

We thank Bill Searcy, Les Beletsky, Jaroslav Picman and two anonymous reviewers for their helpful comments on earlier drafts of this manuscript. This research was supported in part by grants from the National Science Foundation (BNS 84-05221) and the Cullister, Smith, and Haven Funds of Beloit College.

## LITERATURE CITED

- ALTMANN, S. A., S. S. WAGNER, AND S. LENINGTON. 1977. Two models for the evolution of polygyny. *Behav. Ecol. Sociobiol.* 2:397-410.
- BELETSKY, L. D. 1983. Aggressive and pair-bond maintenance songs of female Red-winged Blackbirds (*Agelaius phoeniceus*). *Z. Tierpsychol.* 62: 47-54.
- HURLEY, T. A., AND R. J. ROBERTSON. 1984. Aggressive and territorial behaviour in female Red-winged Blackbirds. *Can. J. Zool.* 62:148-153.
- LANGSTON, N. E., S. FREEMAN, S. ROHWER, AND D. GORI. 1990. The evolution of female body size in Red-winged Blackbirds: the effects of timing of breeding, social competition, and reproductive energetics. *Evolution* 44:1764-1779.
- LAPRADE, H. R., AND H. B. GRAVES. 1982. Polygyny and female-female aggression in Red-winged Blackbirds. *Am. Nat.* 120:135-138.
- LENINGTON, S. A. 1980. Female choice and polygyny in Redwinged Blackbirds. *Anim. Behav.* 28:347-361.
- NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. I. Mating and nesting activities. II. Territoriality. *Wilson Bull.* 68:5-37, 129-150.
- NERO, R. W., AND J. T. EMLEN. 1951. An experimental study of territorial behavior in Red-winged Blackbirds. *Condor* 53:105-116.
- ORIANI, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Tri-colored, and Yellow-headed Blackbirds. *Univ. Calif. Publ. Zool.* 84:1-85.
- PICMAN, J. 1980. Impact of Marsh Wrens on reproductive strategy of Red-winged Blackbirds. *Can. J. Zool.* 58:337-350.
- PICMAN, J., M. LEONARD, AND A. HORN. 1988. Antipredation role of clumped nesting by marsh-nesting Red-winged Blackbirds. *Behav. Ecol. Sociobiol.* 22:9-16.
- RITSCHER, S. E. 1985. Breeding ecology of the Red-winged Blackbird (*Agelaius phoeniceus*): tests of models of polygyny. Unpubl. Ph.D. thesis, Univ. of California, Irvine, CA.
- ROBERTS, L. B., AND W. A. SEARCY. 1988. Dominance relationships in harems of female Red-winged Blackbirds. *Auk* 105:89-96.
- SEARCY, W. A. 1986. Are female Red-winged Blackbirds territorial? *Anim. Behav.* 34:1381-1391.
- SEARCY, W. A. 1988. Do female Red-winged Blackbirds limit their own breeding densities? *Ecology* 69:85-95.
- SEARCY, W. A., AND K. YASUKAWA. 1989. Alternative models of territorial polygyny in birds. *Am. Nat.* 134:323-343.
- SINCLAIR, D. F. 1985. On tests of spatial randomness using nearest neighbor distances. *Ecology* 66:1084-1085.
- TEATHER, K. L., K. E. MUMA, AND P. J. WEATHERHEAD. 1988. Estimating female settlement from nesting data. *Auk* 105:196-200.
- YASUKAWA, K., AND W. A. SEARCY. 1981. Nesting synchrony and dispersion in Red-winged Blackbirds: is the harem competitive or cooperative? *Auk* 98:659-668.
- YASUKAWA, K., AND W. A. SEARCY. 1982. Aggression in female Red-winged Blackbirds: a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.* 11:13-17.

*The Condor* 94:777-781

© The Cooper Ornithological Society 1992

## NESTING FAILURE OF THE WOOD STORK IN A NEOTROPICAL WETLAND<sup>1</sup>

CRISTINA RAMO<sup>2</sup> AND BENJAMIN BUSTO

*Centro de Investigaciones de Quintana Roo (CIQRO), Apartado Postal 424, 77000 Chetumal, Quintana Roo, México*

*Key words:* Wood Stork; breeding phenology; nesting failure; México.

The Wood Stork (*Mycteria americana*) is one of the three New World Ciconiidae, that ranges from the

southern United States to Northern Argentina. During recent decades frequent nesting failures have been associated with a pronounced population decline in southern Florida and a northward shift in the location of colony sites in the United States population (Ogden and Nesbitt 1979, Ogden and Patty 1991, Kushlan and Frohring 1986, Ogden et al. 1987). Although some colonies failed due to high winds or cold weather (Kahl 1964, Clark 1978), the main cause of nesting failure appears to be related to changes in hydroperiod caused by management programs. Here we report a case of generalized nesting failure in an almost pristine tropical

<sup>1</sup> Received 31 December 1991. Accepted 8 April 1992.

<sup>2</sup> Present address: Estación Biológica de Doñana, C.S.I.C., Apartado 1056, 41080 Sevilla, Spain.

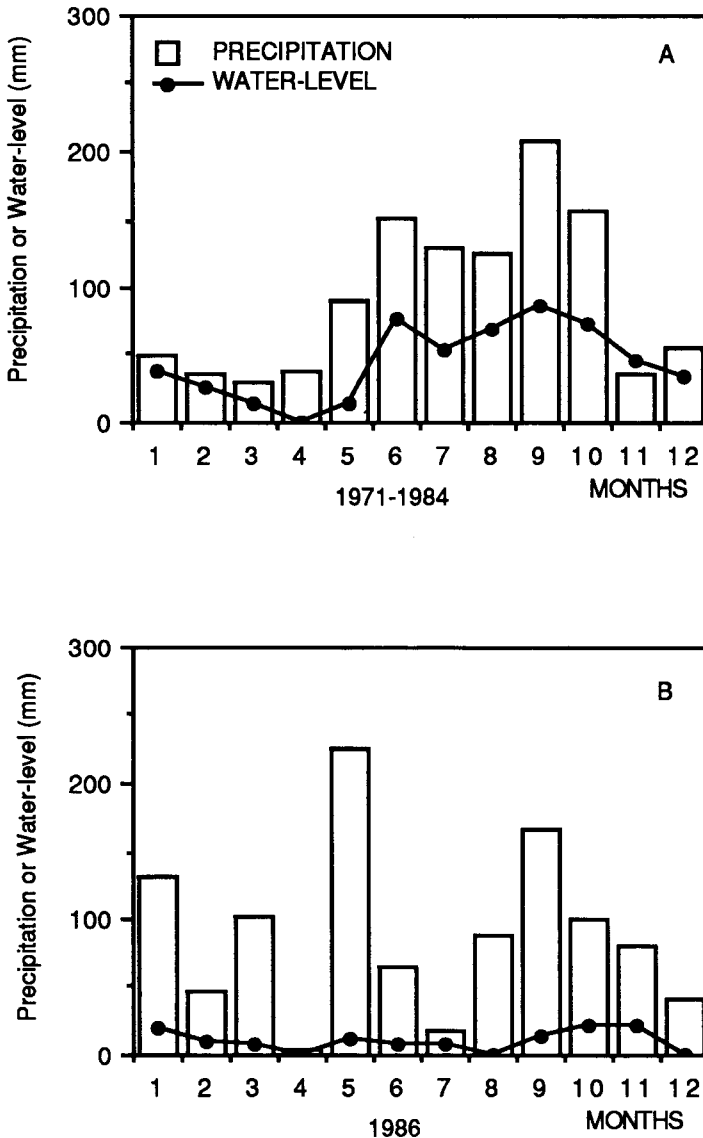


FIGURE 1. Pattern of monthly rainfall and water-level in Sian Ka'an reserve. A: precipitation during 1971-1980, water-level in 1984. B: data of 1986 (rainfall was recorded at Limones, Felipe Carrillo Puerto and Tulum, water depth at a permanent gauging site in the marsh 19°47'N and 87°29'W).

area very similar to the Everglades, but which is not affected by water management schemes.

#### STUDY AREA AND METHODS

The study was conducted during 1986 on Sian Ka'an Biosphere Reserve in Quintana Roo, in the Yucatan peninsula of Mexico (between 20°06' and 19°05'N, and 88°00' and 87°22'W). The reserve comprises 528,000 ha, including marine habitats such as a coral reef, two large bays, coastal lagoons and mangrove fringe (totaling 180,000 ha), forests (150,000 ha), marshes (100,500 ha), and mangrove swamps (61,600 ha) formed

by scrub (1.5-2 m tall) red mangroves, *Rizophora mangle*. Although coastal mangrove swamps are largely marine and salinity may be high, salinity in inland mangrove swamps is usually low. The Wood Stork colonies were located in the red mangroves on four keys, one in Espíritu Santo Bay and three in Ascension Bay totaling 548 pairs. Annual rainfall in the area (1967-1982) ranged from 872.1 mm to 1,436.2 mm, with an average of 1,128 mm (López Ornat 1983). Nearly 75% of annual rain falls during the wet season from May to October, June and September being the most rainy months and March and April the driest months (Fig.

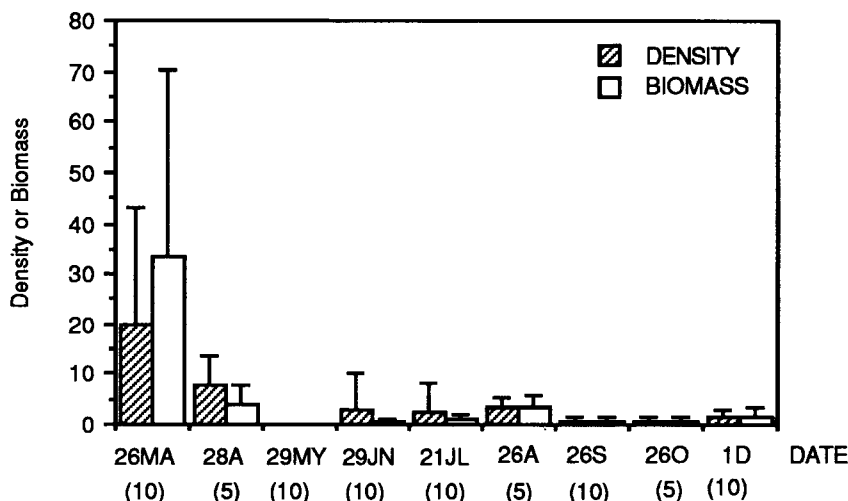


FIGURE 2. Density (fishes/throw trap) and biomass (grams/throw trap) of available prey at a permanent trap station in Sian Ka'an reserve. Lines denote standard deviations. Number of throws is shown in parenthesis.

1A). This variation in rainfall causes a seasonal fluctuation in water levels, which during 1984, a typical year (Olmstead, pers. comm.) showed a maximum from June to October, and a minimum in April (Fig. 1A). Mean monthly temperatures vary little during the year, ranging from 22.7°C in January to 27.5°C in May.

Rainfall during 1986 was recorded at three meteorological stations bordering the reserve: Limones, Felipe Carrillo Puerto and Tulum. We also recorded water depth at a permanent gauging site in the marsh (19°47'N, 87°29'W).

Main feeding sites of storks were located through two intensive aerial censuses on 11 April (from 08:45 to 13:30 hr) and 23 April (from 13:35 to 15:20). We flew at 160 km/hr and 300–400 ft altitude, covering almost the entire marsh and the mangrove surface of the reserve.

Densities of prey were determined from monthly samples at a permanent trap station in one of the main feeding sites for storks. The station was located in a shallow lagoon surrounded by small mangroves, the bottom was mud and the salinity was two parts per thousand on 29 June and 26 September. With a 1-m<sup>2</sup> throw trap (Kushlan 1981) we took a monthly sample of 5 to 10 throw traps, from March to November.

Every 15 days we visited the nesting colonies in Ascension Bay. A colony located in Espiritu Santo Bay was visited twice during the breeding season. During each visit we checked a variable number of nests (from 6–114) for eggs or chicks. We classified chicks into four age categories according to developmental stage (Kahl 1962): small (<2 weeks); medium (2–6 weeks); large (6–7 weeks); and fledging (7–8 weeks). We collected food regurgitated by six nestlings.

## RESULTS

During 1986 annual rainfall was 1,059.2 mm, which was within the normal range, but monthly distribution did not follow the typical pattern (Fig. 1B). The wet and dry seasons were not sharply separated and May

showed twice the average amount of rainfall. Because of the monthly distribution of rainfall, water levels in 1986 did not follow the normal pattern (Fig. 1B). From January to April water levels decreased to a minimum. In May, however heavy rains caused an increase in water levels, flooding large areas rather quickly. Because of low rainfall in June and July, there was a second dry period in August. Following August, water levels reached a second maximum.

Aerial censuses during breeding activities revealed that the main feeding habitat of storks was inland mangrove swamp. Of 159 feeding areas, 91% were in this habitat, 5% in coastal lagoons, 3.4% in grass marshes, and 0.6% in coastal mangrove swamp. Prey density at the permanent station in inland mangrove swamp was highest in March, 20.1 fish/throw trap (Fig. 2). In April the sampling locality was almost dry, and we found some dead fishes, though 30 Wood Storks were feeding 100 m away in deeper water. Following heavy rainfall in May the entire sampling area was deeply flooded, and fishes dispersed, thus sharply decreasing density. Indeed, no fish were caught during May sampling. Densities thereafter remained low, ranging between 0.6 and 3.4 fishes/throw trap, and biomass showed a similar pattern (Fig. 2). Captured species were: *Cichlasoma urophthalmus*, *C. meeki*, *C. salvini*, *C. robertsoni*, *Gambusia yucatanana*, *Astyanax fasciatus*, *Poecilia orri*, *Garmanella pulchra*, *Cyprinodon variegatus* and *Belonesox belizanus*, most of which were also found in stork regurgitations (Table 1).

Although colonies were occupied as early as the middle of February, we did not enter them until 16 March to avoid disturbance during the critical courtship and nest building periods. Nesting chronology followed a unimodal pattern (Fig. 3). Of the nests observed on 16 March, 3 and 19 April, 100%, 93.75% and 21.43%, respectively, contained eggs. On 19 May only one of the 114 observed nests (0.88%) contained eggs. The maximum percentage of nests containing small nestlings occurred on 19 April, medium size nestlings on

TABLE 1. Presence of prey remains in six Wood Stork regurgitations. Percent dominance in samples are shown in parenthesis.

Species	Prey consumed	
	n (%)	Mass (%)
<i>Synbranchus marmoratus</i>	1 (0.86)	84.13 (19.76)
<i>Astyanax fasciatus</i>	4 (3.45)	4.58 (1.07)
<i>Rhamdia guatemalensis</i>	1 (0.86)	7.36 (1.73)
<i>Belonesox belizanus</i>	1 (0.86)	14.70 (3.45)
<i>Heterandria bimaculata</i>	2 (1.72)	4.62 (1.08)
<i>Poecilia orri</i>	2 (1.72)	6.20 (1.46)
<i>Cichlasoma friedrichsthalii</i>	6 (5.17)	116.07 (27.26)
<i>C. urophthalmus</i>	4 (3.45)	10.50 (2.47)
<i>C. meeki</i>	4 (3.45)	25.12 (5.90)
<i>C. robertsoni</i>	2 (1.72)	36.22 (8.51)
<i>C. octofasciatum</i>	50 (43.10)	86.92 (20.42)
<i>Pogonias cromis</i>	39 (33.62)	29.30 (6.88)
Total prey	116	425.72

5 May and large nestlings on 19 May (Fig. 3). Clutch size averaged 2.16 (SD = 0.45; range = 1-3;  $n = 25$ ), size of broods at 6-7 weeks of age averaged 1.97 per nest that produced chicks (SD = 0.45; range 1-3;  $n = 104$ ).

First fledged young were seen on 19 May (14.4% of all chicks). In late May the area was flooded because of the heavy rains, and adult storks abandoned the colonies. On 6 June, six large nestlings were found dead in their nests and one in the water at two close colonies in the Ascension Bay (6.5% of all chicks). In addition, 29 fledglings were walking around the two colonies un-

able to fly. Some nestlings had wet feathers and were very weak. On 22 June there were not any surviving chicks and we found dead nestlings in 25 nests.

#### DISCUSSION

The Wood Stork feeds by groping, a tactile-location method (Kahl 1964). They depend on dense food supplies, especially during the breeding season, when the energetic demands are greatest (Kahl 1962). Undoubtedly for this reason the breeding period takes place in the dry season when water level declines and prey are concentrated; the young must fledge before the rains (Kahl 1964, Spaans 1975, Kushlan et al. 1975, Ayarzagüena et al. 1981). This pattern seems typical of the Wood Stork throughout its range, despite the fact that other ciconiiform birds often breed during the rainy or wet season.

The temporal pattern of stork activity at Sian Ka'an during 1986 is different from that which once occurred prior to 1960 in the Florida Everglades, where birds moved in to the region in October-November, at the beginning of the dry season, and colonies formed in November-January. Reproductive data for other years at Sian Ka'an (López Ornat, pers. comm.) are consistent with the pattern found in 1986.

In the Everglades, colonies that formed after January were rarely successful because they did not have enough time for chick development prior to the onset of the rainy season (Kushlan et al. 1975). At Sian Ka'an the normal end of the reproductive season and the beginning of the rains are rather coincident, so Wood Stork colonies there are also at risk of failure due to early rains.

In southern Florida, heavy rainfall was followed by stork abandonment of nesting colonies (Kahl 1964). In the Everglades, desertion was associated with increases of 3 cm or more in water level within the first two months of nesting (Kushlan et al. 1975), although storks could continue foraging and feeding young despite slowly rising levels in the late nesting period (Ogden et al. 1978). Frederick and Collopy (1989), suggested

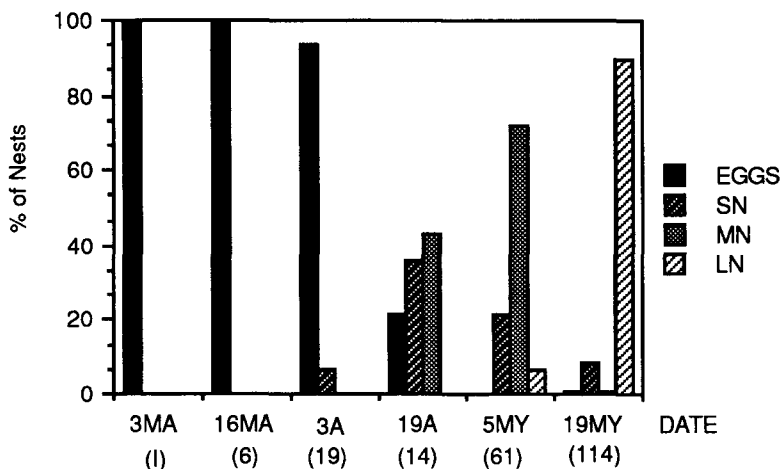


FIGURE 3. Breeding phenology of Wood Storks in Sian Ka'an. SN = small nestling. MN = medium nestling, and LN = large nestling. Number of nests checked shown in parentheses. I = adults incubating.

that colony abandonment by White Ibis (*Eudocimus albus*), a species that also uses tactile methods to forage, appeared to be closely related to decreases in prey densities, which probably were directly affected by water-level fluctuations. At Sian Ka'an the increase in water level was dramatic. Between 26 April and 28 May, we registered an increase of 12.5 cm. In our case, a dramatic decrease in the density of prey caused by a pronounced rise in water level due to heavy rainfall seemed to be a trigger for abandonment. Our results show that the Wood Stork is very sensitive to changes in water level during breeding, and that reproductive failure of storks may be produced by climatic factors in areas where hydrological patterns have not been modified by man.

During the field work, funds were provided by the Centro de Investigaciones de Quintana Roo and the Secretaría de Desarrollo Urbano y Ecología of Mexico. We thank Oscar and Victor Barrera for assistance in the field, W. F. Loftus and M. Navarro for the identification of fishes, and J. A. Amat, P. C. Frederick, J. A. Kushlan, J. C. Ogden and A. López Ornat for manuscript review.

#### LITERATURE CITED

- AYARZAGÜENA, J., J. PEREZ TORRES, AND C. RAMO. 1981. Los garceros del Llano. Cuadernos Lago-ven, Caracas.
- CLARK, E. S. 1978. Factors affecting the initiation and success of nesting in east-central Florida Wood Stork colony, p. 178-188. *In Proc. Colonial Waterbird Group.*
- FREDERICK, P. C., AND M. W. COLLOPY. 1989. Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. *Auk* 106:625-634.
- KAHL, P. 1962. Bioenergetics of growth in nestling Wood Storks. *Condor* 64:169-183.
- KAHL, P. 1964. Food ecology of the Wood Storks (*Mycteria americana*) in Florida. *Ecol. Monogr.* 34:96-117.
- KUSHLAN, J. A. 1981. Sampling characteristics of enclosure fish traps. *Trans. Am. Fish. Soc.* 110:557-562.
- KUSHLAN, J. A. AND P. FROHRING. 1986. The history of the southern Florida Wood Stork population. *Wilson Bull.* 98:368-386.
- KUSHLAN, J. A., J. C. OGDEN, AND A. L. HIGER. 1975. Relation of water level and fish availability to Wood Storks reproduction in the southern Everglades, Florida. U.S. Geol. Survey, Rept. 75-434, Tallahassee, FL.
- LÓPEZ ORNAT, A. 1983. Localización y medio físico, p. 21-49. *In Sian Ka'an. Estudios preliminares de una zona en Quintana Roo propuesta como Reserva de la Biosfera.* Centro de Investigaciones de Quintana Roo, México.
- OGDEN, J. C., KUSHLAN, J. A., AND J. T. TILMAN. 1978. The food habits and nesting success of Wood Storks in Everglades National Park 1974. U.S. Dept. Interior, National Park Service, Natural Resources Report No 16.
- OGDEN, J. C., D. A. MCCRIMMON, G. T. BANCROFT, AND B. W. PATTY. 1987. Breeding populations of the Wood Stork in the southeastern United States. *Condor* 89:752-759.
- OGDEN, J. C., AND S. A. NESBITT. 1979. Recent Wood Stork population trends in the United States. *Wilson Bull.* 91:512-523.
- OGDEN, J. C., AND B. W. PATTY. 1981. The recent status of the Wood Stork in Florida and Georgia, p. 97-103. *In Proc. of the Nongame and Endangered Wildlife Symposium.* Athens, GA. Georgia Department of Natural Resources, Game and Fish Division, Technical Bulletin WLS.
- SPAANS, A. L. 1975. The status of the Wood Stork, Jabiru, and Maguari Stork along the Surinam Coast, South America. *Ardea* 63:116-130.