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SEASONAL VARIATION IN THE FORAGING ECOLOGY OF THE WOOD STORK IN THE SOUTHERN LLANOS OF VENEZUELA[1]

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Abstract. The southern llanos of Venezuela are tropical wet savannas distinguished by a severe flood-drought alternation throughout the year. I analyzed the seasonal variation in use of habitat, foraging behavior and diet exhibited by the Wood Stork (*Mycteria americana*) in response to the changing conditions of this environment. With the beginning of the rainy season, streams and lagoons overflowed and inundated extensive marshes, which became the preferred foraging sites for storks. Amphibians and aquatic invertebrates proliferated in these flooded areas and accounted for half of the food consumed; the remaining half was composed of fish. The Wood Stork population was dispersed over the widely inundated area, and individuals foraged solitarily or in small groups. Groping and foot-stirring were the most common foraging behaviors. These patterns changed gradually with the cessation of rains. Shallow marshes dried up rapidly and became inadequate as feeding sites. Wood Storks then formed large foraging aggregations in the few ponds and lagoons that still kept water, where they foraged by groping together in close proximity. Fish accounted for more than 99% of the diet of Wood Storks during the dry season.

Resumen. Los llanos inundables de Venezuela son sabanas tropicales húmedas caracterizadas por una marcada alternancia inundación-sequía a lo largo del año. Se analizaron las variaciones estacionales exhibidas por el Gabán (*Mycteria americana*) en cuanto a selección de hábitat, comportamiento alimentario y dieta, como respuesta a las condiciones cambiantes del medio. Con la llegada de las primeras lluvias, los caños y lagunas se desbordaron inundando los esteros, que se convirtieron en los hábitats más frecuentados por los Gabanes. Los anfibios e invertebrados acuáticos proliferaban en estas áreas inundadas y constituyeron la mitad de la dieta consumida, estando el resto compuesto por peces. La población de Gabanes estaba dispersa y los individuos se alimentaban en solitario o en pequeños grupos. El tanteo y el pateo fueron las pautas de forrajeo más utilizadas. Todos estos patrones cambiaron gradualmente con el cese de las lluvias. Los bajíos y esteros se secaron rápidamente convirtiéndose en lugares inadecuados para la alimentación. Los Gabanes comenzaron entonces a formar grandes bandadas en los escasos préstamos y lagunas que todavía mantenían algo de agua, donde forrajeaban tanteando juntos en estrecha proximidad. Los peces representaron más del 99% de la dieta consumida por los Gabanes durante la época de sequía.

Key words: *Wood Stork,* Mycteria americana, *foraging ecology, diet, seasonal variation, llanos of Venezuela.*

INTRODUCTION

The Wood Stork (*Mycteria americana*) ranges from southern United States to northern Argentina, east of the Andes (Blake 1977, Kahl 1987). Many studies have been conducted in recent decades on various aspects of its biology in the southeastern U.S. (e.g., Kahl 1964, Kushlan et al. 1975, Ogden et al. 1976). However, almost nothing is known about Wood Stork biology in other parts of its wide distribution range. In the llanos of Venezuela, information about this species is very scarce (Morales 1990, Hancock et al. 1992), although some general data on its status and ecology are available (Morales et al. 1981, Ogden and Thomas 1985, Thomas 1985). No published studies consider variations in foraging ecology and diet throughout the annual cycle.

Human activities have recently introduced a series of alterations in the llanos region that may be affecting severely local wading bird populations, given their great sensitivity to human-induced change in their natural habitats (Custer and Osborn 1977, Morales 1990). These human-induced habitat alterations are the slow but continuous loss of forests which involves a loss of adequate nesting places, recent projects of agricultural expansion, the massive use of pesticides in some parts of the region, furtive hunting and, very especially, the construction of dikes for ar-

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tificial water management. Considering all these threats, it seems urgent to conduct field studies on basic aspects of biology and ecology of wading bird species as a first step towards the development of a global strategy for their management and conservation (Coulter and Rodgers 1987).

In this contribution I try to fill in the absence of information about the feeding ecology of the Wood Stork in the southern llanos of Venezuela. I provide basic data on its foraging behavior, diet and habitat use, with special reference to ecological adaptations to seasonal changes imposed by the severe cycle of drought-flood characteristic of this part of the llanos.

METHODS

STUDY AREA

Field work was conducted on Hato El Frío, a 78,000-ha private cattle ranch located in the southern llanos (flooding llanos) of Venezuela, in the state of Apure, between the villages of El Samán and Mantecal (7°35′–7°55′N, 68°50′–69°00′W). The study area is a tropical wet savanna with a highly seasonal distribution of rainfall. Mean annual rainfall is 1.65 m (n = 20 years), with more than 80% falling between May and October when much of the land is flooded up to 1 m deep (rainy season); rainfall is very scarce between November and April, when much of the land is dry and water is restricted to some streams, lagoons and deepest marshes (dry season).

Following Ramia's (1967) classification of llanos landscape types, the study area belongs to the group called "savannas of *banco, bajío* and *estero.*" At first look, these savannas are totally level, but in fact there is a slight unevenness of up to 2 m, so that during the rainy season some places flood while others stay dry. The local names of banco, bajío and estero apply to the three most common habitats of the region, which differ in depth of water during inundations, as well as in their vegetation and soils. The bancos are sandy raised grounds, never inundated; the bajíos are shallow marshes that become temporarily flooded during the rainy season as a consequence of heavy rainfall over a clay substrate; the esteros are deep marshes, inundated by the overflowing of streams and lagoons, that keep water during the whole rainy season and the first months of the dry season. Caños (local name for streams), permanent lagoons and artificial roadside ponds for gravel extraction (locally called préstamos), complete the landscape of the study area. A detailed and illustrated description of all these habitat types is in Ayarzagüena et al. (1981). More than 80% of the land is occupied by herbaceous savanna vegetation, while the rest is covered by gallery forests and small isolated forested islands, locally called matas. A detailed description of vegetation communities present at Hato El Frío is in Castroviejo and López (1985).

FORAGING BEHAVIOR

I made observations of foraging behavior of Wood Storks using 10× binoculars or a 20× telescope from December 1988 to December 1990. The year was divided into two periods: a dry season (November to April) and a rainy season (May to October). The accumulated total time of observation was 210 hr, 138 in the dry season and 72 in the rainy season. Data were collected from 08:00 to 12:00 and from 15:00 to 19:00. Observations were recorded in written notes or by using a tape cassette recorder. During each observation, a focal bird or group of birds was watched continuously until they left the area or stopped their feeding activities. For each focal sample, I recorded feeding behavior (using the terminology of Kushlan 1978), group size, foraging habitat, water depth, and plant cover.

Kushlan (1978) distinguished and standardized 38 different feeding behaviors in wading birds, 14 of which were used by Wood Storks in my study area. In order to simplify and establish seasonal comparisons, these behaviors were grouped in four major types of foraging techniques:

(1) Active groping: a technique which involves groping while walking slowly, with the bill submerged as the bird moves forward; the movement was sometimes accompanied by a slow head-swinging. In places with dense vegetation or irregular topography, birds used a variation of this behavior consisting of withdrawing and reinserting the bill with each step.

(2) Foot-stirring: the bird, with the bill submerged in water, walked very slowly (13.2 steps/min; range = 4–20), pumping its foot up and down several times with each step before placing it down; this behavior was sometimes accompanied by probing and wing-flicking movements.

(3) Passive tactolocation: the opened bill was

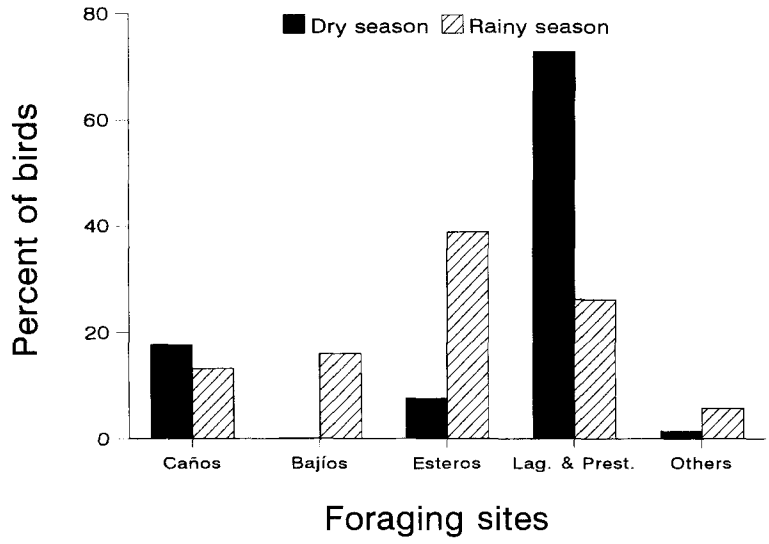

FIGURE 1. Seasonal changes in habitat selection: percentage of Wood Storks foraging in each habitat type.

introduced deeply into the water while the bird remained completely static in that position; this passive behavior was sometimes accompanied by a slight bill-vibrating or a shallow probing.

(4) Visual foraging: all those techniques in which the bird used mainly sight to locate food, including behaviors such as standing, gleaning, running, or hopping.

DIET

I collected regurgitated samples at a colony containing 442 Wood Stork nests and 13 Roseate Spoonbill (*Ajaia ajaja*) nests. Visits to nests were made weekly from late January to the middle of March 1989, always during the morning, and avoiding stormy or rainy days and times of extremely bright sunshine to prevent damage to nestlings (Dusi and Dusi 1978, King 1978). Entering Wood Stork colonies during early nestling stages facilitates predation by Crested Caracaras (*Polyborus plancus*) and may have severe negative effects on reproductive success or even cause the whole abandonment of the colony by nesting storks (González 1993). To avoid this, I began to visit the colony in late January, when most of the nestlings were more than one month old.

Nestling Wood Storks readily regurgitate when handled, and the regurgitation samples represent the food ingested by adults at their feeding sites, so they can be used as an estimate of the diet of the species during the breeding season (Kahl 1964, Jenni 1969, Ogden et al. 1978), which in the llanos corresponds to the dry season (Thomas 1985). Food items were measured to the nearest millimeter, weighed (wet mass) to the nearest gram, and then preserved in 10% formalin solution. Prey were later identified in as much detail as possible. The stomach contents of five adult birds collected while feeding in marshes (esteros) during the rainy season also were analyzed. Comparisons between seasons were made using the chi-square test or the *G*-test (Sokal and Rohlf 1979). Means ± SD are presented in the text.

RESULTS

USE OF HABITAT

I found significant differences in seasonal use of available foraging habitats by Wood Storks ($\chi^2_4 = 16.4$, $P < 0.01$). During the dry season, lagoons and artificial ponds (préstamos) were the most used habitats followed by streams (caños), whereas marshes (esteros and bajíos) were scarcely used as foraging sites. During the rainy season, deep marshes (esteros) became the preferred habitat followed by lagoons and ponds (Fig. 1).

I also found seasonal differences in water depth ($\chi^2_3 = 31.0$, $P < 0.001$) and vegetation height ($\chi^2_3 = 43.4$, $P < 0.001$) selected by Wood Storks at their foraging sites. During the dry season, birds foraged at an average depth of 16.8

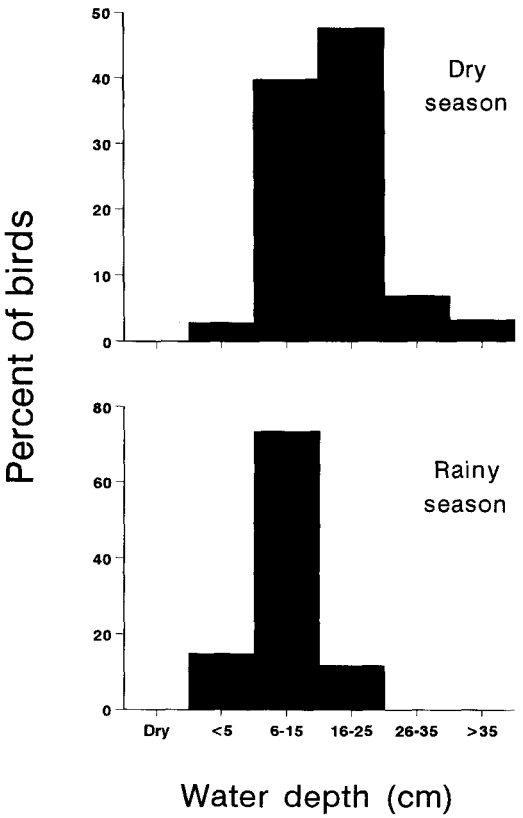

FIGURE 2. Water depth selected by Wood Storks in their foraging sites.

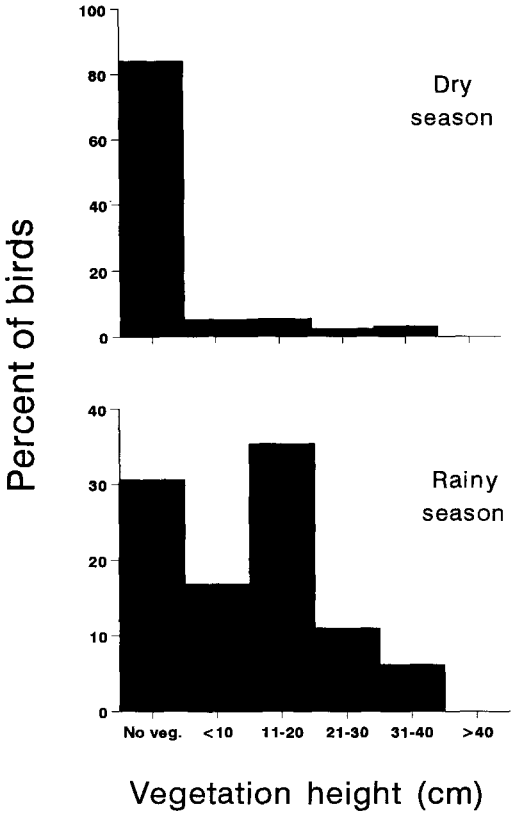

FIGURE 3. Presence/absence of plant cover and height of emergent vegetation in Wood Stork foraging sites.

± 7.6 cm, with 47.5% of the birds foraging in waters 15–25 cm deep. The average foraging depth during the rainy season descended to 10.0 ± 4.4 cm, with 73.4% of the birds foraging in waters 5–15 cm deep (Fig. 2). Wood Storks showed a clear preference for open waters without vegetation during the dry season, whereas they chose areas with abundant emergent vegetation during the rainy season; preferred vegetation heights ranged between 10 and 20 cm above the water surface (Fig. 3). Wood Storks never used completely dry areas or terrestrial habitats as foraging sites.

FORAGING BEHAVIOR AND SOCIAL FORAGING

There were strong seasonal differences in the foraging behavior of Wood Storks ($\chi^2_3 = 21.6$, $P < 0.001$). Active groping techniques were widely preferred by 86.5% of the Wood Storks observed during the dry season, whereas these techniques were used only by 39.7% of Wood Storks during the rainy season. In contrast, Foot-stirring techniques were very common in rainy months and scarcely used in dry months. There also were slight differences in Passive tactolocation and Visual foraging techniques, both of which were more common during the rainy season (Table 1).

TABLE 1. The number and percentage of Wood Storks using each type of foraging technique (see text) during the dry and rainy season.

Foraging behavior	Dry season		Rainy season	
	n	%	*n*	%
Active groping	507	86.5	138	39.7
Foot-stirring	21	3.5	115	33.1
Passive tactolocation	31	5.2	48	13.8
Visual foraging	27	4.6	46	13.2
Total	586		347	

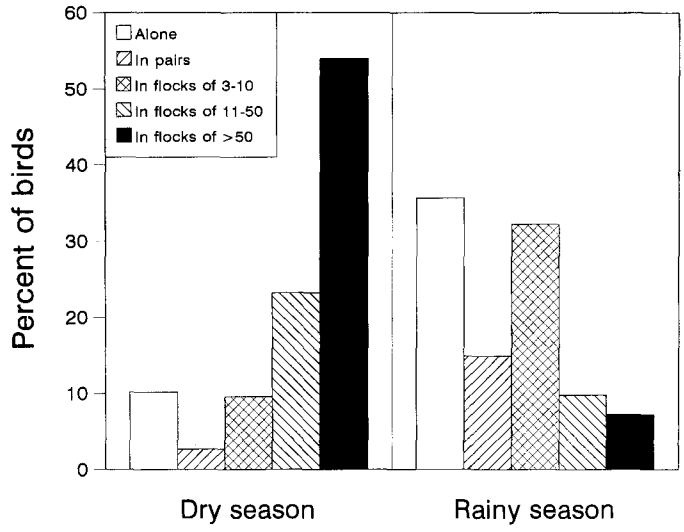

FIGURE 4. Seasonal variation in the foraging sociality of the Wood Stork.

Overall, techniques involving tactile location of food (Foot-stirring, Active groping and Passive tactolocation) were used by 92.2% of the Wood Storks observed throughout the year, whereas Visual foraging techniques were used by the remaining 7.8%. Therefore, Wood Storks in the southern llanos behaved mainly as tactile foragers, which is consistent with observations from other geographic areas (Kahl 1964, Kushlan et al. 1985, Thomas 1985).

Wood Storks in the study area were largely gregarious. Birds formed big foraging flocks of up to 500 individuals to locate food, generally accompanied by other wading bird species (González 1996). The largest group I observed in the llanos contained 670 Wood Storks foraging in close proximity. However, this social character varied significantly between the two seasons of the year ($\chi^2_3 = 22.4$, $P < 0.001$). A clear predominance of foraging flocks with more than 50 storks and flocks with 11–50 storks was observed in the dry season, whereas during the rainy season Wood Storks preferred to forage solitarily or in small groups of less than 10 (Fig. 4).

DIET

I obtained a total of 753 prey items from regurgitation samples collected in 115 Wood Stork nests between January and March 1989. Fish accounted for 99.5% of prey items, with the remaining 0.5% composed of aquatic insects. Overall, 34 species of fish were consumed by Wood Storks in the study area (Appendix I). Three fishes, *Hoplosternum littorale, Hoplerythrinus unitaeniatus* and *Gymnotus carapo,* accounted for more than 50% of the prey; the first two species and *Hoplias malabaricus* represented 59.1% of the biomass consumed by Wood Storks.

Analysis of the stomach contents of five storks collected out of the nesting period revealed the presence of different types of prey (Appendix I), although fish were still the most frequent prey representing 50% of the food items. Other prey consumed during rainy months were crabs (*Dilocarcinus dentatus*), which accounted for 34.8% of prey items, and frogs/tadpoles (*Pseudis paradoxus*), which represented 6.5% of the diet. During the months of June and July, I also observed that Wood Storks ate large quantities of caterpillars that were very abundant on emergent vegetation of flooded marshes.

There was a significant seasonal variation in the diet of Wood Storks in the study area ($G = 61.2$, $P < 0.001$), which in part reflects the seasonal changes in ecology and life cycles of their prey. Using the Shannon-Weaver formulation as an estimator of trophic niche amplitude after grouping prey categories represented in the diet (Colwell and Futuyma 1971), values of 0.03 for the dry season and 0.51 for the rainy season were obtained, reflecting a great dominance of

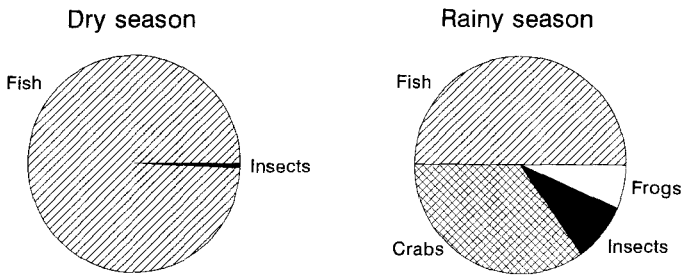

FIGURE 5. Seasonal changes in the food habits of the Wood Stork.

fish during the dry period and a more diversified composition of the diet in the rainy season (Fig. 5).

DISCUSSION

The ecology of tropical wet savannas is dominated by an extreme seasonal variation in rainfall. These systems are characterized by the presence of animal populations that are adapted to the dual stresses of flood and drought (Kushlan et al. 1985). Foraging ecology of Wood Storks in the southern llanos of Venezuela showed changes throughout the year in adaptation to the severe seasonal fluctuation characteristic of the region. Patterns of habitat selection, feeding behavior, social foraging, and diet varied significantly between the two seasons in which the annual cycle is divided (Table 2). The ultimate cause of this variation is related to seasonal cycles in water depth and prey availability.

USE OF HABITAT

The use of available foraging habitats by Wood Storks differed between dry and rainy seasons. Each type of habitat exhibits a different productivity that varies seasonally, which implies important seasonal changes in the biomass of food available for birds. This seasonal variation in productivity, combined with the environmental heterogenity of this region, determine a sequence in the use of available habitats by wading birds throughout the year (Aguilera 1988).

Wood Storks, due to their particular foraging behavior based on tactile location of food, require shallow waters with high prey densities to feed successfully (Kahl 1964, Kushlan 1979). This fact determines the habitat preferences and the feeding ecology of Wood Storks in the llanos.

Lagoons and ponds (préstamos) are the preferred foraging sites during the dry season because water depth descends to 5–20 cm (February-April) and high concentrations of fish occur in them (Kushlan et al. 1985). During the rainy season, lagoons are scarcely used because the water level is too deep for wading and food is too dispersed to be located using Wood Stork tactile foraging techniques.

Marshes (esteros and bajíos) are chosen during the rainy season, when they become inundated up to 20–100 cm deep by rains and overflowing of streams (which supply these habitats with plenty of fish) and, consequently, become suitable for tactile foraging. Most fish, amphibians and aquatic invertebrates begin their reproductive activity during the rainy season in the marshes of the llanos, which guarantees a relatively high abundance of potential prey for Wood Storks in these habitats. With the cessation of rains, seasonal marshes dry rapidly and become inadequate for Wood Stork foraging techniques.

FORAGING BEHAVIOR AND SOCIAL FORAGING

The role of habitat in determining feeding behavior of wading birds is often overlooked, and there are few behavioral studies that have considered this aspect (Willard 1977, Rodgers 1983). Kushlan (1976a) suggests that differences in foraging habitat and availability of prey may determine the feeding behavior and feeding efficiency of birds. My data confirm this suggestion; differences in habitat and microhabitat (water depth and vegetation cover), combined with differences in availability and dispersion of prey, lead to significant variations in foraging techniques used by Wood Storks in the southern llanos.

Although foraging techniques based on tactile location of food prevail throughout the year, I observed significant seasonal differences in the

TABLE 2. Summary table of the seasonal changes observed in feeding ecology of Wood Storks in the study area.

	Dry season	Rainy season
Foraging behavior	Active groping	Foot-stirring and groping
Habitat selection	Lagoons and ponds	Marshes and small lagoons
Mean water depth	16.8 ± 7.6 cm	10.0 ± 4.4 cm
Vegetation cover	Absent	Present
Flock size	Big flocks (>50)	Solitary or small flocks (<10)
Types of prey	Fish	Fish, crabs, frogs, insects

frequency of each technique. Active groping was amply preferred during the dry season but less used during the rainy season, whereas Foot-stirring was commonly used in the rainy season but almost never in the dry season. This variation can be explained by differences in foraging habitat and microhabitat. Groping is a very efficient behavior in shallow waters with high densities of medium-large size prey (drying lagoons and ponds). Foot-stirring, in contrast, is more efficient for capturing small, hidden and slowly mobile prey such as crabs, frogs and aquatic insects in places with dense plant cover (marshes in the rainy season).

All wading birds defend an individual distance around them, which may enlarge or contract according to circumstances (Kushlan 1978). Formation of large foraging aggregations is an interesting adaptation that enhances efficiency in exploiting food resources where they are clumped, ephemeral, and unpredictably distributed (Ward and Zahavi 1973, Krebs 1974, Kushlan 1976b). Foraging in flocks decreases search time between food patches, increases the likelihood of foraging in a suitable location, and decreases the risk of obtaining no food (Kushlan 1981, Erwin 1983). In the case of the Wood Stork in the southern llanos, large aggregations form only when available foraging habitat is reduced by drought and prey are highly concentrated. This occurs during the late dry season, when large flocks of Wood Storks exploit ephemeral suitable habitats intensively during several consecutive days until fish densities become too low to compensate for capture effort. The birds then move to another suitable site where they form a new foraging flock. These movements allow Wood Storks to forage always in places where water depth is temporarily adequate and prey are locally abundant (Kushlan 1981).

During the rainy season, most of the southern llanos are flooded and food is widespread and distributed more uniformly. At this time, Wood Storks tend to feed solitarily or in small groups and, in many cases, defend their foraging territory by facing other storks and even other wading birds that try to use it. When suitable wetlands are abundant and when prey densities are low at almost all foraging sites, there may be little advantage to storks foraging in large flocks (Coulter and Bryan 1993).

DIET

Little was known previously about food consumed by Wood Storks in the southern llanos of Venezuela. Data from other geographic areas compiled from the literature coincide with results obtained in this study for the dry season. Kahl (1964) analyzed seven stomach contents from southern Florida and found only fish. Ogden et al. (1978) also reported that more than 99% of the prey captured by Wood Storks in Everglades National Park were fish. In a Wood Stork colony of east-central Georgia, Depkin et al. (1992) found that fish accounted for 92% of the prey items and 93% of the biomass regurgitated by Wood Stork nestlings.

Seasonal changes observed in foraging habitat and feeding behavior have an effect on food habits of Wood Storks in the southern llanos. The diet of this species has to adapt to seasonal changes in ecology and life cycles of prey. During the dry season, diet of storks is based almost exclusively on fish, whereas during the rainy season it becomes more diverse and includes crabs, frogs, tadpoles and aquatic insects, that represent half of the prey consumed by storks.

The most common prey during the dry season are those fish species resistant to severe droughts. The three species that account for 59% of the diet of Wood Storks have physiological adaptations to subsist in deoxygenated waters and are very abundant in shallow ponds and lagoons where storks feed during the dry season (Machado-Allison 1987). The rainy season, on the other hand, is the reproductive period for amphibians, aquatic invertebrates and most of the fish, which proliferate in recently inundated

marshes. This guarantees the existence of an abundant food supply in those habitats selected by Wood Storks, and explains the qualitative seasonal differences observed in the diet of this species.

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APPENDIX I. Prey found in regurgitated samples of Wood Storks collected in the dry season (n = 753 prey items) and in stomachs of five Wood Storks collected during the rainy season (n = 46 prey items) at Hato El Frío.

Prey	Dry season				Rainy season			
	n	%	B[a]	%	*n*	%	B	%
Fish								
Hoplosternum littorale	211	28.0	2,657	19.5	4	8.7	50	13.3
Hoplerythrinus unitaeniatus	87	11.5	3,065	22.5				
Gymnotus carapo	80	10.6	1,520	11.1				
Cichlasoma orinocense	56	7.4	523	3.8	4	8.7	37	9.8
Hoplias malabaricus	45	5.9	2,336	17.1	1	2.2	52	13.8
Caquetaia krausii	36	4.8	298	2.1	2	4.3	8	2.1
Hoplosternum thoracatum	31	4.1	119	0.8				
Eigenmannia virescens	31	4.1	76	0.6				
Aequidens sp.	24	3.2	114	0.8	1	2.2	4	1.1
Pterigoplichthys multiraddiatus	24	3.2	445	3.2				
Pimelodella gracilis	19	2.5	75	0.5				
Curimata sp.	16	2.1	178	1.3	1	2.2	11	2.9
Prochilodus mariae	15	2.0	518	3.8				
Parauchenipterus galeatus	9	1.2	87	0.6				
Astyanax sp.	8	1.0	11	0.0				
Schizodon isognathus	7	0.9	411	3.0				
Synbranchus marmoratus	7	0.9	81	0.6	1	2.2	6	1.6
Pygocentrus caribe	7	0.9	428	3.1				
Rhamdia sebae	4	0.5	87	0.6				
Astronotus ocellatus	3	0.4	111	0.8				
Charax gibbosus	3	0.4	42	0.3				
Agamyxis albomaculatus	3	0.4	9	0.0				
Markiana geayi	3	0.4	102	0.7				
Roeboides sp.	3	0.4	5	0.0				
Adontosternarchus devenanzi	3	0.4	2	0.0				
Rhamphichtys marmoratus	2	0.2	2	0.0				
Poptella sp.	2	0.2	2	0.0				
Loricarychtys maculatus	2	0.2	16	0.1				
Serrasalmus sp.	2	0.2	21	0.1				
Leporinus friderici	2	0.2	79	0.6				
Pimelodus blochii	1	0.1	8	0.0	4	8.7	32	8.5
Metynnis luna	1	0.1	13	0.0				
Serrasalmus elongatus	1	0.1	3	0.0				
Triportheus sp.	1	0.1	12	0.0				
Hoplosternum sp.					2	4.3	8	2.1
unidentified					3	6.5	12	3.2
Crabs								
Dilocarcinus dentatus					16	34.8	102	27.2
Frogs								
Pseudis paradoxus					3	6.5	45	12.0
Insects								
Belostomatidae	4	0.5	2	—	2	4.3	1	—
Coleoptera					1	2.2	—	—
unidentified					1	2.2	—	—

[a] Total biomass (g) of each type of prey.