been described for *C. boyciana* (Archibald and Schmitt in press). Non-display wing flicking, commonly observed in all three species, appears to be a comfort movement, serving to readjust the wings following physical activity. Derivation of signal patterns from non-signal sources is a fundamental characteristic of animal communicatory behavior (Morris 1957), and comfort movements have been thought to be a major source of display movements. Wing flicking may have evolved to enhance signaling value of the Up-Down in *C. boyciana* and *C. ciconia*. Movement is considered by Hailman (1977) to be the most obvious principal of conspicuousness in signaling. Movement of the wings during displays in penguins (Spheniscidae) is thought to have great signal value in long range displays (Jouventin 1982). Signaling by flicking of the fin has been observed in many fishes; such movements have sometimes developed into relatively complex kinds of communication (Cole and Ward 1977).

Though both *C. boyciana* and *C. ciconia* have some white coloration on the primarily black flight feathers, the white coloration is more obvious in C. boyciana (Vaurie 1965; pers. obs.), the species with the higher wing flicking rate. Wing flicking during Up-Down performances and white wing coloration are both absent in C. maguari; it may be that these characteristics (degree of white wing coloration and wing flicking) are related.

Melanized Wood-Warbler (Emberizidae: Parulinae) feathers have been shown to be less susceptible to abrasion than unmelanized feathers (Burtt 1986). Additional feather strength may account for the preponderance of black wings in otherwise white aquatic birds (Mock 1980b). White coloration (absence of pigment deposit) on the wings of C. boyciana and C. ciconia is more prominent on the secondaries than primaries, and is almost entirely restricted to the outer vane of the feather, though white occurs at the base of both vanes where the barbs lack functional barbules. Above these barbs the white primarily occurs on the teeth and cilia of the distal barbules, and on the white flanges of the proximal barbules (pers. obs., terminology from Pettingill 1971). White coloration is not present on the underside of the feather. Unequally rapid deterioration of the white feather parts compared to the black foundation in C. ciconia is indicated by Cramp (1977) and Vos (pers. comm.), who noted that white areas on wings of adults become patchy prior to molting.

Visibility of white coloration on the wings is thus maximized while the strength of the wing is not severely impaired. Presence of white areas on the wings at the potential cost of feather strength suggests that the white coloration has signal value that may relate to wing flicking.

Wing pumping, an element of Up-Downs observed in wild C. ciconia during "Threat Up-Downs" was not recorded in this study. In the "Threat Up-Down" the performer stands oriented toward an intruder with the tail strongly cocked, and the wings partially opened. The wings are pumped rhythmically up and down when the performer has the neck extended in the forward position; during this phase the neck is swung side-to-side, to ca. 40° from the midline (Kahl 1972a). Kahl (1972a), noting that this variation of Up-Down was performed at the approach of a unfamiliar conspecific and discontinued when the intruder departed, suggested that it is a territorial defense display. Haverschmidt (1949) remarked that "Threat Up-Downs" are frequently performed by lone, unmated individuals when no other stork is in sight, and concluded that performance of this variation is dependent on the internal state of the bird rather than on extrinsic factors.

Although tail cocking and partial spreading of the wings were observed in some Up-Down performances by C. ciconia and C. boyciana in this study, absence of wing pumping in conjunction with them demonstrates that the three elements of "Threat Up-Downs" are not absolutely interdependent. Photographs of wing pumping by C. ciconia (e.g. Kahl 1972a: 228) indicate that this behavior strongly resembles the Begging Display of older nestling Ciconia in posturing (see Begging Display). Tail cocking and wing spreading were not associated with any particular context in this study, and were performed by both mated and unpaired birds.

The hissing element observed in some Up-Downs of C. ciconia and C. boyciana was originally described by Schüz for C. ciconia in a form of the Up-Down that he called "Zichklappern", or "Hiss clattering" (Haverschmidt 1949; Kahl 1972a). This form sometimes precedes the "Threat Up-Down" and probably contains a higher level of hostile motivation than the typical Up-Down (Kahl 1972a). Six of the seven C. boyciana in this study that were heard hissing during performances were also observed touching the ground with their bills in movements resembling nest material manipulation (Arranging) during some performances. Hissing was only recorded three times in C. ciconia, and Arranging not at all.

Ciconia ciconia sometimes engages in nest building behavior at the end of an Up-Down performance (Jovetic 1961; Haverschmidt 1949; Kahl 1972a). Arranging was noted by Archibald and Schmitt (in press) with "Threat Up-Downs" of C. ciconia and C. boyciana. Arranging during Up-Downs of C. maguari (Type C displays) seemed to be more prevalent among some individuals during introductions of conspecifics in this study, but this variation of the Up-Down comprised almost half of all performances in non-introduction situations as well.

Arranging behavior may be a punctuating signal (Hailman 1977), providing syntactic information about the intended message of that performance. Pecking at the ground in a manner that bears some resemblance to nesting activities has been described for threat displays of gulls (Laridae; Hailman 1977) and sparrows (Fringillidae; Moynihan 1955), and are thought to be redirected fighting movements. Arranging movements in this study were somewhat similar to pecking behaviors observed in nestling Begging Displays of C. boyciana and C. ciconia. Presence of this component in Up-Downs of all three species, despite diversity in other components, may indicate that the ground touching Arranging behavior does have a ecumenical function, although its derivation and message remain obscure.

During all forms of Up-Downs of C. boyciana and C. ciconia excluding forms in which the head and bill were immediately brought to the extreme rearward position, a short bout of clattering preceded the primary bout(s) of clapping. The initial short clapping bouts may act as "alerting signals". Such signals are designed to gain the attention of the receiver, and are followed by the message-containing signal. This results in more reliable message transmission, and in a reduced time commitment for receiver attentiveness. Alerting components are particularly suitable to vocalizations used in territorial defense (Wiley 1983).

Posturing, emphasis of subtle visual features, orientation and proximity to the mate, and lack of a highly audible vocalization or mechanical sound indicate that the Up-Down is a short range display in *C. maguari*. Conversely, the highly conspicuous movements in Up-Downs of *C. boyciana* and *C. ciconia* suggest that it is more important as a long-range display in these species. Chopped vocal signals in the form of short identical syllables with large frequency bands are ideal for rapid location of the communicator (Jouventin 1982); this accurately describes the percussion component of bill claps.

Up-Downs of all the Ciconiidae are visual displays accompanied by some sort of sound (Kahl 1972a), though none of the Up-Downs of other Ciconiids are as audible as those of *C. ciconia* and *C. boyciana*. Visual signal intensity cannot be increased above a certain maximum, hence most animals are driven to other means of achieving conspicuousness over long ranges, e.g. employment of auditory signals (Marler 1968). The highly developed auditory element in Up-Downs of *C. boyciana* and *C. ciconia* has probably evolved in response to a need to transmit the signal over a long range.

A consideration in long range displays is the ability of conspecific receivers to discriminate the signal from those of other species that utilize the same space at the same time; this constraint often favors stereotypy of at least some components (Marler 1968). The bill clapping component of _C_. _boyciana_ and _C_. _ciconia_ Up-Downs easily distinguish this signal from signals produced by sympatric species; thus a high degree of species specific stereotypy may not be necessary. Certainly performances observed in this study were highly variable.

Other forms of noise are also present in the environment. These interfering noises influencing behavior are usually proportional to the distance between the communicator and the receiver. Since different environments have different levels of noise, both factors (distance and level of environmental noise) need to be considered. The general rule is that at greater distances, and/or in environments with higher noise levels, redundancy and individual stereotypy are favored (Barlow 1977). Redundancy, the presence of elements beyond those necessary to convey a particular message (Rand and Williams 1970) helps the receiver discriminate between noise and the signal (Bateson 1968), and favors successful message transmission even if some parts are missing (Lewis and

Gower 1980). In biological situations where redundancy is great, noise may not be a problem (Regal 1977). Redundancy in the form of repeated performance of signal elements, and presence of multiple elements conveying the same message, may be high in some forms of Up-downs of *C. boyciana* and *C. ciconia*, but quantification of redundancy is necessary to confirm this.

Though Kahl (1971a) stated that the Up-Down of *C. ciconia* is more highly developed than in any other Ciconiid, the Up-Down of *C. boyciana* appeared to be even more complex. Up-Downs of the latter species were longer, contained more extreme rearward neck movement, were more variable in frequency of the reverberative component of bill clapping, contained clapping at a faster rate, included more wing flicking and exhibited the side-to-side forward clapping absent in *C. ciconia*.

Mock (1980a) stated that there may only be three ways of increasing the amount and rate of information transfer within a display: sequencing (encoding of information into the order of signals), enrichment (encoding extra information into the individual signals themselves; e.g. grading, adding new elements), and speed (accelerating signal performance). Theoretically, information content of the Up-Down of *C. boyciana* may be increased above that of *C. ciconia* in all these dimensions through the differences listed above. However, grading, and presumably some other means of increasing information transfer, are advantages most likely to be exploited in close range signals (Marler 1968; Morton 1982).

Addition and exaggeration of components in the C. boyciana Up-Down may have evolved to increase effectiveness of signal transmission over longer ranges, or in environments with more noise, rather than to increase message content. Characteristics of the side-to-side forward clapping specific to C. boyciana, including changes in sound frequency that result from the neck and head movements, broadcasting of sound in several different directions, and high visibility of the bird due to body and neck movements may serve to make the performer more conspicuous. Such bill clapping was more characteristic of unpaired birds, particularly males; supporting the view that the behavior has an advertising function.

Subtle differences in nesting ecology between C. ciconia and C. boyciana might result in dissimilar signal transmission constraints. Nests of C. ciconia in western and central Europe are typically situated singly in open areas on man-made structures, while nests in northern Africa, Spain, and further east on the Eurasian continent are frequently placed in trees (Haverschmidt 1949; Jovetic 1961). Tree nesting C. ciconia often form colonies that may include 35 nests (Haverschmidt 1949). Ciconia boyciana has sometimes nested on man-made structures (e.g. Gluschenko

1985; Sakomoto 1966), but usually nests singly in trees. Distances between tree nests in the Middle Amur region of the U.S.S.R. range between 200-2000 m, with most nests separated by distances of 500-700 m (Winter 1982). Differences in characteristics of nesting sites in relation to proximity to conspecifics may alter signal transmission effectiveness. Other habitat factors (e.g. dissimilar physical topography) could affect signal transmission, if such differences exist.

It is also possible that Up-Down forms of *C. boyciana* and *C. ciconia* diverged at a time when/if the storks were sympatric, and acted to isolate them behaviorally. If so, unless other factors are now contributing to retention of a complex Up-Down in the repertoire of *C. boyciana*, display simplification would be expected in the interest of signaling economy (Barlow 1977; Hailman 1977). The inversion of hisses of the two species accompanying one form of the Up-Down observed in this study could possibly have developed to aid in species identification, as costs associated with modification of this vocalization might be relatively small.

Kahl (1971a) reported that Up-Downs of *C. maguari* nestlings include a bill clapping component, and appear to be similar to Up-Downs of *C. ciconia*. Thomas (1984) described a nestling *C. maguari* "onk onk onk onk" vocalization consisting of 4-5 notes of descending tones that may be the equivalent of the "grunt" emitted during the "Up" phase of displays performed by nestling C. boyciana and ciconia in this study.

Nestlings of all three species addressed here have gular regions that contrast sharply with body coloration (Table 2). Ciconia maguari nestlings also have a yellow strip of skin extending up the ventral apteria that is no longer present by 20 days of age (Kahl 1971b). Coloration of C. maguari is otherwise quite dark throughout most of the nestling stage, and probably functions as an anti-predator adaptation (Thomas 1984). This indicates that the bright patches of skin do act as a visual signal of some importance, at least in this species.

Motor patterns of C. boyciana, C. ciconia, and C. maguari nestling Up-Downs emphasize the brightly colored areas, unlike motor patterns of the Begging Display of these species. The bright patches of coloration may serve to draw the parents' attention to the young during performance of nestling Up-Downs. Bill movements during clapping may serve the same function: during the early nestling stages, in which Up-Down rates are highest, (Table 10) little sound is produced. This may account for presence of a bill clapping component in the nestling of C. maguari, a component absent in adult performances.

The Up-Down of nestlings probably functions to identify the young to the parents and transmits a "bonding message" (Smith 1969). The decline in performance frequency of nestling Up-Downs throughout ontogeny (Table 10) corresponded with increased motor development; by 8-12 days of age all C. boyciana and C. ciconia nestlings observed could maneuver well by shuffling on the tarsi, and some were also standing. General awareness of the surroundings also increased as frequency of Up-Down performances decreased, e.g. parent-reared nestlings cease performing Up-Downs to non-parental figures at ca. two weeks of age, and nestlings around this age are also less likely to accept novel nestlings into their nests (Schmitt pers. comm.; pers. obs).

The maturation of the Up-Down observed in nestling C. boyciana and C. ciconia at ca. one month of age in this study apparently also occurs in C. maguari. Thomas (1984) reported that nestlings four to five weeks of age begin producing a throaty hiss resembling the Up-Down vocalizations of adults. The vocalization was produced in defensive, agonistic and social situations.

The Up-Down display is absent in the behavioral repertoire of juvenile and sub-adult C. ciconia (Haverschmidt 1949; Schmitt pers. comm.), and may be lacking during these stages in C. boyciana and C. maguari as well. This is particularly meaningful in light of the somewhat generalized function, at least in adults, of the Up-Down. It is possible that absence/presence of the display may aid in assessment of reproductive maturity of individuals by conspecifics, as sub-adults are only subtly different from adults morphologically (Table 2).

Offering

Essential Elements. The stork gathers material (usually vegetation) in its bill and carries the material to a selected site, where it deposits the material while making small shaking movements of the head and bill. The movements resemble those made when lodging nesting materials into the nest structure.

Offerings were observed in all species here, but have not been described for any of the Ciconiidae by Kahl (1966, 1972a, c, d, e, 1973).

Variations. Offerings by C. maguari involved deposition of materials in a frontal or frontal-lateral position next to the enclosure mate (Fig. 20). This behavior was only considered to be an Offering in this species if the action occurred away from the nest, as it was difficult to discern between an Offering and addition of nesting materials at the nest.

Physical contact with the receiver was often an element of Offerings in C. maguari; performers frequently nudged the recipient when depositing the material, and were sometimes observed crossing under the mate's neck multiple times, brushing against the recipient's breast region, prior to setting the material down. A C. maguari making an Offering to a sitting mate often set materials down on the far side of the recipient, so that the performer's neck was momentarily laid across the back of the recipient, a behavior reminiscent of male precopulatory movements (see Copulation Clattering).

Offerings made by C. boyciana and C. ciconia always occurred at the nest when the mate was present, with the exception of one performance by a male C. ciconia that took material to his mate at another site after the pair had ceased defending their nest following unsuccessful incubation. Shaking of the head and bill was less pronounced in C. ciconia and C. boyciana, and physical contact with the mate was rarely observed. Performance of Offering in these two species was distinguished from non-display material additions to the nest by the presence of a hissing vocalization. This was heard up to distances of 14 m, but may have been inaudible under some conditions. Lack of detection of the vocalization would have resulted in recording of Offerings as non-display nest material additions.

Contexts. Offerings in the three species were primarily observed preceding egg laying during the courtship period, but were also recorded at other times (Table 9). Offerings were made between two male C. maguari that built nests together. One male C. boyciana made Offerings while placing nesting material on a perch and in the fence between his enclosure and that of a female with whom he engaged in courtship activities. This male was attempting to build a nest, and accumulated much material at this site. Offering is generally a male behavior, although both sexes do perform the display (Table 11).

Comments. Manipulation of nesting material during courtship behavior is almost universal throughout the Ciconiiformes (Sibley et al. 1969), and the "Twig Grasping Display" is a recognized courtship display in three genera of the Ciconiidae (Kahl 1966, 1972c, e). Offerings observed here were also primarily associated with courtship. Recording of this display 177 times during observation of C. maguari, and the high rate of occurrence relative to the other species addressed here, indicate that this was an important behavior in the repertoire of this species. Thomas (1986) reported that these storks sometimes carried material in their bills during assemblies, but did not make any reference to Offering behaviors.

Observed differences between C. maguari and the other two species in form and orientation (mate vs. nest) of Offerings in captivity may result from differences in nesting ecology. Courtship of C. maguari appears to take place in assemblies, at least initially (Thomas 1986), while that of other storks occurs at the nest (Kahl op.

cit.). Annual deterioration of nests at re-used sites would be expected to be greater for ground nests built from grassy vegetation by C. maguari than for the largely twig constructed nests fabricated by the other two species.

The nests of C. ciconia and C. boyciana have high visibility relative to the typical ground nests of Maguari Storks. Offering behaviors of C. maguari, C. ciconia and C. boyciana share a common visual element, but Offerings of C. maguari contain a tactile element not present in Offerings of the other two species. The auditory element of Offerings performed by C. ciconia and C. boyciana is absent in those of C. maguari.

Hissing and guttural vocalizations of captive male C. ciconia accompanied by nest material manipulation, observed when females approached a defended site during courtship, was reported by Schmitt (1967). Schmitt noted that the behavior had elements common to defensive behaviors. Hissing has been observed in hostile Up-Down displays performed by C. Ciconia, usually by lone storks in response to the appearance of a unfamiliar conspecific (Haverschmidt 1949; Kahl 1972a.). Hissing by C. ciconia and C. boyciana was also recorded in other agonistic situations in this study. Presence of this vocalization, and the limiting of Offerings to performance at the nest suggest that this display has a primarily advertising, rather than pair bonding function in these species.

Manipulation of material is a behavior that appears early in ontogeny of these storks: hand-reared _C_. _boyciana_ and _C_. _ciconia_ were observed arranging nesting material at 23-27 days of age, and carrying nesting material to their nests and food dishes as early as 47-50 days of age in this study. Hissing did not accompany this nestling behavior. Carrying of plant material in the bill was an observed component of play activities of older nestlings, particularly _C_. _boyciana_ (see Play).

Six of eight single adult _C_. _boyciana_ were observed placing plant materials in non-nest locations such as food and water buckets and winter shelters. Eight of 10 non-nesting Maguari Storks also engaged in this behavior. It is not clear whether these activities had any signal function, but their performance does demonstrate the importance of manipulation of materials in behavior patterns of these storks.

Allopreening (Cullen 1963)

Essential Elements. One individual manipulates the feathers of another individual by nibbling movements of the bill. This behavior differs from the stroke type mandibulation of feathers often observed in self-preening of storks. Allopreening was observed in all species studied here. Kahl (1972a) did not describe this behavior for _Ciconia_.

Variations. The head and neck were usually target areas in Allopreening. The breeding pair of _C_. _boyciana_ were often observed nibbling on bare facial areas around the eyes and bill during Allopreening sessions. Mutual Allopreening, in which two individuals preen each other simultaneously, was recorded 10 times in this pair, but never in the other two species. As many as three nestling _C_. _boyciana_ were observed concurrently Allopreening one sibling on several occasions.

All allopreening of _C_. _maguari_ occurred when the recipient was sitting. Recipients were standing in 31% of the Allopreening episodes recorded for adult _C_. _ciconia_; these performances were by birds not currently engaged in reproductive activities. Ninety percent of the Allopreening by adult _C_. _boyciana_ occurred when the birds were standing, including all mutual Allopreening.

Contexts. Allopreening was recorded in all age groups. Juvenile and nestling Allopreening, directed toward siblings, was first observed in nestling _C_. _boyciana_ at 21 days of age (three of four birds) and _C_. _ciconia_ at 14 days. Adult Allopreening, performed by both sexes, was directed toward the mate, potential mate, or offspring. Frequency of Allopreening between breeding pairs varied throughout the reproductive season (Table 9). Number of performances of reproductively active individuals are reported by sex in Table 11.

A courting male and a female _C_. _boyciana_ were observed Allopreening through a chain-link fence on two occasions. Allopreening was observed in _C_. _maguari_ on eight occasions; seven of these performances were by the same female, and involved two different mates. The other performance was by a male, and was directed towards a male mate. These performances were associated with courtship activities.

Removal of feather sheaths during Allopreening of offspring by _C_. _boyciana_ commenced upon emergence of the first contour feathers, i.e. the scapulars. The female raising one chick increased the frequency of this behavior over a four day period, until it comprised 76.2% of her time budget. The chick was then removed as this behavior had resulted in continual bleeding of the incoming feathers.

Comments. Solicitation of Allopreening by assuming postures that elicit this behavior in conspecifics (Harrison 1965; Morris 1956; Sparks 1964) was not observed in this study. Contrarily, recipients often appeared to barely tolerate the behavior, an observation made in other studies of _C_. _ciconia_ and _C_. _boyciana_ (K. Archibald, B. Schmitt pers. comms.). Recipients were occasionally observed withdrawing the head several times prior to submitting to Allopreening overtures.

Allopreening and displays involving this behavior among adults are generally thought to function in reduction of attack tendencies and strengthening of the pair bond (e.g. Blaker 1969; Harrison 1965; Hudson 1965; Mock 1976; Rodgers 1977). Data gathered in this study are consistent with these theories, in that Allopreening frequency is highest during the courtship period (Table 9). Harrison indicated that in Allopreening descriptions involving C. ciconia, the recipient was always sitting, and suggested that temporary dominance brought about by the difference in stature elicited this behavior. As Allopreening in this study was not restricted to recipients in a sitting position this theory cannot generally account for the behavior. Low-lying positioning of the mate may act as stimulus for the behavior, similar to the presence of a chick. Allopreening has been reported to be a typically female behavior in C. ciconia (Schüz in Haverschmidt 1949:42), but no consistent sexual differences were observed in this study (Table 11).

Data from captive birds in this study suggest that Allopreening is more important in behavioral repertoires of C. ciconia and C. boyciana than in C. maguari, which is in agreement with observations in the wild. Thomas (1986) noted that Allopreening by C. maguari infrequently occurred, while the behavior is common in C. ciconia (Cramp 1977; Haverschmidt 1949). Harrison (1965) suggested obligatory close proximity to the mate at the nest site, such as that resulting from the use of nest platforms commonly practiced by Ardeidae, Ciconiidae, Threskiornithidae, and Columbidae, may be a factor in development of Allopreening in these groups. He noted that absence of Allopreening in Botaurinae, a tribe of Ardeidae, might result from greater ease of movement off and on the nest. A similar trend may occur in _Ciconia_: lower incidence of Allopreening in _C_. _maguari_ could be a due this species being a predominantly ground nester.

Allopreening of mates was more prevalent during all phases of reproductive activity in _C_. _boyciana_ than in _C_. _ciconia_ (Table 11). Additionally, _C_. _boyciana_ allopreened mates primarily when standing, thus lower elevation of the mate was not acting as a stimulus, and mutual Allopreening was observed exclusively in this species. Aggression resulting in death and injury of conspecifics has been documented more often in _C_. _boyciana_ than in _C_. _ciconia_ under captive situations (Archibald and Schmitt in press). It may be that Allopreening is a particularly important behavior in reduction of agonistic tendencies between mates of _C_. _boyciana_, but no data are available concerning this behavior in wild individuals.

Feather sheath removal on offspring has been observed in wild _C_. _ciconia_, though persistence in this activity to the extent that damage results has not been reported, and is rarely observed in captive individuals (M. Bloesch,

B. Schmitt, K. Vos pers. comms.). This aberrant behavior has been noted among some other groups in captive situations, and is particularly prevalent in the Psittaciformes (Low, 1986). The same female C. boyciana did not engage in this behavior when rearing three young in 1988 (G. Newark, pers. comm.); possibly increased nestling demands on parental resources acted as a deterrent.

Copulation Clattering

Essential Elements. Standing to one side of the female, the male lifts one leg and then the other onto her back while slowly flapping his wings. The male grips the female's shoulders with his feet, resting his tarsi on her back. The female positions her body horizontally as the male begins to mount, opening her wings slightly to the carpal joint, and retracting her neck so that it lies under the male's breast. The female holds her tail to one side, and the male lowers his, so that cloacal contact is made.

Once the male begins to lower himself onto the female's back he moves his head side to side, irregularly clapping his bill while stroking it through the female's basal neck feathers.

Copulation Clattering was observed in all three species, and resembled Kahl's (1972a) description of this behavior for Ciconia.

Variations. Precopulatory movements observed were strikingly similar among the three species. Males often initiated copulation by suddenly terminating the current activity engaged in and standing with the body motionless for less than 5 s, surveying the surroundings. Immediately following this phase the male would move toward the female, often walking slowly around her. The male stretched his neck across the female's mantle, nibbling with his bill on the far side of her neck and upper body. Precopulatory behaviors were sometimes absent in copulation activities of C. ciconia and C. boyciana.

Circling of both birds during precopulatory activity was sometimes observed during the first week of copulation in C. boyciana, but rarely thereafter. During this period the female also avoided the male by flying from the nest to the perch and the converse. Female C. maguari and C. ciconia rarely circled the nest with their mate during precopulatory activities.

Males mounted the females from the side during copulatory activities, except for one male C. ciconia that attempted to mount from the front in 21% of 24 attempts. This male never made successful cloacal contact with the female when mounting from the front, or side. Reverse Copulations (Haverschmidt 1949) in which females made copulatory advances towards the male were made by one female C. maguari 25 times, and one female C. ciconia 10 times. Precopulatory movements and side mounting resembled that of males in these incidences.

Successful copulation was not observed in Maguari Storks during this study. Copulation activities did not proceed further than the precopulatory behaviors described above in 46% of 108 advances made by three males; these occurrences were coded as Copulation Approaches. The other 54% of advances consisted of Copulation Attempts in which the male endeavored to place at least one leg on the female's back. Mean duration of these activities was 9.5 s (S.D. = 6.7, N = 11) for male "A" and 24.4 s (S.D. = 23.5 N = 23) for male "H". Copulation success of three _C_. _ciconia_ pairs ranged from 73% in 37 occurrences (of copulatory activity) to 0% in 28 occurrences. Copulation Approaches and Attempts were distributed throughout the copulatory period with no discernible pattern. Mean duration of unsuccessful copulation advances by two males was 12.5 s (S.D. = 6.0, N =12). Mean duration of four functional copulations by two males was 25.6 s (S.D. = 9.2).

Copulation was successful in 67% of 89 occurrences in the one pair of _C_. _boyciana_ observed. Rate of copulation success varied throughout the study: activity consisted of Copulation Attempts and Approaches in 79% of 19 occurrences in the first week of copulatory activity, 13% of 60 occurrences throughout the rest of the pre-incubation and incubation periods, and 60% of 10 occurrences after the young were removed.

The clattering typically emitted by males during copulation was always heard during successful copulations. Clattering was also heard during Copulation Attempts in which males mounted females but did not make cloacal contact; this was observed in all species by all reproductively active males. Copulation Clattering was heard once in *C. ciconia* when the male did not actually mount the female. Claps in a sonogram of Copulation Clattering by a male Maguari Stork ranged from ca. 4/s-11/s, with peak frequencies of 5.6-6.8 KHz. Mean clattering rate was 5.2 clatters/s in five performances of this species. Temporal aspects of Copulation Clatters appeared similar between the three storks observed, however more detailed study is needed. Female bill clattering, similar to male Copulation Clattering, was heard during reverse copulations if the female actually mounted the male.

The two egg-laying female *C. maguari* hissed during 11% (N = 108) of male copulatory advances (Approaches and Attempts). The females appeared to be receptive to the male on these occasions, as they assumed the female copulatory posture. Female copulatory hissing was also heard during some copulations of the pair of *C. ciconia* nearest to the observation station, but was not heard in more distant pairs of *C. ciconia*, or in *C. boyciana*.

Copulation Approaches or Attempts by male _C. maguari_ took place when the female was sitting (Fig 21) in 38% of the 108 advances observed. One male attempted to mount his "same-sex" mate three times, all when the mate was sitting. The female _C. maguari_ that performed reverse Copulations attempted to mount the male when he was sitting in 10 of 25 occurrences. Two male _C. ciconia_ made copulation advances when the female was in both sitting and standing positions, while a third did so only when the female was sitting. The breeding male _C. boyciana_ made all advances when the female was standing.

Context. Frequency of copulation was variable between the six egg producing pairs of storks observed here (Table 12). The breeding pair of _C. boyciana_ began copulating 42 days before the first egg was produced. Observations of the other species began after initiation of copulation, thus date of copulation initiation could not be established. In all six pairs, copulation activities ceased within two weeks of laying of the first egg. In four of five pairs copulation was reinitiated for a short time during the post reproductive phase (Table 12). Copulations occurred throughout the day in all species.

Copulation advances made by four male and one female _C. maguari_ occurred at nest sites in only 48% of 136 occurrences. Although copulation activities of the two breeding pairs did not necessarily take place on the nest, they were often associated with Offerings and manipulation of plant material (Table 13). Copulatory behaviors of C. ciconia and C. boyciana always took place on the nest, but were not as strongly related to bringing of nesting material to the nest as those of C. maguari (Table 13).

One of the male C. maguari, "A", was observed performing Copulation Clattering on short (< 25 cm) tree stumps 33 times in the 11 days preceding egg laying and incubation. Mean duration of six performances was 6.7 s (S.D. = 1.7). The behavior sometimes followed copulation advances to the female, and were generally identified with plant material manipulation.

Comments. Preliminary copulatory behaviors observed here have been described for C. ciconia and C. maguari (Haverschmidt 1949; Jovetic 1961; Thomas 1986), and did not appear to differ from wild behaviors in form, despite incompleteness of copulation in many cases.

Pinioning of C. ciconia and C. maguari undoubtedly affected copulatory behavior. Seventy infertile eggs have been produced over an additive six year period by the two breeding female C. maguari studied here, supporting the observation that the males were unable to mount their mates. Performance of Copulation Clattering on tree stumps observed in male "A", the male that tended to abandon unsuccessful copulation advances toward the female more rapidly, indicates that inability to mount was a physically, rather than psychologically, induced phenomenon. Redirection of copulatory activities to substitute objects (protruberances) in the immediate surroundings has been observed in other species when the female providing the initial stimulation becomes unavailable for some reason (Ficken and Dilger 1960).

The one fertile (of three) egg producing pairs of *C. ciconia* (three of five eggs were fertile) was the pair that copulated only when the female was sitting. This modification of copulatory behavior is common in pinioned *C. ciconia*, however some males do not adopt this strategy, and may not fertilize eggs (B. Schmitt; K. Vos; M. Weldon pers. comms.). Copulation when the female was sitting has been observed in wild *C. ciconia* on rare occasion (Kahl 1972a). This behavior was not observed in wild *C. maguari* (B. Thomas pers. comm.).

The copulation pattern observed in full-flighted *C. boyciana* here, in which success increased during the initial copulatory period, has been observed in wild *C. Ciconia* (Haverschmidt 1949). Haverschmidt did not comment on prior experience of birds in which this pattern was observed. The pair of *C. boyciana* produced eggs for the first time the year of observation, but may have copulated previously, as they had been housed together and a pair bond had been established for three years. Potential differences in copulation success within the breeding season could not be assessed since observation of experienced C. ciconia in this study began after copulation was initiated.

Copulation usually begins ca. one week prior to egg production in the Ciconiidae (Kahl 1978). The prolonged copulatory period of seven weeks observed in the breeding C. boyciana here would be unlikely to occur in the wild, as most of the birds arrive at breeding areas only two to three weeks before eggs are laid (Dymin and Pankin 1975; Rosylakov 1977; Winter 1982), and copulation in storks occurs at the nest (Kahl 1978). Copulation has been observed year round, with varying frequency, in free-flying non-migratory C. ciconia of the Dutch reintroduction project for this species. These birds also maintain and defend their nests throughout the year (K. Vos pers. comm.).

Although individual differences existed, patterns of copulation observed in this study resembled those of wild storks insofar as the primary copulation period ended within two weeks of laying of the first egg in all six pairs studied. The brief reinitiation of copulation and nest building after eggs or young were removed or young fledged was seen in all species here and is typical of wild C. ciconia following fledging of young (Haverschmidt 1949). Thomas (1986) also noted that Maguari Storks sometimes commenced nest building after the young left the nest.

Jouventin (1982) reported a recurrence of breeding activity by penguins at the end of the breeding season, and interpreted this as "protogamic" behavior designed to reduce the time needed for courtship the next year in an environment in which reproduction is temporally restricted. Reinitiation of courtship activities may serve a similar function in the storks; it could be particularly important in _C_. _ciconia_ and _C_. _boyciana_, as these species are highly migratory. Indeed, it has been noted that _C_. _ciconia_ arriving at their nests later in the year than is feasible to successfully fledge young prior to migration back to wintering grounds will defend the nests but not produce eggs, or will have low hatchability of eggs (Jovetic 1960; Haverschmidt 1949; Lack 1966; Zink 1967).

Two atypical copulatory behaviors observed in this study are not unknown in wild or semi-wild conditions. Reverse copulation is a behavior that has been observed in some wild _C_. _ciconia_ that also copulated normally and produced young (Haverschmidt 1949). Reverse copulations have also been observed in _Jabiru_ _mycteria_ (Kahl 1973).

Formation of same-sex "breeding" pairs, observed in Maguari Storks in this study, has been documented in free-flying storks in European reintroduction programs. Numerous individuals of the opposite sex were available to these storks during the pairing process, thus the reason for the selections made is unclear. Behavior of the same-sex pairs resembles that of heterosexual pairs; they have even raised young when given fertile eggs (M. Bloesch, K. Vos pers. comms.). Formation of same-sex pairs may occur under natural conditions, but has not been identified.

High occurrence of C. maguari copulatory activities at non-nest locations, and a stronger association between copulation and nest material manipulation than copulation and the nest was observed in this study. Though copulation of C. maguari normally takes place at the nest, the same trends may occur in the wild. Thomas (1986) recorded some copulation advances by male C. maguari in Venezuelan marshes away from the nest, though females were usually unreceptive in these encounters. Thomas also noted an association between nest material and copulation of C. maguari: conveyance of wet grass lining materials to the nest by the male often preceded copulation.

Copulation Clattering involving erratic clapping of the bill is homologous throughout the storks (Kahl 1966, 1972a, c, d, e, 1973). Kahl (1972a) suggested that this display may be derived from ritualized biting, as agonistic tendencies are high between newly formed pair members at the time of most frequent copulation. Hudson (1965) interpreted this behavior in C. ciconia as a form of Allopreening, which may also be an agonistic behavior derived from ritualized biting (e.g. Blaker 1969; Harrison 1965; Mock 1976). It is interesting that bill clapping is present in this display throughout the Ciconiidae, while other elements (e.g. open to slightly open female positioning of the wings, point of contact between the male's bill and the female) are more variable between genera (Kahl 1966, 1972a, c, d, e, 1973).

Begging Display (Kahl 1972a)

Essential Elements. Begging of nestlings was observed from the first day of age, but this behavior changed markedly through ontogeny. Begging of both *C. boyciana* and *C. ciconia* included a bisyllablic vocalization that resembled a cat's "meow" in cadence.

The Begging Display of *Ciconia*, described by Kahl (1972a) for four species, including *C. maguari*, was found to differ little among species. Begging was observed in both hand- and parent-reared nestlings in this study. The display of older nestlings was similar to the *Ciconia* Begging Display described by Kahl.

Variations. Sonograms showed that the begging meow was a broad banded vocalization, with the pitch between 7 and 2 KHz. Within this range two or three discernible bands of sound occurred that were variable in form (Fig. 23). The cadence of this vocalization remained the same throughout the nestling period, but some change in pitch frequency occurred as the young developed. Pitch was also audibly different between the two species; in this and all other vocalizations, that of _C_. _ciconia_ was lower.

The meowing vocalization was emitted almost continuously during feeding when chicks were very young, perhaps to 10-15 days, but sometimes was only produced at the beginning of the feeding session thereafter. There was noticeable individual variation in frequency of performance.

While producing the meowing vocalization, chicks up to ca. 10 days of age typically extended the neck forward and "pecked" at the substratum, with the bill barely open. The neck was not raised beyond the vertical axis between pecks, and the bill remained at least 30° below the horizontal. Bobbing head movements continued to accompany the begging sounds even when the chicks ceased the pecking behavior.

Wings were usually folded during begging until the chicks were ca. 25-30 days of age, but were sometimes held slightly from the body, with the tips dropped close to the ground. When actually picking up pieces of food the chicks sometimes raised the wings, so that the humerus was rather horizontal in position, and the wing open to ca. 90° at the carpal joint.

Begging Displays were often interspersed with performances of Up-Downs during the first 10 days of life, but these gradually decreased in frequency thereafter

(Table 10). A monosyllabic "yip" was commonly emitted when chicks were actually picking up food during the first 10 days. The yip was also produced when two or more nestlings were vying for the same piece of food, a frequently occurring situation once the chicks were 10-15 days of age. Peak frequencies of this vocalization ranged between ca. 3-8 KHz, and were usually ca. 0.2 s in duration. Changes in pitch frequency of "yips" occurred during nestling development. This sound was indistinguishable from sounds the chicks made when they were uncomfortable (e.g. too hot or cold).

Nestlings, particularly C. ciconia, often tugged on their sibling's crop or wings when begging. This behavior was most prominent during the first few day of life, but persisted throughout the nestling stage. The tugging did not seem to be particularly hostile. Parent-reared chicks began touching the bill to that of a feeding parent at 12-14 days of age while emitting the meowing begging vocalization; this was observed in both C. boyciana and C. ciconia. Older chicks sometimes grabbed the parents bill in their own, but not as vigorously as in many other wading birds, including some Ardeidae.

Chicks at 25-30 days began to hold their wings in a distinctive posture during begging: the humerus was raised and tilted back so that it is angled 30-50° from the horizontal axis, the radius and ulna were dropped, with an angle of ca. 60° formed at the carpal joint, and the wing tips were held horizontally (Fig. 22). Chicks of this age sat up on the tarsi when performing Begging Displays, rather than directly on the ground as they did when younger. When begging, the base of the chick's neck was lowered almost to the ground, and the neck extended, forming an angle of 40-50° with the horizontal axis.

Begging chicks of 25-30 days of age occasionally began to flap their wings, holding them in the above described position. Flapping was erratic until the storks were about 55 days of age, then the flapping usually proceeded rhythmically, at a rate of 8-9 flaps/s. Rapid head bobbing and the meowing vocalization were still components of the display. The tail was cocked ca. 40° above the horizontal axis. Wing flapping chicks sometimes pecked at the substratum, similar to the behavior observed in very young nestlings.

Standing chicks would drop to the tarsi to perform Begging Display. This was often seen after the chicks began standing for prolonged periods (35-45 days of age). Hand-reared nestlings sometimes approached or followed their human caretaker for several m while shuffling on the tarsi in the begging posture.

<u>Contexts.</u> Hand-reared chicks usually began begging when they saw their caretaker, even if food was available.

When the chicks were 60-70 days of age they became more wary of humans, and usually moved well away when anyone approached. When the chicks at this stage were fed, they sometimes dropped to the tarsi and performed a Begging Display before moving away. After the hand-reared chicks left the nest (but were still fed by the parents), they returned to the nest and dropped into the begging posture when the caretaker put stork food in the enclosure. This suggests that the chicks associated this event with feeding by parents.

Comments. Kahl (1978) reported that nestling storks rarely seemed satiated, and would intermittently perform Begging Displays whenever one of the parents was present on the nest. Parent-reared chicks in this study were sometimes disinterested in food, and did not perform Begging Displays even when a parent was regurgitating food. The male *C. ciconia* invariably regurgitated food when he got on the nest, so food was usually abundantly available to the nestlings.

Progression of Begging Display variations throughout nestling development was noted by Haverschmidt (1949) in wild *C. ciconia*: he reported that begging took the form of "bill clattering" (Up-Downs) when the nestlings were small, but was replaced by wing flapping when nestlings were able to stand. The similarity of the begging vocalization to the meowing of a cat was also remarked upon. Winter (1982) described vocalizations similar to those heard here for wild C. boyciana.

The close association of the nestling Up-Down with begging behaviors demonstrates the value of the Up-Down in gaining parental attention, as securing food is probably the most critical consideration in survivorship of the young. Since the Up-Down is replaced during ontogeny by the wing flapping display, it can be assumed that the latter is more effective in prompting feeding, at least in the later nestling stages.

Absence of wing flapping in very young chicks could be due to at least two factors: motor development may not have proceeded sufficiently to allow performance, or the flapping is not then visually effective. Wing flapping begins only after the primaries, secondaries and scapulars are well grown; presence of these feathers greatly accent movements involved.

The Begging Displays of nestling C. ciconia and C. boyciana are remarkably similar, and appear to resemble those of C. maguari, at least during the late nestling stage.

Nestling Bill Snapping

Essential Elements. The nestling strongly erects the head, upper back and all neck feathers, and rapidly snaps the bill for ca. 2-5 s with the hyoid apparatus lowered.

The head is held stationary throughout the display. This display was observed in both _C_. _boyciana_ and _C_. _ciconia_ nestlings, but was not described by Kahl for any species of _Ciconia_.

Variations. Nestlings performing this display while standing would hold the neck straight, but extended forward at a 30° angle from the vertical. The bill was oriented slightly downward, ca. 45° below the horizontal axis. Nestlings also performed the display when being handled: though not standing, the performer erected the feathers and emitted bill snaps.

Contexts. Nestling Bill Snapping was first recorded in _C_. _boyciana_ at 24 days of age when they were handled. This behavior was thereafter observed throughout the nestling period. Some individual variation existed- one of the four nestlings never Bill Snapped when being handled. Further, Bill Snapping was never observed during handling of _C_. _ciconia_.

Nestling Bill Snapping performed while standing was first observed in _C._ _boyciana_ at 40 days of age. Four performances were observed between 40-50 days of age: one was directed at nestling _C_. _ciconia_, and one at Common Peafowl (_Pavo_ _cristatus_) in adjacent enclosures, and two were directed towards unfamiliar humans. The one performance recorded in _C_. _ciconia_ occurred at 55 days of age, and was directed toward nestling _C_. _boyciana_.

Comments. Bill snapping heard during this display sounded more uniform in frequency than that of claps emitted during Up-Downs. This was probably a result of the stationary position of the head, which did not allow frequency alterations due to changes in shape of the sound chamber (gular sac) to occur.

Nestling Bill Snapping was obviously an agonistic behavior, based on posturing, feather erection, and the contexts in which it was observed. Erection of the head and neck feathers by nestling hand-reared _C_. _boyciana_ was often observed when unfamiliar humans approached; this behavior was performed from ca. 25 days of age to the end of the nestling period. Erection of the head feathers and all neck feathers was not observed during any bill clapping display of adults.

Haverschmidt (1949) also observed a bill clapping display in a nestling approaching fledging age. He noted that erection of the neck feathers was the most outstanding component of this behavior. The display was performed whenever the author made his presence (at a blind) obvious to the stork. Haverschmidt reported that the display was certainly threatening in function, and also noted that neck feather erection was unlike any adult display. Although the neck was moved more rearward in performances observed by

Haverschmidt, it seems likely that this is a variation of the same display observed in this study: in both cases it was performed by older nestlings, neck feather erection was a visible component, and it was performed in a "threatening" context.

Thomas (1984) reported that *C. maguari* nestlings began bill clapping and snapping in defense at two weeks of age. Though no details were provided on posturing of performers during occurrences, it seems likely that the behavior observed in her study was also a Nestling Bill Snapping Display.

Bill snapping was also observed during nestling agonistic interactions in which the Nestling Bill Snapping Display was not performed; both *C. ciconia* and *C. boyciana* species were recorded snapping the bill when jabbing at siblings, humans, and nestlings of the other *Ciconia* species studied. During such encounters the snapping was erratic, and performed only a few (less than 5-10) times. This type of behavior was observed from 25 days of age in *C. boyciana* and 22 days of age in *C. ciconia*, and continued throughout the nestling period.

Kahl (1972a) described the performance of a bill clapping display by a roughly three week old Woolly-necked Stork (*Ciconia episcopus*) in response to the presence of a House Crow (*Corvus splendens*). This display showed some similarities to the Up-Down of adult *C. episcopus*, involving some Up-Down head movement. More data is needed to determine whether these are homologous displays, and whether the behavior is characteristic of Ciconia. A "Nestling Defense Display" was described by Kahl (1972a) for C. maguari. It was quite unlike the agonistic display described here, but resembled begging in posturing, and involved striking at the (human) opponent with the bill, while emitting a "shrill, rasping scream".

Akinesia (Schüz 1943c in Haverschmidt 1949:46)

Essential Elements. The performer becomes motionless, and can be manipulated without responding in any obvious manner.

This behavior has been documented in all three species addressed here (Haverschmidt 1949; Jovetic 1961; Thomas 1984; Winter 1982) but was not considered to be a social signal in Ciconia by Kahl (1972a). Because it is a widespread behavior in storks, and because the precise function of this behavior, or the message conveyed (if any) is not well understood, it is addressed herein.

Variations. Akinesia occurs when the bird is in a stressful situation. Duration of the display is possibly dependent on the length of time that the stress stimulus is present. Schmitt (1967) reported that reversion to the normal state is gradual.

Contexts. Akinesia was observed in *C. ciconia* parent-reared nestlings 46 and 48 days of age when closely approached by a human. A hand-reared nestling *C. ciconia* 63 days of age performed this behavior following introduction into the enclosure holding the *C. ciconia* group, when attacked by an adult. A *C. boyciana* nestling 18 days of age showed Akinesia when removed from its parents.

Comments. Akinesia reportedly occurs in wild *C. ciconia* to seven weeks of age (Haverschmidt 1949), in *C. maguari* during the first two weeks of life (Thomas 1984), and *C. boyciana* from 12-40 days of age (Winter 1982). Behavior of captive parent-reared *C. ciconia* here was similar to that reported by Haverschmidt, i.e. Akinesia was still performed at 46-63 days of age. Winter (1982) noted that wild *C. boyciana* nestlings began performing Akinesia in response to human approach at 15 days of age; younger chicks begged and performed Up-Downs instead. Behavior of parent-reared nestling *C. ciconia* and *C. boyciana* studied here was similar: a *C. boyciana* chick removed from the parents at 5 days of age, and parent-reared *C. ciconia* handled at 1-10 days of age also responded with Up-Downs and Begging.

Nestlings of all three species perform Akinesia in response to signals (the clapping sometimes associated with Neck Stretches) communicated by their parents, and possibly other nearby adults (see Neck Stretch).

Generally, Akinesia has been considered a nestling behavior. However, Schmitt (1967) has frequently observed it in captive adults when cornered by a caretaker, or during battles between conspecifics. He reports that when the behavior is performed during a fight, the opponent becomes confused, repeatedly circles the performer while pecking at the head, then leaves and may also become Akinetic. Akinesia must have some signal value if performance of this behavior by one individual causes its opponent to cease aggressive behavior, and/or also become Akinetic. Thomas (1984) suggested that Akinesia may be an anti-predator strategy, designed to give young nestlings an egg-like appearance. This is certainly not the only function in C. ciconia, as Akinesia is still practiced in adult-sized nestlings. Haverschmidt (1949) considered the behavior to be "sham death," a strategy employed by nestlings for protection against injury during nest invasion by conspecifics. Akinesia may, at least in some situations, act as a "white flag of surrender", signaling an aggressor that the performer will not engage in fighting.

Akinesia was replaced by increasing active defense by C. maguari during handling at 9-14 days of age (Thomas 1984). Kahl (1972a) also recorded active defense by nestling C. maguari by three weeks of age. This is much earlier than the seven weeks reported for C. ciconia

(Haverschmidt 1949), and the 35-50 days reported by Winter (1982) for C. boyciana.

The earlier age at which Akinesia commences, and also is replaced by active defense in C. maguari suggests that this species has developed specialized anti-predator strategies. Thomas (1984) made the same observation, but pointed out that Wood Storks also begin active nest defense at early ages. Possibly Wood Storks also have greater predation pressure than some of the other storks; e.g. American Wood Storks (Mycteria americana) in a nesting colony in Georgia suffer heavy nestling losses from raccoons (Procyon lotor) when water around the colony recedes (M. Coulter pers. comm.). Unattended nestlings are also subject to avian predation (Van Meter 1985).

Kahl (1972a) did not observe the Nestling Defense Display of C. maguari in other Ciconia, but his observations of Ciconia nestlings was limited. Though it may occur in other species, references to such a display have not been located.

Play

Essential Elements. The bird engages in bouts of physical activity that include hopping locomotion. Performance of play is not obviously related to any external stimulation. Performance of behaviors categorized as play herein were not described by Kahl (1972a).

Variations. Play activities were observed in juveniles and nestlings. Juvenile play of *C. ciconia* usually involved lateral hops, with both legs pushing off the ground simultaneously (Daanje 1950), that sometimes carried the performer a distance of ca. 2 m. Wings were raised, with the line of the humerus ca. 25-45° above the horizontal axis, and the tail spread. The performer often turned the orientation of the body ca. 90-180° during the hops, while flapping the wings. When performing hops the birds tended to stay in a relatively small area, e.g. within a 3-5 m. radius.

Bill snapping, during which the bill was raised well above the horizontal axis, was also commonly performed between hops of juvenile *C. ciconia*. Posturing and bill snapping movements resembled those observed in the Neck Stretch of *C. ciconia* and *C. maguari* described above. Snaps were usually produced at a rate of fewer than 1/s.

Juveniles performing hops alone often jabbed at vegetation, both above and to the side the bird, between the hops. Sometimes two to all four of the juveniles engaged in hopping during the same time period. Interactions involving physical contact (e.g. Bill Duelling, non-display jabbing) were interjected between hopping bouts. The interactions observed had a dancing quality about them, as the birds often reoriented in a rotating fashion during the interactions, and movements alternated back and forth in the direction of the participants.

Play of nestlings tended to involve more wing flapping and hopping with the feet pushing off asynchronously than did play of juveniles. Nestlings ca. two months of age often traversed the length of their 14 m pens several times in succession when performing this activity, gliding as much as 4 m between hops. Interactions between sibling nestlings similar to that observed in juvenile _C_. _ciconia_ occurred when the nestlings engaged in play activities.

Play was dissimilar between _C_. _ciconia_ and _C_. _boyciana_ nestlings. When engaging in play, nestling _C_. _ciconia_ often (85% of 13 sessions) snapped the bill in a manner similar to that of juvenile _C_. _ciconia_. Conversely, nestling _C_. _boyciana_ were not observed bill snapping during Play. This species typically picked up small objects, i.e. paper, twigs, and plant or nesting materials and carried them around in the bill during play: this was recorded in 79% of 39 play sessions. Nestling _C_. _ciconia_ only performed this behavior in 15% of 13 play sessions. Nestling _C_. _boyciana_ were commonly observed attempting to wrest materials from each other during Play.

Contexts. Play was observed in nestlings from ca. 45 days of age. Performance of this behavior was preceded in ontogeny by wing flapping without hopping; wing flapping was first observed in birds 22-26 days of age. Play was not associated with any particular activity in either juveniles or nestlings. Play of multiple individuals appeared to be initiated by the performance of this behavior by a single bird.

Comments. Exercising of the wings accompanied by vertical jumps prior to fledging has been reported for all three species addressed in this study (Jovetic 1961; Thomas 1984; Winter 1982). The behavior described as nestling Play here is probably preparatory for flight, however presence of bill snapping and material carrying components, as well as frequent physical sibling interactions, preclude description of the behavior as merely exercising. Enhancement of muscular development in young animals is thought to be a primary function of play (Beach 1945; Ficken 1977).

Beach (1945) listed "the main types of play" under the following categories: 1) general bodily activity, chiefly of locomotor character, in which considerable amounts of +energy are expended, 2) youthful practices of adult behaviors, including mock battles and sexual activities, 3) exploration and experimentation, such as pecking, scratching, pulling and biting at objects in the environment, and 4) social responses that seem to lack any practical outcome, e.g. "tilting matches" of birds, dancing of young primates. Play of storks observed in this study had elements included in all of the above categories.

Social play is uncommon in birds, though imitation of non-social play is common (Ficken 1977). Both were observed among siblings in this study. Cross-species imitation was not observed however; the difference in nestling play (carrying of object by _C_. _boyciana_ vs. bill snapping by _C_. _ciconia_) occurred despite the fact that these species were in virtually identical environments, and had visual as well as limited physical contact with each other. Play is somewhat species-specific (Beach 1945), thus it is possible that play forms (carrying of materials vs. bill clapping are species specific behaviors, though more data are needed for comparison. The presence of bill snapping in play of juvenile _C_. _ciconia_ not genetically related to the nestlings observed here, or in contact with these individuals, does suggest that bill snapping is a characteristic of play in this species rather than a personality variation.

Acoustic play has been established as a valid form of play in birds (Ficken 1977). Manipulation of objects is a common component of avian play, though manipulation of nesting materials does not by itself constitute play (Ficken 1977). This difference was also distinguished in this study; non-play manipulation of nesting materials was observed in both _C_. _ciconia_ and _C_. _boyciana_.

Play, as defined in this study, was restricted to juveniles and nestlings. The bill snapping play of

C. ciconia strongly resembled Neck Weave of adult C. maguari. Neck Weave may be a form of adult solitary play, or at least be derived from play.

CHAPTER V

DISCUSSION

Characteristics of Social Signals Used

Signals in Repertoires

Most social signals described for C. boyciana, C. ciconia, and C. maguari are common to all three storks (Table 14). Only three displays, the Head Shaking Crouch, Mock Resting and the Nestling Defense Display, are likely to be absent in the repertoire of one or more of the species. Behavior of Ciconia maguari seems to differ the most: the Head-Shaking Crouch may be absent in this species, while Mock Resting and the Nestling Defense display may be specific to it.

Ten of the 21 behaviors presented as social signals were not reported by Kahl, but six of the ten were described in recognizable form in the literature by others (Table 14). Three of the four previously undescribed signals, Arch Gape, Offering, and Wing Flash, were used predominantly by Maguari Storks. The other signal, Play, was restricted to juveniles and nestlings in this study. Identification of new behaviors in juveniles and nestlings would not be unexpected, as signals of these two age classes have not been well studied.

Twenty displays listed in Table 14 are included in the behavior repertoire _C. maguari_, and 19 in repertoires of _C. boyciana_ and _C. ciconia_, including signals specific to nestlings. Moynihan (1970) suggested that there is a maximum display repertoire (ranging somewhere between 10 and 37 major displays) that the communication system of a species can support without losing transmission effectiveness. Other authors have found the mode for birds to be 19 to 21 displays (Barlow 1977). Though what is considered a "major display" is somewhat arbitrary, it is generally agreed that the number of displays in the repertoire of a given species will be small (Barlow 1977; Beer 1975; Hailman 1977).

Variability in Signal Form and Signal Usage

There was a marked difference in usage of the signals among species: e.g. _C. maguari_ tended to perform the short range hostile displays, Arch-Gapes and Wing Flashes, more than _C. ciconia_, while _C. ciconia_ characteristically performed the longer range Forward Display in agonistic situations. _Ciconia maguari_ also relied more on Basal Neck Feather Erection to convey messages. Offerings were more typical of interactions between C. maguari pairs than of the other two species during the courtship period, and allopreening more prevalent in C. boyciana and C. ciconia.

Moynihan (1970) postulated that displays decay and eventually disappear from repertoires, being replaced by others in accordance with changing intrinsic and extrinsic selection pressures; thus the number of displays in repertoires do not exceed the optimal number. Differences in usage of signals common to the three storks observed in this study may support Moynihan's hypothesis if the storks addressed here are viewed as phylogenetically closely related entities that are behaviorally diverging to meet new ecological constraints as they expand into new environments.

Form, usage, and repertoires of nestling behaviors were quite similar for C. ciconia and C. boyciana, excluding the differences in nestling Play discussed. Kahl's (1972a) description of the Begging Display of C. maguari resembled that of the other two species as well. One or more of the prominent visual components of the Begging Display; tail cocking, wing positioning and wing movements, were observed in adult signals of C. ciconia and/or C. boyciana but not C. maguari. Such displays included the Nest Covering Display, "Threat Up-Down", and Head Shaking Crouch. Kahl (1972a) suggested that wing pumping is derived from flight intention movements, i.e.

pursuit of the opponent. One element of nestling Begging Displays, pecking at the substrate, was an element in some variations of the Up-Down of all three species.

Incorporation of these nestling signal elements in adult behaviors may be due in part to their high visibility, which presumably provides strong signaling value. Also, the central nervous system favors stereotypy when faced with a familiar task, giving priority to more essential patterns of coordination (Barlow 1977). In light of this, it is interesting that most of these signaling elements are not present in displays of C. maguari.
Use of these elements in several displays emphasizes the importance of context; it is improbable that the Begging Display and a "Threat Up-Down" carry the same message.

Use of video tapes in this study permitted quantification of display elements. Generally, displays were found to be more variable in form than those described in previous studies, but were clearly recognizable. Recent work has shown that although there may be a "typical intensity" of signal form (Morris 1957), there is also considerable form variation (Barlow 1977; Lewis and Gower 1980; Stamps and Barlow 1973). It is assumed that variability observed here was not an artifact of captivity because descriptions of behaviors under field conditions also exhibit considerable variability.

Though caution must obviously be used in interpretation of results, study of behavior in captive situations has three inherent advantages: 1) it allows observation at closer range than would often be possible under natural conditions, 2) more opportunities are possibly provided for observation of social interactions than in wild situations due to forced close proximity of individuals, 3) functions of social signals may be more obvious when performed in unnatural conditions, particularly if contexts can be compared to those in natural conditions.

Sexual differences in signal usage included predominantly male performance of Offerings and Nest Covering Displays, and typically female performance of Mock Resting. Some variations of the Up-Down seemed to be characteristic of males, and others characteristic of females. Results from this study are consistent with previous work; Kahl (1971a) commented that he had seen almost all behaviors that were characteristic of one sex at least occasionally performed by the other sex. Further exploration of sexual variations in signal usage in relation to contextual components must be undertaken before any meaningful conclusions concerning adaptive survival value of variations can be made.

Signaling Sensory Modalities

Social signals of the three species involved auditory, visual and tactile characteristics. Although the sensory modalities used to transmit a signal sometimes varied among species, the overall number of signals employing the different modalities was consistent (Table 15). The only social signal used by the storks that did not appear to have a highly visual component was Allopreening. As all three species forage by sight, vision plays an important role in their behavior. "It is a truism, but nevertheless necessary to say, that visual signaling develops hand in hand with visual abilities" (Lewis and Gower 1980). Three of the 21 signals here (Akinesia, Basal Neck Feather Erection, Forward) appeared to employ only this modality in all species addressed.

Auditory elements were present in 15 of the 21 signals, in at least one species. Storks do not have functional syringeal muscles (Terres 1980), and only a poorly developed tracheal syrinx (Ligon 1967), hence vocal powers are quite limited. The only sounds emitted by the species studied here are hisses, and mechanically produced bill claps that are enhanced by reverberation in the gular sac. Yet it is in auditory modality that signaling varied the most between C. maguari and the other two storks. Auditory elements of C. boyciana and C. ciconia signals were similar; in six signals in which presence and form (hiss and/or claps) of an auditory element could be identified they were the same for both species (Table 16).

Nestling C. ciconia often bill snapped during play, but C. boyciana did not. The only auditory distinction in adult behaviors was that hissing by the breeding female C. boyciana was never recorded during copulation, however, most copulations by the C. boyciana pair were observed at distances at which this would probably be inaudible to the observer. It is probable that the vocalization would be heard in close range study of Copulation Clattering performed by C. boyciana. Though observed in both C. ciconia and C. maguari, female hissing was not consistently present in Copulation Clattering of either species. That female hissing during copulation is infrequent and practically inaudible is supported by the lack of mention of this behavior in the literature.

Auditory elements of signals produced by Ciconia maguari were of the same form (hiss or clap) as that of C. boyciana and/or C. ciconia in six signals: Aerial Clattering, Begging, Copulation Clattering, Neck Stretch, Neck Weave, and Nestling Bill Snapping. An auditory element was present in the Arch-Gape and Upright Display of C. maguari, but absent in the same signal in the other two species. Conversely, two signals, Wing Flash and Offering, had auditory components in performances by C. ciconia and/or C. boyciana, but not in those of C. maguari. Auditory components were present, but different in form, in the Nest Covering Display and Up-Down of all three storks

(Table 16).

Ciconia maguari bill clapped during three agonistic displays and Copulation Clattering, but only hissed during Up-Down Displays and Courtship Clattering. Conversely, C. boyciana and /or C. ciconia bill clapped during the Up-Down, but primarily hissed during agonistic encounters, and "Threat Up-Downs". Nestling C. ciconia and C. boyciana, as well as juvenile C. ciconia, bill clapped in agonistic displays or non-display agonistic encounters. Nestlings were not heard hissing during any signals. Nestling vocalizations ("grunts", "meows", and "yips") lacked the chevron configuration of adult hisses. Whether this difference during ontogeny is due to physical maturation, and/or is behaviorally adaptive, remains unclear.

Ecology and Signaling

Differences in signal repertoire, usage, and form among the species studied can be viewed in terms of their (probable) adaptive character in order to gain insight into likely pathways of evolutionary change (Tinbergen 1962). The adaptive significance of behavioral differences discussed in this paper seems to be related to differences in reproductive ecology and foraging habits; behaviors not so related appear to be similar in the three species.

Courtship, Nest Site, and Timing of Breeding

Banding studies have shown that some C. *ciconia* travel 19,200-22,400 km annually to and from the breeding site (Kahl 1978). The nesting cycles of C. *ciconia* must proceed rapidly; eggs are usually produced within two weeks of arrival at the nest, and late arriving birds frequently fail to nest (Haverschmidt 1949, Jovetic 1961). A need to quickly complete reproduction might favor courtship at the nest in this species, and also in the other migratory species, C. *boyciana* (Table 3). The need to rapidly locate conspecifics may have been a factor in the evolution of the acoustically conspicuous Up-Down display of these storks. As sub-adult birds often attempt to take nests (Jovetic 1961; Haverschmidt 1949), absence of the Up-Down in their behavioral repertoire may aid adults in quickly assessing the reproductive status of these individuals.

Use of elevated nests by C. *ciconia*, and presumably C. *boyciana* has reduced predation potential, thus the need to compromise display length and visibility because of exposure is reduced. Kahl noted that compared to other storks, initial pair bonding of C. *ciconia* is quite violent, and suggested that this may be due to the fact that the female must alight directly on the nest when attempting to gain entrance to the nest. This, and the forced close proximity of mates at the nest may have been instrumental in the evolution of what seems to be an advertising complex, including Offerings, frequent Allopreening, and the highly conspicuous Up-Down. The constant threat of marauding conspecifics may also have acted on evolution of these displays.

Ciconia maguari is primarily a nomadic tropical breeder, although some may migrate (Table 3). Reproductive behavior of C. maguari is apparently synchronized with rainfall, i.e. breeding occurs when water levels are high (Thomas 1985; Weller 1966). Yet eggs are not necessarily rapidly produced; nest building continued for over two months before eggs were laid in one nest observed by Thomas (1986), and one young was successfully reared. A longer reproductive period may be a factor leading to group courtship of this species. It is unlikely that more time availability alone is responsible for group courtship in C. maguari, as most storks are tropical, but still court at the nest (Kahl 1978).

There are two obvious advantages to group courtship in C. maguari: increased visibility to potential mates and reduced susceptibility to predation. Use of a highly audible display including bill clattering would increase conspicuousness of potential mates in high vegetation, but also would probably increase likelihood of predator detection. The ability to monitor the environment would possibly also be reduced. It may be significant that all three Up-Down forms of _C_. _maguari_ were shorter than Up-Downs of _C_. _ciconia_ and _C_. _boyciana_, as longer displays would decrease monitoring time.

The presence of the specialized Nest Covering Display and Mock Resting defense tactics employed by _C_. _maguari_ suggests that terrestrial predation has been a selective force in behavioral evolution of this stork. The dark coloration of _C_. _maguari_ nestlings, acquired by the time that nestlings are left alone at the nest, was suggested by Kahl (1971b) and Thomas (1984) to be an adaptation to aerial predation, but could also serve to make nestlings less visible to ground predators. Caldwell (1986) recently showed that predation is an important selective force on tropical Ardeids. Thus it seems likely that the emergence of a courtship strategy involving less conspicuous display elements in a social group context (more eye scanning for predators) could evolve easily in a bird with the Maguari's natural history.

The performance of _C_. _maguari_ courtship behaviors at sites other than the nest in the wild has apparently translated into a reduced association of reproductive activities with the nest in captivity: copulations and Offerings frequently occurred at sites other than the nest. Use of nesting material in courtship activities, a frequently observed phenomenon, may represent in this species what the nest does in _C_. _boyciana_ and _C_. _ciconia_.

It is possible that C. maguari does not employ a long range Up-Down for reasons other than potential increased predation on themselves and/or their offspring. Since Maguaris often nest in tall vegetation, and apparently court in groups, a primary reproductive signal visible from a long range would be superfluous. Courtship activities of Maguari Stork pairs described by Thomas (1986) were not reported to be highly agonistic. The courtship of these storks in a non-restricted and undefended site, and less forced proximity of mates at the nest could be at least in part responsible for signaling trends observed, including a higher rate of Offerings (that may carry a different meaning in this species), and a lower rate of Allopreening.

Offerings of Maguari Storks may serve to initiate and promote contact with potential mates in a non-restricted situation. Thomas did not observe this behavior in Maguari Storks nesting in Venezuela, but noted that flooding of the savannahs during breeding activities would have precluded such behavior (pers. comm.). Thomas (1986) did report that birds sometimes carried material in their bills during assemblies; these events may have been Offering intention movements. The behavior was so prevalent in captive individuals that it is unlikely that it does not occur in wild ones as well.

General Habitat Considerations

Ciconia boyciana and C. ciconia are typically found in more open habitat than C. maguari: C. ciconia prefers short vegetation and shallow waters for foraging (Bogucki and Ptaszyk 1986; Cramp 1977; Profus and Mielczarek 1981), and Ciconia boyciana usually forages in expansive shallow waters (Gluschenko 1985; Wang in press). In contrast, vegetation of habitats utilized by Maguari Storks can become quite tall and dense (Hanagarth and Riberia 1985; Gibson 1880; Weller 1967).

Habitat differences may be responsible for signaling trends observed in agonistic encounters. Ciconia ciconia tended to perform the longer range Forward when initiating an agonistic encounter, while Wing Flashing and Arch-Gapes, short range agonistic displays, were more common in C. maguari. Basal Neck Feather Erection, another short range display, was much more common in Maguari Storks. This display may have a generalized function when performed alone, and is also an important component of the C. maguari Up-Down.

Ciconia maguari consistently held the wings higher than the other two species in Wing Flashes and other spread-wing activities such as running and wing drying. Ciconia maguari rarely participated in such activities with the wings lower than 50° above the horizontal axis, while

C. ciconia and *C. boyciana* often held their wings at 10-30° above the horizontal. Positioning of wings in spread-wing activities may also be habitat related; *C. maguari* may carry their wings higher in tall vegetation to increase signal value of actions or to facilitate movement.

Another behavioral difference observed in this study may indirectly relate to habitat: *C. ciconia* was less likely to perform defensive or agonistic behaviors in response to humans in both the nestling and adult stages than were the other two storks. This difference was also observed by Archibald and Schmitt (in press) concerning *C. ciconia* and *C. boyciana*. *Ciconia ciconia* also reproduces much more readily in captivity than the other two species (Johnson et al. 1987), and can be kept in close group situations more successfully. The long association that *C. ciconia* has had with humans has may make them more conformable to the captive situation than *C. boyciana* or *C. maguari* (e.g. they may habituate to forced close proximity to humans and conspecifics more readily).

Phylogeny and Classification

Phylogenetic relationships within the Ciconiidae, and among Ciconiiforms have not been well established (Ligon 1967; Sibley and Alquist 1972). The earliest fossil Ciconiiform, dating from the Cretaceous Period, was found in Denmark. Lambrecht (in Howard 1950:9) suggested that the storks originated in Africa, where the earliest stork fossil, resembling *Ephippiorhynchus* and dating from the Oligocene, was discovered. The paucity of early fossils makes it difficult to establish origins (Howard 1950). Regardless, it is quite probable that *Ciconia* originated on that continent as four of the five present species recognized by Kahl (1971a, 1972a, 1972b) are found there.

Analyses of systematic characters in *Ciconia* have not increased understanding of phylogenetic relationships within the genus, or in relation to other Ciconiidae. Karyotyping studies indicate that *C. maguari*, *C. ciconia*, and *C. boyciana* chromosomes are almost identical, but these are also almost identical to *Ephippiorhynchus*, the Saddlebill and Black-necked Storks, and *Leptoptilos javanicus*, the Lesser Adjutant Stork. Contrarily, chromosomes of *C. nigra*, the Black Stork, appear to resemble those of *Leptoptilos crumeniferous*, the Marabou Stork, more closely than they resemble those of congenerics (Belterman and de Boer 1984; de Boer and van Brink 1982; Takagi and Sasaki 1974). Belterman and de Boer (1984) concluded that it was tempting to say that the chromosomal arrangement observed in the former group is ancestral, as it is shared by three genera, further, it is unlikely that the arrangement observed in the latter group arose independently. Morphological and behavioral studies have not suggested that *C. nigra* and *L. crumeniferous* have a close affinity, however (Kahl 1966, 1971a, 1972a; Wood 1983, 1984).

Based on a phenetic study of continuous osteological characters in the Ciconiidae, Wood (1983, 1984) found that in six analyses the most similar species to *C. maguari* was always *C. ciconia*, but that the converse was not always true. Howard (1942) analyzed skeletal characteristics of the Pleistocene North American Stork, *C. maltha*, and concluded that this stork was intermediate between *C. ciconia* and *C. maguari*, and unlike *Jabiru* or *Leptoptilos*. Kahl (1972a) suggested that *C. maltha* might be the link between *C. ciconia* and *C. maguari*. Feduccia (1973) felt that *C. maltha* more closely resembled *Jabiru*, and suggested that the matter be reopened.

Kahl (1971a, 1972a, b) recommended that the three monospecific genera *Euxenura* (= *C. maguari*), *Dissoura* (= *C. episcopus*), and *Sphenorhynchus* (= *C. abdimii*), be placed in the genus *Ciconia* along with *C. ciconia* (including *C. c. ciconia*, *C. c. boyciana*, and *C. c. asiatica*) and *C. nigra*. Unification of these storks was proposed based on presence of the Head-Shaking Crouch (with the possible exception of this in *C. maguari*), and only partial opening of the female's wings during copulation. Neck Weaving, only observed in *C. abdimii* by Kahl (1972a) may also set this group apart. Morphological similarities tabulated by Kahl include a similar black-white plumage pattern, feathered head and neck, long basal neck feathers, bare skin on the lores and around the eyes, and an essentially straight bill. Base on morphology, Delacour and Mayr (1945) had recommended the same treatment as Kahl for these storks.

Characteristics that Kahl thought to be particularly relevant in assessing relationships within the genus were differences in Up-Downs and tail morphology; bill clapping during Up-Downs is almost entirely absent in *C. nigra*, and though present in *C. abdimii* and *C. episcopus*, it is much less developed than in *C. ciconia*. The bisyllabic hissing vocalization is present in Up-Downs of all species excluding *C. ciconia*. The tail is notched in *C. abdimii*, deeply forked and shortened in *C. episcopus* and *C. maguari*, and elongated and square in the Palearctic migrants, *C. nigra* and *C. ciconia*.

Based on these characteristics, but assuming that the Up-Down of *C. maguari* also has a bill clapping element, Kahl (1971a, 1972a, b) proposed the following sequence to reflect phylogenetic relationships: *C. nigra*, *C. abdimii*, *C. episcopus*, *C. maguari*, and finally *C. ciconia*. This sequence reflected the presumed primitive absence of bill clapping in *C. nigra*, and the evolution of a deeply forked tail in *C. episcopus* and *C. maguari*, as well as the similarity in plumage patterns of *C. maguari* and *C. ciconia*. Body coloration is primarily black in the other three species. This arrangement does not account for the elongated squared tail of C. nigra and C. ciconia, which were placed on both ends of the spectrum.

Evidence from the present study suggests an alternative interpretation of relationships. The Up-Downs of C. abdimii and C. episcopus include both a bill clapping and vocal element, as do those of other genera, Leptoptilos and Mycteria. This condition would seem to be ancestral, with the variously modified Up-Downs of C. ciconia, C. nigra and C. maguari adapted to new environmental selective forces encountered in South America and Eurasia.

Although C. ciconia and C. nigra are both palearctic migrants, they breed in dissimilar habitats: C. nigra breeds singly in trees of heavily wooded forests (Kahl 1972a). Of possible significance, the two species of Ciconia lacking a bill clattering component in the Up-Down, C. maguari and C. nigra, are the only two that also nest in heavily vegetated situations.

A C. abdimii-like ancestor to the present members of this genus would seem most likely, as this species is intermediate to the extremes of the others in several traits. It nests in trees, on cliffs, and on village huts (even in man made baskets) (Brown et al. 1982). The notched tail of this species could easily develop in either direction, squared or deeply forked. Although considered to be a truly migratory species because it travels across the equator, *C*. *abdimii* does not undergo the extensive migrations of *C*. *ciconia* and *C*. *nigra*, but it is more migratory than *C*. *episcopus* and *C*. *maguari* (Kahl 1971c).

A number of what may be primitive characteristics are also found in *C*. *abdimii*. First, it is the smallest of all of the storks (Kahl 1978). It is also highly gregarious in the non-breeding season, and is the only truly colonial breeder of the genus *Ciconia* (Kahl 1972a). As such, *C*. *abdimii* has the (probably primitive) social pattern most typical of the Ciconiidae (Kahl 1978). Colony size of *C*. *abdimii* does not usually exceed 20 pairs (Brown et al. 1982), a size smaller than other colonial storks (Kahl 1971c, 1978), but perhaps a step towards the more solitary breeding habits of other *Ciconia*.

The phylogenetic relationships of *Ciconia* are probably not linear: the development of Up-Downs lacking a bill clapping component in *C*. *nigra* and *maguari* could have evolved independently, as is likely for the large size and proportionally longer bills of *C*. *maguari* and *C*. *boyciana* (Table 1). The large bills may well be tied to foraging habits, as these two species are almost entirely aquatic feeders. The primarily white plumage of *C*. *ciconia* and *C*. *maguari* could also be independently acquired: white body plumage is common in Ciconiiforms that forage in flocks (e.g. Kushlan 1977).

Because variation in morphological and behavioral characteristics cited here are in fact somewhat continuous, it would seem that lumping of species now included in Ciconia within this genus is justified. The overall character divergence of C. maguari from the others is so great, however, that additional in depth study may tip the scales in favor of resurrection of a monotypic genus for it.

Based on the close morphological and behavioral similarities of C. ciconia and C. boyciana it is certain that these two storks are quite closely related, though the question of their status as full species remains problematical. Crosses of these storks in captivity can produce viable F2 offspring (K. Murata, pers. comm.), thus they are not reproductively, but rather geographically, isolated. Biologists adhering strictly to a " Biological Species Concept" Mayr (1969, 1982), might be prompted by such information to consider the allopatric forms as subspecies.

If one takes the approach of Cracraft (1983), utilizing the phylogenetic species concept, in which a species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent, C. boyciana and ciconia would surely be considered separate species. In this approach subspecies cannot have ontological status as evolutionary units. The difference observed in this study in the Up-Down of these two populations alone indicate that they are indeed different evolutionary units, responding to distinctive environmental factors. Since one purpose of classification is to define such important differences, it would seem that treatment of the two storks as separate species is valid.

The sub-species of C. ciconia found in central Asia, C. c. asiatica, nests in trees in groups of one to three pairs, and on buildings, and is thus somewhat intermediate reproductive behavior between C. c. ciconia and C. boyciana. The range of C. c. asiatica is not entirely known, but does not appear to overlap with that of C. c. ciconia or C. boyciana (Demente'ev et. al. 1951). This stork is generally intermediate in morphology between the western population of C. ciconia and C. boyciana (Demente'ev et al. 1951; Vaurie 1965). Study of the the population of C. c. asiatica, a now unknown entity, may clarify the relationship between the three Palearctic populations.

CHAPTER VI

CONCLUSIONS

Summary

Signaling behaviors of three storks, _C_. _ciconia_, _C_. _boyciana_, and _C_. _maguari_, in captivity are described, and the effects of captivity on signaling evaluated. Though some alterations may occur, performances of displays observed here were comparable to descriptions of displays in natural situations. Some displays that have not been previously described were observed in this study.

The three storks share many of the same displays but variations occur among the species in usage and form. _Ciconia_ _ciconia_ and _C_. _boyciana_ were more similar to each other in behavior than either were to _C_. _maguari_. Ecological considerations relating to signaling are discussed; it is apparent that ground nesting habits of _C_. _maguari_ have markedly its influenced signaling behaviors. Though _C_. _ciconia_ and _C_. _boyciana_ are quite similar behaviorally, major differences in the form of the Up-Down, a signal considered to be a valuable taxonomic character, justifies their treatment as separate species.

Suggestions for Future Research

Continued study of the Up-Down in these species, and in other Ciconiids, in relation to their ecology would be helpful in further assessing their relationships, and in understanding the ecological constraints impinging on them. For example, lowering of the tail and tail movements observed in performances by _C_. _maguari_ but not _C_. _ciconia_ or _C_ _boyciana_ were also observed in Up-Down performances of full-flighted captive _C_. _abdimii_ (pers. obs.). Comprehensive study of the relationship between tail movements, tail morphology and vocalizations may help to further elucidate the relationship of these storks, which are very different ecologically (Kahl 1972a; Luthin 1987). _Ciconia_ _episcopus_ is sometimes separated into three subspecies, one of which (_C_. _e_. _stormii_) is now extremely rare, and may well deserve full-species status (Luthin 1987).

It is apparent from this study that subtle differences in forms of bill clapping and hissing occur both among species, and within a species, dependent on context. A detailed analysis of sounds produced by adults, and the ontogeny of these sounds could be quite fruitful in understanding the phylogenetic relationships among these storks, and the function of signals.

To date, little attention has been given to ecological factors shaping the evolution of signals in these species. Studying the behavior of the birds in relation to predation, nesting sites and foraging behavior would be quite valuable. Thomas (1985) has already studied foraging group size in _C_. _maguari_, in a comparative evaluation of foraging of the three New World storks, with interesting results.

Social organization of all three species varies throughout the year, and is situational during both the non-breeding and breeding season. Ecological factors that might determine social organization have not been studied. Little work has been done in the area of adult and non-breeding behavior; certainly these aspects of the natural history of the storks must be addressed before a thorough understanding of their behavior is achieved.

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APPENDIX A

ACTIVITY CATEGORIES

Prior to taking time budget data for the study, Maguari Storks were observed at the Oklahoma City Zoo for several days to identify activity categories appropriate to the captive situation. Minor modifications were made as the study progressed. Some categories were based on descriptions from Kahl (1966).

AG: AGONISTIC BEHAVIOR
Several forms of agonistic behavior were recognized: displacement of an individual, blows delivered by bill or obvious intention movements, and agonistic displays as defined in Chapter IV.

AP: ALLOPREENING
Preening of another individual.

BA: BATHING
Using wings to splash water onto head and body, dipping body down while standing in water.

BC: BILL CLAPPING
Applied to *Ciconia ciconia* and *Ciconia boyciana*. The "Up-Down" display, in which the bill is rapidly clattered, and the head moved vertically.

CA: COPULATION ATTEMPT
Male (or female) attempts to place at least one leg on its mate's back.

CD: COMPLETE "UP-DOWN DISPLAY"
Applied to Maguari Storks only. The head is thrown back, a hiss-wheeze vocalization is emitted, then the head is lowered and the ground jabbed at several times.

CO: COPULATION
Male successfully mounts the female, contact is maintained for several seconds.

CP: COPULATION APPROACH
Male (or female) circles its mate, possibly nibbling on its back, but does not attempt to mount.

DR: DRINKING
from Kahl (1966)

EP: EXPLORATORY
Stationary or mobile, probing or nibbling randomly.

EX: EXERCISING
Rapid locomotion (walking quickly, running or jumping) with wings flapping or extended but not flapping, not obviously agonistic.

FE: FEEDING
Eating food items provided by zoo personnel.

FL: FLYING

FO: FORAGING
Stationary or mobile, observed probing non-randomly, or grasping with bill at a place after looking there intently, or actually swallowing an item.

GB: GRABBING
Applied to nestlings only. Grabbing at available articles including conspecifics or nearby objects.

ID: INCOMPLETE "UP-DOWN" DISPLAY
Applied to Maguari Storks only. A display with some but not all of the components of the complete "Up-Down" display.

IN: INACTIVE, ALERT
Stationary but alert

MO: MOBILE
Moving, not engaged in any activity other then locomotion.

NA: NEST ARRANGING
Manipulating plant material (e.g. grasses, twigs, leaves) with bill, small head shaking movements made.

NG: NEST GATHERING
Gathering plant materials with bill, then moving them to another location.

NS: NECK STRETCH
Bill is pointed upward, a weaving motion is made with the neck.

OT: OTHER
Any behavior unspecified in this ethogram.

PR: PREENING
From Kahl (1966)

RE: RESTING
Not glancing around, head often tucked such that the bill rests against partially or completely erected neck feathers.

SC: SCRATCHING
from Kahl (1966)

ST: STRETCHING
from Kahl (1966)

SU: SUNNING
Wings partially or fully extended, possibly flapping (e.g. wing drying) in sunlit area of enclosure.

APPENDIX B

TABLES

TABLE 1: Body weight, exposed culmen length, and tarsus length of adults.

	C. boyciana[a]		C. ciconia[a]		C. maguari[b]	
	males	females	males	females	males	females
Body weight (Kg)	5.1 (9)	4.1 (8)	3.6 (43)	3.3 (28)	4.2 (9)	3.8 (5)
	[Archibald pers.comms.; Murata 1987]		[Bauer and Glutz 1966; Murata 1977]		[King, unpubl.data; Thomas 1985]	
Exposed culmen length (cm)	25.5 (32)	23.2 (26)	18.7 (13)	17.4 (8)	24.1 (9)	21.3 (5)
	[Archibald 1985; Winter pers. comm; Murata 1987]		[Archibald and Schmitt in press; Murata 1987]		[King, unpubl.data; Thomas 1985]	
Tarsus length (cm)	28.5 (31)	25.4 (26)	24.5 (14)	22.1 (8)	26.3 (4)	23.8 (4)
	[Murata 1987; Winter pers. comm.		[Archibald and Schmitt in press; Murata 1987]		[Thomas 1985]	

(n) = number of measurements

[a] data from captive and wild individuals

[b] data from captive individuals exclusively

TABLE 2: Summary of morphological characteristics.

	C. boyciana	C. ciconia	C.maguari
Body Plumage Coloration			
Hatching	sparse down: off white [Winter 1982]	sparse down: off white [Schröpel 1984]	sparse down: white [Thomas 1984]
1 wk-2 mo	white [Winter 1982]	white [Schröpel 1984]	black [Thomas 1984]
Fledging	similar to adult, but brown tinges also some grey [Winter 1982]	similar to adult, but brown tinges [Cramp 1977]	black [Thomas 1984]
Adult	white [Kahl 1972a]	white [Kahl 1972a]	white [Kahl 1972a]
Flight Feather Coloration			
Juvenile	similar to adult, but more white [Winter 1982]	similar to adult, but more white [Cramp 1977]	like adults [Thomas 1984]
Adult	black, extensive grey patches [Vaurie 1965]	black, some grey [Cramp 1977]	iridescent black [Blake 1977]
Tail Shape	square [Kahl 1972a]	square [Cramp 1977]	deeply forked [Kahl 1972a]
Tail Coloration	white [Kahl 1972a]	white [Kahl 1972a]	black [Kahl 1972a]
Bill Coloration			
Hatching	grey-white [Winter 1982]	black [Cramp 1977]	grey [Thomas 1984]
1 wk-2 mo	progressively darker, yellow tones present [Winter 1982]	progressively redder, yellow tones present [Schröpel 1984]	black [Thomas 1984]

TABLE 2 (CONTINUED)

	C. boyciana	*C. ciconia*	*C.maguari*
Fledging	dark grey, yellow streaks [Winter 1982]	pale red dark streaks [Jovetic 1961]	black [Thomas 1984]
Adult	black, some red marginally [Vaurie 1965]	bright red to orange-red [Cramp 1977]	blue-grey, maroon distally [Kahl 1971b]
Iris Coloration			
1 wk-2 mo	dark brown, progressively lighter [Winter 1982]	dark brown progressively lighter [Archibald and Schmitt in press]	dark [Thomas 1984]
Adult	pale yellow [Archibald and Schmitt in press]	brown to grey [Cramp 1977]	pale yellow [Blake 1977]
Leg and Foot Coloration			
Hatching	fleshy [Winter 1982]	fleshy [Schröpel 1984]	pinkish-grey [Thomas 1984]
1 wk-2 mo	progressively deeper orange [Winter 1982]	patchy grey [Schröpel 1984]	black [Thomas 1984]
Fledging	bright orange [Winter 1982]	pale red [Schröpel 1984]	black, some pink [Thomas 1984]
Adult	red [Vaurie 1965]	red [Kahl 1972a]	red [Kahl 1972a]
Orbital and Lore Coloration			
1 wk-2 mo deeper orange	progressively deeper orange [Winter 1982]	black [Archibald and Schmitt in press]	black [Thomas 1984]

TABLE 2 (CONTINUED)

	C. boyciana	*C. ciconia*	*C.maguari*
Fledging	orange-red [Winter 1982]	black [Cramp 1977]	black [Thomas 1984]
Adult	red [Vaurie 1965]	black [Cramp 1977]	orange-red to deep red [Kahl 1972a]
Orbital Region Texture:Adults	smooth	smooth	carunculated
Gular Region Coloration			
Hatching	pink-orange [Winter 1982]	black [Archibald and Schmitt in press]	whitish-yellow [Thomas 1984]
1 wk-2 mo	progressively more orange [Winter 1982]	black, orange developes [Cramp 1977]	progressively more orange [Thomas 1984]
Adult	red [Vaurie 1965]	black, red-orange near chin feathers [Cramp 1977]	red [Kahl 1972a]

TABLE 3: Adult behavioral and ecological characteristics.

	<u>C</u>. <u>boyciana</u>	<u>C</u>. <u>ciconia</u>	<u>C</u>. <u>maguari</u>
Courtship location	nest [Kahl 1971a]	nest [Kahl 1971a]	assemblies [Thomas 1986]
Typical nest sites	tall trees, some other elevated structures not over or in water [Gluschenko 1985; Winter 1982]	buildings, ruins, trees, haystacks, artificial sites not over or in water [Cramp 1977; Haverschmidt 1949]	on ground in marshes, some in low trees over, or in, water [Kahl 1971b; Thomas 1986; Hudson 1920]
Relationship of nests to humans	avoided [Winter 1982]	close [Jovetic 1961]	avoided [Thomas 1986]
Nesting patterns	solitary, loose aggregates, small groups [Dymin and Pankin 1985; Winter 1982]	solitary, loose aggregates, small groups [Havershmidt 1949]	solitary, loose aggregates, small groups [Kahl 1971b; Thomas 1985]
Nest structure	exterior: twigs, interior: soft materials [Fei et al. 1983; Winter 1982]	exterior: twigs, interior: soft materials [Haverschmidt 1949]	pile aquatic vegetation, twig exterior in tree nests [Kahl 1971b; Thomas 1985]
Incubation	32-35 days [Fei et al. 1983]	32-35 days [Jovetic 1961]	29-32 days [Thomas 1986]
Migratory habits	migratory [Luthin 1987]	long distance migrant [Luthin 1987]	most nomadic, some migrate [Short 1975; Thomas 1986]
Climatic Zone	temperate [Kahl 1972a]	temperate [Kahl 1972a]	tropical [Thomas 1986]

TABLE 4: Ages in day at which selected nestling behaviors have been observed.

	C. boyciana	*C. ciconia*	*C. maguari*
Defecate over nest edge	21-26 [Winter 1982]	14-20 [Jovetic 1961]	28, some before [Thomas 1984]
Stand	21-26 [Winter 1982]	22-24 [Jovetic 1961]	22-38 [Thomas 1984]
Manipulate nest material	21 [Winter 1982]	13 [Schröpel 1984]	No Data
Active defense	35-50 [Winter 1982]	20-30 [Jovetic 1961]	14 [Thomas 1984]
Fledge	65-70 [Winter 1982]	58-64 [Cramp 1977]	65-67 [Thomas 1984]
Independent of parents	No Data	7-20 [Cramp 1977]	42 [Thomas 1984]

Table 5: Observation sites, schedules, and inventory of *C. boyciana*, *C. ciconia* and *C. maguari* studied.

Ciconia species	site observed	period observed	hours observed	inventory M.F.U.[a]
Adults				
C. maguari	OKC[b]	Apr-Aug 1985 Feb-May 1986	578	3.1.0
C. maguari	MIL[c]	May-Jun 1986	201	1.1.0
C. maguari	GPZ[d]	Jun-Jul 1986	132	2.2.0
C. ciconia	VW[e]	Mar-Aug 1987	169	4.3.0
C. boyciana	VW	Mar-Aug 1987	440	5.5.0
Juveniles (hatched in 1986)				
C. ciconia	VW	Mar-Aug 1987	*	0.0.4
Nestlings (hatched in 1987, 1 - 76 days of age)				
C. boyciana	VW			
hand-reared		May-Aug 1987	136	1.3.0
C. ciconia	VW			
hand-reared		Jun-Aug 1987	**	0.0.2
parent-reared		May-Aug 1987	*	0.0.2
Totals			1656	16.15.8

[a] males.females.unknown sex

[b] OKC = Oklahoma City Zoo, Oklahoma City, Oklahoma, USA.

[c] MIL = Milwaukee County Zoo, Milwaukee, Wisconsin, USA.

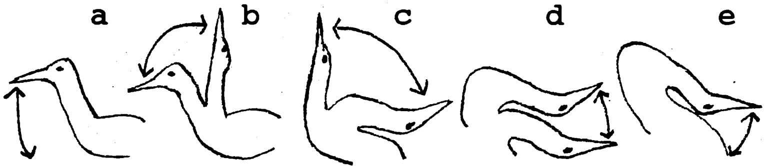
[d] GPZ = Gladys Porter Zoo, Brownsville, Texas, USA.

[e] VW = Vogelpark Walsrode, Walsrode, West Germany.

* = included in observation schedule of adult *C. Ciconia*.

** = included in observation schedule of nestling *C.boyciana*

TABLE 6: Relative frequencies (in percent) of degree rearward bill movement during Up-Down displays of C. boyciana (N = 266) and C. ciconia (N = 75)



	none	a	b	c	d	e
C. boyciana	5%	1%	14%	9%	3%	68%
C. ciconia	7%	11%	12%	11%	56%	7%

[a] below frontal horizontal axis.
[b] between frontal horizontal and vertical axes.
[c] between vertical axis and 79° beyond
[d] between 10° above and 10° below rear horizontal axis.
[e] beyond 10° below the rear horizontal axis.

TABLE 7: Relative frequencies (in percent) of selected orientations of breeding pairs to the mate during performance of Up-Downs.

Orientation	↗↖	↗↑	↑↑	↓↑	↓ ↑	Other	N
C. boyciana[a]	11%	0%	32%	24%	11%	22%	46
C. ciconia[b]	37%	12%	29%	11%	11%	0%	38
C. maguari[c]	51%	22%	11%	3%	5%	8%	98

[a] Hours observed: 352; data for one pair.

[b] Hours observed: 169; data totaled for three pairs prds I and II, for two pairs prd III.

[c] Hours observed: 285; data for two pairs.

TABLE 8: Relative frequencies (in percent) of Up-Downs associated with activities or interactions for breeding pairs[a].

	C. boyciana	*C. ciconia*	*C. maguari*
Human activity	31%	8%	9%
Agonistic encounters/ enclosure disturbances	10%	7%	0%
Nest defense[b]	0%	12%	19%
Join mate	13%	25%	44%
Copulation	1%	2%	5%
Nest material collection	1%	4%	13%
Nest duty exchange	0%	5%	3%
Not identified	44%	37%	7%
N	250	281	187

[a] includes performances by one or both birds

[b] does not include nest defense against humans.

TABLE 9: Frequency (incidence/hr observation) of Allopreening, Offerings, and Up-Downs for breeding pairs throughout the reproductive period.

	Allopreening			
	prd I	prd II	prd III	Mean
_C_. _boyciana_[a]	.38	.04	.14	.20
_C_. _ciconia_[b]	.16	.01	.26	.08
_C_. _maguari_[c]	.06	0.0	0.0	.02
	Offerings			
	prd I	prd II	prd III	Mean
_C_. _boyciana_[a]	.07	.01	0.0	.03
_C_. _ciconia_[b]	.06	.01	.02	.02
_C_. _maguari_[c]	.78	.10	.12	.36
	Up-Down			
	prd I	prd II	prd III	Mean
_C_. _boyciana_[a]	1.18	.13	1.40	.71
_C_. _ciconia_[b]	1.30	.49	1.31	.78
_C_. _maguari_[c]	1.07	.34	.47	.64

prd I = courtship period, prd II = incubation/chick rearing, prd III = post-reproduction.

[a] Hours observed: prd I - 148, prd II - 163, prd III - 41; data and hours for one pair.

[b] Hours observed: prd I - 22, prd II - 96, prd III - 44; data and hours averaged for three pairs prds I and II, for two pairs prd III.

[c] Hours observed: prd I - 54, prd II - 60, prd III - 58; and data averaged for two pairs prds I and II.

TABLE 10. Frequency (incidence/hr) of Up-Downs performed by nestling _C_. _boyciana_ and _C_. _ciconia_ through development

	Days of Age					
	1-10	11-20	21-30	31-40	41-50	51-60
_C_. _boyciana_[a]						
complete	4.80	1.80	.11	.15	.02	0.0
incomplete	.15	.25	0.0	0.0	.01	0.0
	(11)	(23)	(19)	(23)	(21)	(17)
_C_. _ciconia_[b]						
complete	2.84	1.56	.56	.56	.12	.09
incomplete	.16	.33	.20	.27	.08	0.0
	(16)	(21)	(20)	(28)	(12)	(23)

[a] data averaged for three individuals days 1-10, for four therafter.
[b] data averaged for two individuals.
(N) = hours averaged/individual.

TABLE 11: Sexual differences in incidences of Allopreening and Offerings of reproductively active individuals.

	Allopreening		
	males	females	N
_C_. _boyciana_	48%	52%	71
_C_. _ciconia_	64%	36%	36
_C_. _maguari_	13%	87%	8
Total	50%	50%	115

	Offerings		
	males	females	N
_C_. _boyciana_	89%	11%	18
_C_. _ciconia_	44%	56%	9
_C_. _maguari_	94%	6%	177
Total	91%	9%	204

TABLE 12: Frequency (incidence/hr observation) of copulation activities for breeding pairs throughout the reproductive period.

	Prd I	Prd II	Prd III	Mean
C. boyciana (one pair)	.53 (148)	.01 (163)	.19 (41)	.25
C. ciconia (three pairs)	.56 (22)	.07 (83)	0.0 (64)	.11
	1.16 (22)	.11 (83)	.06 (64)	.23
	1.16 (22)	.10 (122)	.04 (25)	.22
C. maguari (two pairs)	.59 (51)	.11 (74)	* *	.30
	1.10 (56)	.48[a] (46)	.03 (58)	.54

Prd I = courtship, Prd II = incubation and chick rearing, Prd III = post reproduction.
(N) = hours observed.
* = data not taken for this pair during Prd III.
[a] pair abandonded nest after 10 days of incubation.

TABLE 13: Percent copulation activities of breeding pairs occurring on the nest and associated with nest materials.

	Nesting Material				
	Arranging	Gathering	Total	Occur on nest	N
C. boyciana[a]	18%	1%	19%	100%	89
C. ciconia[b]	14%	21%	35%	100%	93
C. maguari[c]	36%	31%	67%	53%	123

Arranging = manipulation of plant material by small shakes of the bill within 2 min of copulation.

Gathering = carrying of plant material to the nest or mate immediatly before or after copulation.

[a] Hours observed: 352; data for one pair.

[b] Hours observed: 169; data totaled for three pairs prds I and II, for two pairs prd III.

[c] Hours observed: 285; data totaled for two pairs.

TABLE 14: Summary of social signals used by C. *boyciana*, C. *ciconia* and C. *maguari*.

	C. *boyciana*	C. *ciconia*	C. *maguari*
Aerial Clattering	NP	OO	OO
Akinesia	O	O	OO
Allopreening	O	O	O
Arch-Gape	O	O	O
Begging	O	O	OO
Bill Duel	O	O	O
Copulation Clattering	O	O	O
Forward	NP	O	O
Head Shaking Crouch	O	OO	NM
Mock Rest	NM	NM	O
Neck Feather Erection	O	O	O
Neck Stretch	O	O	O
Neck Weave	NP	O	O
Nest Covering Display	O	OO	O
Nestling Bill Snapping	O	O	OO
Nestling Defense Display	NM	NM	OO
Offering	O	O	O
Play	O	O	NP
Up-Down	O	O	O
Upright Display	NP	O	O
Wing Flash	O	O	O

O = observed in this study, OO = observed by others, but not observed in this study, NP = not observed in this study or by others, but probably is part of behavioral repertoire, NM = not observed in this study or by others, may not be part of behavioral repertoire.

TABLE 15: Summary of number of sensory modalities used in social signals.

	C. boyciana	*C. ciconia*	*C. maguari*
visual	16	17	18
auditory	9	10-11	11
tactile	5	5	5
Number Signals[a]	17	18	19

[a] data totaled for the number of signals in which the modalities are apparent in at least some forms of the signal.

TABLE 16: Summary of sound (mechanical and/or vocal), present in social signals[a].

	C. boyciana	*C. ciconia*	*C. maguari*
Aerial Clattering Threat	?	clap	clap
Akinesia	none	none	none
Allopreening	none	none	none
Arch-Gape	none	none	clap
Begging	meow	meow	meow
Bill Duel	none	none	none
Copulation Clattering	M-clap F-?	M-clap F-hiss	M-clap F-hiss
Forward	?	none	none
Head Shaking Crouch	hiss	?	?
Mock Rest	?	?	none
Neck Feather Erection	none	none	none
Neck Stretch	clap	clap	clap
Neck Weave	?	clap	clap
Nest Covering Display	hiss/clap	?	clap
Nestling Bill Snapping	clap	clap	clap
Nestling Defense Display	?	?	scream
Offering	hiss	hiss	none
Play	none	clap	?
Up-Down	hiss/clap	hiss/clap	hiss
Upright Display	?	none	clap
Wing Flash	A/J-hiss N-clap	A-hiss N-clap	none

[a] data totaled for the number of signals in which the sounds are apparent in at least some forms of the signal. ? = unknown- may not occur, M = male. F = female, A/J = adults and juveniles, N = nestlings.

APPENDIX C

FIGURES

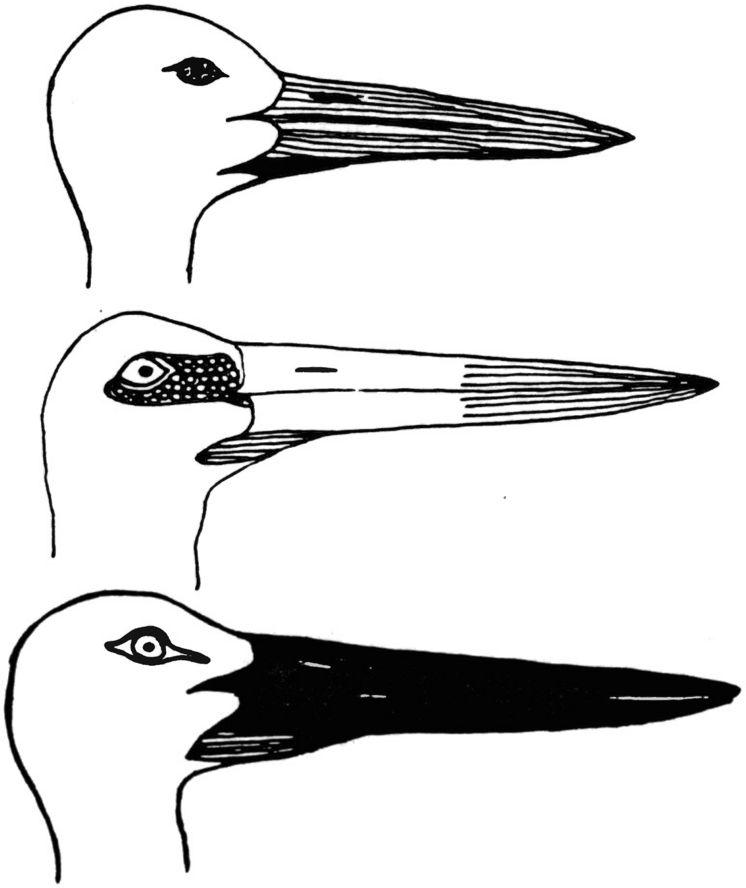


Fig. 1: Heads of adult storks, bill lengths proportional to data in Table 1, averaged for males and females. top: *C. ciconia*, middle: *C. maguari*, bottom: *C. boyciana*

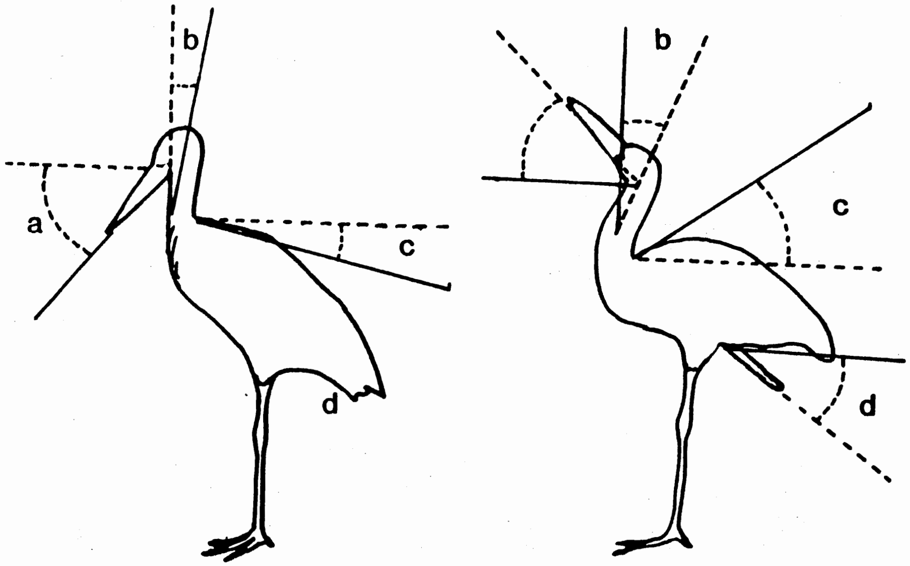


Fig. 2: Measurements for analysis of extreme posturing of performers during social signals. Left figure: Angles of measurement a) bill - from horizontal axis, b) neck - from vertical axis c) back (mantle) - from horizontal axis, d) tail - from horizontal axis, here "normal position", hidden by wings. Right figure: Example of measuring technique a) bill raised 44° above horizontal, b) neck retracted 22° behind the vertical, c) back arched 22° above the horizontal, d) tail lowered 35° below the horizontal.

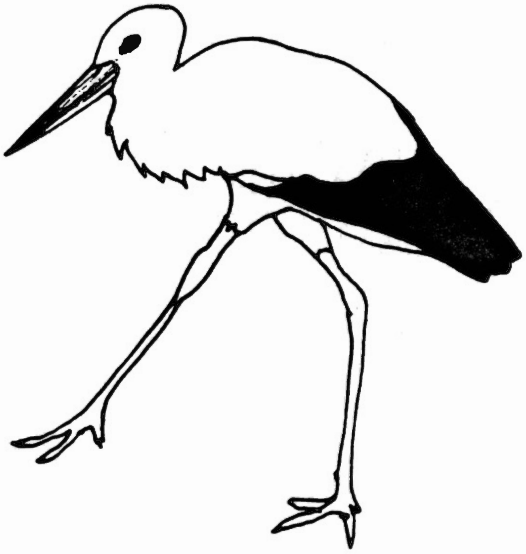


Fig. 3: Forward performed by a male adult *C. ciconia*.

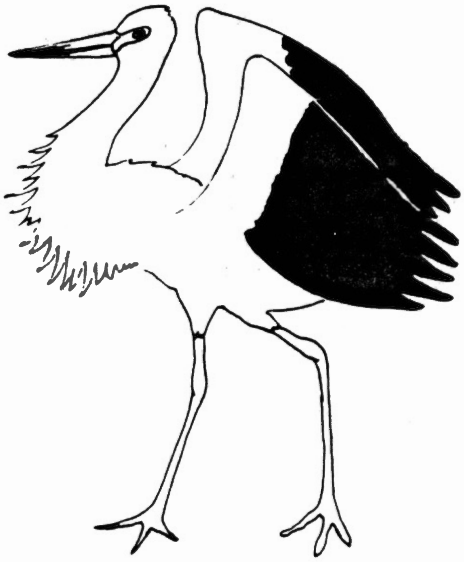


Fig. 4: Wing Flash performed by a male adult _C_. _maguari_.

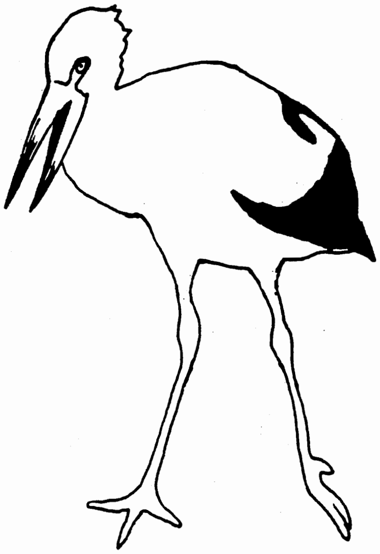


Fig. 5: Arch-Gape performed by female adult C. maguari.

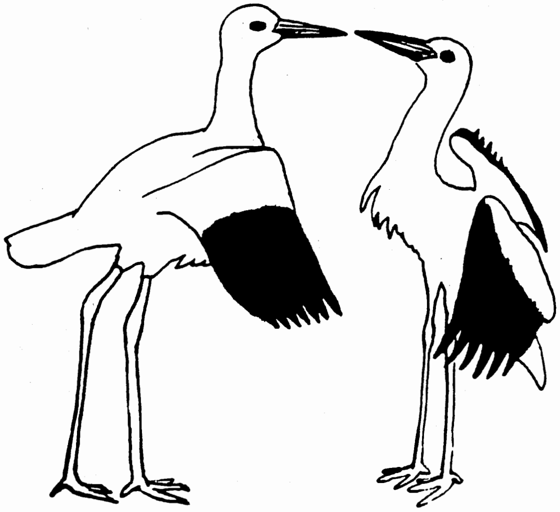


Fig. 6: Bill Duel performed by C. boyciana nestlings.

Fig. 7: Upright Display (Type 2) performed by a female <u>C</u>. <u>maguari</u>.

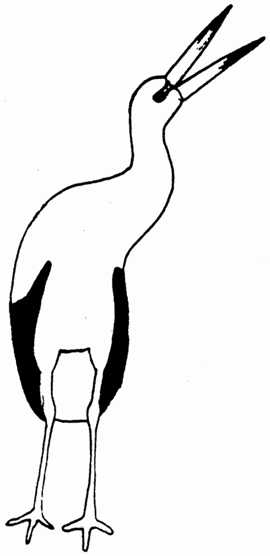


Fig. 8: Neck Weave, performed by adult male C. maguari.

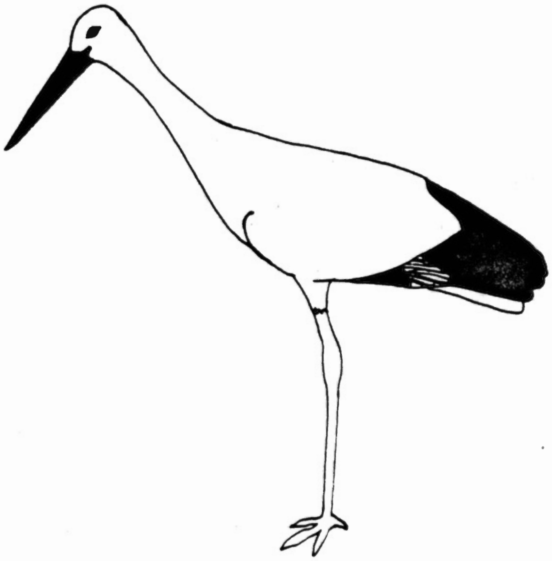


Fig. 9: Neck Stretch, performed by a female *C. boyciana*.

Fig. 10: Head-Shaking Crouch performed by a male _C_. _boyciana_.

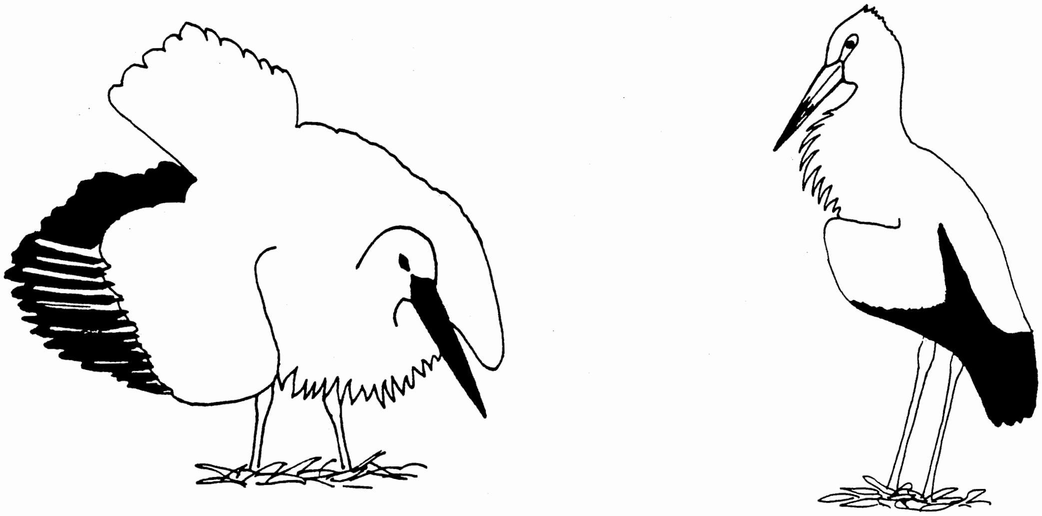


Fig. 11: Nest Covering Displays performed by males.
left: *C. boyciana*, right: *C. maguari*.

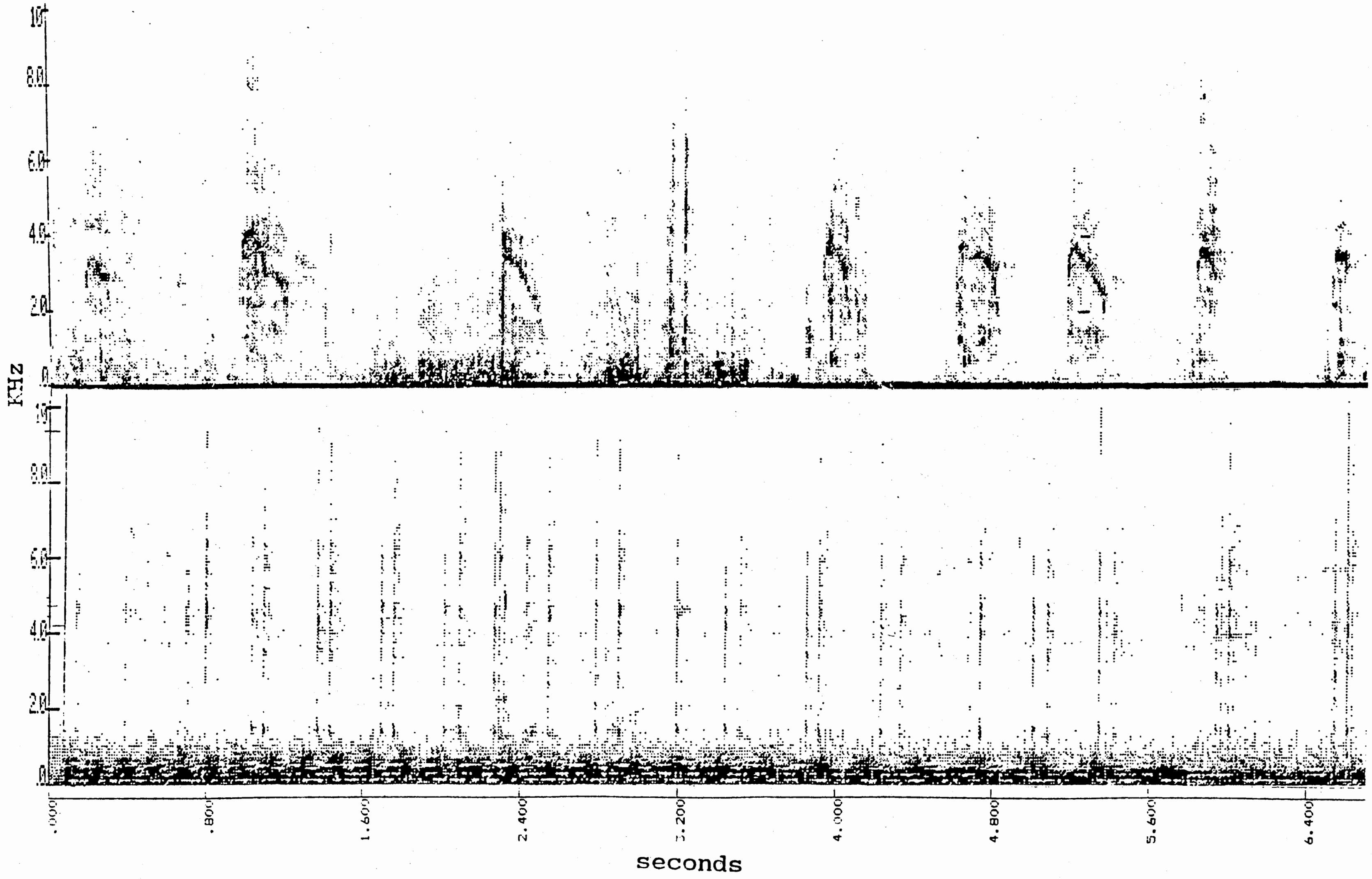


Fig. 12: Sonograms of male Nest Covering Displays. top: *C. boyciana*, bottom: *C. maguari*.

Fig. 13: Mock Rest performed by a female C. maguari.

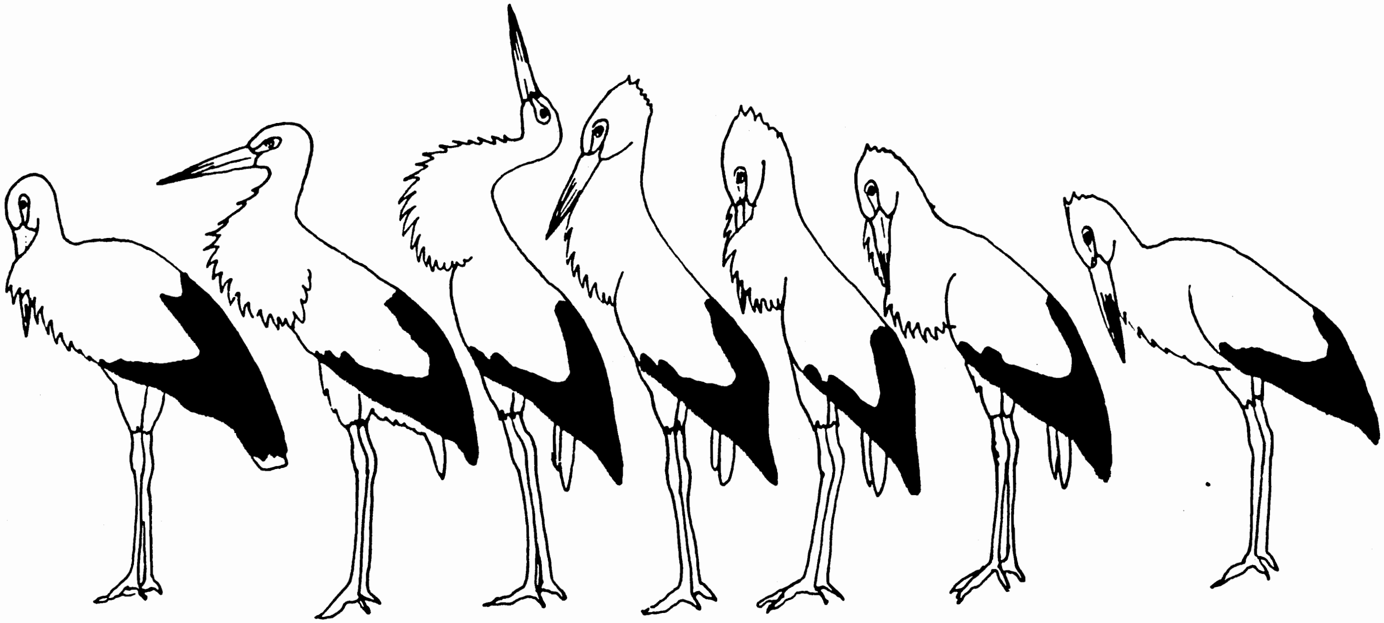


Fig. 14: Up-Down (Type B) performed by a female C. maguari.

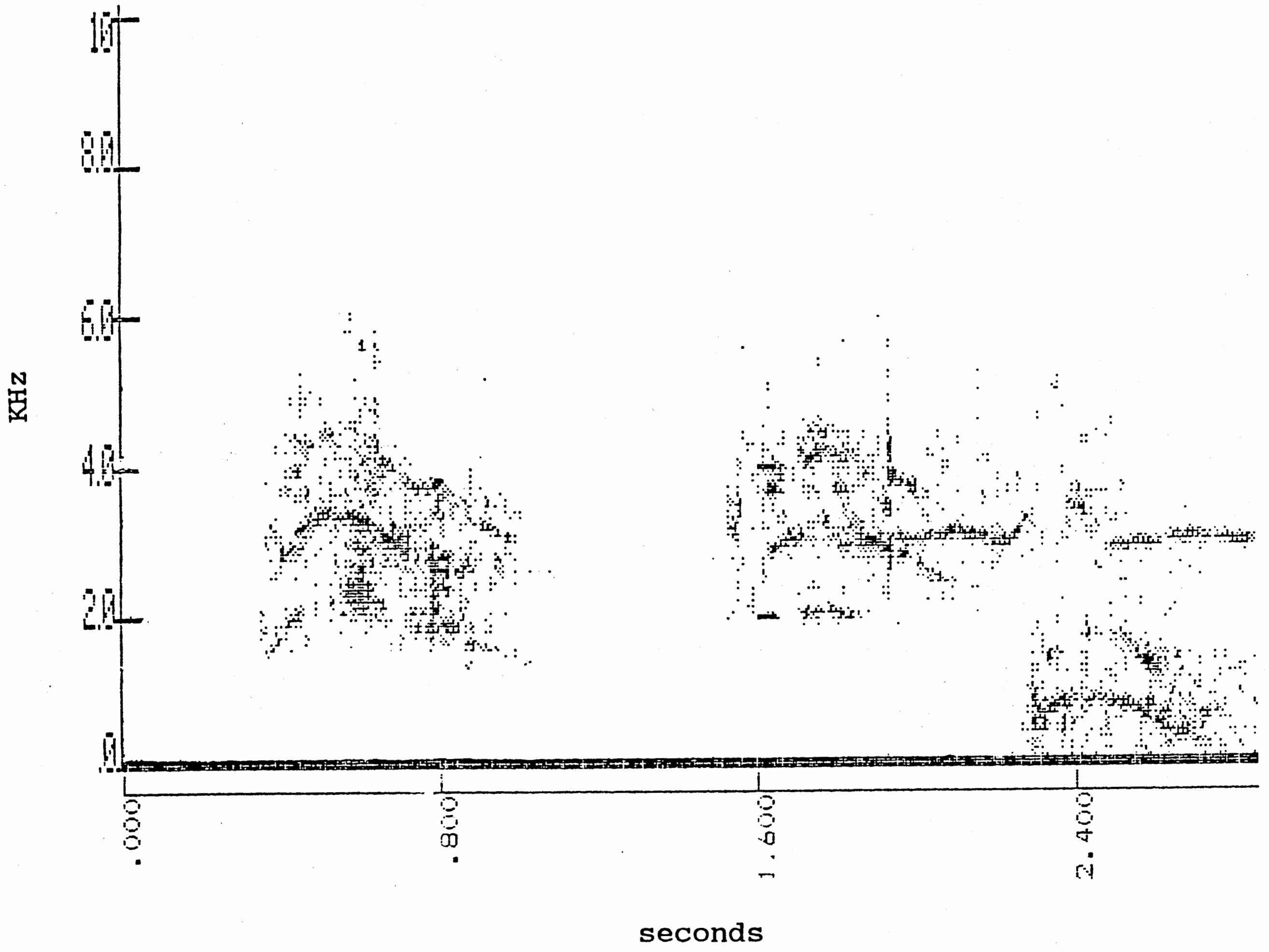


Fig. 15: Sonogram of Up-Down vocalizations produced by C. maguari.

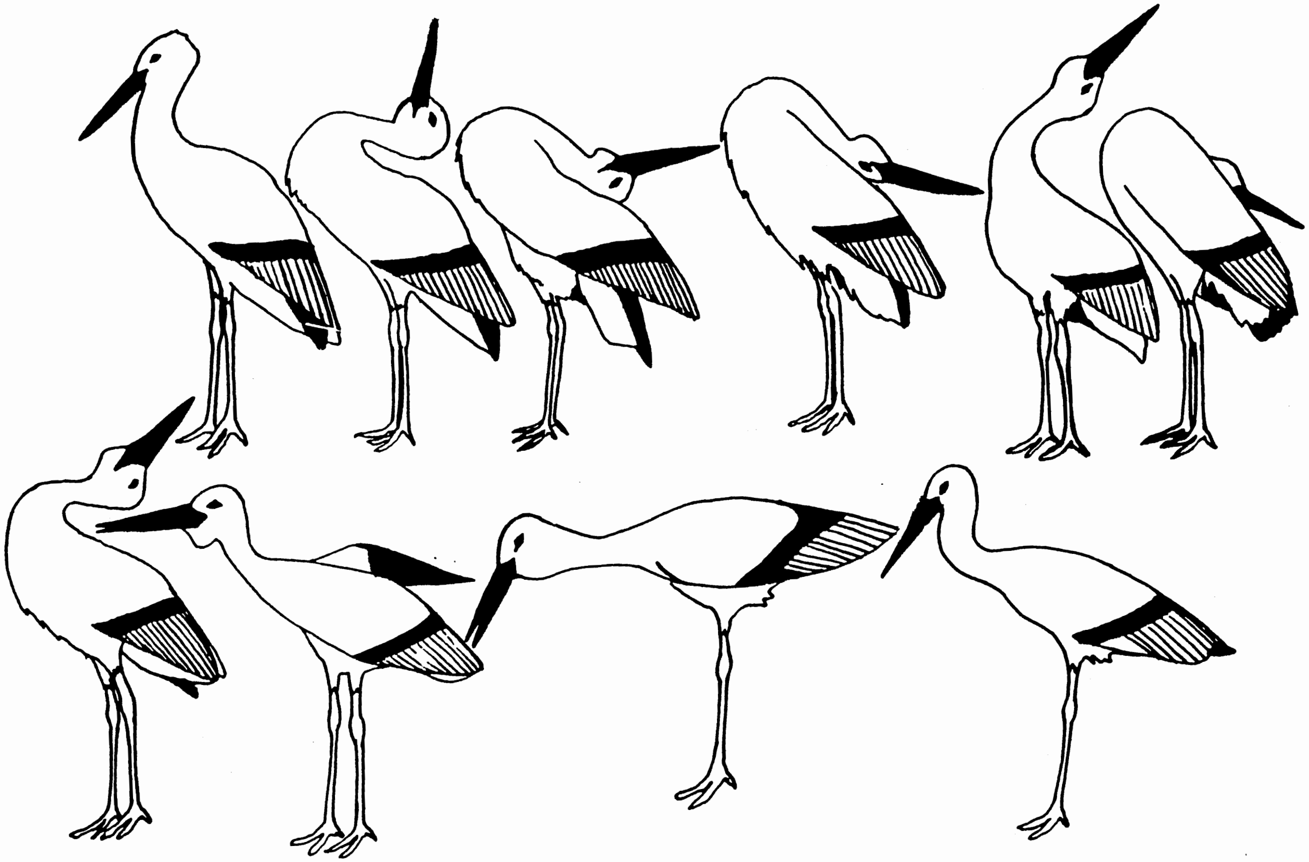


Fig. 16: Up-Down performed by a male C. boyciana.

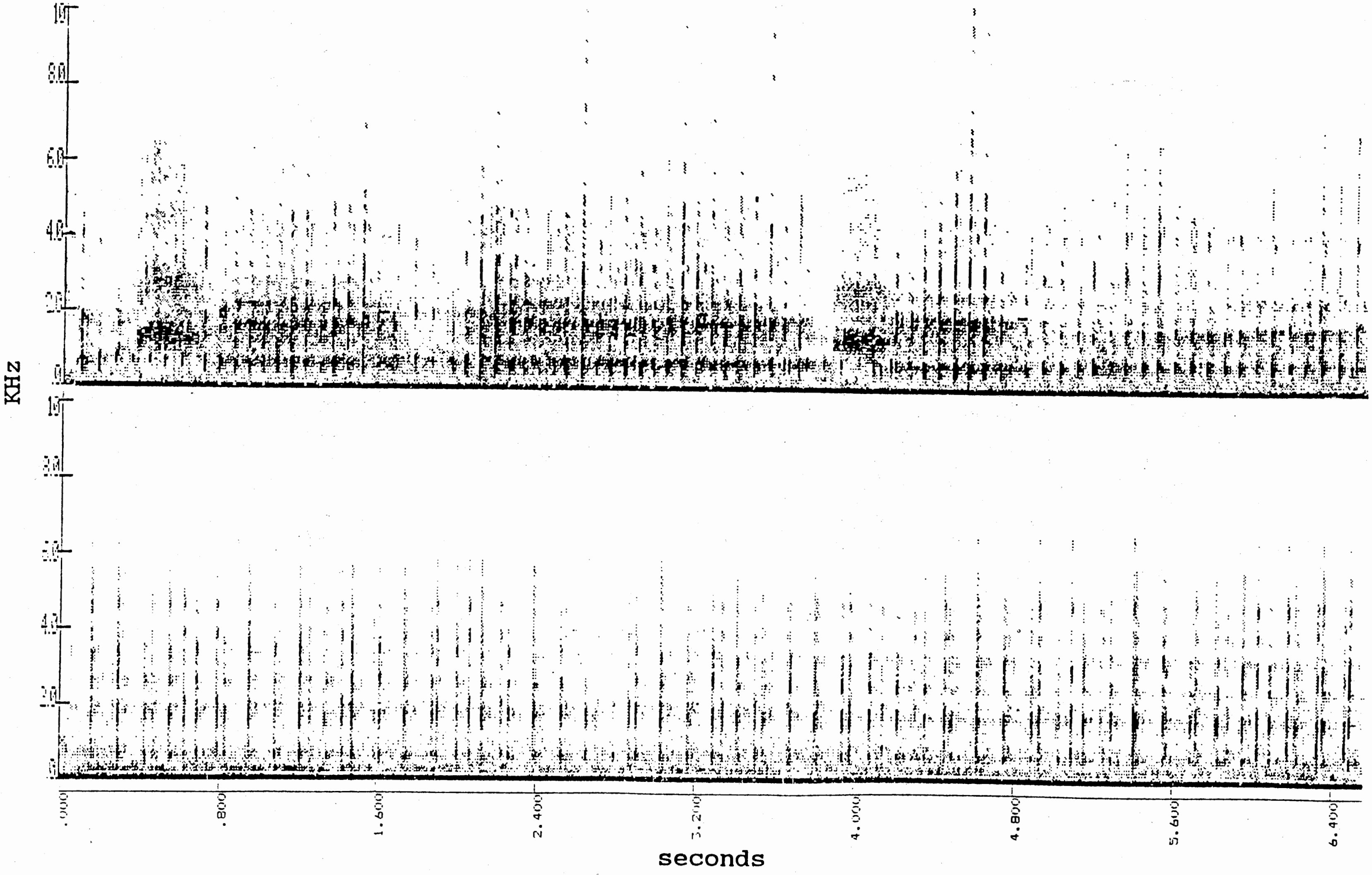


Fig. 17: Sonograms of Up-Down bill clapping. top: C. boyciana, bottom: C. ciconia.

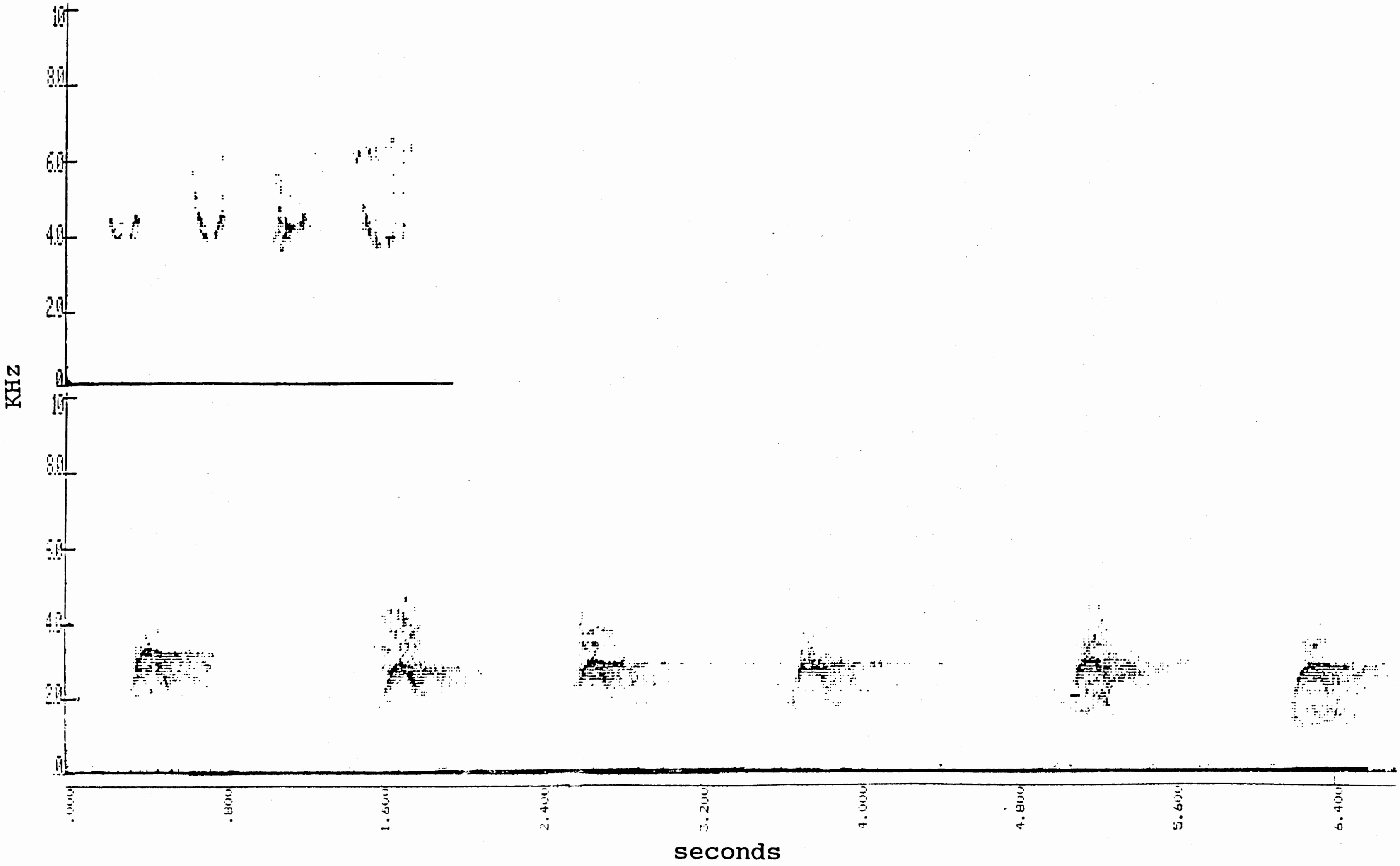


Fig. 18: Sonograms of hissing vocalizations preceding bill clattering in Up-Downs. top: C. ciconia, bottom: C. boyciana.

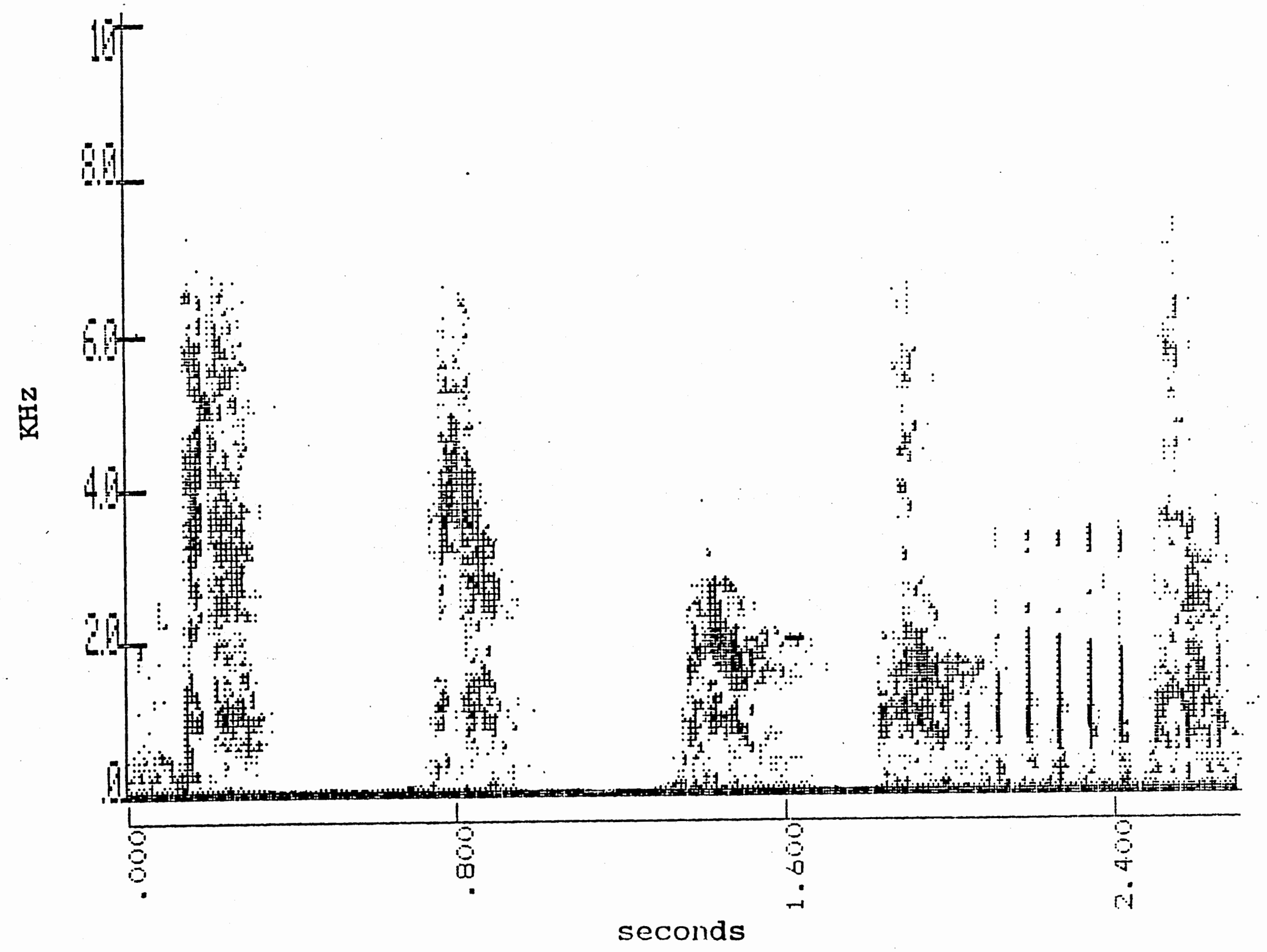


Fig. 19: Sonogram of Up-Down performed by a nestling C. boyciana.

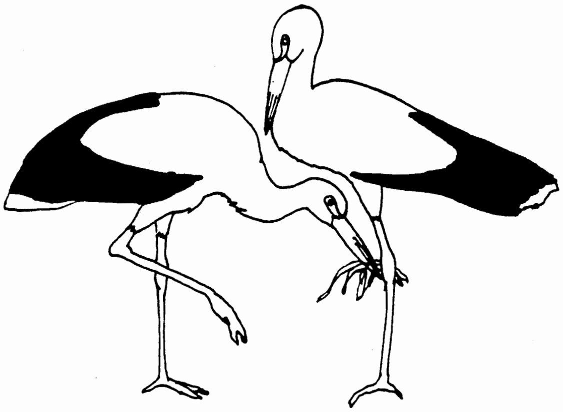


Fig. 20: Offering performed by a male C. maguari.

Fig. 21: Male C. maguari attempting to mount a sitting female; the female is hissing.

Fig. 22: Begging Display performed by nestling _C_. _boyciana_.

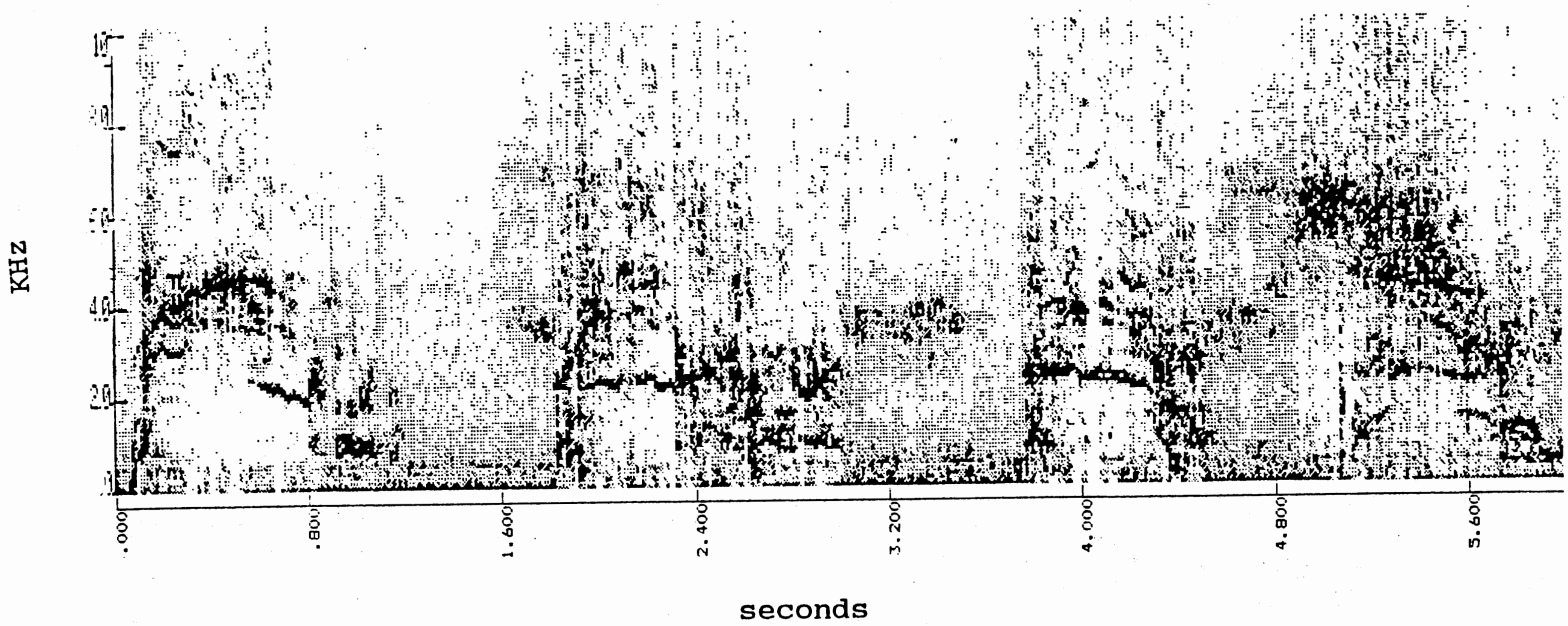


Fig. 23: Sonogram of "meowing" begging vocalization produced by a nestling C. boyciana.

VITA

2

Catherine E. King

Candidate for the Degree of

Master of Science

Thesis: AN ETHOLOGICAL STUDY OF THREE STORKS: *CICONIA BOYCIANA*, *C*. *CICONIA*, AND *C*. *MAGUARI*

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- American Ornithologist's Union
- Animal Behavior Society
- Cooper Ornithological Society
- Oklahoma Academy of Science
- Phi Kappa Phi Honor Society