Kleptoparasitism in Mixed-Species Foraging Flocks of Wading Birds During the Late Dry Season in the Llanos of Venezuela

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Abstract.—Mixed-species foraging flocks of wading birds were studied between February and April 1990 in the southern llanos of Venezuela to document the occurrence and significance of kleptoparasitism. Intra- and interspecific food robbery was a very common behavior during the late dry season, when most of the land was dry and wading birds concentrated in dense aggregations around ponds and lagoons that still had enough water to sustain fish populations. A total of 15 species of wading birds formed these foraging aggregations including three Ciconiidae, six Ardeidae and six Threskiornithidae. Seven of these species were occasionally involved in prey-robbing attempts, with a 51.5% overall success rate. The Jabiru Stork (*Jabiru mycteria*), the Wood Stork (*Mycteria americana*) and the Cocoi Heron (*Ardea cocoi*) were more frequently associated with kleptoparasitic behaviors. *Received 22 February 1996, accepted 14 July 1996.*

Resumen.—Se estudiaron las bandadas mixtas de aves ciconiiformes entre febrero y abril de 1990 en los llanos inundables de Venezuela para documentar la existencia e importancia del cleptoparasitismo. El robo de presas intra- e interespecífico resultó ser un comportamiento muy común durante la época de sequía, cuando la mayor parte del territorio se encontraba seco y las aves ciconiiformes se concentraban alrededor de las escasas charcas y lagunas que todavía tenían suficiente agua para mantener poblaciones de peces. Un total de 15 especies de aves ciconiiformes formaban parte de estas agregaciones, incluyendo tres Ciconiidae, seis Ardeidae y seis Threskiornithidae. Siete de estas especies estuvieron, en alguna ocasión, implicadas en tentativas de robo de presas, con un 51.5% de efectividad global. El Garzón Soldado (*Jabiru mycteria*), el Gabán (*Mycteria americana*) y la Garza Morena (*Ardea cocoi*) fueron las especies más frecuentemente asociadas con los comportamientos de cleptoparasitismo.

Key words.—Ciconiiformes, foraging flocks, kleptoparasitism, llanos of Venezuela, prey- robbing, wading birds.

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Social foraging is posited as an adaptation enhancing the efficiency of wading birds in the exploitation of ephemeral or unpredictable food supplies (Krebs 1974, Kushlan 1981, Erwin 1983, Kushlan *et al.* 1985). In the llanos of Venezuela, foraging aggregations take place especially during the late dry season (February to April), when most of the land is dry and only a few ponds hold sufficient water to sustain fish populations. I observed concentrations of up to 15 different species of wading birds foraging together in these small and ephemeral ponds (González 1993).

Although trophic niche partitioning has been well documented in the llanos for ibises (Aguilera 1988, Frederick and Bildstein 1992), herons (Morales 1982, Kushlan *et al.* 1985) and storks (Thomas 1985, González 1993), such dense aggregations of birds provide a good opportunity for the development of negative interactions such as prey robbery, that has sometimes been reported in wading birds (Kahl 1966a, Recher and Recher 1972, Kushlan 1978, Caldwell 1980, Mock and Mock 1980, Kushlan *et al.* 1985, Frederick and Bildstein 1992). In this paper, I document the occurrence and significance of intra- and interspecific food robbery in flocks of wading birds during the late dry season in the llanos of Venezuela.

STUDY AREA AND METHODS

I conducted the field work on Hato El Frío, a 78,000-ha cattle ranch located in the state of Apure, between the villages of El Samán and Mantecal (7°35'-7°55' N, 68°50'-69°00' W). The area is distinguished by a marked seasonal alternation between flood and drought. Mean annual rainfall is 1,653 mm (N=20 years), most (>80%) falling between May and October, when most of the land becomes flooded (rainy season). Between November and April, most of the flooded area becomes dry and water is restricted to a few streams, lagoons, ponds and deep marshes (dry season). The climate is tropical and mean monthly temperature is reasonably uniform throughout the year, with a maximum in March (28.6°C) and a minimum in July (25.4°C). Most of the area is covered by herbaceous savanna vegetation, with less than

20% occupied by forests (*matas* and gallery forests). Landscape and vegetation communities of the ranch are described exhaustively in Ayarzagüena *et al.* (1981), and Castroviejo and López (1985).

During the late dry season of 1990 (February to April), field surveys were conducted to determine density and composition of foraging flocks. A total of 123.8 km were surveyed monthly encompassing a wide variety of habitats. When a mixed-species foraging aggregation of wading birds was found, I recorded the number of species involved and the total number of individuals of each species present. A bird was considered belonging to a flock when foraging less than 10 m from its nearest neighbor. Some flocks containing more than five species were observed for periods of 2-6 hours using a 20× telescope or 12× binoculars. Intra- and interspecific aggressive behaviors and prey-robbing interactions were recorded on a tape recorder or transcribed directly to notes. To determine the effectiveness of food piracy, a large mixed-species flock was observed for two days (0710-1850), recording all the unsuccessful robbing attempts and all the effective ones. As the main focus of study was the three storks that coexist in the llanos (*Mycteria americana*, *Ciconia maguari* and *Jabiru mycteria*), only flocks containing at least one of these species were considered (González 1993).

RESULTS

All the mixed-species foraging flocks observed (N=39) contained Wood Storks (*Mycteria americana*), while Jabiru Storks (*Jabiru mycteria*) were associated with 74.3% of the flocks. Cocoi Herons (*Ardea cocoi*), Roseate Spoonbills (*Ajaia ajaja*) and Great Egrets (*Casmerodius albus*) were also present in more than 60% of the foraging aggregations. Another 10 wading bird species were present in less than 50% of the mixed-species foraging flocks (Table 1).

I recorded prey-robbing attempts between seven species of wading birds. During two days of observation focused on a single mixed-species foraging flock (composed of species in Fig. 1), I recorded a total of 99 kleptoparasitic attempts, 51.5% of which resulted in successful prey robbery. The Jabiru Stork was the most common robber, probably due to its size, as it is much larger than any other bird in the llanos. Jabirus stole food mainly from Cocoi Herons, Wood Storks and Maguari Storks (*Ciconia maguari*), with 78.5% effectiveness (range: 75-100%). Intraspecific piracy was also very common between Jabirus, with 65.2% of the robbing attempts being successful (Table 2).

In dense flocks that formed during the late dry season around the few places that retained water, each capture of medium-large size prey (10-40 cm, generally a fish), was always followed by several interactions including fights for its possession. This was due to the prey handling before swallowing (González 1993). When a heron or a stork captured small prey (<10 cm), it was swallowed immediately, but if the prey was big enough to require some handling, the bird retired quickly to the shore to avoid the pursuit of its proximate neighbors. During this handling time, Jabirus would run towards their victim and force them to drop the prey. If victims took flight, Jabirus pursued them in the air until the prey was dropped. In-

Table 1. Wading bird species that foraged in mixed-species flocks during the late dry season in the southern llanos of Venezuela, and the number and percentage of aggregations in which each species was present (N=39 flocks).

Scientific name	Common name	N	Freq. (%)
Mycteria americana	Wood Stork	39	100.0
Jabiru mycteria	Jabiru Stork	29	74.3
Ardea cocoi	Cocoi Heron	26	66.6
Ajaia ajaja	Roseate Spoonbill	25	64.1
Casmerodius albus	Great Egret	25	64.1
Eudocimus ruber	Scarlet Ibis	20	51.2
Egretta thula	Snowy Egret	19	48.7
Ciconia maguari	Maguari Stork	17	43.5
Bubulcus ibis	Cattle Egret	8	20.5
Phimosus infuscatus	Whispering Ibis	5	12.8
Plegadis falcinellus	Glossy Ibis	2	5.1
Egretta caerulea	Little Blue Heron	1	2.5
Theristicus caudatus	Buff-necked Ibis	1	2.5
Syrigma sibilatrix	Whistling Heron	1	2.5
Cercibis oxycerca	Sharp-tailed Ibis	1	2.5

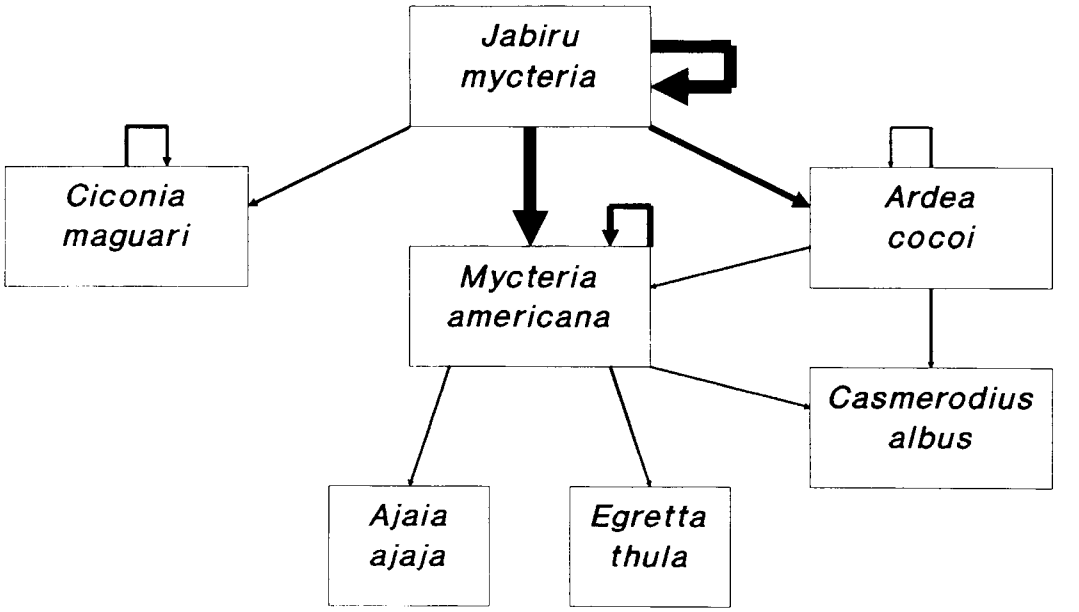

Figure 1. Successful prey-robbing interactions observed during the late dry season in the southern llanos of Venezuela. Arrows indicate the direction from robber to victim. The thickness of the arrows are proportional to the frequency of the interactions.

traspecific fights between Jabirus for possession of prey also occurred. The falling of robbed prey from the air was sometimes used by opportunistic birds such as the Crested Caracara (*Polyborus plancus*) to appropriate the food before the wading birds involved in fights descended to the ground.

As an example of the complexity of these interactions, I recorded an intraspecific robbery in which eight Jabirus fought for a freshwater eel (*Synbranchus marmoratus*) about 55 cm long. The bird that initially captured the eel was persistently pursued by the other seven Jabirus, and finally forced to take flight. The pursuit continued in flight, until the eel was dropped to the ground close to a pond where other wading birds were foraging. There, one Jabiru descended quickly, took the eel, and the same competitive sequence recurred. Prey ownership was transferred six times before one of the Jabirus succeeded in evading the others, quickly swallowing the eel.

Intra- and interspecific kleptoparasitism was also common for Wood Storks. Interspecific victims were mainly other smaller wading birds foraging in close proximity, such as Roseate Spoonbills, Great Egrets or Snowy Egrets (*Egretta thula*) (50-100% efficiency). Food piracy by conspecifics was very common in dense Wood Stork foraging flocks, due to the close proximity of the birds when groping together in small ponds (Kahl 1964, Kushlan 1978). The efficiency of intraspecific piracy between Wood Storks was lower, at 23% of successful attempts (Table 2). Individual size, hunger level and physiological state of the birds involved were probably the factors contributing to the success or failure of robbery attempts.

The Cocoi Heron also stole prey from Great Egrets, Wood Storks and conspecifics. Due to its great aggressiveness, this heron was the only wading bird observed stealing prey from larger birds like Wood Storks, although efficiency was only 20% in such instances. I also observed two cases of intraspecific food piracy between Maguari Storks, both successful.

DISCUSSION

Food kleptoparasitism is widespread among several groups of birds such as gulls,

Table 2. Effectiveness of the most frequent[a] prey-robbing interactions occurring in a mixed-species foraging flock of llanos wading birds during two days of observation.

Robber	Victim	N attempts	N successful	% success
Mycteria americana	*Mycteria americana*	26	6	23.0
Jabiru mycteria	*Jabiru mycteria*	23	15	65.2
Jabiru mycteria	*Mycteria americana*	18	14	77.7
Jabiru mycteria	*Ardea cocoi*	8	6	75.0
Ardea cocoi	*Mycteria americana*	5	1	20.0

[a]Only prey-robbing attempts observed more than three times are considered (see Fig. 1 for other minor interactions).

terns, skuas, and grackles (Sprunt, Jr. 1941, Hatch 1970, Ashmole 1971, Hopkins and Wiley 1972, Dunn 1973, Anderson 1976, Elston *et al.* 1977, Fuchs 1977, Thompson 1986). This behavior has also been reported in wading birds (Kushlan 1978, Kushlan *et al.* 1985). Mock and Mock (1980) estimated that Goliath Herons (*A. goliath*) at Lake St. Lucia (South Africa) lost 11% of captured prey as the result of robbing attempts by other fish-eaters. Intraspecific food piracy has also been documented in White Ibis (*Eudocimus albus*) colonies (Frederick 1985). Marabou Storks (*Leptoptilos crumeniferus*) steal carrion torn from carcasses by other scavengers (Kahl 1966a,b), a behavior that is also used by the Maguari Stork during the annual harvesting of capybaras (*Hydrochoerus hydrochaeris*) in the llanos of Venezuela (González 1993).

Few studies document kleptoparasitism between wading birds in the llanos of Venezuela. In foraging aggregations of ibises, Frederick and Bildstein (1992) reported three species attempting prey robbery, with a minimum success rate of 13%, Scarlet Ibises (*E. ruber*) were the most aggressive and the most likely to attempt food robbery. Kushlan *et al.* (1985) reported intraspecific prey-robbing interactions among seven species of wading birds in the llanos: two ibises, three egrets, one heron and one stork; interspecific piracy was rare, with only two species acting as robbers and two others being victims. My observations indicate that both intra- and interspecific food piracy are common in mixed-species foraging flocks during the stressful late dry season in the southern llanos, with at least four species (26.6%) acting as robbers and seven (46.6%) serving as victims (Fig. 1).

Kushlan *et al.* (1985) report that prey-robbing interactions are more complex in the Everglades than in the llanos, suggesting these differences relate to greater prey availability in the llanos that make such interactions unnecessary. I agree with this argument during the rainy season, when most of the llanos are flooded, and when food abundance is high and prey (fish, amphibians and aquatic invertebrates) are widespread (Lowe-McConnell 1975, Kushlan *et al.* 1985). However, during the dry season, as water level drops, wading birds concentrate around the few ponds and lagoons maintaining enough water to sustain fish populations (Kushlan 1976, Morales *et al.* 1981, González 1993). It is easy, then, to observe aggregations of more than a thousand wading birds per hectare. For example, on 2 March 1990, I observed 108 Jabirus, 90 Maguari Storks and more than 400 Wood Storks, accompanied by lower numbers of Great Egrets and Cocoi Herons, in a half-hectare pond. A second similar pond, situated less than 500 m from the first, contained another 83 Jabirus and 280 Wood Storks. In situations like this, high prey density is not sufficient to prevent continuous interactions between birds.

Kushlan (1978) suggests that the tendency to rob depends on size, with small birds lacking potential victims; larger birds have a high probability of success, but also a large energy expenditure. This could explain why medium-sized birds are often the predominant prey robbers in foraging aggregations

in the Everglades (Kushlan 1978). In the llanos, the Jabiru Stork (not present in the Everglades) is the largest wading bird and also the most common robber (37.3% of the attempts observed). I estimated that more than 20% of the fish consumed by Jabirus in mixed-species flocks during the late dry season came from intra- or interspecific piracy (González 1993). The Wood Stork, another large wading bird, is also a common robber in the llanos (30.3% of the attempts) stealing prey from conspecifics. With at least three other species of potential victims, interspecific parasitism for llanos Wood Storks is similar to that in the Everglades (Kushlan *et al.* 1985). Both species of storks seem to be very efficient as interspecific robbers (78.5% and 75% of successful attempts, respectively).

Other cases of food piracy between medium size ibises and herons are described in Frederick and Bildstein (1992) and Kushlan *et al.* (1985). As I focused only on aggregations containing storks formed during the late dry season, I did not record other kinds of kleptoparasitism in the llanos (especially in flocks of smaller wading birds). Since my study was conducted only during the late dry season, the results cannot be extrapolated to other times of the year.

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