ORNITOLOGÍA NEOTROPICAL
(2022) 33: 124–132
ORIGINAL ARTICLE

DIET AND FOOD RESOURCE PARTITIONING AMONG SIX IBIS SPECIES IN THE VENEZUELAN LLANOS

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Abstract · This work is the first study to provide simultaneous information on the diet of all six ibis species inhabiting the Venezuelan Llanos, which was obtained by analyzing gizzard contents of birds collected in 1979-1982 (between 59 and 11 per species). The percentage of prey number for the ibis species was determined: for the Scarlet/White ibis (*Eudocimus ruber/E. albus*), the main prey were Coleoptera, Diptera, and Heteroptera in the dry season, and Coleoptera and Odonata in the wet season. For the Barefaced Ibis (*Phimosus infuscatus*), main prey included Coleoptera and Ephemeroptera in the dry season, and Oligochaeta, Ephemeroptera, and Coleoptera in the wet season. For the Glossy Ibis (*Plegadis falcinellus*), Spinicaudata, Coleoptera, and plant material were the main items consumed in the dry season, and Coleoptera, Decapoda, Odonata, and Heteroptera in the wet season. For the Sharptailed Ibis (*Cercibis oxycerca*), Pisces, Lepidoptera, Coleoptera, and Orthoptera were mainly consumed in the dry season, and Coleoptera, Orthoptera, and Oligochaeta in the wet season. For the Buffnecked Ibis (*Theristicus caudatus*), main prey were Coleoptera, Orthoptera, Arachnida, and Lepidoptera in the dry season, and Coleoptera and Orthoptera in the wet season. Finally, for Green Ibis (*Mesimbrinibis cayennensis*), we found that Coleoptera, Gastropoda, and Orthoptera were the most consumed in the dry season, without data for the wet season. We also found that rainfall seasonality has a great influence on the prey eaten by the ibises: diet overlap between the dry and wet season varied between 0.07 and 0.45 (Schoener's index), depending on the species. Moreover, diet overlap between pairs of species showed extremely low to medium values (0.13-0.44 in the dry season, 0.03-0.60 in the wet season, according to Schoener's index), which suggests that the coexistence of these species is largely facilitated by food resource partitioning.

Resumen. Dieta y partición de recursos alimentarios entre seis especies de ibis en Los Llanos de Venezuela
Este trabajo es el primero en proporcionar información simultánea sobre la dieta de seis especies de ibis en Los Llanos de Venezuela, obtenida a través del análisis de los contenidos estomacales (entre 59 y 11 por especie) de ejemplares colectados durante 1979-1982. Se determinó el porcentaje del número de presas para las especies de ibis: para los corocoros rojo y blanco (*Eudocimus ruber/E. albus*), las presas principales fueron Coleoptera, Diptera y Heteroptera en la estación seca, y Coleoptera y Odonata en la estación húmeda. Para la zamurita (*Phimosus infuscatus*), Coleoptera y Ephemeroptera en la estación seca, y Oligochaeta, Ephemeroptera y Coleoptera en la estación húmeda. Para el corocoro castaño *(Plegadis falcinellus*), Spinicaudata, Coleoptera y material vegetal en la estación seca, y Coleoptera, Decapoda, Odonata y Heteroptera en la húmeda. Para el tarotaro (*Cercibis oxycerca*), Pisces , Lepidoptera, Coleoptera y Orthoptera en la época seca, y Coleoptera, Orthoptera y Oligochaeta en la húmeda. Para el tautaco (*Theristicus caudatus*): Coleoptera, Orthoptera, Arachnida y Lepidoptera en la época seca, y Coleoptera y Orthoptera en la húmeda. Para el corocoro de monte (*Mesimbrinibis cayennensis*), Coleoptera, Gastropoda y Orthoptera en la estación seca, y no hay datos para la húmeda. También encontramos que la estacionalidad de las lluvias tuvo una gran influencia sobre las presas consumidas: el índice de solapamiento de Schoener entre la estación seca y húmeda varió entre 0,07 y 0,45 dependiendo de la especie. Además, los índices de solapamiento de Schoener entre la dieta de estas especies mostraron valores extremadamente bajos o medianos (0,13-0,44 en época seca, 0,03-0,60 en época húmeda), lo que sugiere que estas especies pueden coexistir en simpatría gracias a la partición de los recursos alimentarios.

Key words*: Cercibis oxycerca · Eudocimus albus · Eudocimus ruber · Mesembrinibis cayennensis · Phimosus infuscatus · Plegadis falcinellus · Theristicus caudatus*

INTRODUCTION

South American ibises are among the least known species of the subfamily Threskiornithinae, despite the fact that they are locally common and most of them live in open habitats (Hancock et al. 1992). Seven of these ibises live in sympatry in the Llanos of Venezuela: four of them —White Ibis (*Eudocimus albus*), Scarlet Ibis (*E. ruber*), Glossy Ibis (*Plegadis falcinellus*), and Barefaced Ibis (*Phimosus infuscatus*)— are predominantly gregarious during foraging, while the other three —Sharptailed Ibis (*Cercibis oxycerca*), Buffnecked Ibis (*Theristicus caudatus*), and Green Ibis (*Mesembrinibis cayennensis*)— are solitary or forage

Submitted 26 April 2022 · First decision 5 July 2022 · Acceptance 15 August 2022 · Online publication 29 September 2022
Communicated by Karolina Fierro-Calderón & Carlos Bosque

Table 1. Diet of the Scarlet/White Ibis in the Venezuelan Llanos (source of information: Aguilera et al. 1993). N = number of prey, %N = percent of prey number, %F = percent of gizzards in which prey were found. [1] Prey items, [2] Gizzards.

Prey type	Dry season			Wet season		
	N	%N	%F	N	%N	%F
Coleoptera	1625	73	98	247	82	92
Adults	1245	72	98	344	81	92
Carabidae	424	25		3	<1	
Curculionidae				2	<1	
Dytiscidae	75	4		1	<1	
Elmidae	38	2				
Staphylinidae	1	<1				
Hydrophilidae	233	14		6	1	
Scarabaeidae	461	27		323	76	
Undeterminined	13	<1		9	2	
Larvae	20	1	15	3	<1	8
Dytiscidae	2	<1		3	<1	
Scarabaeidae	15	<1				
Undetermined	3	<1				
Dermaptera	2	<1	4			
Diptera (larvae)	202	12	4	4	<1	17
Calliphoridae	193	11				
Chironomidae	8					
Culicidae				4	<1	
Undetermined	1	<1				
Heteroptera	99	6	55	4	<1	25
Belostomatidae	44	3		4	1	
Naucoridae	51	3				
Nepidae	3	<1				
Undetermined	1	<1				
Odonata (larvae)	36	2	19	38	9	50
Anisoptera	36	2		38	9	
Orthoptera	11	<1	9	4	<1	17
Ephemeroptera	24	1	4			
Undetermined insect larvae	1	<1	2			
Arachnida	5	<1	11			
Chilopoda	1	<1	2			
Decapoda (crabs)	15	<1	23	8	2	67
Gastropoda	23	1	26	15	4	8
Ampularidae	17	<1		15	4	
Planorbidae	6	<1				
Bivalva	1	<1	2	1	<1	8
Oligochaeta	1	<1	2			
Pisces	32	2	34	2	<1	8
Ciclidae	2	<1				
Lebiasinidae	1	<1				
Synbranchidae	19	1			<1	
Undetermined	10	<1				
Anura	6	<1	13		<1	17
Sauria	1	<1	2			
Ophidia	1	<1	2			
Lygophis lineatus	1	<1				
TOTAL	1726[1]		47[2]		425[1]	12[2]

in small groups (Ogdem & Thomas 1985, Aguilera 1988, Frederick & Bildstein 1992).

The distribution of the White Ibis ranges from coastal North America to Venezuela (Hancock et al. 1992, Heath et al. 2020), while the Scarlet Ibis is distributed from Venezuela to the coast of Brazil (Hancock et al. 1992, Matheu et al. 2020a). The species delimitation of these ibises is not clear: Ramírez et al. (2014) showed that the Scarlet Ibis from Brazil and the North American White Ibis are two different lineages, suggesting that they are separate species and that the contact zone needs further investigation. In the Venezuelan Llanos, both ibis coexist, and the Scarlet Ibis is much more abundant (Ramo & Busto 1987, Aguilera 1988). They nest in the same colonies, where hybridization is very frequent, and show the same breeding behaviour (Ramo & Busto, 1985, 1987). Furthermore, both species show no differences in foraging behaviour or foraging habitat (Frederick & Bildstein 1992); therefore, and following Ramo & Busto (1982), we considered the White and the Scarlet Ibis as a single species (*E. ruber*). It is worth noting that the food habits of the White Ibis are well known in North America (Nesbitt et al. 1974, Kushlan & Kushlan 1975, Kushlan 1979, Bildstein et al. 1990, Boyle et al. 2012, among others), and the diet of the Scarlet Ibis has been studied in Brazil and Venezuela (Aguilera et al, 1993, Olmos et al. 2001, Marín et al. 2003, Martínez 2004).

On the other hand, the Buffnecked Ibis (*Theristicus caudatus*) has two subspecies (Matheu et al. 2020b), and there are data on the food habits of *T. c. caudatus* in southwestern Colombia (Fierro-Calderón 2010) and *T. c. hyperorius* in Uruguay (San Martín 1960). Moreover, the Glossy Ibis is the most widespread species (Hancock et al. 1992, Davis Jr. & Kricher 2020), and its diet has been studied in Cuba (Acosta et al. 1996), Spain (Macías et al 2004), Romania (Petrescu 1999), and Algeria (Samraoui et al. 2012). Lastly, and unlike the rest of the ibis species, available information about the food habits of the Sharptailed, Barefaced, and Green ibises is merely anecdotal (Hancock et al. 1992, Villegas-Retamal 2015, de Lima and Bernardes 2020).

Table 2. Diet of the Barefaced Ibis in the Venezuelan Llanos. N = number of prey, %N = percent of prey number, %F = percent of gizzards in which prey were found. [1] Prey items, [2] Gizzards.

Prey type	Dry season			Wet season		
	N	%N	%F	N	%N	%F
Coleoptera	3740	73	100	334	14	100
Adults	903	18	100	208	9	100
Carabidae	415	8		65	3	
Cicindelidae	2	<1		1	<1	
Curculionidae	1	<1				
Dytiscidae	4	<1				
Elmidae	9	<1				
Gyrinidae	1	<1				
Hydrophilidae	18	<1		1	<1	
Scarabaeidae	442	9		137	6	
Undeterminined	11	<1		4	<1	
Larvae	2836	55	79	126	5	68
Dytiscidae	13	<1		83	4	
Elateridae	1	<1				
Hydrophilidae	104	2		43	2	
Scarabaeidae	2715	53				
Undetermined	3	<1				
Pupa	1	<1	3			
Dermaptera	1	<1	3			
Diptera	35	<1	18	20	<1	36
Chironomidae	1	<1				
Tabanidae	30	<1		3	<1	
Undetermined	4	<1		17	<1	
Heteroptera	12	<1	15			
Belostomatidae	2	<1				
Naucoridae	2	<1				
Undetermined	8	<1				
Lepidoptera	53	1	12	4	<1	9
Odonata	8	<1	15			
Anisoptera	8	<1				
Orthoptera	63	1	38	4	<1	14
Gryllidae	49	1				
Gryllotalpidae	14	<1		4	<1	
Ephemeroptera	1008	20	29	449	19	32
Arachnida	102	2	38			
Decapoda				1	<1	5
Gastropoda	4	<1	12	6	<1	18
Ampularidae	3	<1		5	<1	
Planorbidae	1	<1		1	<1	
Oligochaeta	126	2	24	1521	65	82
Pisces	4	<1	3			
Synbranchidae	4	<1				
TOTAL	5156[1]		34[2]	2339[1]		23[2]

The foraging habitat of these species has been previously described in the Llanos (Kushlan et al. 1985, Frederick and Bildstein 1992); however, except for the Scarlet and the White Ibis (Aguilera et al. 1993), their diets in this region are unknown, even though this aspect is fundamental to understand their ecology. Therefore, we analyzed in this study the food items of these species in an area of sympatry in this geographical region, with the objectives of providing quantitative data on their diet, and describing their seasonal changes and food resource partitioning among species.

METHODS

Diet was analyzed through the examination of gizzard contents (stored in 70% ethanol) of birds deposited in the Museo de Ciencias Naturales of the Universidad Nacional Experimental de Los Llanos Occidentales Ezequiel Zamora (UNELLEZ). Specimens were collected from 1979 to 1982 in Hato El Frío (7º35'N, 68º50'W) and nearby cattle ranches located in the Western Llanos (Apure, Venezuela). This area belongs to the flooded savanna type, according to Ramia's (1967) classification, and its climate is characterized by a seasonal period of rainfall with a mean annual precipitation of 1,650 mm, over 80% of which falls between May and October (González 1997).

We examined 57 gizzards of Barefaced Ibises, 32 of Glossy Ibises, 21 of Sharptailed Ibises, 21 of Buffnecked Ibises, and 11 of Green Ibises. In addition, Aguilera et al. (1993)

Table 3. Diet of the Glossy Ibis in the Venezuelan Llanos. A = Animal prey, N = number of prey, %N = percent of prey number, %F = percent of gizzards in which prey were found, [1] Prey items, [2] Gizzards. B = Plant material, %V = percent of plant volume, %F = percent of gizzards in which plant material was found.

A	Dry season			Wet season		
Prey type	**N**	**% N**	**%F**	**N**	**% N**	**%F**
Coleoptera	736	18	93	42	51	33
Adults	728	18	93	42	51	33
Carabidae	396	10				
Curculionidae				4	5	
Dytiscidae	125	3		2	2	
Elmidae				6	7	
Hydrophilidae	61	2		28	34	
Scarabaeidae	140	3		2	2	
Undeterminined	6	<1				
Larvae	8	<1	7			
Dytiscidae	4	<1				
Hydrophilidae	4	<1				
Diptera (Larvae)	1	<1	3			
Chironomidae	1	<1				
Heteroptera	35	<1	41	7	8	33
Belostomatidae	15	<1	2	7	8	
Naucoridae	19	<1				
Nepidae	1	<1				
Lepidoptera	1	<1	3			
Odonata	26	1	21	8	10	67
Anisoptera	26	1		8	10	
Orthoptera	2	<1	7			
Gryllidae	1	<1				
Gryllotalpidae	1	<1				
Ephemeroptera	26	1	3			
Decapoda (crabs)				23	28	67
Spinicaudata	3207	79	31			
Limnadiidae	1483	37				
Lynceidae	1724	42				
Gastropoda	20	<1	24	3	4	33
Ampularidae				3	4	
Pileidae	17	<1				
Planorbidae	3	<1				
Bivalvia	1	<1	3			
Pisces	8	<1	3			
TOTAL	4063[1]		29[2]	83[1]		3[2]

B	Dry season		Wet season	
Category	**% V**	**%F**	**% V**	**%F**
Plant material	18	69		
Pontederia subovata (stem tubers)	17			
Others	2			
Gastroliths		86		67
TOTAL		29[2]		3[2]

had previously examined 59 gizzards of White and Scarlet Ibises from the same location and years, and we combined this data for the two ibises for the present study with the purpose of documenting dietary overlap with the other species. The content of each gizzard was examined using a binocular microscope, and prey were identified in as much detail as possible following Roth (1973) and Macan (1975).

To study seasonal variation, we divided the year into two periods: a dry season, from November to April, and a wet season, from May to October. Diet overlap was compared among species and seasons using Schoener's index, considering the numerical proportion of each prey type consumed and discarding undetermined items and plant material (resulting in 47 prey categories). This index estimates overlap adequately over most of the potential range of overlap (Linton et al. 1981) and it ranges from 0 (no overlap in the use of food resources) to 1 (complete overlap). We considered five categories of overlap: 0-0.19 = extremely low; 0.20-0.39 = low; 0.40-0.59 = medium; 0.60-0.79 = high; 0.80-0.99 extremely high.

RESULTS

Scarlet/White Ibis. Most of the prey in the dry season were adult coleopterans (73%, Table 1), with two terrestrial families (Scarabeidae and Carabidae) predominating over aquatic

Table 4. Diet of the Sharptailed Ibis in the Venezuelan Llanos. N = number of prey, %N = percent of prey number, %F = percent of gizzards in which prey were found. [1] Prey items; [2] Gizzards.

Prey category	Dry season			Wet season		
	N	% N	%F		% N	%F
Coleoptera	112	27	100	181	35	100
Adults	108	27	100	167	32	100
Carabidae	49	12		41	8	
Curculionidae	2	<1		3	<1	
Dytiscidae	10	2				
Hydrophilidae	12	3				
Scarabaeidae	34	8		123	24	
Undeterminined	1	<1				
Larvae	4	<1	36	14	3	30
Dytiscidae	3	<1		1	<1	
Hydrophilidae				13	3	
Undetermined	1	<1				
Dermaptera	1	<1	9			
Diptera (larvae)	7	2	27			
Chironomidae	1	<1				
Tabanidae	5	1				
Undetermined	1	<1				
Heteroptera	6	1	36	1	<1	10
Belostomatidae	3	<1		1	<1	
Naucoridae	3	<1				
Lepidoptera	112	28	18	2	<1	20
Noctuidae	112	28		2	<1	
Odonata (larvae)	8	2	18			
Orthoptera	23	6	64	172	33	100
Gryllidae	10	2		32	6	
Gryllotalpidae	13	3		140	27	
Arachnida	9	2	27	6	1	40
Chilopoda				1	<1	10
Decapoda				1	<1	10
Gastropoda	2	<1	9	2	<1	20
Pileidae	2	<1		2	<1	
Oligochaeta				151	29	90
Pisces	121	30	100	3	<1	20
Synbranchidae		30			<1	
Anura	1	<1	9			
Leptodactylidae	1	<1	9			
TOTAL	403[1]		11[2]	520[1]		10[2]

forms. Diptera were the second most common prey, with Calliphoridae larvae accounting for 11% of total prey; however, all of them came from only one gizzard. Heteroptera (6%) were the third most common prey, and in the wet season the predominance of adult terrestrial Coleoptera was more pronounced (82% of prey in 81% of gizzards) —especially the family Scarabeidae—, followed by Odonata larvae and Gastropoda (9% and 4%, respectively). The similarity index of food consumed between seasons was low (overlap index of 0.36).

Barefaced Ibis. The most important prey in the diet of this ibis during the dry season were coleopterans (Table 2), namely Scarabeidae larvae (53%) and Carabidae and Scarabeidae adults (8% and 9%, respectively), followed by Ephemeroptera (20%). By contrast, coleopterans were much less consumed in the wet season (14%), when earthworms (Oligochaeta, 65%) were the most consumed prey, and insects in the order Ephemeroptera were consumed in the wet season in similar proportion to that of the dry season (20% and 19%, respectively). The similarity index of food consumed between seasons was low (overlap index of 0.33).

Glossy Ibis. This species was the only one that included plant material in its diet: during the dry season, plants were present in 69% of the gizzards, representing 18% of total diet volume, with *Pontederia subovata* tubers as the main item (Table 3). Moreover, gastroliths were present in 86% of the gizzards. Numerically, clam shrimps (Spinicaudata) were the main animal prey (79%), followed by adult coleopterans (18%). In the wet season, plant material and clam shrimps were not consumed, but a new item was ingested —crabs (*Dilocarcinus dentatus*, 28%)—, and Coleoptera, Heteroptera, Odonata, and Gastropoda were consumed in a greater proportion (51%, 8%, 10%, and 4%, respectively) than in the dry season. The similarity index of food consumed between seasons was extremely low (overlap index of 0.07).

Sharptailed Ibis. During the dry season, the main component in the diet of the Sharptailed Ibis was the freshwater eel (*Synbranchus marmoratus*, 30%), which was found in all gizzards (Table 4). These were followed by caterpillars (Noctuidae, 28%), adult coleopterans (27%) — mainly Carabidae and Scarabeidae—, and orthopterans (6%). During the wet season, eels virtually disappeared from the ibis' diet, but

Table 5. Diet of the Buffnecked Ibis in the Venezuelan Llanos. N = number of prey, %N = percent of prey number, %F = percent of gizzards in which prey were found. [1] Prey items, [2] Gizzards.

Prey category	Dry season			Wet season		
	N	%N	%F	N	%N	%F
Coleoptera	546	43	100	526	56	100
Adults	272	21	100	518	55	100
Carabidae	137	11		28	3	
Cicindelidae	5	<1				
Dytiscidae	2	<1				
Elateridae	1	<1				
Hydrophilidae	5	<1		3	<1	
Scarabaeidae	119	9		487	52	
Undeterminined	3	<1				
Larvae	274	21	40	8	<1	36
Dytiscidae	2	<1		3	<1	
Scarabaeidae	272	21		4	<1	
Undetermined				1	<1	
Dermaptera	2	<1	20	1	<1	9
Diptera				7	<1	27
Tabanidae				6	<1	
Undetermined				1	<1	
Heteroptera	4	<1	30			
Belostomatidae	3	<1				
Undetermined	1	<1				
Lepidoptera	73	6	30	21	2	18
Orthoptera	542	42	100	329	35	100
Acridoidea	5	<1				
Gryllidae	320	25		54	6	
Gryllotalpidae	217	17		175	29	
Arachnida	91	7	100	36	4	36
Chilopoda				2	<1	9
Decapoda	2	<1	20	3	<1	27
Gastropoda				4	<1	36
Pileidae				4	<1	
Anura	12	1	50	5	1	45
Bufonidae	8	<1		2	<1	
Leptodactylidae	4	<1		3	<1	
Sauria	3	<1	20	1	<1	9
Teiidae	3	<1		1	<1	
TOTAL	1276[1]		10[2]	935[1]		11[2]

its absence was compensated by the consumption of more orthopterans (33%), mainly mole crickets (Gryllotalpidae), and by the appearance of a new taxon, Oligochaeta or earthworms (29%). Coleopterans were also present in all gizzards with a higher frequency during the wet season (35%). The similarity index of food consumed between seasons was low (overlap index of 0.26).

Buffnecked Ibis. During the dry season, this species mainly fed on Coleoptera (43%) and Orthoptera (42%), which were present in the whole sample of gizzards. Arachnida were also present in all gizzards, but comprised a low proportion of the prey items (7%) (Table 5). Coleoptera (56%) and Orthoptera (35%) were the main components of its diet during the wet season, with half of the coleopterans being larvae in the dry season and almost all of them adults during the wet season. There was also a seasonal variation in the proportion of orthopteran families in the ibis' diet: crickets were more abundant (Gryllidae, 25%) during the dry season, whereas mole crickets (Gryllotalpidae, 29%) were mostly consumed during the wet season. Furthermore, the proportion of Arachnidae was slightly lower than in the dry season, and the similarity index of food consumed between seasons was medium (overlap index of 0.45).

Green Ibis. Coleoptera was the most important component in the Green Ibis' diet during the dry season —comprising about 75% of the total prey number—, and the order was found in the entire gizzard sample (Table 6). Mostly adults were found among the Coleoptera, with more terrestrial (mainly Sarabeidae and Carabidae) than aquatic families, although aquatic coleopterans were mainly Hydrophilidae larvae (10%). Orthoptera made a minor contribution to the number of prey (6%), and we have no data on the ibis' diet during the wet season.

Interspecific differences. Diet overlaps among species during the dry season were lower than 0.5 (Table 7). The Scarlet/White Ibis and Green Ibis showed the highest diet similarity (0.44, medium overlap), followed by the Barefaced Ibis and Buffnecked Ibis (0.43, medium overlap). By contrast, the Glossy Ibis showed the lowest overlap with other ibises (between 0.13, extremely low, and 0.22, low), and the overlap values of the Sharptailed Ibis with other ibises were intermediate (between 0.19, extremely low, and 0.35, low). In the wet season, the values of overlap indices were slightly higher

Table 6. Diet of the Green Ibis in the Venezuelan Llanos. N = number of prey, %N = percent of prey number, %F = percent of gizzards in which prey were found. [1] Prey items, [2] Gizzards.

Prey category	Dry season		
	N	%N	%F
Coleoptera	438	75	100
Adults	255	44	100
Carabidae	35	6	
Curculionidae	4	<1	
Dytiscidae	25	4	
Hydrophilidae	13	2	
Scarabaeidae	163	28	
Tenebrionidae	14	2	
Undeterminined	1	<1	
Larvae	183	31	36
Dytiscidae	2	<1	
Hydrophilidae	59	10	
Scarabaeidae	121	21	
Undetermined	1	<1	
Diptera	2	<1	9
Heteroptera	18	3	64
Belostomatidae	13	2	
Naucoridae	2	<1	
Nepidae	3	<1	
Lepidoptera	2	<1	9
Odonata	9	2	27
Anisoptera	9	2	
Orthoptera	36	6	45
Gryllidae	23	2	
Gryllotalpidae	13	4	
Hymenoptera	5	<1	9
Formicidae	5	<1	
Undetermined insect larvae	17	3	18
Arachnida	2	<1	18
Gastropoda	39	7	18
Pileidae	4	<1	
Planorbidae	35	6	
Oligochaeta	2	<1	9
Pisces	10	2	18
Synbranchidae	10	2	
Anura	1	<1	9
Leptodactylidae	1	<1	
TOTAL	581[1]		11[2]

than in the dry season (Table 7). Furthermore, the highest overlap index was between the Scarlet/White and the Buffnecked Ibis (0.60, medium), the Sharptailed and the Bufnecked Ibis (0.57, medium), and the Barefaced and the Sharptailed ibis (0.40, medium). The remaining overlap values varied between 0.03 (extremely low) and 0.20 (low). As in the dry season, the Glossy Ibis showed the lowest overlap with other species.

DISCUSSION

Knowing about a species diet is fundamental to understand its ecology. With this in mind, the most valuable contribution of this paper is providing quantitative data on the food consumed by six species of sympatric ibises in the Venezuelan Llanos. All six ibis were mainly insectivorous, although clamp shrimps, worms, crabs, and plant material constituted important diet items for some of them.

In addition, we found differences between our results and those presented in other studies conducted in other sites: for instance, crayfishes, fishes, and crabs were primarily eaten by the White Ibis in North America (Nesbitt et al. 1974, Kushlan & Kushlan 1975, Bidstein et al. 1990), while estuarine crabs constituted the main prey of the Scarlet Ibis in coastal mangroves in Brazil (Olmost et al. 2001, Martínez 2004). In the Llanos, the main prey consumed by both ibises were insects (mainly coleopterans), and crabs and fishes were eaten in a very low proportion. Furthermore, ants were the main prey consumed by the Buffnecked Ibis in Colombia, accounting for 91% of the prey identified in its fecal samples (Fierro-Calderón 2010); nevertheless, this type of prey was absent from this ibis' diet in the Llanos, while coleopterans and orthopterans were the most consumed preys. The Glossy Ibis is the only ibis among the six studied species that fed on plant material in the Llanos, namely *P. subovata* tuber, but there have been reports of it feeding on rice grains in Cuba and aquatic plant seeds in Spain (Acosta et al. 1996, Macías et al 2004). Moreover, the most consumed prey by the Glossy Ibis in the Llanos during the dry season were clam shrimps, which were absent from the ibises studied in Cuba, Spain, and Romania (Acosta et al. 1996, Petrescu 1999, Macías et al 2004). By contrast, amphibians and fishes, consumed

Table 7. Schoener's overlap indices between pairs of species in the Venezuelan Llanos during the dry (November to April) and wet season (May to October).

Dry season	Scarlet/White	Barefaced	Glossy	Sharptailed	Buffnecked	Green
Scarlet/White	1.00	0.22	0.22	0.32	0.24	0.44
Barefaced		1.00	0.13	0.22	0.43	0.30
Glossy			1.00	0.19	0.14	0.13
Sharptailed				1.00	0.35	0.25
Buffnecked					1.00	0.31
Green						1.00

Wet season	Scarlet/White	Barefaced	Glossy	Sharptailed	Buffnecked
Scarlet/White	1.00	0.08	0.20	0.26	0.60
Barefaced		1.00	0.03	0.40	0.10
Glossy			1.00	0.03	0.03
Sharptailed				1.00	0.57
Buffnecked					1.00

by this ibis in Spain, were absent or found in very low proportions in the Llanos.

Due to rainfall seasonality in the Llanos, there is a wet period in which most part of the savanna remains flooded and most of the insects, amphibians, and fishes proliferate (Kushlan et al. 1985, Winemiller 1989), and a dry period, when aquatic fauna is concentrated in the few places that remain flooded. This seasonality had a great influence on the prey eaten by the ibises: all of them fed largely on insects —mainly coleopterans, which were consumed in varying proportions throughout the year—, but other important prey, such as earthworms (Oligochaeta) for the Barefaced and the Sharptailed Ibis, and crabs (*Dylocarcinus dentatus*) for the Glossy Ibis, were consumed mainly in the wet season, while clam shrimps (Spinicaudata) and plant material —important for the Glossy Ibis—, as well as freshwater eels (*Synbranchus marmoratus*) and caterpilars (Noctuidae), in the case of the Sharptailed Ibis, were consumed in the dry season. Furthermore, at an intraspecific level, the overlap indices showed little similarity between seasons in the diets of all ibises, a result likely due to the different availability of foraging habitats and prey types. The highest value reached 0.45 in the Buffnecked Ibis, the most terrestrial of them, thus suggesting that the species is less dependent on flooded habitats. This seasonality is also evident in other wading bird species in the Llanos, such as the Wood Stork (Mycteria americana), as its diet during the dry season is based almost exclusively on fish, whereas during the rainy season it includes crabs, frogs, tadpoles, and aquatic insects (González 1997).

In addition, diet overlap between pairs of ibis species showed extremely low to medium values even in the dry season, when the availability of water could be a limiting factor and the reason for competition among ibises (0.22-0.44 in the dry season, 0.03-0.60 in the wet season). Frederick and Bildstein (1992) found interspecific differences in the use of foraging habitats in the Llanos during the dry season: for instance, the Buffnecked Ibis used dry land, Sharptailed and Barefaced ibises were recorded in moist soils —and occasionally in standing water—, Green Ibises were found in the water's edge, and Scarlet, White and Glossy ibises were almost always standing in the water. Moreover, these authors found considerable overlap in habitat use among the three aquatic foragers: the Scarlet, the White and the Glossy ibises.

Considering their foraging habitats and diets, the partitioning of resources becomes more evident. The greatest diet overlap we found in the dry season was between the Scarlet/White and the Green Ibis (0.44), and between the Buffnecked and the Barefaced Ibis (0.43), all of which used different foraging habitats. On the other hand, although White/Scarlet and Glossy ibises shared the same foraging habitat, diet overlap was very low (0.22). Additionally, the presence of the Glossy Ibis in the Llanos is relatively recent, as the species was first recorded in 1965 (Gochfeld 1973), and it is currently the second most abundant ibis species after the Scarlet Ibis (Aguilera 1988). Furthermore, the low overlap indices with other species with regards to animal preys (0.13-0.22, in the dry season, 0.03-0.20 in the wet season) suggest that the invasion of the Llanos by the Glossy Ibis may have been facilitated by the occupation of an empty food niche, which might help it avoid competition with other ibises. Therefore, all these data suggests that the coexistence of these species is largely facilitated by food resource partitioning.

ACKNOWLEDGEMENTS

We would like to thank the Museo de Ciencias Naturales of the Universidad Nacional Experimental de Los Llanos Occidentales Ezequiel Zamora and the Biological Station of El Frío for allowing the analysis of ibis gizzards. We are also grateful to S. Reid for fish identification, and to M. Báez and J. Gélvez for insect identification. We also thank JA Amat, AJ Green, and three anonymous reviewers for their comments on the manuscript.

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