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THE BEHAVIOR AND BREEDING OF ADULT MAGUARI STORKS[1]

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Abstract. An 11-year study of the Maguari Stork (*Ciconia maguari*) in the *llanos* (flatlands) of Venezuela is reported. Stork behaviors are described in the following contexts: arrival flocks, roosting, pre-nesting social assemblies, nest site choice, nest building, copulation, nestling care and defense, adult feeding, sun and water bathing. The storks nested in bushes and short trees. Nesting was both colonial and solitary, and nest defense behaviors varied accordingly from mobbing to distraction display. Nesting success during three years was greater for colonial nesters (67%) than for solitary nesters (42%).

Key words: Maguari Stork; storks; nest building; copulation; nestling care; Venezuela.

INTRODUCTION

Although the Maguari Stork (*Ciconia maguari* = *Euxenura galeata*) is large and conspicuous in its usual marshland habitat, no previous long-term observations have been made. The only other published field study is that of Kahl (1971a), who worked for three months in Argentina. I studied it from 1972–1982 in the *llanos* of Venezuela. Originally my interest in this stork concerned how it lived in sympatry with the other two Western Hemisphere storks (Thomas 1985). The Maguari Stork was the least known and the most accessible to me so I concentrated my efforts on it. Elsewhere I have given information on nestling growth and behavior (Thomas 1984), philopatry, and decrease in numbers (Thomas, in press [a]), also a comparison to the White Stork *C. ciconia* (Thomas, in press [b]). This paper covers my observations of adult Maguari Stork behavior and morphology, some of which may be significant to the birds' conservation. The life history data of a presumed normal population are important because the Maguari Stork, like its nearest congener the White Stork of the Eastern Hemisphere, will be particularly vulnerable to rapid human alteration of its South American wetland habitat.

STUDY AREA

My principal study area was in the Venezuelan state of Guárico, on Fundo Pecuario Masaguaral, a 4,000-ha cattle ranch roughly in the center of the *llanos* (08°31'N, 67°35'W). These *llanos,* covering approximately 200,000 km^2, consist of grassland savannas with small clumps of trees and occasional gallery forests, although the habitat is classified under the Holdridge system as dry tropical forest (Ewel and Madriz 1968). Because the altitude of the ranch is only 63 m, the climate is tropical and has a small annual temperature variation of 14 to 33°C (Troth 1979). The mean annual rainfall was 1.48 m (n = 24 years), with most of it (>85%) falling between May and November, with much of the land flooded up to 1 m deep (June to October). During the dry season (December to April) small lagoons were maintained on Masaguaral by means of deep wells and diesel pumps. The vegetation of this ranch was described by Troth (1979) and the avifauna by Thomas (1979). The area used by Maguari Storks on Masaguaral covered about 690 ha (Fig. 1; hereafter called the study area). I used binoculars, a telescope and a stop watch to observe the storks. Data were recorded in written notes or by using a tape cassette recorder. In the largest breeding colony, the Busaca, I used a blind on a 2-m high platform, but I also frequently made observations by climbing trees adjacent to stork nests and near marshes, or by using a jeep for a blind. My observations were concentrated during the breeding months, June through November, but because I spent time on this ranch in every month of most years, some data are from other months.

From the middle of the 1973 breeding season through the end of the 1976 breeding season, I banded all nestling storks in the study area (n = 128) with a numbered aluminum band on one leg and two to three color bands on the other. Nestling handling techniques are in Thomas (1977). When I worked at stork nests I observed adults from as close as 1 m. Immature storks were determined by iris color (Thomas 1984).

RESULTS

ARRIVAL OF STORKS ON THEIR BREEDING GROUNDS

Generally the first storks arrived on their breeding grounds in flocks, but the month of arrival varied from March to late May. The

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extremely variable beginning of the seasonal rains, which in some years was as early as late March and in others not until June, strongly influenced the beginning of nesting (Thomas 1985) and seemed to influence stork arrival time as well.

Early on the morning of 5 April 1981 a group of 20 adult birds stood together where they had spent the night on the nearly bare, dry ground along the east side of the San Juanera Lagoon (Fig. 1). The storks were in a loose group; several showed an interest in a small armadillo (*Dasypus novemcinctus*) but did not attack it. A few storks rested on their tarsi. At about 1000 they flew away together. The following morning at 0650, at the same place, 74 birds stood in three discrete groups in an area about 100 m in diameter. By 0800 group distinctions had blurred as some storks foraged for arthropods in the dry grass and under dry cow excrement. Several storks stood with their neck semiplumes greatly expanded; other birds preened. These birds did not spend the day on Masaguaral; they flew away in mid-morning, probably because they are visual feeders (Thomas 1985) and no clear water marshes had yet formed on the ranch. That evening at dusk (1850) many storks returned to the same roosting place.

On 10 April only 18 birds roosted at the same site, and I watched them from 0640 to 1025. There was one brief bill-duel, after which the loser stepped quickly away and the winner continued to forage on the same spot. The birds stayed together in a group 12 to 27 m in diameter; the distance between individuals was about 1.5 m. There appeared to be no established pairs although several individuals stood with greatly expanded neck feathers, which may be a social signal. By 0735 three birds had flown away, and among the remaining 15 storks three were immatures (i.e., born during the previous breeding season).

I recorded the behavior of each stork in the group at 5-min intervals from 0840 to 1020. Two thirds of the point counts showed that about 60% of the birds stood without doing anything, about 20% preened, and a few foraged. The immature birds were more restless than the adults, but during the last hour they sat more often on their tarsi or lay down with their ventral surface on the ground than did the adults. At 1025 the birds left as a group, circling overhead as they rose on thermal air currents.

No returning immature Maguari Storks ever remained on the study area for more than a few days. A Maguari Stork was collected on 4 June 1951 at Caicara in the Venezuelan state of Monagas, a site far from any known breeding area. It had brown irides, gray bill, and dull red feet (Specimen #448555 U.S. Nat. Mus., Friedmann and Smith 1955). When I examined this specimen, I confirmed from plumage that it was an immature bird.

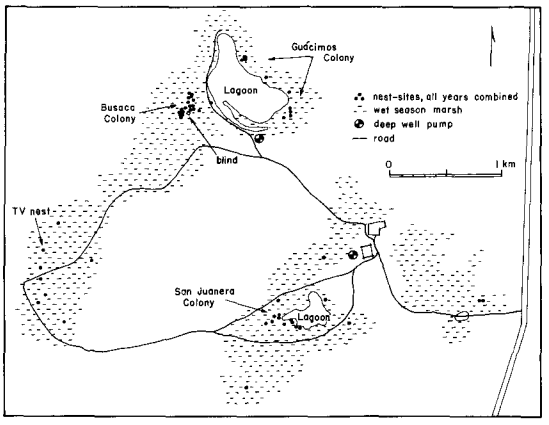

FIGURE 1. Maguari Stork study area with nest sites from all years.

PRE-NESTING SOCIAL BEHAVIOR

After flocks returned, but before heavy rainfall formed freshwater marshes, several birds that may already have been paired sometimes frequented areas near the artificial lagoons adjacent to the most used nesting sites. But after rain-fed, freshwater marshes filled to about 20 cm deep and marsh vegetation was 10 to 50 cm above the water surface, groups of 20 to 35 male and female Maguari Storks congregated there. The storks were particularly shy and difficult to observe at this time. Pair-formation and/or reuniting of birds mated in the previous year may have taken place in these assemblies. The storks stood or walked about in a stiff-legged manner some 1.5 to 2 m apart. When two birds met, both displayed by expanding their neck feathers, throwing their heads back then forward in a deep bow, ending with the bill pointed down at the substrate (up-down; Kahl 1972). A deep throaty hiss accompanied this display. Other birds stood for many minutes with their neck feathers fully expanded. Occasionally birds strutted about with bills full of wet grass.

At the assemblies, which took place in the morning and lasted 2 to 7 hr, no birds fed, although sometimes a stork scooped up a drink of water. Occasionally there were short running attacks by one bird at another, but these aggressions never resulted in either bird leaving the assembly. Once a male and a female walked stiffly and purposefully, directly toward each other over a distance of 150 m. When they met they displayed (up-down) facing each other, then turned and walked side

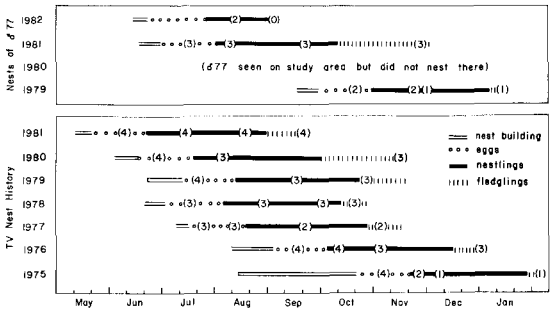

FIGURE 2. Breeding phenology of the nest of Male # 77 and of the TV nest. Months are divided into 10-day intervals. Numbers indicate how many eggs or young were in or at the nest on the dates of the abscissa. Nest building began on the date of closed-end lines; open-end lines indicate an unknown date of nest beginning.

by side leaving the assembly, and eventually they flew away together. Occasionally birds behaving like a pair stayed apart from the group and performed up-down displays while standing parallel to each other. Although assemblies may be the time of choosing mates, some stork pairs probably nested together in more than one year (see below). I was unable to determine whether these storks returned as a pair to the breeding area or whether they met on the familiar assembly ground or on a nest site of the previous year.

Usually a few days after an assembly, the storks began to build nests in colonies adjacent to the assembly site. By this time many of the birds appeared to be paired, but lone individuals remained around colonies and attempted to take over nest sites for one to two weeks.

SOLITARY VERSUS COLONIAL NESTING AND NEST SITES

Most storks built nests in colonies of 5 to 15 nests; sometimes 3 to 6 nests were within 50 cm of conspecifics in the same tree or in the single canopy of a clump of short trees. Other storks selected isolated nest sites, even though there were unused nest sites at colonies in all years. For example the TV nest (Fig. 1) was nearly 2 km from the nearest other stork nest in five of the seven years it was used. Neither of the TV-nest adults was banded, but from their behavior each year I believe they were the same individuals. This nest was large and well-made; it had a hard, matted vegetable base that lasted from year to year and reduced preparation time in succeeding years (see year 1975 vs. 1979, Fig. 2). Most nests disintegrated completely after use and were built new each year, although identical sites were regularly reused.

I examined all the nest sites on the study area in 1975 and 1976 ($n = 28$) and found that 57% were on the tops of short, thick-trunked trees, and the other 43% were on their side branches. The mean nest height from the ground to the bottom of the nest was 3.65 m (SD 1.33, range 1.4 to 6.3). The mean *dbh* of the supporting tree trunk was 21.6 cm (SD 12.2, range 4 to 50). The tree species used were *Hecastostemon completus, Ficus pertusa, Ficus* spp. and *Randia venezuelensis.* One nest site was used for 7 years, 3 sites were used for 6 years, 2 sites for 5 years, 4 sites for 4 years and the other 18 sites were used from 1 to 3 years. Of these nest sites, 23 (82%) were in isolated trees or tree clumps, and 5 (18%) were in trees that faced the marsh on the nest side but adjoined a wooded copse on the other. No nests were built where branches overhung the nest, and all nests were in trees surrounded by seasonal water.

NEST BUILDING

The base of nests was 20 to 75 cm thick, and composed of sticks, few of which were more than 2 cm in diameter and usually less than 1 m long. A frequently used stick was the dead rachis of the palm (*Copernicia tectorum*). At the beginning of nest construction, males appeared to bring most of the material, but females also brought sticks and nest-lining material, which both members of the pair arranged in the nest.

In colonies there was considerable theft of nest material. Consequently, perhaps, pairs took turns guarding nest sites. Early during nest building, however, colony birds generally stopped about 1330 and all departed, presumably to feed, and did not return until the next morning. Such colony sychronization at this stage could keep nests from being vandalized by conspecifics. As the season progressed, storks remained on their nests later in the day; by laying time the nest was never left unguarded.

After the nest base was about 1 m wide, the pair began to line it, mostly with wet grass gathered nearby. This material was worked into the nest with sharp jabbing motions. In the intense sun, the grass soon dried to a hard smooth surface which gently sloped toward the center 5 to 7 cm deep. Nests with lining material 1 to 1.2 m in diameter had enough space for 3 to 4 chicks to exercise their wings without falling out. Storks sometimes laid eggs in nests no more than 0.7 m wide, and loss of eggs and young from these small nests was frequent (Thomas 1984).

Nest material, especially the lining, was brought throughout the incubation and brooding periods. Some pairs added material to disintegrating nests after their young had fledged.

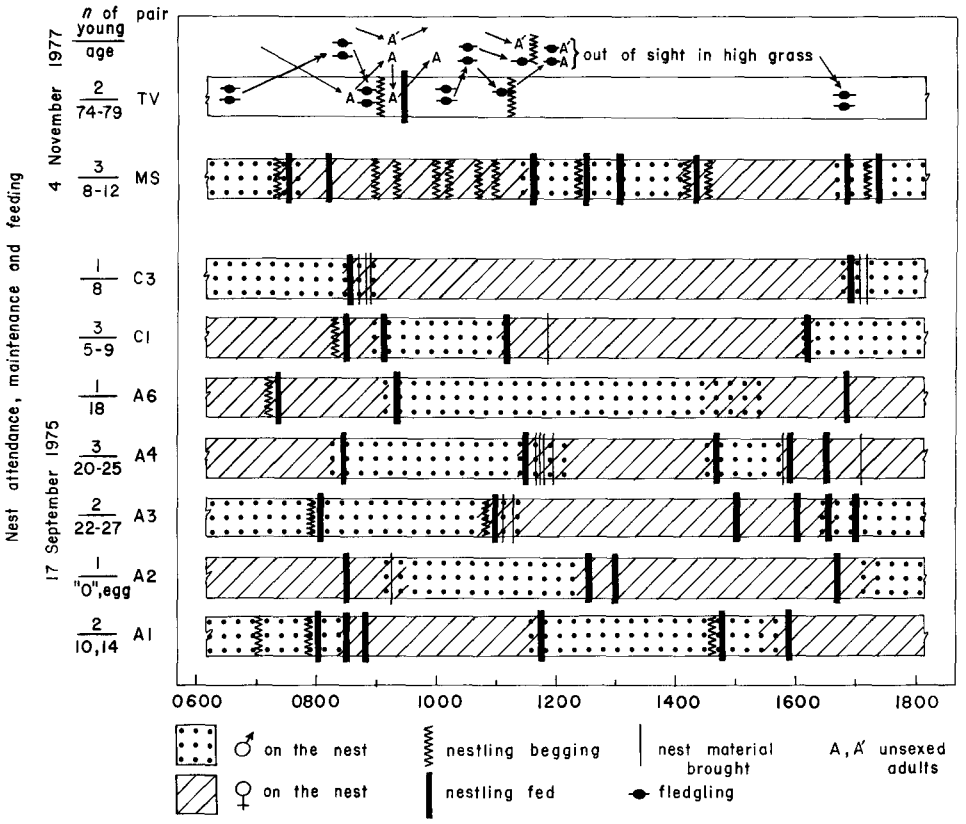

FIGURE 3. Adult behavior at the nest showing nocturnal and diurnal nest attendance, nestling feeding, and nest maintenance. Clutch of Pair A2 was a replacement. The arrows at the TV nest show the direction of movements of fledglings and adults; double-headed arrows indicate birds moving together. Age of young is given in days. All nests were observed continuously from 0600 to 1830.

Nests were used as a feeding site for fledglings and as a roost by them up to six weeks after fledging (Fig. 3). In the *llanos* of western Apure, 12 nests in a colony were made entirely of grass, probably because there were few bushes and trees and no palms in the area for nest base material.

Storks in colonies competed actively for certain nest sites with bill-clattering, bill-jabbing, and fighting. Bill-clattering was used in both intraspecific and interspecific situations. The mean duration of bill-clattering was 2.5 sec (SD 1.02, range 1.5 to 3.5, $n = 24$). In 1974 at a nest in the Busaca colony, the male repeatedly fought with, and drove off, an intruding bird. Once the female of this nest severely bit the neck of the intruder when it landed near the pair on their nest. Thirty minutes later a bird, probably the same intruder, again flew on to the nest beside the pair and pushed them with its body, whereupon the female shoved it off the nest.

Attacking birds were mostly males, judged from their bill lengths, and at times they landed on the back of another male and a fight ensued. During one such encounter, a male intruder fell from a top nest into the thorny side branches of the nest tree. His right wing and neck were badly caught and became more so as he struggled. As the entangled bird dropped parallel with a lower nest, the male from it attacked by jabbing the trapped bird on its head and rump while it hung with its legs dangling, unable to gain a footing.

The most unusual aspect about this incident was that as the attack on the entangled stork continued, all the noise and activity of the entire colony ceased and every stork ($n = 25$), except the two males on their nests in the disputed nest tree, gathered in a tight group in the marsh facing the caught bird. These spectators, some of them standing in pairs, watched intently from a distance of 5 to 10 m while the stork alternately struggled and hung limply, and blood stained its upper tail coverts. Finally after 35 min the bird wrested free of the tree and fell into the water below. Blood spots were also on its neck and underneath its wing, the latter possibly from the thorns. The bird limped, then walked, through the assembled storks to a fence about 150 m away. It was briefly followed by a smaller bird, probably a female, and the rest of the storks promptly returned to their nest building. An hour later

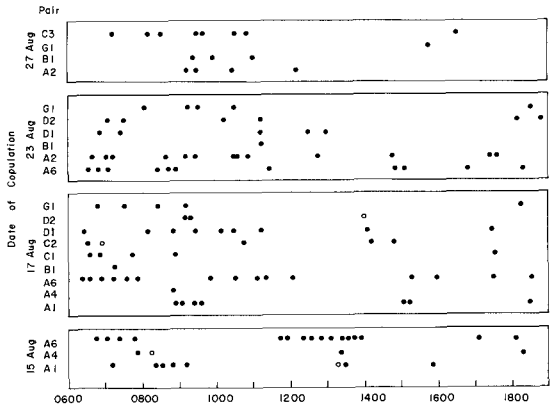

FIGURE 4. Copulation at the Busaca colony over a period of 13 days in 1974. Note no pairs copulated over the full observation period. Nests A1, 2, 4 and 6 were in the same tree clump and 25 m from other nests. Closed circles indicate successful copulations; open circles, unsuccessful copulation attempts. Observations were made continuously from 0600 to 1830.

the injured bird flapped its wings and preened; it had recovered enough to fly away. Schüz (1944) reported that fighting at nests is frequent among White Storks: 77 deaths resulted from 2,660 fights.

Until nests had a firm and solid lining, Maguari Storks were able to stand only in an unsteady and wavering manner on branches of the nest tree. When they did so, they usually chose to stand at branch intersections so that the toes of one or both feet were braced with the web against a fork. They maintained their balance, especially if there was a wind, by body and wing movements. Unlike Wood Storks (*Mycteria americana*; pers. obs.), Maguari Storks do not grasp with their hallux. This difference has affected the life of these storks; they rarely stand in trees. They roost on the ground, and nestlings cannot leave the nest until they can fly (Thomas 1984).

In most years, well after the beginning of the breeding season late-arriving storks began to build nests, few of which were finished. One bird attempted to place nest lining before it had a nest base; another used unsuitable material such as cow pats for a base. A few nests were made on palm trees; the first nest of Male #77 was in a low palm (Fig. 2). Late nests and palm nests were often made by inexperienced individuals, and they had a low rate of success (Thomas 1984).

COPULATION

When nests were essentially completed, pairs of storks stood together on them for many hours. Frequently they gave the up-down display while facing each other on the nest. This was the same display used in the marsh at assemblies and later in nest relief. But single storks of both sexes also directed up-downs to nearby neighbors in their nest tree and occasionally to storks flying overhead. The mean duration from the beginning of the display until its completion was 9.2 sec (SD 1.4, range 7.8 to 12.0, $n = 7$).

The up-down display was not a prelude to copulation. Copulations often followed the return of the male with a bill full of wet grass nest-lining material, which one or both birds incorporated into the nest. The male then moved behind the female, occasionally shuffling back and forth several times. If she remained still, he placed one foot on her back, then hopped up by flapping his wings. She spread her wings slightly and he slipped his toes into the notch formed between her body and wings. Then he reached forward to grab her bill in his. The female raised her bill somewhat and usually pressed her head underneath the male. During actual coition the male generally nibbled on the female's bare neck area or the feathers around it, or the pair snapped their bills together in a noisy duel. Males dismounted by stepping backward, unlike Jabirus (*Jabiru mycteria*) that dismounted forward (Thomas 1981). The mean time of 13 successful mounts was 8.77 sec (SD 1.15, range 7.25 to 10.50).

Some copulations were preceded by the male allopreening or nibbling the female's neck feathers. At other times males raised a foot and touched the female's back, but perhaps lacking an affirmative response, proceeded no further. One male did this seven times in three hours without mounting. Infrequently a female solicited by pressing her body against her mate.

Most copulations took place before noon, and often they appeared to be stimulated by the behavior of nearby pairs. Some birds copulated frequently, others rarely (Fig. 4, see Pair A6 vs. B1). A few copulations were attempted by males while females stood in the marsh; generally these females walked away. After copulation both members of the pair usually preened by nibbling their primaries in a ritualized manner, or the male left the nest briefly and returned with more nest material.

CARE OF THE EGGS AND YOUNG

Egg laying was highly synchronous among storks that had closely adjacent nests, perhaps as a result of socially stimulated copulations. After egg laying, intraspecific tensions and fighting terminated and the colony was transformed into well-coordinated group behavior. Lone birds, which had caused much of the turmoil, had either paired or left the area.

Circumstantial evidence suggested that some pairs roosted together on the nest before egg laying, but beginning with incubation only one bird stayed on the nest at night. The sexes alternated incubation and brooding during the day. The night session at some nests alternated between the parents; at others, it did not (Fig. 3). Diurnal nest exchanges were accompanied by up-downs, but the greeting decayed in some pairs, e.g., one brooding female displayed without standing up. In other pairs the display remained strong and unambiguous throughout nesting.

Eggs were laid on alternate days, and hatching was asynchronous. The incubation period was 29 to 32 days, and nestlings fledged at the age of 60 to 72 days (Fig. 2; Thomas 1984). At five nests, eggs were replaced soon after total early loss. Although none of these birds were banded, I believe that replacement clutches were laid by the same females. Twelve days after the loss of both nestlings (5 to 6 weeks old), Male #77 and his unusually small mate again copulated on their nest. It had been 2.5 months since that female had laid eggs, and she failed to produce a replacement clutch.

From before egg laying until nestlings were about six weeks old, nests were always guarded (Fig. 3). At the Busaca colony off-duty (loafing) storks spent their time together in a marsh 200 to 500 m west of the colony, where water was never as deep as that around nest trees. They were joined there by storks from other nests in the study area. In this marsh the storks displayed and preened; a few hunted for food.

Nest relief at the Busaca colony consisted of 2 to 4 exchanges each day varying with the number and ages of the young (Fig. 3). In response to disturbance in the colony, all adults stood up on their nests and looked toward the disturbance. Brooding adults bill-clattered, and nestlings usually lay down flat on the nest, the youngest in akinesia (Thomas 1984). Within a minute the off-duty birds arrived and made overflights (mobbing), during which they flew over the colony at heights of 10 to 50 m. They flew in tight circles clattering their bills, and some birds returned to stand beside their mates on nests. Storks defended nest trees with overflights even before nests were built. The proximity of the loafing marsh greatly facilitated the birds' fast response to colony disturbance.

Colonial and solitary nesters differed in their nest defense tactics. At both kinds of nests, incubating and brooding storks were unwilling to leave even when a human was less than 1 m away. Some adults stood on their nests while I removed their young one at a time for banding. Often adult colonial storks attacked and bit me or hit my back with their bills while I worked at their nests. One colonial nesting male climbed 1 m below his nest to jab me on the head a week after I had banded his young.

Contrarily, I was never physically attacked by solitary nesters. They used a different defense technique that I called *lead-away*. Once a solitary nesting male walked up to less than 10 m behind another person and me in a marsh while we observed his newly fledged young about 75 m away. He clattered his bill, and when we turned around he turned and walked slowly away from us. Each time we stopped, he stopped and clattered until we moved toward him. Another solitary nesting male once flew to and landed in shallow marsh less than 4 m from me as I left his nest area. He clattered his bill, stretched up his neck, and expanded his neck feathers in display. I waited; he walked about five steps away from me, then turned and looked back, clattering. If I followed, he led me away from his nest but clattered when I stopped. I tested him by going back toward his nest 30 m; he turned and followed me, never letting the distance between us become more than 12 m or less than 2 m. Thus he escorted me over 300 m away from his nest, where the female stood with their nestlings. Three days later I returned, and he repeated the behavior; for 23 min we alternately led and followed each other as before. Other solitary males behaved similarly. These observations suggest that overflights (mobbing) and physical attacks by Maguari Storks were used by colonial nesters, but that solitary nesters used the lead-away (distraction display).

The nest success of all nests over three years, determined by whether adults fledged at least one young as compared to unsuccessful nesters that laid eggs but fledged no young, was 67% for colonial birds compared to 42% for solitary nesters (Table 1).

FOOD AND FEEDING BEHAVIOR

Before and after the breeding season, adults occasionally foraged in short-grass, dry fields. Far more often they used wet or shallow marshes with emergent vegetation 10 to 30 cm high. One adult regurgitated a food bolus on its nest, when it only had eggs; the bolus consisted of 11 aquatic rats (body length = 6 to 18 cm) and a small frog. Nestling food was entirely aquatic: frogs, fish, freshwater eels, rats, crabs, and water insects (Thomas 1984). Adults probably fed on similar food at that time.

The Maguari Stork is a visual forager (Thomas 1985). One male spent 95 min foraging in water 5 cm deep with vegetation 1 to 1.5 m high. He walked slowly with his bill open. Three times he pawed the air with a foot; once he opened his wings and ran two steps

TABLE 1. Comparison of solitary and colonial nesting success. Only nests that contained eggs are considered.

Year	Nests *n*		Solitary nests (%)	Colonial nests (%)
1974	29		6 (21)	23 (79)
		successful	3 (50)	13 (57)
		unsuccessful	3 (50)	10 (43)
1975	32		8 (25)	24 (75)
		successful	3 (37)	14 (58)
		unsuccessful	5 (63)	10 (42)
1976	24		5 (21)	19 (79)
		successful	2 (40)	17 (89)
		unsuccessful	3 (60)	2 (11)
Total nests *n* (%)			19 (22)	66 (78)
		successful	8 (42)	44 (67)
		unsuccessful	11 (58)	22 (33)

forward just after he had spread and shaken his wings. Often he stood on one foot with the other poised out of the water, ready to move forward quickly. He caught and swallowed some unidentified small prey. (Small fish and tadpoles were in the water.) No prey capture resulted from either the wing spread or aerial pawing. Another adult foraged in open water 10 to 25 cm deep, a less common habitat. During 10 min it walked slowly, jabbing the water with its open bill at the rate of 37 jabs per min. In this way it caught a 50-cm freshwater eel and a crab.

COMFORT BEHAVIORS

Maguari Storks frequently preened and stretched bilaterally. Once I saw water-bathing. At 1430 during nest building in the Busaca colony, several birds flew singly and in pairs to bathe in water about 15 cm deep. They sat in water that covered their breasts, spread their wings out on the surface and flapped both at the same time while stretching their necks out in the water in front of them. The birds repeated this 3 to 4 times standing and shaking vigorously in between. Afterward, the birds preened their primaries and upper breasts. Some held out their wings and fanned the tail like Cathartid vultures, while standing with their backs to the sun. Occasionally non-bathing storks held their wings spread with their backs to the afternoon sun. Houston (1980) has shown that sunning behavior in large soaring birds results in restoration of feather curve after distortion during soaring.

While standing on nests, the storks often opened the wrists laterally with their backs to the sun while they shaded eggs or nestlings. This delta-wing posture was reported in six other stork species by Kahl (1971b), but not for Maguari Storks. On hot afternoons, birds on nests opened the bill, panted, gular-fluttered, and raised the nape, neck, and throat feathers in apparent thermoregulation. Although storks at night roosts excreted on their legs (urohidrosis; Kahl 1963), adult storks on nests never did so; they excreted over the nest edge. Large nestlings, however, used urohidrosis for thermoregulation during the last one to two weeks before fledging (Thomas 1984).

Maguari Stork nests were kept very clean, although some nestlings had ectoparasites. The mite (*Ornithonyssus bursa*), found at several nests, was the same species reported from the Asian Openbill Stork (*Anastomus oscitans*) in a breeding colony in Thailand (McClure and Kwayuen 1973). Adults and nestlings rarely allopreened.

POST-BREEDING BEHAVIOR

Parent storks continued to guard and feed fledglings up to six weeks after fledging (Thomas 1984). At this time, seasonal rains ended and the marshes dried quickly. Because their usual food was no longer available, Maguari Stork breeders and young left the study area. In mid-January 1980 I found 24 storks standing together in a dry field at 1000 about 35 km south of the ranch. The flock was in an area about 150 m in diameter; a few birds foraged and others preened. Their behavior was similar to that of arrival flocks. On the afternoon of the same day these birds were gone, but 18 storks foraged together in a marsh 20 km further south. In the dry season, wetter areas prevailed for a longer time south of the ranch. After their first departure, no banded nestlings were ever found on the ranch until they returned as mature breeding birds—three-year-old males and four-year-old females (Thomas, in press [a]).

DISCUSSION

Kahl (1971a) found that in northern Argentina Maguari Storks nested on the ground. This is unusual for a stork, as Kahl pointed out, and he suggested that ground-nesting might be a result of the storks' recent invasion of a treeless habitat. J. Ogden (pers. comm.) also found Maguari Storks in Argentina nesting on the ground on small vegetated islands surrounded by meter-deep marshes. In Venezuela, however, they nested in bushes and trees, both on my study area and at three other sites 40 to 200 km away. Zahl (1954) also found them nesting in high bushes in central Apure, Venezuela.

Maguari Storks are gregarious and colonial. They arrived on the breeding area in flocks and they roosted together. Pairing seemed to take place in group assemblies. Nests were sometimes built within 50 cm of conspecifics

and often in colonies of up to 15 nests. Off-duty birds loafed and defended colonies together, and the storks departed from the breeding area in flocks. Juveniles, as soon as they left the nest, had the same gregarious tendencies.

In all years there were unused nest sites in colonies, so a shortage of sites does not explain why 22% of nests examined in three years were solitary. Lack (1968) suggested that solitary vs. colonial nesting in the same species is an adaptation to different food densities; this is not the case with Maguari Storks, because both types of nesters foraged at the same places. Solitary nests were less successful, but their success rate for the years examined were remarkably constant (Table 1). No single explanation seemed to fit solitary nesting. It is possible that first-time breeders that arrived later than experienced breeders may not have been attracted to well-established colonies where behavior had passed the nest-building and copulation stage. Or due to the precision of philopatry, storks may select nest sites as close to their natal tree as possible, which three or more years after their birth may no longer be suitable for a colony (Thomas, in press [a]). Perhaps solitary nesting may be simple predator avoidance; the highest nest losses during the study were from snake predation on eggs in colonies (Thomas 1984).

A sharp drop in the number of breeding pairs in 1977 was followed by a slow but steady decline on the study area and within 50 km (Thomas, in press [a]). This precluded the possibility of learning whether colonies subsequently formed around successful solitary nests, such as the TV nest. However, the diminished number of breeding pairs indicated clearly that the storks were tenacious to their preferred nest areas: in 1981 there were only four nests on the study area, one each in the Busaca, Guácimos and San Juanera colonies, plus the TV nest; the only three nests in 1982 were one each in the three colony areas (Fig. 1).

The social stimulation of colonial nesting in Maguari Storks may have resulted in highly synchronized egg laying. This may be advantageous in swamping predators or reducing colony risk-time to predation (Emlen and Demong 1975). But perhaps equally important for Maguari Storks is age synchrony for fledglings and juveniles. Gregariousness begins for like-aged young as soon as they leave the nest (Thomas 1984) and is probably an anti-predator defense.

South America is undergoing an unprecedented human population expansion. This is causing rapid land-use changes, much of it in the interior of the continent. Natural wetlands, the supporting habitat of the Maguari Stork, are under heavy pressure everywhere from modern agriculturalists. Furthermore, the Maguari Stork is a large, conspicuous, and gregarious bird, which is taken for human food in Venezuela (Thomas 1984) and probably elsewhere. The increased human population in the natural wetland habitat will directly affect the stork. Thus life history data collected about the species during the presumed normal years (1972 to 1976) should be useful in its conservation.

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