FORAGING NICHE RELATIONS OF WADING BIRDS IN TROPICAL WET SAVANNAS

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ABSTRACT. The foraging niche relations of ciconiiform wading birds in hyperseasonal wet savannas are influenced by seasonal fluctuations in rainfall, water depth, and food abundance and availability. The ciconiiform wading bird community of the Venezuelan Llanos includes 22 species, that of the Florida Everglades includes 15. Both faunas contain more species of herons than ibises, spoonbills, or storks. The Llanos supports terrestrial ibises, very large storks, and species that live in mated pairs year-round, types of wading birds not found in the Everglades. The wading bird community of the Everglades is numerically dominated by a single species, whereas abundances are more equitably distributed among species in the Llanos. Seasonal cycles of prey availability, bird migration, and fluctuating water depth influence packing of species in the wading bird community of both savannas. The Llanos includes relatively more terrestrial habitat than does the Everglades and supports a greater variety and amount of potential prey. Thus the Llanos provides more diverse foraging opportunities. Wading bird species found in both areas feed on analogous types of prey, although the diets of some species in the Llanos include types of prey with no analogue in the Everglades, the fish fauna of which is derived from temperate North America.

RESUMEN. Las relaciones de los nichos de forraje de la comunidad de aves zancudas ciconiformes en savanas excesivamente húmedas están influenciendas por las fluctuaciones estacionales de lluvias, profundidad del agua y abundancia y disponibilidad de comida. La comunidad de aves zancudas ciconiformes de los llanos venezolanos incluye 22 especies, mientras que la de los Everglades en Florida, E.E.U.U. incluye 15. Ambas avifaunas contienen mayor cantidad de especies de garzas que de ibis, picos de espátula o cuchara y cigueñas. En los llanos se encuentran ibis terrestres, cigueñas muy grandes y especies que viven en pareja duranta todo el año, tipos de aves zancudas que no se encuentran en los Everglades. La comunidad de aves zancudas de los Everglades está dominada en el aspecto numérico por una sola especie, mientras que la abundancia de especies de los llanos está distribuída de manera más equitativa. Ciclos estacionales de disponibilidad de presas, migración de aves y fluctuación de la profundidad de las aguas son quienes influyen en el compactamiento de las especies de la comunidad de aves zancudas de ambas savanas. Los llanos incluyen relativamente mayor cantidad de habitats terrestres que los Everglades y poseen una mayor variedad y cantidad de posibles presas. Así los llanos preveen diversidad de oportunidades de forrajeo. Las aves zancudas encontradas en ambas áreas se alimentan en tipos de presas análogas, aunque las dietas de algunas especies de los llanos incluyen presas que no tienen análogos en los Everglades, la ictiofauna que se deriva del clima templado de América del Norte.

Wet savannas are among the most extensive of tropical ecosystems (Beard 1953; Cole 1960; Blydenstein 1967; Walter 1969; Sarmiento and Monasterio 1975). Although tropical and subtropical in character, these systems are far from climatically stable in that rainfall, generally over 1000 mm per year is highly seasonal, concentrated in a five to eight month period. In the western hemisphere, such wet savannas occur from southern North America, through para-equatorial regions, to southern South America. Their faunal components are determined by both ecological constraints and biogeographical considerations. Ecologically, the dramatic climatic fluctuations could be expected to impose fundamental constraints on the invasion and persistence of animal populations. These savannas are hyperseasonal marshes, in the terminology of Sarmiento and Monasterio (1975), and are characterized by the presence of plant and animal populations that are adapted to the dual stresses of flood and drought. Biogeographically, the fauna is constrained by the availability of suitably-adapted species in

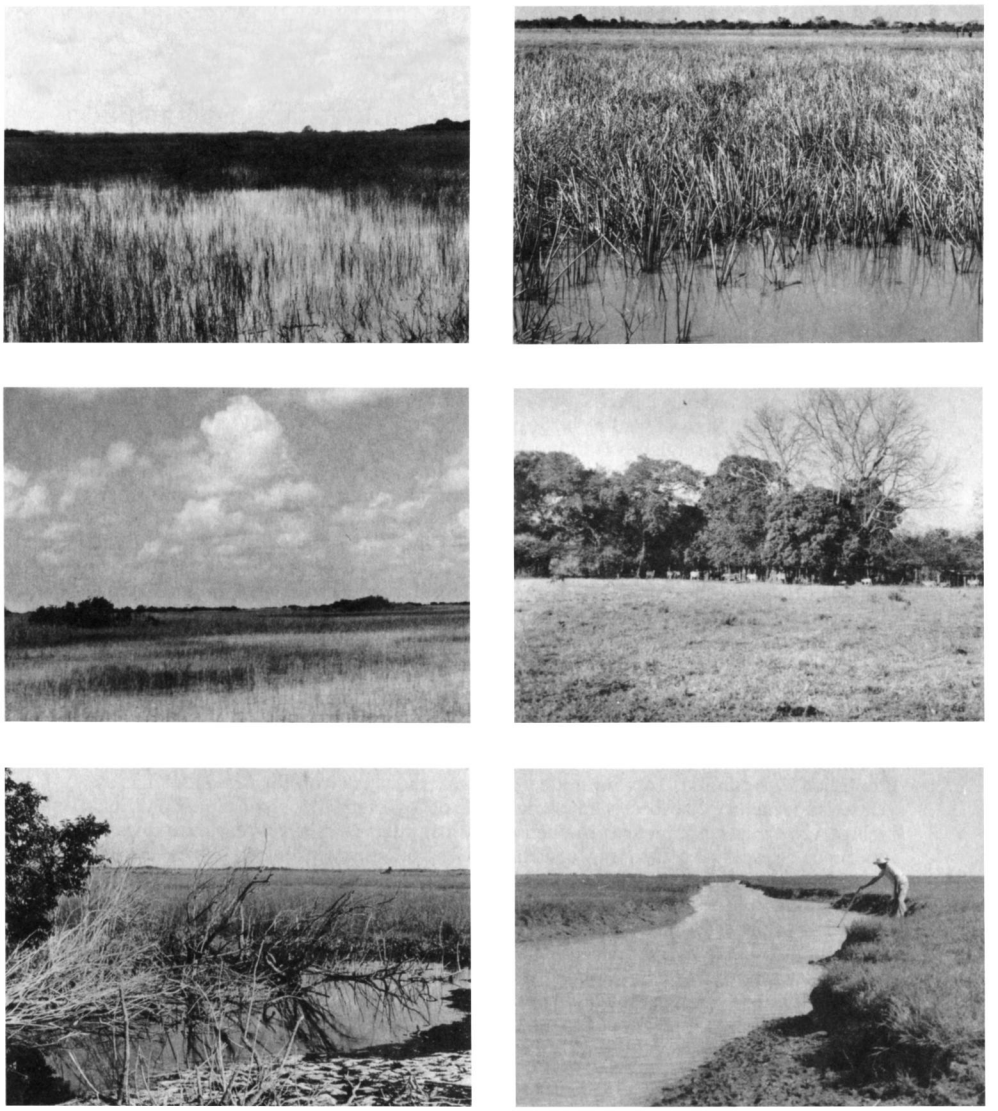

FIG. 1. Habitats of the Everglades (left) and Llanos (right). From top to bottom: Everglades wet prairie—Llanos estero; Everglades tree islands—Llanos wooded banco, with cattle; Everglades pond in the dry season—Llanos caño in the dry season. Llanos photographs courtesy of Dr. Mauricio Ramia.

that these savannas are relatively young in their current incarnation. In South America, glacial refugia undoubtedly provided sources for aquatic species having a long history of adaptation to tropical marshes, whereas in North America nonvolant species are derived from a temperate fauna.

Two of the largest Neotropical wet savannas are the South American Llanos, situated in the Orinoco River Basin of Venezuela (Ramia 1967), and the North American Everglades, situated on the southern tip of the Florida peninsula. The ecological and biogeographic similarities and differences of these two marshes provide a natural experiment in the assembly of animal communities. In such comparisons species may be found that exhibit ecological equivalency. A similar comparison of entire communities may reveal both equivalencies and divergences that result from environmental or biogeographic constraints peculiar to each system, and so can further our understanding of system effects and community responses.

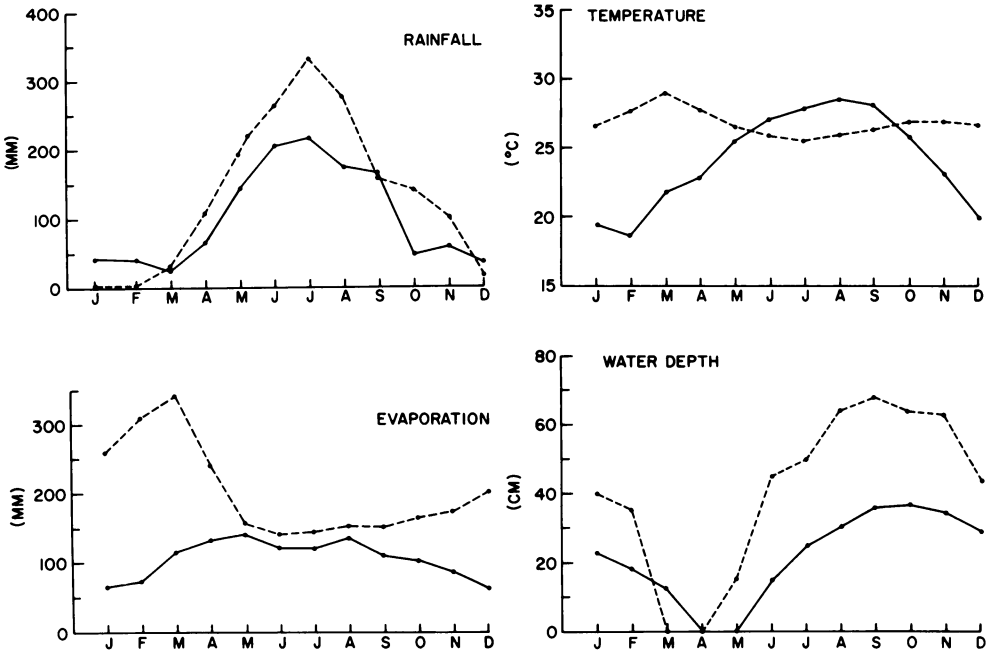

FIG. 2. Seasonal variation of environmental conditions in the Everglades (solid line) and Llanos (dashed line). Data plotted are monthly averages for 1972–1980, except for water depth in the Everglades, which includes data from 1962–1982.

Ciconiiform wading birds are useful for such a comparison. They are large and abundant species that are especially suited to make use of the seasonal variability in prey populations that occurs in wet savannas (Kushlan 1978a, 1979a, b, 1981a; Pinowski et al. 1980) and may be influential in the flow of energy and materials within the system (Kushlan 1976a; Morales et al. 1981). Wading birds are a community of morpho-ecologically similar species, some of which occur in both North and South America. In this paper we compare the wading bird communities of the Florida Everglades and Venezuelan Llanos with respect to species composition, abundance structure, and foraging niche relations, and we consider particularly how differences and similarities are the result of biotic, environmental, and biogeographic constraints. Our goal is to understand the patterns of community composition and to suggest explanations for the patterns observed.

STUDY AREAS

The Llanos is in South America in the states of Apure, Barinas, Guarico, and Bolivar, Venezuela, at 6–9°N latitude. The Everglades is in North America in the state of Florida, United States, 25–27°N latitude. We examined the wading bird communities of study areas as representative of the two ecosystems. The Everglades study area was the fresh-water marshes west of Miami, Florida, 25°N, 81°W. The Llanos study area was in the low Llanos near Mantical, Apure, 7°N, 69°W (Ramia 1974). The seasonal hydrological pattern was wetter than the more extensive high Llanos and therefore more similar to that of the Everglades.

The landscapes (Fig. 1) of both savannas are mosaics of marsh and woody vegetation (Loveless 1959; Tamayo 1961; Ramia 1967; Troth 1979). The highest ground, occupied by trees, palms, and shrubs, is not normally flooded. In the Llanos, such high ground, called bancos, is variable in size and shape ranging from small islands and river banks to extensive, continuous sandy ridges (matas). High ground in the Everglades is restricted to small tree islands of fewer than 2 ha that occupy discontinuous rock outcrops. Slightly lower elevations are marshes (bajíos) dominated by sawgrass (*Mariscus*) in the Everglades and by *Panicum* and *Leersia* in the Llanos. Even lower elevations support wet prairies (esteros) dominated by aquatic sedges and grasses, *Eleocharis, Panicum,* and *Rhynchospora* in the Everglades and

TABLE 1

CICONIIFORM WADING BIRD FAUNAS OF THE FLORIDA EVERGLADES AND VENEZUELAN LLANOS AND THE RELATIVE ABUNDANCE OF VARIOUS SPECIES

Scientific name	English name	Spanish name	Occurrence (rel. abund.)[2]	
			Everglades	Llanos
Botaurus lentiginosus	American Bittern	Mirasol	X[1]	
Ixobrychus exilis	Least Bittern	Garza Enana	X	
Ardea herodias	Great Blue Heron	Garzón Cenizo	X (8.6)	
A. cocoi	White-necked Heron	Garza Morena		X (4.3)
Casmerodius albus	Great Egret	Garza Real	X (5.8)	X (17.2)
Egretta thula	Snowy Egret	Garza Chusmita	X	X (2.7)
E. caerulea	Little Blue Heron	Garcita Azul	X (2.1)	X (3.1)
E. tricolor	Tricolor Heron	Garza Pechiblanca	X (1.2)	
Bubulcus ibis	Cattle Egret	Garza Garrapatera	X	X (32.3)
Butorides striatus	Green-backed Heron	Chicuaco Cuello Gris	X	X (3.1)
Syrigma sibilatrix	Whistling Heron	Garza Silbadora		X (0.4)
Pilherodius pileatus	Capped Heron	Garciolo Real		X
Nycticorax nycticorax	Black-crowned Night-Heron	Guaco	X	X (3.1)
N. violacea	Yellow-crowned Night-Heron	Chicuaco Enmascarado	X	X
Tigrisoma lineatum	Rufescent Tiger-Heron	Pájaro Vaco		X (2.1)
Theristicus caudatus	Buff-necked Ibis	Tautaco		X
Cercibis oxycerca	Sharp-tailed Ibis	Tarotaro		X
Mesembrenibis cayennensis	Green Ibis	Corocora Negra		X (12.6)
Phimosus infuscatus	Bare-faced Ibis	Tara		X (2.8)
Eudocimus albus	White Ibis	Corocora Blanca	X (78.3)	X (0.2)
E. ruber	Scarlet Ibis	Corocora Roja		X (10.3)
Pelgadis falcinellus	Glossy Ibis	Corocora Castaña	X	X (0.6)
Ajaia ajaja	Roseate Spoonbill	Garza Paleta	X[1]	X (0.2)
Jabiru mycteria	Jabiru	Garzon Soldado		X (1.5)
Mycteria americana	Wood-Stork	Gabán	X (3.7)	X (2.2)
Euxenura maguari	Maguari Stork	Gabán Peonío		X (1.4)

[1] Present but not nesting.

[2] Relative abundance is the percent of all birds present. Species for which no relative abundance is given were present but in relatively small numbers and were not adequately censused.

Hymenachne, Eleocharis, and *Luziola* in the Llanos. Floating and submerged species occur in deeper areas. In the Everglades deep pockets contain ponds, maintained by alligators. In the Llanos small seasonal streams, called caños, provide deep water habitats. In both areas, canals and borrow pits (préstamos) have been excavated for drainage, road fill, or levees. In some situations these hold water after natural habitats have dried.

Soils in the Everglades are peat and marl overlying highly permeable limestone. When the limestone is saturated, the ground water level rises above the surface, flooding the marshes. In the Llanos, the soil is a heavy clay that impedes vertical drainage, leading to surface flooding from rainfall and from overflow of permanent and seasonal rivers.

Rainfall in both areas exceeds 1200 mm per year and is heavily seasonal, peaking in July (Fig. 2). Both areas are, therefore, covered in the boreal summer and fall by moderately deep water, which recedes in the winter to a low point in spring. The low Llanos differs from the Everglades by being wetter in the wet season. Higher wet season water levels in the low Llanos result from a 25 percent greater annual rainfall, 1540 mm per year compared to 1225 mm per year in the Everglades. In the dry season the Llanos experiences less rainfall and higher rates of evaporation owing to higher temperatures.

TABLE 2

FAUNAL SIMILARITY OF THE WADING BIRD COMMUNITIES OF THE EVERGLADES AND VENEZUELAN LLANOS

	Bitterns	Herons	Tiger-Herons	Ibises	Spoonbills	Storks
Nesting in Everglades	1	9	0	2	0	1
Present but not nesting in Everglades	1	0	0	0	1	0
Total in Everglades	2	9	0	2	1	1
Present and nesting in Llanos	0	10	1	7	1	3
Common faunal elements	0	7	0	2	1	1
Faunal similarity[1]	0	0.58	0	0.29	1.00	0.33

[1] Jaccard similarity coefficient.

METHODS

Faunal lists were constructed by considering only those species that occur in the freshwater marshes of each geographic area. Species abundances were determined using monthly censusing along transects conducted by car and by airplane. Census results are expressed as the percent of the annual total number of each species occurring in each month. Observations of birds at feeding sites were made using cars as hides. Qualitative descriptions of foraging behavior, using the terminology of Kushlan (1978a), foraging sociality, interactions, and habitat use as presented in this paper are based on quantitative 1 or 5 min observations of randomly selected individuals. Food habits were quantified by collecting specimens and examining regurgitates of adults and nestlings, which had the same diets (Kushlan 1979a; Morales et al. 1981). Fish standing crop was sampled using enclosure traps, net traps at culverts, and poisoning (Kushlan 1981b; Ramos et al. 1981). Size of birds was indexed by one measurement of tarsal length: the distance from the point of the joint between the tibia and metatarsus to the point of the joint at the base of the middle toe in front.

Faunal similarity was calculated using the Jaccard similarity coefficient, $S_j = a/(a + b + c)$, where a = the number of common faunal elements, b = those only in Everglades, c = those only in the Llanos. Diversity was calculated using the Simpson index, $D = 1/\Sigma p_i^2$, where p_i is the proportion of individuals in the *i*th species. Climatological and hydrological data were obtained at permanent stations within each study area.

RESULTS

SPECIES RICHNESS

In the Everglades, the wading bird community consists of 15 species (Table 1). The Reddish Egret (*Egretta rufescens*) is not included in the faunal list because it is rarely found in the inland freshwater marshes, occurring more commonly in the south Florida marine habitats. Although also primarily a marine species in south Florida, the Roseate Spoonbill is included because it occurs regularly in the Everglades marshes in small numbers. The American Bittern is included because it winters there, although it does not nest in the Everglades.

Twenty-two species of wading birds are found in the Llanos (Table 1), and all of these species nest there although not necessarily in the study area. The Pinnated Bittern (*Botaurus pinnatus*) occurs in the high Llanos (M. Gochfeld, pers. comm.) but is not considered in this paper because it is not recorded from the study area.

Wading birds comprise a larger proportion of the total bird fauna in the Llanos (12%) than in the Everglades (4%) (Kushlan and Morales, unpubl. data). The species richness of wading birds in the Llanos exceeds that of the Everglades by seven species, and its nesting fauna is greater by nine species. Of six higher taxa (families and subfamilies) occurring in the two areas (Table 2), herons dominate both faunas, comprising 60 percent of the species in the Everglades and 45 percent of those in the Llanos. The seven extra species of ibises and storks in the Llanos account for much of the difference in species richness between the wading bird communities of the two areas.

Despite these differences, over 40 percent of the total number of wading bird species found in the Everglades and Llanos are common to both areas (Jaccard's coefficient = 0.42). The

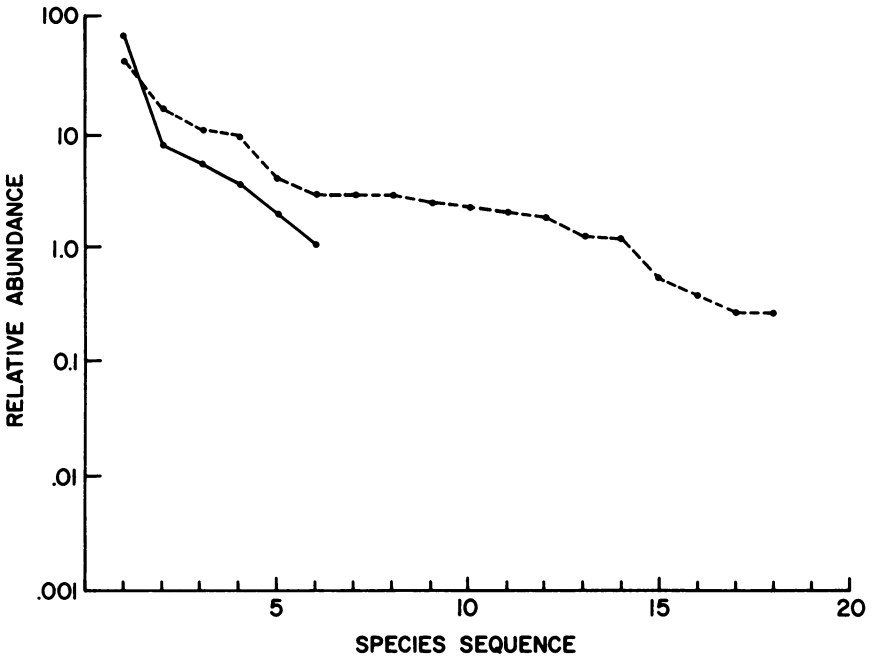

FIG. 3. Relative abundances of wading bird species in the Everglades (solid line) and Llanos (dotted line). Relative abundance is the proportion of the combined wading birds population represented by each species, plotted in sequence of species from the most to the least abundant. The steeper the curve, the greater the dominance of one or a few species.

ecological commonality of the two areas is understated by recognized taxonomy (Hancock and Kushlan 1984). The Great Blue Heron and the White-necked (Cocoi) Heron are closely-related species that are geographic replacements, and probably ecological equivalents. Similarly, the White and Scarlet Ibises, treated as separate species in our analyses, are closely related and are thought to be conspecific (B. Busto and C. Ramo, pers. comm.).

COMMUNITY STRUCTURE

The Llanos and the Everglades differ in the relative abundances of wading bird species comprising the respective communities (Table 1). In the Llanos, the herons are the most abundant wading birds, while in the Everglades a single species, the White Ibis, constitutes more than 75 percent of the total wading bird fauna, a situation that apparently has always been the case (Kushlan and Frohring, unpubl. data). Cattle Egrets, which comprise half the heron fauna in the Llanos, are scarce in the Everglades marsh although abundant in terrestrial habitats of southern Florida (Kushlan and White 1977).

The distribution of relative abundances among species implies differences in community structure that may be fundamental (Fig. 3). The low species diversity of the Everglades fauna (Simpson's Index = 1.60) reflects the strong dominance of the single species, whereas the higher diversity of the Llanos fauna (Simpson's Index = 5.98) reflects a more even representation of species. The distribution of relative abundances in the Everglades, the relatively rapid fall of the curve in Figure 3, is similar to that expected of a non-equilibrial community in contrast to the more equitable situation suggested by the relatively slowly falling curve (Fig. 3) for the Llanos fauna. (See May [1976] for a discussion of such curves.) Thus the Llanos wading bird community may be closer to an equilibrium condition, with an equitable distribution of abundances spread out over a greater number of species.

SEASONALITY OF PREY AND FORAGING HABITAT

In the wet season, surface water in both the Llanos and the Everglades stands over all of the savanna except the tree islands (bancos). Wet season (June–December) water depths in

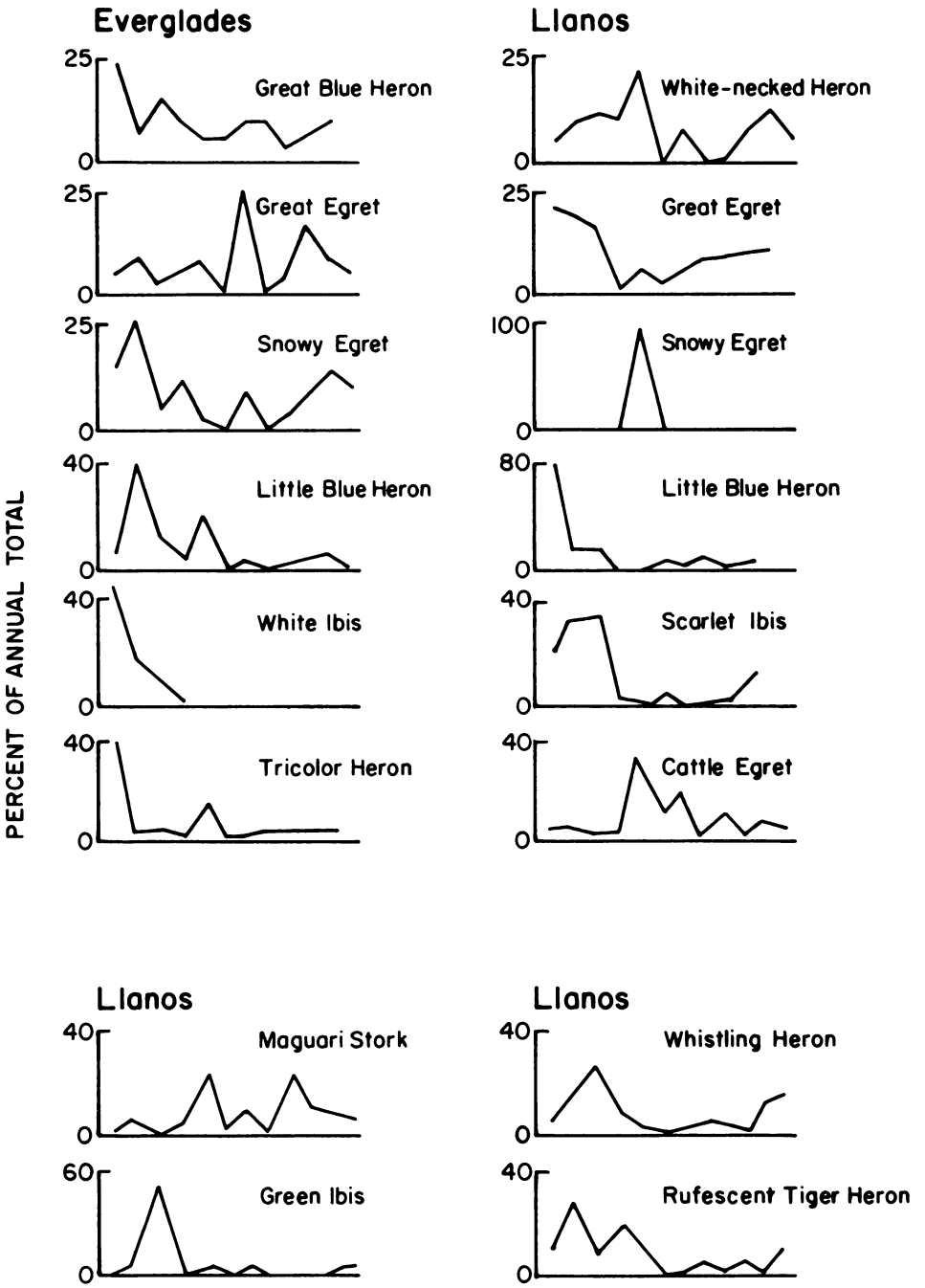

FIG. 4. Seasonal variation in abundance of wading bird species in the Everglades and Llanos. Abundance is expressed as the monthly percentage of the yearly total count for each species (based on monthly censuses), beginning in January and ending in December.

the marshes (38 cm in the Llanos and 24 cm in the Everglades, on average) (Fig. 2), can restrict foraging by wading birds. During this season many species migrate to higher ground or to coastal habitats, resulting in a seasonal variation in wading bird use of the savannas (Fig. 4). Most species tend to be more abundant in the late winter–spring dry season than in the fall wet season. Great Blue Herons and White-necked Herons remain throughout the year, as do Great Egrets in both areas. In the Llanos, Maguari Storks remain in numbers throughout the wet season. In the Everglades wet season, Tricolor Herons, Little Blue Herons, and American Bitterns occur in small numbers in the shallower marshes. Green-backed Herons and Least Bitterns, which feed by perching and are less restricted by deep water, remain in the Everglades year-round. Ibises typically migrate out of both savannas during the wet season, except for the territorial Buff-necked and Sharp-tailed Ibises in the Llanos.

The wet season is the period of reproductive activity for most fishes, amphibians, and aquatic invertebrates in both the Llanos and the Everglades (Lowe-McConnell 1975; Kushlan and Kushlan 1980; Kushlan, unpubl. data). Thus, the wet season is a time of relatively high abundance of potential prey. Ecological density, however, is low as the prey are spread over large expanses of marsh making them less available than if they were concentrated. In the Llanos, we estimated fish standing stock in the wet season to be about 60 to 70 kg/ha. In the Everglades fish standing stock is less, 50 kg/ha of marsh during the wet season.

In the drying season, receding water levels result in increased densities of prey, as prey become concentrated in progressively smaller areas of remaining water (Kushlan 1976a), including deep marshes (esteros), natural ponds, excavation pits (préstamos), and streams (caños). As marshes dry, wading birds form mixed-species flocks and feed on these concentrated prey. Flocking herons and storks use still-flooded marshes and ponds in both areas. In the study area in the Llanos, nearly-dry marshes are used by ibises; in the Everglades, ibises feed in wetter marshes.

The drying season standing crop of fishes is similarly high in marshes of both areas, about 90 kg/ha. In the Llanos, shallow excavation pits can contain up to 1300 kg/ha of fishes. In south Florida, alligator ponds in most years may contain about 500 kg/ha, 40 percent of the Llanos value. In the driest period wading birds seldom use dry Everglades marshes. In the Llanos, damp and dry areas continue to be used by Cattle Egrets, Whistling Herons, and Buff-necked and Sharp-tailed Ibises.

When the rainy season begins in the Everglades, remnant fish stocks move out of ponds via surface water that rises uniformly throughout the marsh system. Prey densities decrease rapidly, and birds disperse to more elevated habitats. In the Llanos, streams overflow and flood the savanna, carrying fishes from their dry-season refugia. Wading birds follow the flooding, initially using newly flooded marshes. These birds include, especially, Whistling Herons, Little Blue Herons, Maguari Storks, and ibises. As the savannas flood further, the wading bird community continues its adjustment toward the high water conditions noted previously.

The seasonal interrelationships of wading birds to their prey are complex in wet savannas. Deeper and permanent bodies of water serve as dry-season refugia for fishes. In sites shallow enough for wading, the feeding of wading birds can regulate the survival of some of these prey populations. In south Florida, wading birds can reduce prey populations as much as 76 percent (Kushlan 1976a); in the Llanos the reduction is more than 50 percent (Morales et al. 1981). Because birds do not consume all fishes present, if ponds or other deep-water habitats do not dry completely, bird predation prevents local extirpation of prey populations by preventing catastrophic mortality of the fish (Kushlan 1974b). In the Llanos, heavy predation by birds on juvenile predatory fishes (*Serrasalmus, Hoplias*) may reduce the subsequent abundance of adults.

Another aspect of the seasonality of wading bird predation is related to the presence of crocodilians (Kushlan 1974a; Staton and Dixon 1977; Seijas and Ramos 1980). Alligators (*Alligator mississippiensis*) in the Everglades and Spectacled Caiman (*Caiman crocodilus*) in the Llanos, also feed on aquatic prey and so may affect fish diversity. In the Everglades, alligators dig and maintain the ponds in which wading birds feed and in which the fish populations persist through dry seasons.

Foraging Niches

The foraging niches of wading birds may be interpreted to include axes related to food, habitat, and behavior. In our analysis of the wading bird communities of seasonal savannas, it is useful to consider macrohabitat, feeding strategy, size of bird, microhabitat, including

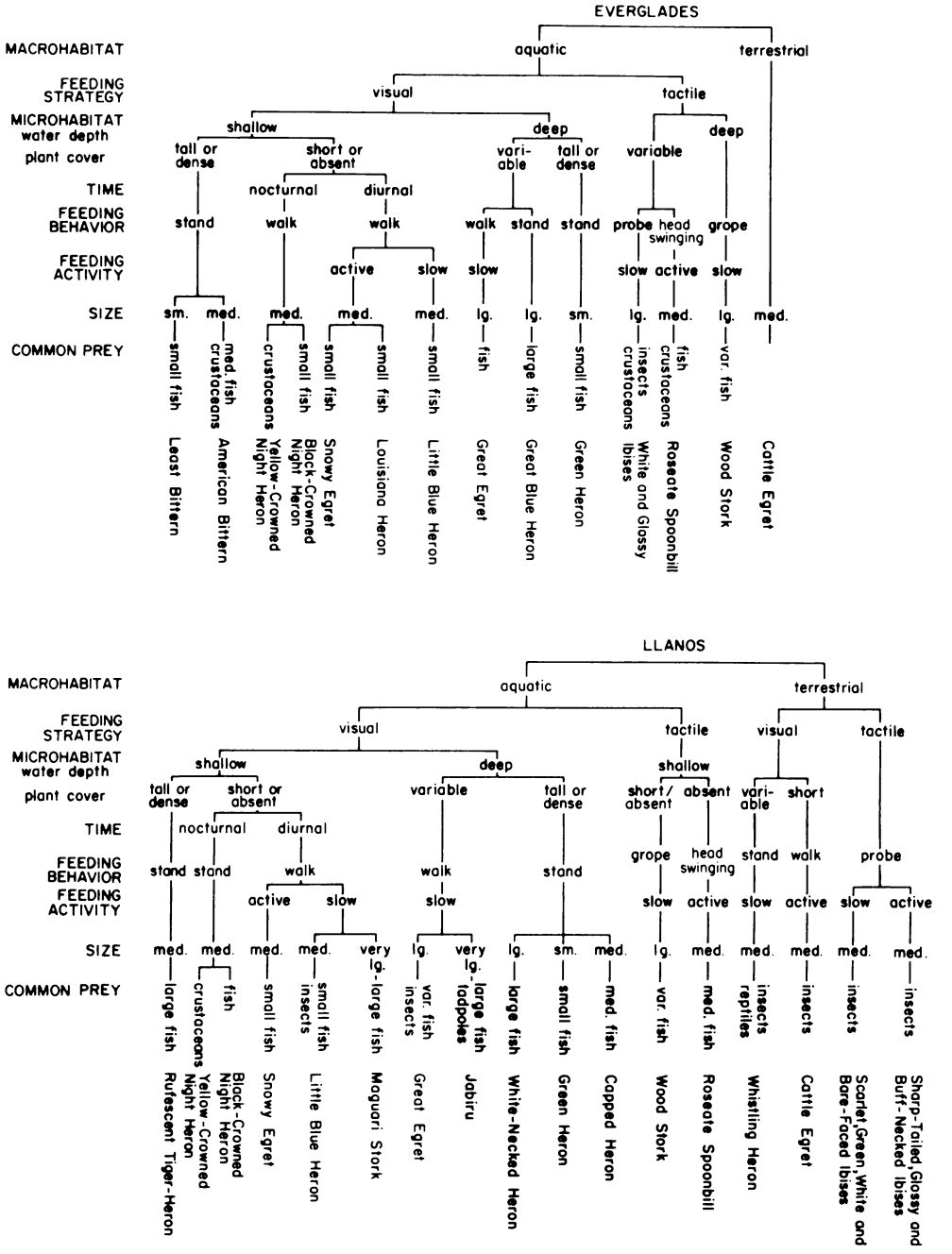

FIG. 5. Difference in niche characteristics within wading bird communities in the Llanos and Everglades.

water depth and plant cover, time of foraging, feeding behavior and activity, and prey consumed. We have qualitatively evaluated the differences among species with respect to these aspects of foraging niche in both the Everglades and Llanos (Fig. 5).

Macrohabitat.—Wading birds may forage in aquatic or terrestrial habitats, but most are primarily aquatic (Table 3). Terrestrial foraging could be an effective strategy in wet savannas only if topographically high areas or the length of the dry season were sufficiently extensive.

TABLE 3

CHARACTERISTICS OF FEEDING SITES USED BY WADING BIRDS IN THE EVERGLADES AND THE LLANOS[1]

	Aquatic								Terrestrial		
	Water depth				Plant cover				Plant cover		
	Shallow		Deep		Short		Tall		Short		Tall
American Bittern	E						E				
Least Bittern	E						E				
Great Blue Heron			E		E		e				
White-necked Heron				L		L		L			
Great Egret	E		E	L	E	L	e	L			
Snowy Egret	E	L			E	L					
Little Blue Heron	E	L			E	L					
Tricolor Heron	E				E						
Cattle Egret									E	L	
Green-backed Heron	E	L	E	L			E	L			
Whistling Heron		l				l				L	L
Capped Heron		L		L		L		L			
Black-crowned Night Heron	E	L			E	L					
Yellow-crowned Night Heron		L				L					
Rufuscent Tiger-Heron		L						L			
Buff-necked Ibis		l				L				L	
Sharp-tailed Ibis		l				L				L	
Green Ibis		L				L				L	
Bare-faced Ibis		L				L				L	
White Ibis	E	L			E	L			e	L	
Scarlet Ibis		L				L				L	
Glossy Ibis	E	L			E	L			e	L	
Roseate Spoonbill		L				L					
Jabiru				L				L			
Wood Stork	e	L	E	L	E	L					
Maguari Stork		L						L			

[1] Capital letters indicate primary feeding sites, small letters indicate secondary feeding sites in Everglades (E, e) and Llanos (L, l).

The two savannas appear to differ in this regard in that dry ground in the Everglades is limited both seasonally and areally. The wading bird communities reflect the differences in availability of terrestrial habitat. The Whistling Heron, the typical heron of neotropical savannas (Kushlan et al. 1982), feeds on ground that is dry or very shallowly covered by water. This species does not occur in the Everglades. The Cattle Egret, a dry-ground forager occurring in both areas, is the typical heron of paleotropical savannas, where it originated. It is the most abundant heron in the Llanos, but it rarely feeds in the Everglades marsh. That it is common in southern Florida on higher ground suggests that it is excluded from feeding in the Everglades marsh by water depths.

The two ibises that occur in the Everglades feed primarily in aquatic habitats. Although capable of foraging terrestrially, they do so only when aquatic habitats are unavailable. In the Llanos the same species, although often foraging in wet marshes, seem also to be terrestrial, especially in the drying season, choosing the drier sites of those available. The Buff-necked, Bare-faced, and Sharp-tailed Ibises characteristically feed on dry or damp ground, the White, Scarlet, and Glossy Ibises somewhat less so. Thus, in the Llanos, although ibises forage in both aquatic and dry habitats, they can especially use the latter in the drying season. It appears, then, that the permanent and facultative terrestrial component of the fauna is expanded in the Llanos; the addition of terrestrial foraging opportunities affects both heron and ibis species found there.

Feeding strategy.—Wading birds can be partitioned dichotomously into those locating prey primarily visually and those locating prey by tactile mechanisms (Kushlan 1978a). Herons and bitterns are primarily visual hunters; ibises and spoonbills are primarily tactile. Heavy cover and seasonally high densities of food enhance the effectiveness of tactile foraging in wet savannas. Four tactile foragers (two ibises, Roseate Spoonbill, and Wood Stork) occur in the

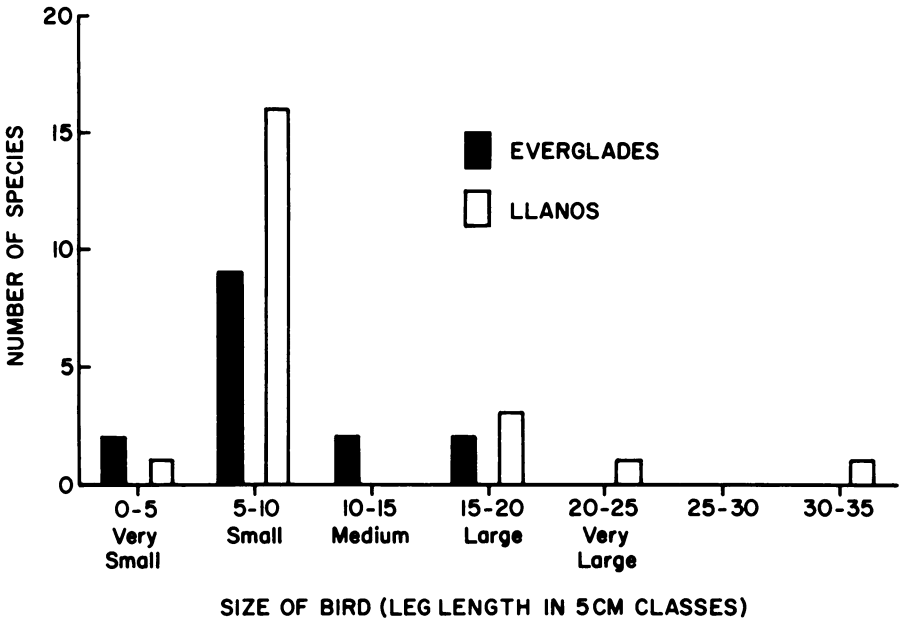

FIG. 6. Distribution by size of wading bird species in the Everglades and Llanos. Leg length is used as an index of size.

Everglades, but the Llanos supports five additional tactile-foraging species of ibises. The addition of these tactile-foraging ibises accounts for five of the seven species added to the Llanos fauna over that of the Everglades.

Size of the bird.—Body size is an important aspect of wading bird niche breadth, in that it is correlated with feeding strategy (Kushlan 1978a). Leg length appears to be the most crucial morphological feature in determining foraging sites available to the various species (Kushlan 1976a; Custer and Osborn 1977). Geographically and seasonally variable water depths in wet savannas provide conditions suitable for use by birds of different leg lengths. Based on this characteristic, we divided the savanna wading bird community into five classes of very small, small, medium, large, and very large species (Fig. 6). The species present in the Llanos, but not in the Everglades, are mostly small (the ibises) but also include the very large Jabiru and Maguari Storks, the latter two species having no equivalent in the Everglades.

Some size differences occur in similar species found in the two areas. Great Egrets in the Everglades are smaller than those in the Llanos (14.1 vs 16.1 cm tarsus length), and Great Blue Herons in the Everglades are larger than White-necked Herons in the Llanos (18.9 vs 17.9 cm). As a result, the Great Blue Heron and Great Egret are more dissimilar in size in the Everglades than are the White-necked Heron and Great Egret in the Llanos. The Great Egret in the Everglades is, in fact, situated along the leg-length gradient midway between the Great Blue Heron and the three small day herons (Little Blue Heron 9.6 cm, Snowy Egret 9.6 cm, Louisiana Heron 9.9 cm). This comparison suggests that size compensation has occurred in the Everglades. That the Great Blue Heron in the Everglades has not become even larger, and that the Wood Stork, the other large species, has not diverged at all from its size in the Llanos (19.8 cm in both areas) suggest the existence of minimal selective pressure to fill a niche space occupied by very large birds in the Everglades wading bird community.

Microhabitat.—Niche distinctions can be drawn with respect to characteristics of feeding sites, particularly water depth and plant cover (Table 3). Primary habitats are those used by a species most of the time, and those in which a species is expected to be found. All primarily aquatic species use shallow water. Very small species (Least Bittern, Green-backed Heron) and some medium-sized species are able to stand on vegetation and so can use deep water as well, as can larger species. The very large species that occur in the Llanos (Fig. 6) are capable of using the greater water depths found there (Fig. 2). In both areas, the cryptic bittern-like

TABLE 4

FORAGING BEHAVIORS USED BY WADING BIRDS IN THE EVERGLADES (E) AND LLANOS (L)[1]

	Number of behaviors recorded		Standing		Walking slowly		Walking quickly		Probing		Head swinging		Foot stirring		Gleaning		Groping	
	E	L	E	L	E	L	E	L	E	L	E	L	E	L	E	L	E	L
American Bittern	4	—	X		(X)													
Least Bittern	4	—	X		(X)													
Great Blue Heron	7	—	X		X				(X)									
White-necked Heron	—	2		X		(X)												
Great Egret	10	7	X	X	(X)	X				(X)					(X)	(X)		
Snowy Egret	20	7	X		X		X	X					X	X				
Little Blue Heron	13	6	(X)		X	X	(X)			(X)						X		
Tricolor Heron	12	—	X		(X)		X						(X)					
Cattle Egret	12	7	(X)		(X)		X	X	(X)						X	X		
Green-backed Heron	9	2	X	X	(X)								(X)					
Whistling Heron	—	6		X		X		(X)										
Capped Heron	—	2		X		(X)												
Black-crowned Night-Heron	4	1	X	(X)	(X)													
Yellow-crowned Night-Heron	5	1	X	X	(X)													
Rufescent Tiger-Heron	—	3		X		(X)												
Buff-necked Ibis	—	2								X								
Sharp-tailed Ibis	—	2								X								
Green Ibis	—	3								X								
Bare-faced Ibis	—	3								X								
White Ibis	5	3	(X)		(X)				X	X	(X)							
Scarlet Ibis	—	3								X								
Glossy Ibis	5	2	(X)						X	X	(X)							
Roseate Spoonbill	7	3	(X)		(X)			(X)			X	X						
Jabiru	—	2		(X)		X												
Wood Stork	7	6	(X)	(X)	X	X							X	X			X	X
Maguari Stork	—	2		(X)		X												

[1] X indicates the behavior used predominately by a species in an area; (X) indicates a behavior used less frequently.

TABLE 5

FORAGING SOCIALITY OF WADING BIRDS IN EVERGLADES AND LLANOS[1]

	Flocking		Paired		Single	
	E	L	E	L	E	L
American Bittern					X	
Least Bittern					X	
Great Blue Heron					X	
White-necked Heron						X
Great Egret	X	X				
Snowy Egret	X	X				
Little Blue Heron	X				X	X
Tricolor Heron					X	
Cattle Egret	X	X				
Green-backed Heron					X	X
Whistling Heron				X		
Capped Heron				X		
Black-crowned Night Heron					X	X
Yellow-crowned Night Heron					X	X
Rufescent Tiger-Heron						X
Buff-necked Ibis				X		
Sharp-tailed Ibis				X		
Green Ibis				X		
Bare-faced Ibis		X				
White Ibis	X	X				
Scarlet Ibis		X				
Glossy Ibis	X	X				
Roseate Spoonbill	X	X				
Jabiru		X				
Wood Stork	X	X				
Maguari Stork						X

[1] Species categorized by their predominant behavior.

birds, i.e., American and Least Bitterns, Rufescent Tiger-Heron, and Green-backed Heron, prefer dense plant cover. Other species tend to feed in the open marsh and pools typical of savannas.

Time of foraging.—Most wading birds are diurnal, and some can feed nocturnally as well. The latter include the Great Blue Heron and Wood Stork. Some species, however, typically forage at night. In both areas, these include the two night-herons. This activity pattern distinguishes the night-herons from similarly sized herons that forage during the day.

Feeding behavior.—The behavioral aspects of the foraging niche of wading birds in savannas are complex because each species can be flexible in its behavior and activity level in response to habitat and prey availability. One aspect of a bird's response is its behavioral repertoire and the relative frequency of use of each behavior. We recorded the behaviors we have observed in each area and determined which were used most frequently (Table 4).

It appears that wading birds have a larger repertoire of foraging behaviors in the Everglades than in the Llanos. On average, herons had repertoires of 8.0 behaviors per species in the Everglades and 4.1 behaviors per species in the Llanos. For ibises the comparison is 5.0 behaviors per species in the Everglades versus 2.6 in the Llanos. For storks it is 7.0 versus 3.3. Such differences between the two areas also hold when individual species that occur in both areas are compared. The known behaviors of various species in the Everglades and Llanos respectively are: Great Egrets, 10 and 7; Snowy Egrets, 20 and 7; Little Blue Herons, 13 and 6; Cattle Egrets, 13 and 7; Roseate Spoonbill, 7 and 3. Such differences in known repertoires are not a function of observation effort, which was about the same in both areas, but rather seem to reflect differences in the diversity of behaviors needed to forage in each area.

The predominant behaviors used by species that occur in both areas were similar (Table 4), and most of these were the relatively inexpensive techniques that involve standing or walking slowly. It appears that birds in the Everglades have additional, rarer and usually more

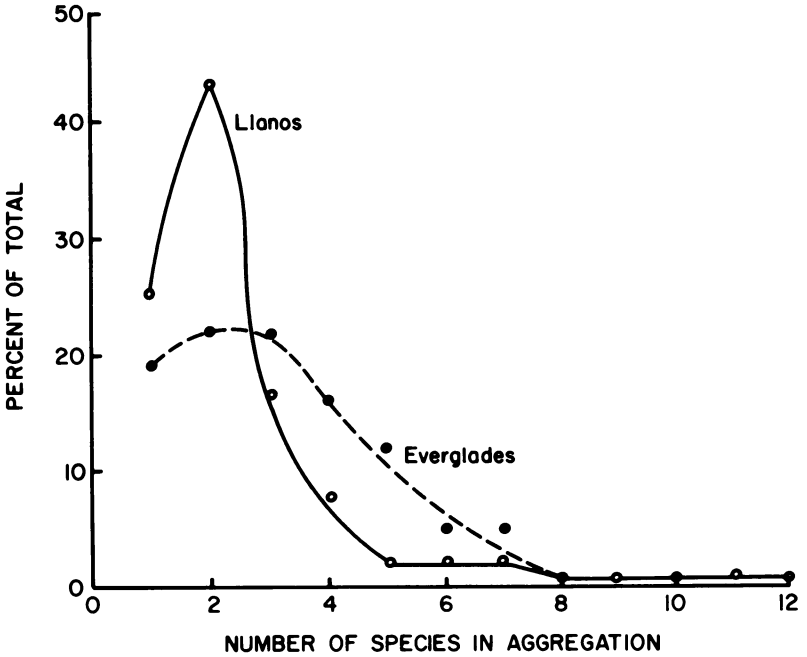

FIG. 7. The percentage of all aggregations censused in the Florida Everglades (solid circles) and Venezuelan Llanos (hollow circles), respectively, that contained specific numbers of species.

energy-demanding behaviors. The higher abundance of prey in the Llanos may make a prey item less difficult to catch and, therefore, specialized behavior unnecessary.

Wading birds typically forage in tropical savannas and similar areas by aggregating at locations of high food availability (Kushlan 1976a; Caldwell 1981). A previous comparison of aggregation structure in a temperate marsh and in the Everglades demonstrated that the maximum and mean number of species in aggregations was higher in the Everglades with its greater overall wading bird species richness (Kushlan 1978a). This led to the hypothesis that aggregation diversity would continue to increase with increasing species richness. The results of the current study do not support this expectation, entirely; mean species richness of aggregations in the Llanos, 2.7 species per aggregation, did not surpass that of aggregations in the Everglades, 3.1 species per aggregation (Fig. 7). This result was due to the addition, in the Llanos, of species that occur primarily in mated pairs (Table 5), tallied as single-species aggregations. Such species, which appear to hold large, generally exclusive feeding territories and remain in pairs year round, include two herons and two ibises and represent a strategy that does not occur in the Everglades.

Maximum species richness, however, did increase in Llanos aggregations (Fig. 7), and one may hypothesize that interspecific interactions would be more common and complicated in such a species-rich community, thereby in part determining feeding behavior. For one such behavior, prey robbing (Kushlan 1978b; Caldwell 1980), we were able to obtain comparable information in both areas. However, contrary to expectations, prey robbing interactions appeared to be more complex in the Everglades than in the Llanos (Fig. 8). The species involved do not appear to be a factor contributing to the differences observed between areas, in that all the species shown to interact in the Everglades are also present in Llanos (if Great Blue Heron = Cocoi Heron). Rather, it seems likely that differences in prey robbing may be related to food availability. We suggest that the higher prey availability in the Llanos makes such interactions unnecessary. Thus, direct competition among species in the Llanos may be mitigated for much of the year by higher prey levels there.

Prey.—The prey consumed by a wading bird is a crucial component of its foraging niche. If one considers higher taxonomic categories of prey, some remarkable similarities in prey

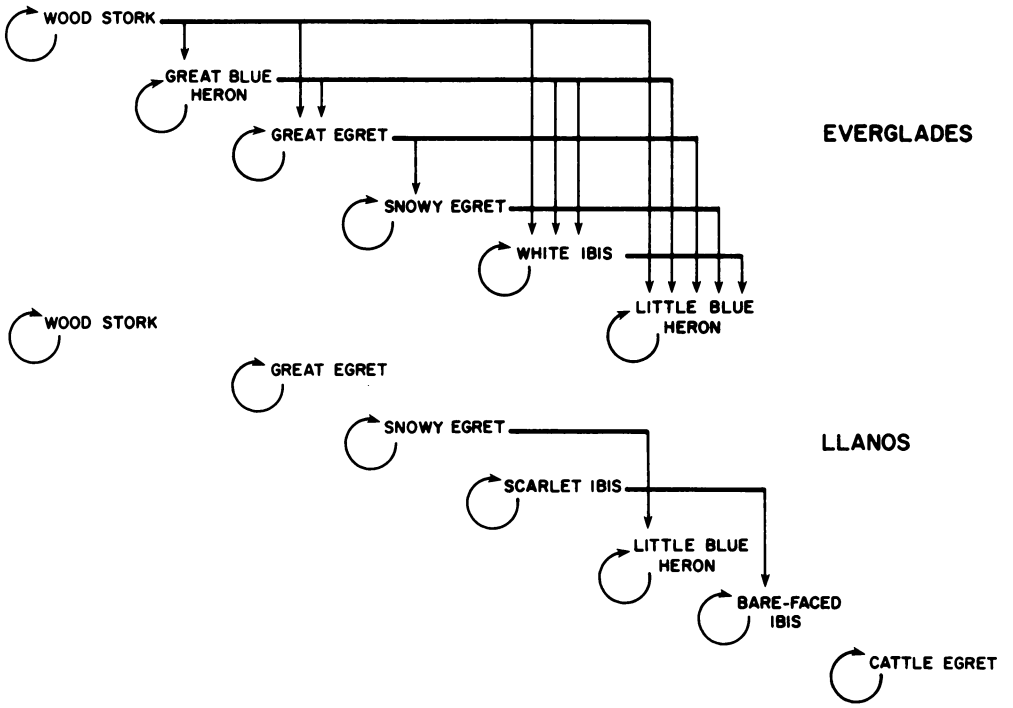

FIG. 8. Prey robbing interactions in the Everglades and Llanos. Arrows show direction of prey robbing from robber to victim.

consumption exist for wading birds that occur in both areas (Table 6). Wood Storks in both areas consume fish almost exclusively. Fish predominate in the diets of Great Egrets, Snowy Egrets, and Little Blue Herons in both areas. White Ibis exhibited the greatest difference in prey selection taking insects in the Llanos and crustaceans and fish in the Everglades. This difference seems to support the interpretation that ibises forage more terrestrially in the Llanos and more aquatically in the Everglades (Table 3).

In that the primary prey of most herons and storks is fishes, it is useful to examine the fish faunas of the two savannas. The Everglades fish fauna of 80 species is less than 30 percent as rich as the Llanos fauna of 286 species, and the species compositions of the two faunas are completely different (Mago-Leccia 1967, 1970; Loftus and Kushlan in press), meaning that the species of fish consumed by wading birds in the two areas by necessity differed taxonomically (Table 7).

Nonetheless the diets of wading birds in the two areas often contain ecologically-similar prey. For example, South American cichlids and North American centrarchids (sunfishes) are to a considerable extent ecological equivalents and are consumed by Great Egrets and Wood Storks where they occur. Similarly, cyprinodontid killifishes and poeciliid livebearers in the Everglades are similar to tetras (*Hyphessobrycon*; characins) and lebiasinids in the Llanos. These fishes are eaten by Great Egrets and Snowy Egrets in their respective locations. Wood Storks consume catfishes in both areas, callichtyid armored catfish (*Hoplosternum littorale*) in the Llanos and ictalurid bullheads in the Everglades.

Some dietary components in the Llanos have no analogue in the Everglades. For example, Great Egrets consume eel-like gymnotid electric fish (*Gymnotus carapo*) in the Llanos, and Snowy Egrets consume deep-bodied (*Markiana nigripinnis*) and compressed-bodied (*Ctenobrycon spirulus*) characins. There are no similar species in the Everglades.

Part of the dietary differences may owe to differing adaptations of the fish species. In the Llanos Snowy Egrets consume curimatas, a group similar to *Notemigonus*, which occurs in south Florida. However, *Notemigonus* is not eaten in the Everglades, because it occurs in

TABLE 6

DIETS OF FIVE SPECIES OF WADING BIRDS OCCURRING IN BOTH THE EVERGLADES (E) AND THE LLANOS (L)

	Percentage of total diet[1]									
	Great Egret		Snowy Egret		Little Blue Heron		White Ibis		Wood Stork	
	E	L	E	L	E	L	E	L	E	L
Worms							T			
Millipedes							T			
Spiders			T		T					
Crustaceans	T	14	15	5	21		52		T	T
Insects	T	8	4	6	4	21	14	100		
Snails	T				T		7			
Amphibians	3	3	T		11		2			
Reptiles	T	2								
Fishes	94	72	79	89	64	79	19		99	100

[1] Percentage of prey items consumed, except for White Ibis, which is expressed as the percentage biomass consumed because of the high degree of masceration. T = less than 2 percent of diet.

deep open water in the wet season and, being very susceptible to deoxygenation, is among the first fish to die during drying periods (Kushlan 1974b). Such factors make these fishes relatively unavailable to wading birds in the Everglades marsh.

The way in which fishes accommodate to the dry season may differ significantly between the two study areas. Llanos fishes generally possess adaptations for survival in deoxygenated waters; such adaptations are rare in Everglades fishes. As a result, dry season conditions affect large fishes in the Everglades more severely than in the Llanos (Kushlan 1976b). This difference influences the standing stocks and sizes of fishes available to birds in the two areas.

Other than for the Wood Stork, large fishes play an unimportant role in the diets of Everglades wading birds. Even the Wood Stork, capable of eating fish in excess of 22 cm long, consumed prey that averaged only 2.6 cm long (Ogden et al. 1976) in the Everglades. In contrast, large fishes in the Llanos are eaten by several birds including White-necked Herons, Great Egrets, and Jabiru, Maguari, and Wood Storks. These birds consume electric fishes, river eels (*Synbranchus marmoratus*), armored catfish, trahiras, caribe (*Serrasalmus*) (a characin), and large cichlids. The only equivalently-sized species in the Everglades marsh, bass (*Micropturus salmoides*), bowfin (*Amia calva*), and gar (*Lepisosteus platyrhincus*), are rare and not often taken by wading birds. Thus, the abundant and diverse large-item component of the fish fauna of the Llanos is not available to wading birds in the Everglades.

DISCUSSION

The Everglades and Llanos share a major portion of their wading bird fauna. However, as might be expected of the more tropically-situated ecosystem, the Llanos supports more species. Although the species compositions of the wading bird communities of both areas are dominated by herons, much of the increase in the Llanos is due to the terrestrial ibises and two very large storks, in addition to the Whistling Heron, a characteristic neotropical savanna species, and the Capped Heron, an Amazonian species.

Differences in the wading bird faunas in these two wetland ecosystems may in part be attributable to historical and biogeographic factors. An impoverishment of the vertebrate fauna in general exists in both the Everglades and the Llanos, and in the Everglades this in part reflects its location at the end of a temperate continental cline of decreasing species richness (Simpson 1964; Robertson and Kushlan 1974; Tramer 1974). Both savannas are also relatively young, perhaps less than 10,000 years old. South American savannas, however, were probably readily re-invaded by tropical species that had persisted in glacial refugia, and as a result the species there have had a longer time to adapt to conditions in fluctuating marshes. This would apply to birds directly as well as to their prey species. In contrast, the Everglades is isolated from South American refugia by a barrier of unsuitable marine habitat, inhibiting the invasion of many species characteristic of neotropical inland marshes, especially those unable to use intervening island and marine habitats of the West Indies. Thus the wading bird community of the Everglades is only a selection of that of South America, and the prey

TABLE 7

COMPARISON OF THE FISHES EATEN BY FIVE WADING BIRDS IN THE EVERGLADES (E) AND LLANOS (L)

	Percentage of total diet									
	Great Egret		Snowy Egret		Little Blue Heron		White Ibis		Wood Stork	
	E	L	E	L	E	L	E	L	E	L
Gar	T[1]								T	
Freshwater eels	T									
Characins		19		21						
Electric-fishes		28								
Suckers	T		T							
Bullheads	T								2	
Killifishes	26		28		12		T		75	
Livebearers	47		50		49		2		13	
Sunfishes	13		T		2				9	
Cichlids	T	19	T	2						83
Sleepers					T					
Lebiasinids		6		32						
Armored catfish										17
Curimatas				34						
Trahiras						79				
Other fishes	8		T		T		16			

[1] T indicates less than 2 percent of diet.

fauna is entirely derived from temperate forms, poorly adapted to fluctuating tropical wetlands. Differing periods of evolutionary time and access, therefore, may be responsible for differing species richness in these systems.

Ecological factors must also have played an important role in structuring the wading bird communities in the Llanos and Everglades, which differ not only in numbers of species, but in their relative abundances as well. The dominance of one species, the White Ibis, in the Everglades and the greater equitability of species in the Llanos may reflect differing responses to resource availability. Higher equitability may suggest that a larger proportion of the wading bird community has accommodated to conditions in the Llanos as a result of niche compression or more likely because of more abundant and diverse resources.

In both the Everglades and the Llanos, differences among species can be characterized along several axes of their foraging niches, including foraging behavior, prey selectivity, and habitat use. In the Everglades a greater range of foraging behaviors are used and the larger herons are more widely separated along a morphological niche dimension. It is possible that direct competition is of greater consequence in structuring this community, an idea supported by the greater complexity of robbing interactions and the higher average number of species that feed together in aggregations. We hypothesize that a lower prey abundance and diversity in the Everglades may decrease the long-term effectiveness of foraging there as contrasted with the Llanos.

Prey selectivity by wading birds results primarily from the size and behavior of their prey. Thus the diets of wading birds in both savannas show a surprising degree of ecological similarity despite taxonomic differences in the prey taken. Although characteristics of the fish faunas converge in the two systems, a greater species richness, including types of fishes not found in the Everglades, occurs in the Llanos, as in many tropical freshwater systems (Lowe-McConnell 1975). This may provide more opportunities for predators and to some extent account for the greater richness of wading bird species in the Llanos. The presence of very large storks, for example, may in part be due to the opportunity to take advantage of the large-sized prey available there.

Another factor that may affect species composition is habitat diversity, which would increase the types of feeding areas available while decreasing the need for niche overlap. The savanna specialists, such as the Buff-necked Ibis, Sharp-tailed Ibis, and Whistling Herons, occur primarily in very shallow to dry habitats near high ground, which is more extensive and continuous in the Llanos than in the Everglades. These species are permanent residents, main-

taining pair-based social and territorial systems not found in the Everglades. Such shallow and dry habitats provide foraging sites for small-sized tactile foraging ibises in the Llanos. These birds often migrate out of the area during the wet season when such habitats are no longer available.

An exception to the pattern of taking advantage of increased foraging opportunities in the Llanos can be seen in the ibises. These species overlap along niche dimensions and in the drying season feed together using similar behaviors and feeding sites. Although additional study of these species is needed (S. Ramos and B. Busto, pers. comm.), we hypothesize that during the dry season prey overlap should be high. However, because prey availability will also be high during these periods, competition may be minor, if it occurs at all. It is possible that differing patterns of habitat use in the wet season may separate the ibis species in the Llanos.

The ecology of hyperseasonal savannas is dominated by the fluctuation in water depths, which results in the seasonal alternation of floods and droughts. Greater fluctuations in water depth occur in the Llanos than in the Everglades, a result of higher rainfall, temperatures, and evapotranspiration, with the more tropical system therefore being the more variable. With a more diverse fish community in the Llanos, prey availability is higher there during the dry season. Because of their adaptations to stressful conditions, more fish species are available to birds in the Llanos later in the dry season, and more species and individuals survive to repopulate the marshes during the following wet season. In general, the maintenance of prey species diversity in tropical savannas depends on the complex interaction of biotic factors and fluctuating water levels. In both the Llanos and the Everglades, fish species richness may be affected by wading birds and crocodilians. During the dry seasons of both areas, deep-water areas provide refugia for fish populations while predation pressure is concommitantly increased.

Wading bird niche relations must therefore be elaborated within a context of seasonal variability of prey and habitat. Many characteristics of wading birds adapt them to such seasonal water depth cycles. Their relatively long legs permit them to use shallowly-flooded marshes, and some species are also able to forage terrestrially. Another important adaptation is seasonal migrations which take birds out of parts of the savannas during the wet season when water is too deep for wading. In the drying season, shorter movements permit foraging at sites where water depths are temporally suitable and prey are locally abundant. These ephemeral but superabundant food supplies, in addition to terrestrial habitat availability, support wading bird populations in the dry season.

Amid the apparently stressful cycles of prey availability, wading bird communities reflect specific accommodations of the species to the savanna environment. That the Llanos and the Everglades differ in the structure of their wading bird communities may be another instance of the general pattern of higher diversity and productivity seen in many tropical ecosystems as contrasted with their more temperate counterparts. In both systems, and probably in tropical savannas in general, it seems clear that cyclical and random fluctuations of environmental factors, together with biogeographic constraints, play primary roles in structuring constituent animal communities.

ACKNOWLEDGMENTS

We thank our many associates, especially C. Casler, K. Dobrowolski, F. Gómez, N. J. León, M. Madriz, C. F. Naranjo, O. T. Owre, J. Pacheco, and J. Pinowski. L. Bulla, W. Loftus, A. Machado, R. Martinez, R. Martinez-E., G. Pereira, D. Rada, and C. R. Robins provided information on prey species. Members of the Grupo de Ecología of the Instituto de Zoología Tropical were always encouraging and supportive, and we especially thank J. Pacheco for making our collaborations possible. E. Szeplaki made critical translations. M. Ramia supplied the Llanos photographs. Financial support was provided by the Maytag Chair of Ornithology at the University of Miami, Consejo de Desarrollo Cientifico y Humanístico of Universidad Central de Venezuela (Projects of C. 05.02/78 and C. 05.4/78), and CONICIT (Projecto Pima 7). We thank P. A. Buckley, G. S. Caldwell, M. S. Foster, M. Gochfeld, T. Jacobsen, C. S. Luthin, and D. Mock for comments and suggestions on the paper.

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