MAGUARI STORK NESTING: JUVENILE GROWTH AND BEHAVIOR

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ABSTRACT.—Although it has a wide range in tropical South America, the Maguari Stork (*Ciconia maguari*) is poorly known. In an 11-yr study of its breeding biology in the llanos of Venezuela I found the mean clutch size for 3 yr to be 3.2 eggs. The young hatched asynchronously at 29–32 days and usually made their first flight at 60–72 days. Data on egg sizes, weights, and a probable dump egg are given. The weight and growth of two siblings, plumage succession, and nestling and fledgling behaviors are described. The fledging success of eggs from 55 nests, over 9 yr, was 61%. Loss of eggs (presumably from snake predation) was higher than nestling loss. Although the asynchronously hatched young in a clutch varied greatly in weight and continued this difference throughout nestling life, no case of brood reduction was found in 123 nests during the study. Nestlings were fed mainly frogs and tadpoles, fish, eels, and aquatic rats; food classes and food sizes brought by adults varied with the age of their young. Maguari Stork nestlings do not grasp with their hallux and so are confined to their nests until they can fly. I suggest that the two black plumages of nestlings, between the white hatching down and the white first basic plumage, are for crypsis of the nest-bound young. *Received 29 August 1983, accepted 1 March 1984.*

THE Maguari Stork (*Ciconia maguari* = *Euxenura galeata*) is found only in South America and is less widespread than the other two storks of the Western Hemisphere, the Wood Stork (*Mycteria americana*) and the Jabiru (*Jabiru mycteria*), both of which range farther to the north (Blake 1977). Although the three species are largely sympatric in South America, the wide ranges indicated on distributional maps are somewhat misleading, because these storks are ecologically restricted to tropical, low-elevation wetlands and adjacent nonforested areas. In Venezuela the three storks are found together in the interior of the country, a vast savanna called the llanos.

Mayr and Amadon (1951) and Kahl (1971a) have suggested that this stork is closely related to the White Stork (*Ciconia ciconia*), and this paper gives a broader basis for a comparison of the young with those of the better known White Stork (Schüz 1942, 1943, 1944; Haverschmidt 1949). The principal published information about the Maguari Stork is from 2 months of observations of nesting birds in Argentina (Kahl 1971b). For 11 yr I followed the seasonal breeding of all Maguari Storks on a ranch in the llanos of Venezuela. I give data on the eggs and on the asynchronously hatched young from the day of hatching to the postfledging period. Perhaps because of abundant food on the study site, no incident of brood reduction was observed in 123 nests. The manner and size of food presented to the young and sibling growth data, however, suggest that brood reduction may not occur in this species or may be rare. Loss of eggs, presumably to snakes, was higher than nestling losses from all causes combined.

One puzzling aspect of Maguari chick development is the succession of two different black plumages, between the white hatching down and the white first basic plumage (Humphrey and Parkes 1959) acquired at fledging. I suggest that the black plumages are for crypsis because of their timing and the fact that Maguari Stork nestlings, like adults, do not grasp with their hallux and thus cannot leave their nests to escape predators.

STUDY SITE AND METHODS

The study site (08°31'N, 67°35'W) was a cattle ranch located roughly in the center of the Venezuelan llanos, about 45 km south of Calabozo in the state of Guárico. Troth (1979) provided an account of the vegetation of this ranch and Thomas (1979a) an annotated list of its bird species. The llanos are grassland savanna with scattered palms and clumps of other trees. During the rainy season (generally May to November) Maguari Storks nest, usually from June to October (Thomas in press), when much of the sa-

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TABLE 1. Maguari Stork hatching and fledging success.

Year	Number of nests	Eggs			Young		Total success (%)
		Laid	Hatched	Percentage hatched	Fledged	Percentage fledged	
1973	2	5	5	100.0	4	80.0	80.0
1974	16	43	24	55.8	18	75.0	41.8
1975	15[a]	47	24	51.0	19	79.1	40.4
1976	10	36	28	77.7	24	85.7	66.7
1977	2	7	4	57.1	4	100.0	57.1
1978	5	14	9	64.2	5	55.5	35.7
1979	1	4	3	75.0	3	100.0	75.0
1980	1	4	3	75.0	3	100.0	75.0
1981	3	11	10	90.9	9	90.0	81.8
Total	55	171	110	71.8	89	85.0	61.5

[a] In 1975 all the young were taken from five nests by poachers. Four of these nests are included here, because their nine young storks were nearly old enough to fledge.

vanna is flooded to a depth of 5–100 cm. Maguari Storks on the study site used an area of approximately 690 ha. I studied the birds from 1972 through 1982, and from 1973 to 1976 I banded all nestlings (n = 128). The details of handling techniques are reported elsewhere (Thomas 1977). Some observations of nestling behavior were made during banding; other data were from dawn-to-dusk observations from blinds and from field censuses during all nesting stages.

I used 8 × 32 binoculars, a 15–60× telescope, spring balance Pesola scales of 100, 300, 1,000, and 2,500 g, a grocer's scale that registered to 10 kg, a vernier scale calibrated to 0.1 mm, and a stop watch. I took notes by hand or by using a portable tape recorder. Color notes were made by comparison with color swatches in hand (Smithe 1975). Only nests where the number of eggs laid and number hatched were known are listed in Table 1. Standard deviations and ranges are given for egg sizes and weights. The length of food items was either measured from collected samples or estimated to the nearest centimeter, and the weight was calculated from preserved samples of food species.

RESULTS

Nests.—Both members of Maguari Stork pairs share in all phases of nest building, incubation, brooding, and feeding the young. In Venezuela their nests were built on bushes and in small trees 1.4–6.3 m high (Thomas MS) but not on the ground, as Kahl (1971b) found in Argentina. Nests were platforms of sticks about 1 m in diameter covered with grass sloping slightly down toward the center. Most nests were in small colonies (77%), but some (23%) were solitary. Details of nests and nest-building will be reported elsewhere.

Eggs.—Maguari Storks laid eggs from May to November; in any one year, however, the nesting season lasts no more than about 4 months. The timing difference is caused by the variation in the beginning of the nesting period and amount of rainfall (Thomas in press). The only pair that laid eggs in late May did not relay after their young fledged in late August. Nesting in October was by late-returning birds, usually young inexperienced individuals. The eggs were small in relation to the size of the adult female ($\bar{x}$ egg is ca. 3.3% of female weight), and the clutch size was usually 3–4 eggs. The mean was 2.8 eggs (n = 20 clutches) in 1974, 3.4 (n = 17) in 1975, and 3.6 (n = 12) in 1976, for an overall mean of 3.2 eggs per clutch. Late rains and low precipitation during May–June in 1974 may have been associated with the smaller clutches.

Eggs are oval to subelliptical (Palmer 1962). They are nearly smooth and dull white but may become stained during incubation. The mean length of 54 eggs from 5 yr was 75.19 mm (± 3.29, range = 69.1–85.0) and their mean width was 52.56 mm (± 2.66, range = 46.0–57.0). Mean weight of 42 fresh eggs, within a week of laying and only slightly incubated, was 116.4 g (± 9.42, range = 100–140). One fresh egg was separated into its component parts and weighed: the shell was 14 g (11%), the yolk 25 g (21%), and the albumen 83 g (68%). The yolk was Flame Scarlet (Smithe 1975), perhaps because of the carotenoids, which are the components of some fish and crustacea (Roudybush et al. 1979); White Stork eggs are also red-yolked (Goldsmith 1965).

At three closely watched nests, the storks laid their eggs on alternate days, and full-time incubation began with the second or third egg. Thus, in a clutch of four, there was sometimes a difference of a week in the age of the asynchronously hatched young.

I found one presumed instance of a dump egg. In a nest with three eggs where incubation had progressed for about 21 days, a fourth egg appeared. Three days later a broken stork egg shell was underneath the nest. No eggs were missing from nearby nests, and the three eggs of this nest hatched 2–5 days apart. Therefore, the shell below the nest was probably that of the dump egg. This nest might have been particularly vulnerable to dumping, because it was the highest and most exposed of a cluster of nests. Unlike the Jabiru, which usually nests in isolated sites where an interloper is easily seen and attacked (Thomas 1981), Maguari Storks sometimes nest less than 0.5 m apart, so there are close conspecific neighbors, and a strange female might not be immediately conspicuous. Yom-Tov (1980) suggested that intraspecific parasitism is more common in "good" years: this year had the largest number of nests (29) during the study.

The chick at hatching.—The incubation period of Maguari Stork eggs was 29–32 days, counted from the last egg laid until the last chick hatched in two nests. At one nest the first chick of three eggs began to break through its shell at 1130. At 1316 the attending adult, the male, stood up, cleaned the nest, picked up one half of the egg shell with the tip of his bill, and tossed it over one side of the nest. The other half he threw in the opposite direction. Then he resumed incubation. At 1430 the chick's white down was dry, and it had a dull gray-colored bill with a small gray egg tooth. The young bird's gape was pink, the gular area was whitish yellow, the legs and feet pinkish gray, and the body skin light gray. The skin of some chicks at hatching is darker, nearly black. The nestling weighed 90 g, and it opened its eyes briefly and made soft peeps when handled. The second chick of this nest, which hatched 4 days later, weighed 83 g approximately 2 h post-hatching. Three other "day 0" nestlings weighed 76, 78, and 88 g. Daily measurements of these two siblings are given in Figs. 1–4. The third egg was infertile.

Plumage sequence.—On its first full day, the Maguari nestling is well covered by expanding white down on the capital, spinal, humeral, alar, and ventral tracts. By day 4, emerging black semiplumes (Lucas and Stettenheim 1972: Fig. 45) cover the frontal, coronal, and occipital areas to the dorsal cervical line. Subsequently, black semiplumes also cover the auricular, malar, and submalar areas, as well as the ventral, lateral, and dorsal cervical areas. At 1 week, a second generation of down, which is Blackish Neutral Gray, starts to appear on the body. The first white down is protoptile and the second black down mesoptile (Van Tyne and Berger 1971).

The second downy feathers push out the first white downy feathers, many of which remain attached to the tips, and the effect is that of regularly spaced white stars (Thomas 1979b). The second down is extremely dense, and it bleaches to Olive-brown by 3 weeks. On the 18th day, the first glossy black remiges begin to emerge from their sheaths. At 5 weeks, young storks are well covered with black juvenal plumage. At this age the distinctively different head and neck semiplumes, which are black, lanceolate, and plumulaceous, are 2–3 cm long. These feathers are often erected when nestlings are excited and occasionally for thermoregulation.

A third generation of down, which is white, begins to appear at about the age of 7 weeks, and soon afterward a few white semiplumes edge the bill on the malar tract, quickly followed by white semiplumes in the postauricular area. Just after 2 months of age, white contour feathers become clearly visible on the interscapular tract. Around the time of the appearance of the first white semiplumes (ca. 60–65 days), most young storks make their first flights. By the age of 3 months, the juvenile stork's first basic plumage looks like that of the adults. The sequence of these plumages and molts is illustrated in Fig. 5.

Other morphological changes.—The egg tooth appears to be absorbed, as it is only slightly visible by day 9. By the 5th day the nestling's legs, toes, orbital area, and bill are black. When the chick reaches its 16th day, the hallux, which previously lay folded forward with the other toes, becomes loose and flexible. Four days later, the hallux flexes backward, but nestlings often do not stand on their feet until they are a month or more old. Neither the nestling nor the adult Maguari Stork uses its hallux to grasp (Thomas MS).

By the nestling's 5th day, the gular area is

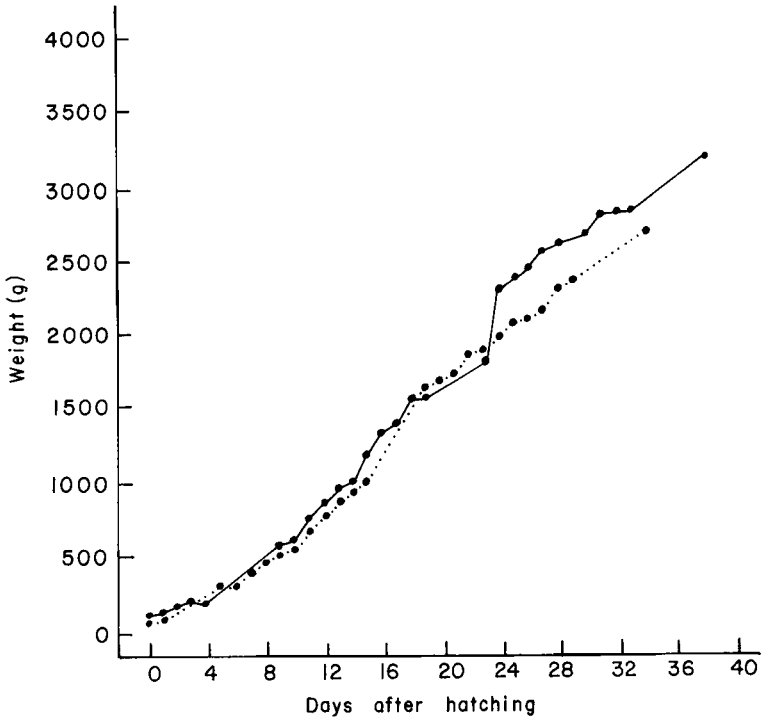

Fig. 1. Weight gain of nestling Maguari Stork siblings. Solid line represents the older, dotted line the 4-day younger bird.

Pale Sulphur Yellow, and it becomes a progressively stronger color: Orange Yellow at 3 weeks and Spectrum Orange 2 weeks later. At this time, some black dots speckle the gular along the edge of the bill, but the amount and pattern vary among nestlings. When the young first fly, the gular is pale Scarlet. The orbital area, which is red in adults, stays black for per-

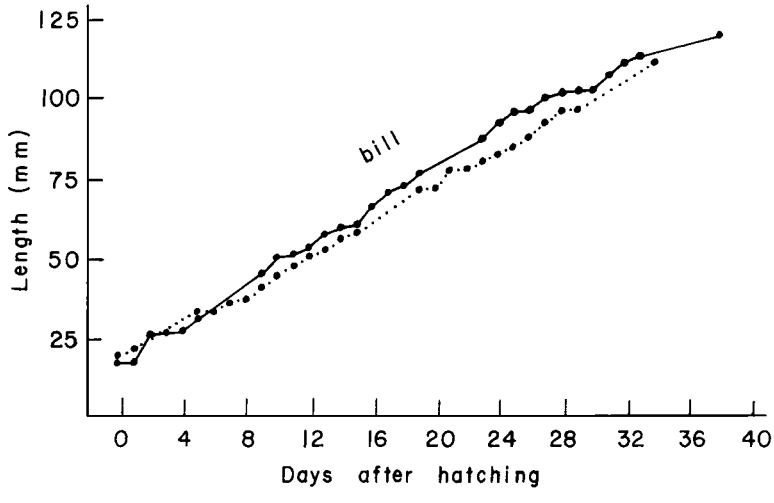

Fig. 2. Exposed culmen growth of siblings different in age by 4 days. Symbols as in Fig. 1.

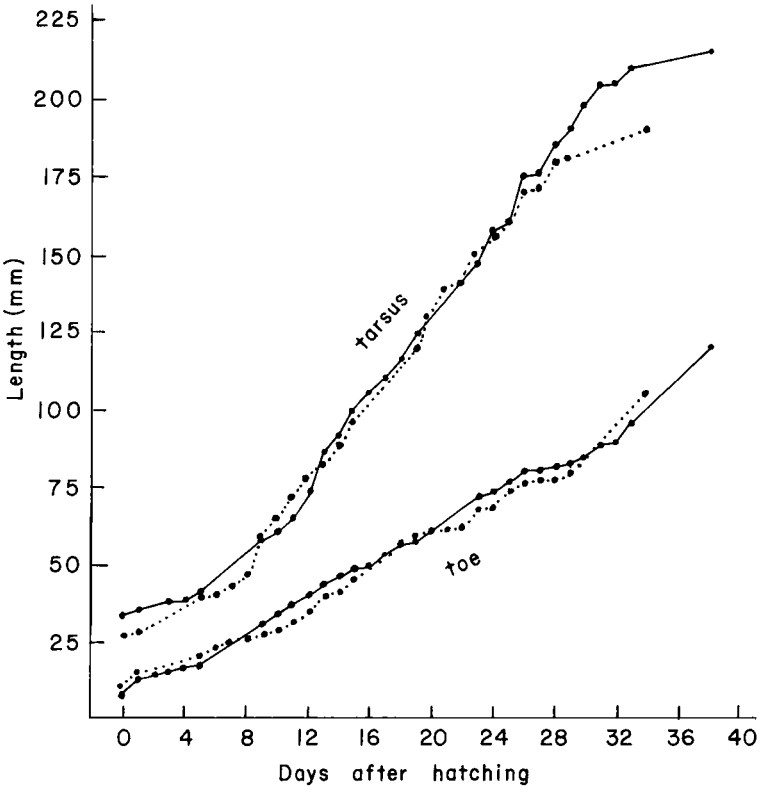

Fig. 3. Tarsal and largest (middle) toe growth of siblings different in age by 4 days. Symbols as in Fig. 1.

haps a year, however. At 3 months, the bill begins to become bicolored, similar to the adult bill, and the legs and feet of some young start to turn pinkish. Both sexes of adult Maguari Storks have lighter than Cream Color irides, but the nestling iris is Raw Umber. This color does not change significantly before young storks leave their natal area and probably not in their first calendar year (Thomas MS). Dark iris color is the best field mark for identifying young Maguari Storks.

Nestling food and feeding.—Nestling Maguari Storks were fed almost entirely upon aquatic organisms. Parents carry food to the nest as a large bolus in the throat or crop. They regurgitate it onto the nest, often bit by bit when the chicks are young and as a large mass to older nestlings. There it is picked up and eaten by the nestlings. Feedings are copious but infrequent (Thomas MS).

Food brought to the nest was always fresh, whole, and undigested; occasionally small fish and eels were still alive. Representative samples of food were collected for identification. The classes of food, in the order of their numerical importance, were: frogs (*Pseudis paradoxus, Leptodactylus fuscus, L. ocellatus*); fish (*Petenia kraussi, Cichlasoma* spp., *Gymnotus carapo, Pterolebias* spp., *Hoplias malabaricus, Rhamdia* spp., *Aequidens* spp., *Hoplosternum littorale, Trachycorystes galeatus*); freshwater eels (*Symbranchus marmoratus*); rodents (*Holochilus brasilensis, Zygodontomys brevicauda*); crabs (*Dilocarcinus dentatus*); insects [*Lothocerias grandis* (Belastomatidae), *Dytiscid* larva, dragonfly nymph, grasshopper]; earthworms (*Lumbricus* spp.); snake (*Lygophis lineatus*); and bird [one unfeathered nestling (not identified)].

The relative importance of food items and classes in 54 boli is illustrated in Fig. 6. Although I identified some food items from a blind rather than collecting them, it appeared that different food classes dominated by weight in different years (see Methods): *Pseudis para-*

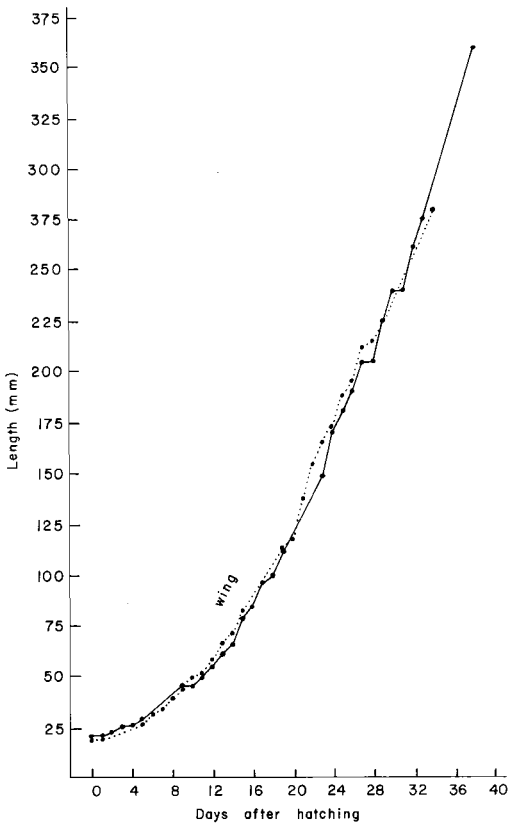

Fig. 4. Wing growth of siblings different in age by 4 days. Measured from the bend of the wing to the tip of the longest primary. Symbols as in Fig. 1.

doxus tadpoles in 1973, eels in 1974, and rodents in 1975. *Pseudis paradoxus* tadpoles were up to 12 cm long and weighed as much as 18.5 g; sometimes 5–6 were in a single bolus. A large eel (60 × 2.5 cm, 326 g) was fed to an 18-day-old nestling, which took several hours to swallow it. By the age of 4 weeks young storks were able to eat rodents with bodies 16 cm long. The most closely observed nestlings regurgitated their first pellets at the ages of 21 and 25 days (42.3 × 78.3 mm, 75 g, and 42.2 × 53.7 mm, 30.5 g; weighed when fresh and wet). At this age the young are first fed rodents, and pellets reflected the larger amount of indigestible fur, in addition to insect and crab exoskeletons.

The quantity and size of food brought by parent storks depended greatly on the age of their nestlings, a variation that Kahl (1964) reported in Wood Storks. When Maguari nestlings are very young, many small items, like frog eggs, earthworm-sized eels, and fish less than 5 cm, are brought. After an adult drops food on the nest, it looks at the bolus and, sorting the food with its bill, quickly picks up and swallows large items, including all rodents if the chicks are small. Sometimes a relieving adult deposited food before the other left the nest, and its mate picked through the boli and ate some of the largest items. Most boli were made up of a variety of food classes. For example, two nestlings 2.5–3 weeks old received 3 baby rats and 2 each of frogs, small fish, small crabs, and insects in a single meal. Three nestlings 6–7 weeks old were fed in a meal 10 rats (5–12 cm body-size, 350 g combined), 31 fish (2–10 cm, 145 g), a tiny eel (1.5 g), 4 crabs (2–5 cm, 45 g), and 2 large insects (10 cm, 46 g), for a total of 588.5 g.

Adult Maguari Storks do not disgorge food until all their nestlings are resting on their tarsi facing the center of the nest, where they beg by flapping their wings. During the transition period between fledging and independence, the young are still largely dependent on adult feeding. Fledglings are fed both on the nest and in the marsh for 5–6 weeks. As a result of this kind of food transfer, young storks receive a fairly equal share of food; the largest nestling usually grabs the largest items, while smaller sibs eat smaller ones. This could lead to disproportionate growth, but, by the time the largest chick swallows a large fish or eel, the smaller ones have eaten many items.

Sibling rivalry was rare and mild. During the study, there was no instance of brood reduction through smaller siblings starving, perhaps because of food abundance in the study area. The weights of asynchronously hatched Maguari Storks in the same nest varied greatly. It was common to find 500–1,400-g weight differences between the largest and smallest siblings in 3–4 chick clutches, yet the smallest birds fledged successfully. At hatching, the younger of the two chicks in the most closely observed nest weighed 46% of the weight of its 4-day-older sibling. A difference in weight between the two continued with age, but the percentage decreased (calculated at 5-day intervals, the smaller chick's weight being 47%, 54%, 60%, 88%, 74%, and 87% of the larger). Nevertheless, their growth rates as seen in Figs. 1–4 were very similar.

The growth rate (Fig. 3) of the bill (exposed

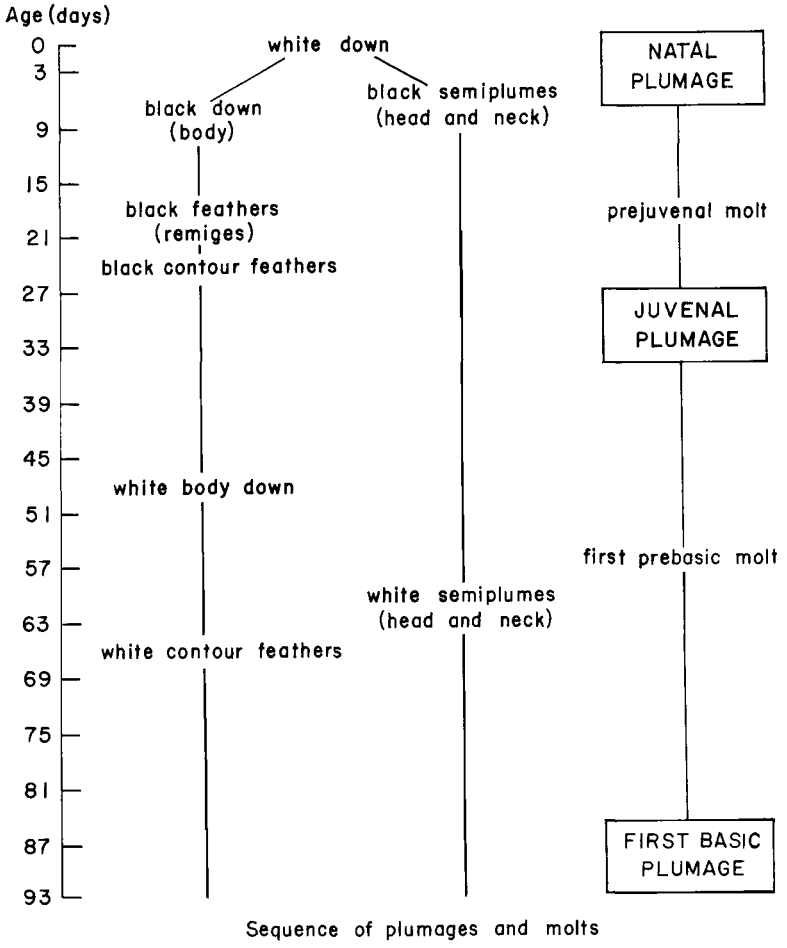

Fig. 5. Sequence of plumages and molts in young Maguari Storks. The age indicated is the first time that the plumage generation is clearly visible, or (later) the time when feathers first begin to break out of their sheaths.

culmen) was close to that of Wood Storks (Kahl 1962); the tarsus (Fig. 3) grew like that of a Wood Stork for the first 3 weeks, and then it grew faster. The longest Maguari toe, however, was slower growing and remained shorter than the Wood Stork toe. Wing measurements (Fig. 4) are not comparable, because Kahl measured the longest primary and I measured from the bend of the wing to the end of the longest primary. Not unexpectedly, Maguari Stork nestling weight (Fig. 1) was always higher than that of Wood Stork nestlings, and it increased at a more accelerated rate; young Wood Storks weigh about 2,500 g at fledging, whereas Maguari Storks weigh about 4,000 g at that time.

Behavioral development.—On its first full day, the Maguari nestling sits and moves with agility on its tarsi and begs with its neck arched and bill open. Its eyes are wide open, and it grabs accurately at the nest surface. By day 9, the elder of the two closely observed chicks began to defend its nest against my approach by gobbling fiercely and biting my hand, while the 4-day-younger sibling lay flat on the nest in akinesia, a form of deliberate immobility. The following day both chicks used this form of defense. Gradually, these two nestlings grew increasingly aggressive, and after 5 weeks I stopped handling them lest they injure themselves. By contrast, the parents, who attacked

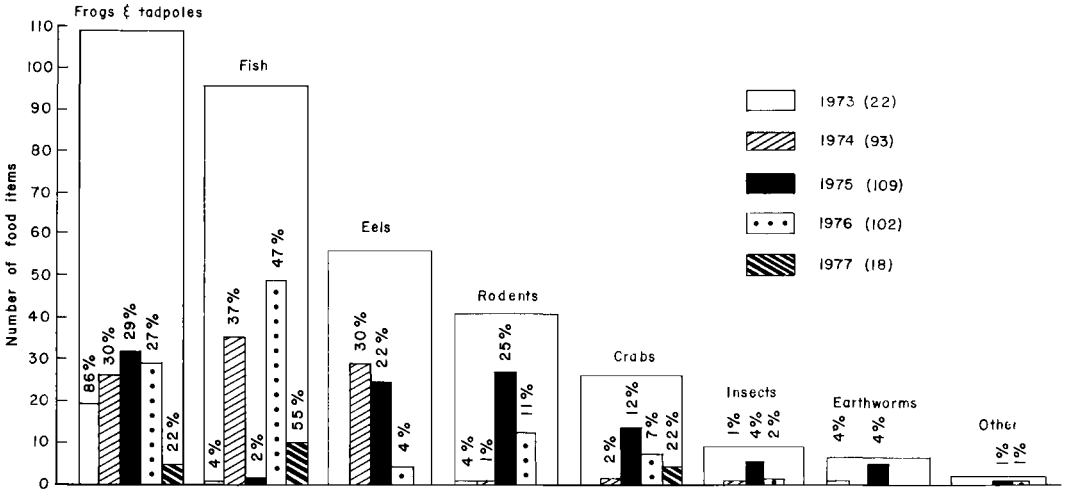

Fig. 6. Food items fed to Maguari Stork nestlings from 54 boli ($n = 344$), all sizes combined. Total items per class shown in the wide unshaded columns; number of items per year in the narrow bottom columns, with the percentage of each food class by year above. Total number of items identified each year is shown to the right of the year symbol.

me during my early nest visits, gradually grew tranquil as they became habituated to my daily nest inspections.

The younger nestling stood on its feet at 22 days, whereas its sibling did not do so until 38 days old. There was great variation among nestlings in regard to this behavior. Young nestlings attempt to defecate over the edge of the nest from the tarsal stance, but by 4 weeks of age, when most stand on their feet, they always defecated over the nest edge. During the last weeks of nest life young Maguari Storks begin to whiten their legs with excreta. This "urohidrosis" is a thermoregulatory behavior of Wood Storks (Kahl 1963). By the age of 6 weeks, when they are left unattended on the nest, the young sometimes gape, pant, gular flutter, and use ptilorerection to dissipate heat during midday.

At 1 month, most nestlings begin a strong defense of their nests by flapping their wings, moving toward the intruder, snapping, biting, and making various defensive sounds (see below). Maguari Stork nests are often less than 0.5 m apart, but these close nests are always constructed at different heights, with no vertical overlap. The defended territory is the nest proper and the airspace directly above it. Seven times when I was banding nestlings at closely spaced nests, the young of one nest stepped down onto a neighboring nest to escape me. In each case only the resident young defended the nest by attacking me; the intruders always stood behind them and hissed.

Vocalizations and other sounds.—Although the Maguari Stork does not have a wide repertoire of vocalizations, it does make some sounds, one of which is mechanical. The ages when I first heard sounds from nestlings, their mnemonic notations, and my interpretations of their meanings are:

(1) First sound at 2.5 h: a thin peeping (begging).
(2) Day 4: *ehehe ehehe ehehe* (rapid begging).
(3) Day 9: gobbling like a turkey [defense against nest intrusion by humans and Carib Grackles (*Quiscalus lugubris*)].
(4) Days 10–14: *onk onk onk onk*, 4–5 notes in descending tones given by nestlings both before and after eating; sometimes I could induce this vocalization by stroking a nestling on the head/nape (subdued begging, contentment?).
(5) Week 2: bill clapping and snapping; when the chicks are very young, hardly any sound results because of the softness of the tomia (defense).
(6) Week 3: grunts, occasional (protests at handling).

(7) Weeks 4–5: throaty hiss, similar to the adult sound that accompanies the adult Up-Down display (Kahl 1972) (defense, agonistic, social).

Fledging and roosting behavior.—Around the age of 6 weeks, nestling Maguari Storks begin to exercise their wings with increasing vigor. Gradually, they add small vertical jumps, with their wings widespread, while they face strong morning breezes; then they land again on the nest. As the young grow, the nest becomes crowded, and, if an empty neighboring nest exists, often a nestling will exercise from it by jumping a meter or more above its surface.

The siblings that I measured daily were first left unattended during the day when they were 41 and 45 days old. As the time for fledging approached, they were fed less and less, although the parents flew low overhead and perched nearby watching over them. Each time a parent returned to the area, the large chicks flung themselves down on their tarsi, faced the center of the nest, and begged with wildly flapping wings and loud vocalizations. If the adult flew away, the young promptly stopped begging and stood up. When a parent did bring a few small bits of food, they were consumed ravenously by the young birds. On its 67th day, the elder of the two made its first flight. These nestlings had not been fed at all for a minimum of 18.5 h preceeding the flight. By 1116, while exercising its wings, the nestling flew off in a gust of wind, circled the nest tree, and landed in the marsh nearby. An adult Maguari Stork, which I believe was its male parent, flew down beside it in the marsh, but after 8 min the fledgling flew directly back up to its nest. During this time, the bird's sibling and two younger storks in an adjacent nest ceased all activities and watched it intently. The younger sib made its first flight 2 days later at 65 days old. The ability to fly back to the nest is important for a fledgling, because the nest is still used by parent birds as a feeding site, and it is a place of safety. Young storks often return to stand on their nests when they are disturbed in the marsh during early postfledgling days, and young usually roost at night on their nests for up to 6 weeks after fledging.

Postfledging behavior.—By day, siblings stay close together in the marsh surrounding their nests. They stalk through high vegetation and begin to hunt visually in water that is seldom more than 20 cm deep at this time of year. Gradually, the young of a colony coalesce into a loose flock, and younger chicks from a single colony often fledge earlier than normal to join these flocks. Fledglings never wander or fly away from the group alone except to return to their nests. Apparently, young storks and their parents are able to recognize each other individually. The young birds constantly scan the sky, and, when one sees a parent circling to land in or near the marsh, it and its sibs hurriedly walk toward the parent. When they reach it, they drop down on their tarsi and beg before they are fed. Such feedings occur 100–900 m from the next. Frequently, several adults stay in the marsh with the fledglings, and, occasionally, a hungry juvenile attempts to beg food from an unrelated adult. In such cases, it is ignored, rebuffed, or mildly attacked.

I was able to watch the activity of three 14–15-week-old siblings for 3.5 h, because they stayed in a dry field with low vegetation. The behavior of each bird was recorded every 5 min for 1.5 h and then every 2.5 min for 2 h (for a total of 177 point samples). Individual differences in their behaviors were small. Collectively, they spent 10% of the time foraging, 34% preening, 32% standing still, 10% resting with the head retracted, 9% walking (not foraging), and 5% flying. Their banded father flew to the field once and fed them. Their mother came 2.5 h later, perhaps in response to a Jabiru harassing them, and all flew away with her. Three-month-old Maguari Storks occasionally supplanted smaller waterbirds at marsh feeding sites (Thomas in press). The young storks remained in the study area, gradually moving to wetter sites as marshes dried, but by 3.5–4.5 months postfledging all young of the year were gone from their natal area.

Losses of eggs and nestlings.—The 55 nests that I observed over 9 yr had a hatching success of 71.8% and a fledging success of 61.5% (Table 1). I found no eggs broken in a nest, a common indicator of egg shell thinning from pesticide contamination, nor were any deformed chicks seen, although adult storks probably fed in an area of intensive rice cultivation that was less than 3 km from the study site and was subjected to a broad spectrum of chemical applications. Five unhatched eggs from five nests were infertile, 3 eggs fell out of very small nests, and

3 eggs in one nest were deserted and promptly eaten by a Crested Caracara (*Polyborus plancus*). During the 2 yr of highest stork-nest concentration, a minimum of 32 eggs disappeared gradually; they were probably taken by boa constrictors (*Constrictor constrictor*). Lower numbers of eggs were lost in the same pattern in other years at other sites.

Maguari Storks lost these eggs one at a time, the other eggs being left unharmed and the nest undamaged. Yet, in all but one case, the entire clutch gradually disappeared. The exception was a nest from which 3 of 4 eggs disappeared. At this time I found two boas (ca. 1.5 m long, a male and a female) resting in a tree where stork eggs had disappeared during the preceding 18 h. One of the snakes was injured and bled from a spot near its head. The following year, close to the same place, there were additional losses of stork eggs, and I began to monitor the clutches of other species of waterbirds nesting in close proximity to the storks. Entire clutches of other birds disappeared overnight: three 3-egg and two 1-egg clutches of the Bare-faced Ibis (*Phimosus infuscatus*) and one 3-egg clutch of a Striated Heron (*Butorides striatus*). The combined weights of the 3-egg ibis clutches were 104.5 g, 84.5 g, and 77.3 g, whereas the weight of the heron clutch was 51.3 g. Thus, a clutch of these birds' eggs weighed less than a single stork egg. I found a 1.3-m boa resting on an empty ibis nest that had held three eggs and was 0.5 m below and underneath a stork nest containing two fresh eggs. The next morning one stork egg was missing, and the boa was still on the ibis nest. The second stork egg was gone 4 h later, and the boa was resting as before on the ibis nest. Snake predation on eggs of colonial birds nesting over water has been reported by other workers (Dusi and Dusi 1968, Dickerman and Gavino T. 1969, Wiley and Wiley 1980).

Fewer Maguari Stork nestlings were lost than eggs. Two hatchlings of a very late nest disappeared, and the third hatchling may have been deserted. One 3-day-old chick fell out of its nest and apparently died while caught in branches within the reach of its parents' bills. One medium-sized nestling (ca. 1,500 g) disappeared from the top-most nest of a colony on an extremely moonlit night while its two sibs remained unharmed. It may have been taken by either a Collared Forest-Falcon (*Micrastur semitorquatus*) or a Great Horned Owl (*Bubo virginianus*), both of which frequent the study area. Ten nearly fledged and banded nestlings were taken as food by human poachers.

The greatest nestling losses were large young (2,200–3,000 g) that fell out of undersized nests that contained 3–4 chicks. In each case that I observed ($n = 6$), the lost bird was the largest or next-to-largest. Early in the study I returned such birds, which were banded, to their nests, but I found that the same overcrowded nest lost the same or a sibling bird again before it could fly. One such bird lived for several days in the water beneath its nest, but all of these birds eventually disappeared, probably from attack by spectacled caiman (*Caiman crocodilus*), which are abundant in water surrounding stork nests.

During the study, five nests (3%) were built on the tops of palm trees. Four of these nests (4–5 m high) were broken off by wind, with a minimum loss of 10 small nestlings. All nests in palms were small in diameter, made late in the season, and probably were made by inexperienced birds. The fifth palm nest was only 3 m high, and it was the first nest of a 3-yr old banded male; one large nestling fell out and died below it, but the other nestling survived. The much heavier Jabiru (Thomas in press) always made its massive nest on the tops of the same palm species in the study area and successfully raised as many as five young (Thomas 1981). The Jabiru, however, uses the top of a living palm, whereas the Maguari Storks used dead palms, which cannot support the weight of the nest and young during strong winds.

Discussion

Two morphological differences between Maguari Stork nestlings and other ciconiiformes are the inability to grasp with the hallux and the two black nestling plumages: these differences may be related. In sympatric colonial herons, egrets, and ibises that bred in the study area and in closely related species elsewhere, the young leave the nest at an early age and climb around in the nest tree long before fledging (McVaugh 1972, Snow 1974, Kushlan 1977a, Maxwell and Kale 1977, Werschkul 1979). Presumably, this early nest leaving is to elude predators or to survive the destruction of flimsy nests (Dickerman and Galvino 1969). In these

species the legs and feet develop relatively rapidly. Compared with Wood Storks (Kahl 1962) and White Ibis (*Eudocimus albus*) (Kushlan 1977a), however, Maguari Stork nestlings have slow-growing toes, they are slow to stand on their feet, and they are not able to cling to branches using their hallux. Therefore, Maguari Stork nestlings are nest bound and unable to escape predators.

Being nest bound may be related to the two black plumages of a bird that is white as an adult. In a review of the selective advantages of black versus white plumage, Mock (1980) has listed five possible reasons for the advantage of one color over the other. The first, that black feathers are stronger, may be irrelevant for nestlings. The second, for thermal regulation, remains controversial, evidence having been found in favor of both black and white in different species under different conditions (Heppener 1970, Lustick 1971, Ellis 1980, Walsberg 1982). Maguari Stork nestlings do not appear to need their dark color for thermal regulation. A few adults deliberately brought water back to the nest, which they drooled on to their young at midday. Nestlings are brooded or shaded continuously by their parents until they are more than 5 weeks old, after which they thermoregulate by gular flutter, panting, ptiloerection, and urohidrosis.

It seems more likely that the two black nestling plumages are for crypsis. Unquestionably, in the sharp chiaroscuro of tropical light, a dark bird is harder to see than a white one, both from above and in a horizontal plane (Kahl 1971b, Kushlan 1978, Mock 1980), but it is the timing of the black nestling plumages that most strongly suggests their role in crypsis. All other stork nestlings that have been described hatch with white down, and all young storks probably have the same plumage successions during the first 3 months, even though the plumages are not conspicuous when the series is all white. In contrast both the second down and the juvenal plumage of the Maguari Stork are black (ca. 10–75 days). Maguari chicks exhibit akinesia only during their first 2 weeks, when they are still mostly white, and the effect is that they look like white eggs. Nestlings of the White Stork continue this presumably predator-avoidance behavior up to the age of 7 weeks (Schüz 1942, 1943; Haverschmidt 1949). After 2 weeks of age, when the Maguari chicks are black, their behavior toward an intruder changes to aggressive physical and vocal defense. It must be pointed out, however, that Wood Storks become aggressive at this age too (Kahl pers. comm.).

The timing of the rapid acquisition of white first basic plumage coincides with the fledging of Maguari Storks. White is no doubt more advantageous for social signaling (Kushlan 1977b, Mock 1980) such as keeping fledglings together and aiding adults in finding fledglings in the marshes for feeding. In addition, probably an appearance similar to more wary and experienced adults could be of survival value to a young, inexperienced bird. A final reason for white plumage at this age has been demonstrated by Mock (1980), who showed that white plumage is less conspicious to prey fish against a bright sky. Thus, the color series, and timing of Maguari Stork plumage (black for crypsis and white for social signaling and hunting strategy) support three of Mock's five selective arguments.

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