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SEASONAL AND GEOGRAPHICAL VARIATION IN RESIDENT WATERBIRD POPULATIONS ALONG THE PARAGUAY RIVER

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ABSTRACT. I conducted 47 censuses of resident waterbirds at the Bahía de Asunción, a shallow "bay" of the Paraguay River, from October 1987 to October 1989. I also conducted four shipboard censuses of waterbirds along 859 km of the Paraguay River between Asunción and Bahía Negra during June, August and October 1988 and January 1989. Forty-seven species of waterbirds were recorded during these censuses. Virtually all species of waterbirds were most common during periods of low water levels, from November to March; lower water levels presumably expose a larger surface area of potential feeding habitat. Interannual variation in abundance appears to be related to local patterns of precipitation and habitat availability. The densities of several species increased toward the north as the Paraguay River narrowed. Waterbird populations are good indicators of environmental changes, and should be further censused in order to monitor the effects of chemical contamination and other changes due to the proposed Hidrovia waterway in the river's watershed.
Key words: waterbirds, seasonal, variation, geographical variation, Paraguay River, Paraguay.

Variaciones estacionales y geográficas de las poblaciones de aves acuáticas residentes a lo largo del río Paraguay

RESUMEN. Se realizaron 47 censos de aves acuáticas residentes en la bahía de Asunción, una bahía no muy profunda del río Paraguay. También se realizaron cuatro censos de aves acuáticas desde barcos a lo largo de 859 km del río Paraguay entre Asunción y Bahía Negra durante los meses de junio, agosto y octubre de 1988 y enero de 1989. Durante estos censos se registraron 47 especies de aves acuáticas. Casi todas las especies de aves acuáticas fueron mas comunes cuando los niveles de agua eran bajos, desde noviembre a marzo; los niveles bajos de agua presumiblemente resultan en una mayor superficie de hábitat de forrajeo. La variación interanual de la abundancia parece estar relacionada con los patrones locales de precipitación y de disponibilidad de hábitat. Las densidades de algunas especies aumentaron hacia el norte mientras el ancho del río Paraguay disminuyó. Las poblaciones de aves acuáticas son buenos indicadores de cambios ambientales, y se recomienda realizar más censos para monitorear los efectos de la contaminación química y otros cambios debido al propuesto proyecto Hidrovia en la cuenca del río.
Palabras clave: aves acuáticas, variación estacional, variación geográfica, Río Paraguay, Paraguay.

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Waterbirds of many species are a conspicuous component of wetlands throughout South America. However, relatively little is known about their abundance and seasonal movements in many areas, especially in freshwater wetlands in the interior of the continent (e.g., Olrog 1974, 1975, Antas 1983, 1994, Scott and Carbonell 1986). Because of the accelerating rate of environmental degradation of wetlands in central South America (Alho *et al.* 1988) and the impending development of the Hidrovia navigation, irrigation and flood control projects along the Paraguay River (Bucher *et al.*, 1993), information on waterbird populations is urgently needed in order to monitor the long term responses of waterbird populations to changing environmental conditions.

The Republic of Paraguay, a small country situated in the interior of South America, possesses an abundance of wetlands, most of which are concentrated in the Paraguay River watershed (López 1986). Previous studies of waterbirds in Paraguayan wetlands have focused on live-trapping cormorants (Foster and Fitzgerald 1982), seasonality and ecology of migratory and resident shorebirds at the Bahía de Asunción (Hayes *et al.* 1990, Hayes and Fox 1991), densities of storks, ibises and spoonbills in the Chaco (Brooks 1991), densities of waterbirds along three tributaries of the Paraná River (Hayes and Granizo Tamayo 1992), and censuses of waterbirds in various parts of the country (López 1993). The status of all waterbirds in various geographical regions of Paraguay was briefly summarized by Hayes *et al.* (1991) and Hayes (1995).

The Paraguay River is a broad, sluggish river subject to extreme variations in water levels (Anonymous 1985, Hayes 1991, Hayes and Fox 1991, Bucher *et al.* 1993). In contrast with most rivers, water levels of the Paraguay River are highest during the dry season, from May to August, and lowest during the wet season, from November to January (e.g., Hayes 1991, Hayes and Fox 1991). This inversion of the typical pattern for rivers has been attributed to the "sponge effect" of the Pantanal just north of Paraguay, where wetlands absorb excess water and delay the release of flood waters into the Paraguay River by about six months (Bucher *et al.* 1993). Since 1978, flooding of the Paraguay River has reached unprecedented proportions, perhaps due to the increased runoff of precipitation resulting from extensive deforestation in the river's watershed (Hayes 1991, Hayes and Fox 1991); a similar situation exists along the upper Amazon River (Gentry and López Parodi 1980). Increased flooding may also be due to siltation of the Pantanal wetlands as a result of erosion, thus reducing the effectiveness of the "sponge effect" (Hayes 1995).

The cycle of flooding and drying along the banks of the Paraguay River directly affects the quantity of water and this, the concentrations of aquatic plants and animals in wetlands associated with the river. However, the impact of fluctuating water levels on populations of birds has been reported only for raptors along the Paraguay River (Hayes 1991) and for shorebirds at the Bahía de Asunción (Hayes and Fox 1991). This paper documents seasonal and geographical variation in resident waterbird populations at the Bahía de Asunción and along a major portion of the Paraguay River, and discusses the factors that may cause variation.

STUDY AREAS AND METHODS

I conducted two separate studies of resident waterbird populations along the Paraguay River. The first study examined seasonal variation of waterbird populations during a two-year period at the Bahía de Asunción. The second study examined seasonal and geographical variation of waterbird densities during four shipboard transects conducted during an eight-month period along a major portion of the Paraguay River.

Waterbirds are defined as including all species from avian families generally regarded as aquatic; hence, aquatic species of raptors and passerines are not included. Data for Nearctic shorebird migrants are given elsewhere (Hayes *et al.* 1990, Hayes and Fox

1991). Although some of the resident waterbird species observed appear to be partially migratory, the patterns of their migrations are poorly known (e.g., Antas 1994, Hayes *et al.* 1994, Hayes 1995). All species mentioned in this text have been observed in Paraguay during the austral summer and are presumed to breed in the country (Hayes 1995). The waterbirds were identified by consulting Narosky and Yzurieta (1987).

BAHIA DE ASUNCION

From 20 October 1987 to 30 October 1989, I conducted 47 censuses of resident waterbirds (except kingfishers, which were not censused) at the Bahía de Asunción, a shallow bay of the Paraguay River situated on the outskirts of Asunción. Roughly 4 km long and up to 2 km wide, the bay covers a variable surface area of 2-5 km^2 (Hayes and Fox 1991). Its width and depth vary greatly, due to fluctuating water levels along the Paraguay River. The southern and eastern banks of the bay are densely populated by poor human squatters; as a consequence, garbage and raw sewage are ubiquitous. The northern bank, which is lower in elevation and thus subject to inundation, is inhabited by only a few families when water levels are low; garbage is less conspicuous. A deep water port and government buildings are located on both sides of the bay at the western end, where it opens up onto the main channel of the Paraguay River. The bay is bordered on its northern and eastern edges by small patches of forest and, during low water levels, variable-sized lagoons, ponds, marshes, grassy fields and mudflats. Approximately a dozen humans visit the more pristine parts of the bay each day; fishing is their primary activity, although a few occasionally hunt birds (mostly cormorants and ducks) with rifles.

During each census I covered the same areas of the bay by foot, rowboat or by both methods. With the aid of 7X binoculars, I counted individual birds or estimated their numbers when in large flocks. All birds seen were counted, including those flying overhead; flying birds were most always identifiable by their characteristic size and shape. Care was taken not to count the same birds twice when they flushed to another part of the bay. Because of the highly variable quantity of habitats, densities based on the number of waterbirds per unit area could not be obtained. Most of the censuses (79%) were conducted during the morning. Censuses averaged 150 min in duration (range = 70-255 min). More time was required when large numbers of waterbirds were present.

Data on water levels were obtained from the Dirección de Hidrografía y Navegación of the Armada Nacional in Asunción (Fig.1). Water levels were used as an inverse measure of habitat availability. For species observed during 10 or more counts (>20% of counts), Spearman rank correlation coefficients (r_s statistic; Zar 1984) were used to compare the abundance (defined as number of birds observed during a census) of each species with water levels. To infer whether the prevailing habitat of the bay had an effect on waterbird populations, I compared the abundance of each species when: (1) land was exposed (water level<400 cm) and water levels were falling (prevailing MUD substrate); (2) land was exposed (water level< 400 cm) and water levels were rising (prevailing GRASS substrate); and (3) when the land was covered by WATER (water level>

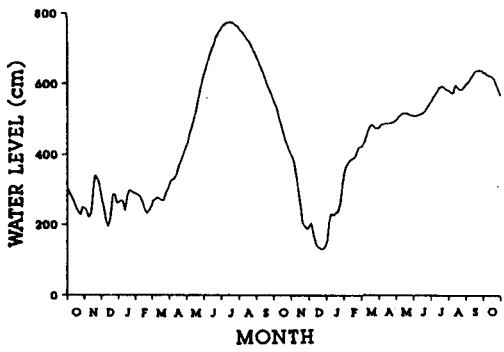

Figure 1. Water levels at the Bahía de Asunción, Paraguay, from October 1987 to October 1989.

400 cm). Kruskal-Wallis tests (*H* statistic; Zar 1984) were used to compare the mean counts of each species during these three habitat conditions; a posteriori multiple comparisons were computed using Mann-Whitney *U* tests (*U* statistic; Zar 1984) with Bonferroni adjustments of the alpha level (divided by number of comparisons, in this case three; see Lentner and Bishop 1986). Mann-Whitney *U* tests were also used to compare abundance during the austral summers of 1987-1988 and 1988-1989, when water levels were < 400 cm.

PARAGUAY RIVER

From June 1988 to January 1989, I conducted four censuses of waterbirds (including kingfishers) from ships along 859 km of the Paraguay River between Asunción and Bahía Negra (Table 1). The habitats along the margins of the Paraguay River comprise sandbars and mudflats when water levels are low, grassy marshes, brush-choked channels and oxbow lakes, wet or dry palm savannas, grasslands (mostly man-made) and subtropical riparian deciduous forest. As one proceeds northward from Asunción, the river gradually narrows, becomes increasingly subdivided by channels, and marshes bordering the river become more extensive. Although human habitations are scattered along the entire length of the river, they become more widely spaced farther north. Most of the habitat along the river's banks remains relatively undisturbed, especially farther north, and the general appearance of the river remains rural except in small ports and in a few densely populated areas (e.g., Asunción, Concepción, Porto Murtiño and Bahía Negra).

All waterbirds seen within 500 m on both sides of a ship-based observation post (8-10 m above the river) were counted during 10 min periods. The censuses were conducted aboard the identical passenger ships Presidente Stroessner (subsequently renamed Bahía Negra) and Presidente Carlos Antonio López. No counts were taken during periods of rain, within 30 min of sunrise or sunset, or in areas densely populated by humans (Asunción, Concepción, Porto Murtinho, Bahía Negra). Ship speed (Table 1) was calculated by timing the interval between fixed km markers. Because the ship often stopped to embark or unload passengers and supplies, I censused waterbirds only while the ship was cruising at full speed.

To determine whether the densities of waterbirds varied geographically, I compared counts along four different geographical sectors: (1) from Asunción, Dept. Central, to Rosario, Dept. San Pedro; (2) from Puerto Tacurú Pytá, Dept. San Pedro, to Puerto Itapucú Mí, Dept. Concepción; (3) from Puerto Valle Mí, Dept. Concepción, to Fuerte Olimpo, Dept. Alto Paraguay; and (4) from Puerto Mihanovick, Dept. Alto Paraguay, to Bahía Negra, Dept. Alto Paraguay (Fig. 2).

Kruskal-Wallis tests were used to compare the density of each species during different seasons and in different geographi-

Table 1. Dates, min of observation, km surveyed, ship speed (km/hr) and water levels (cm) during four censuses along the Paraguay River (from Hayes 1991).

Transect Dates	Min of Obs.	Km Surveyed	Ship Speed (km/hr)	*Water Levels* [1]			
				Asunción	Concepción	Fuerte Olimpo	Bahía Negra
14-17 June 1988	580	138.2	14.3	706 +	823 +	958 -	685 -
09-11 Aug. 1988	680	159.8	14.1	739 -	763 -	823 -	583 -
25-28 Oct. 1988	780	195.0	15.0	425 -	417 -	432 -	298 -
24-27 Jan. 1989	870	185.6	12.8	260 +	316 +	346 +	247 +

[1] Plus sign (+) denotes rising water levels; minus sign (–) denotes falling water levels. The zero mark is arbitrary at each site; hence, comparisons between sites are relative rather than exact.

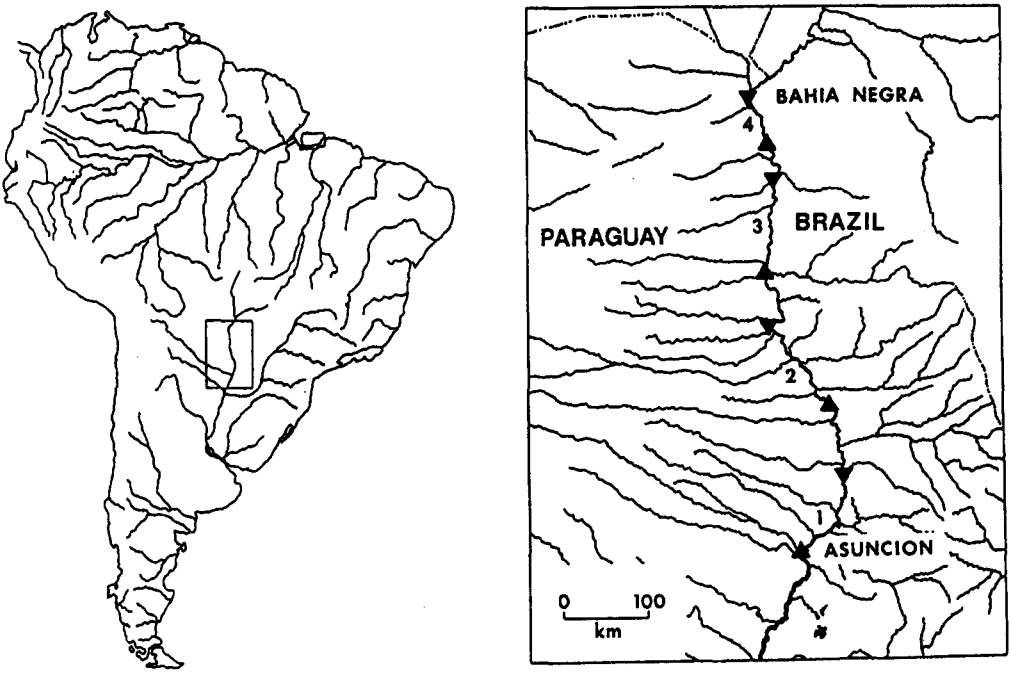

Figure 2. Major South American river systems, and Paraguay River (inset) showing the locations of geographical sectors 1-4. From Hayes (1991); used with permission of Journal of Raptor Research.

cal sectors. Chi-square tests (X^2 statistic; Zar 1984) were used to compare the number of 10 min count periods in each geographical sector during the four censuses. All statistical tests were computed with Statistix 3.1 software (Anonymous 1990).

RESULTS

Forty-seven species of resident waterbirds were recorded during both studies combined. The English and scientific names of these species are given in Table 2.

Table 2. English and scientific names of birds recorded during censuses at the Bahía de Asunción and along the Paraguay River. The nomenclature and sequence of species follow Hayes (1995).

English Name	Scientific Name	English Name	Scientific Name
Least Grebe	*Tachybaptus dominicus*	Plumbeous Ibis	*Theristicus caerulescens*
Pied-billed Grebe	*Podilymbus podiceps*	Buff-necked Ibis	*Theristicus caudatus*
Neotropic Cormorant	*Phalacrocorax brasilianus*	Roseate Spoonbill	*Ajaia ajaja*
Anhinga	*Anhinga anhinga*	Jabiru	*Jabiru mycteria*
Rufescent Tiger-Heron	*Tigrisoma lineatum*	Wood Stork	*Mycteria americana*
Whistling Heron	*Syrigma sibilatrix*	Maguari Stork	*Ciconia maguari*
Cocoi Heron	*Ardea cocoi*	Southern Screamer	*Chauna torquata*
Great Egret	*Casmerodius albus*	Fulvous Whistling-Duck	*Dendrocygna bicolor*
Snowy Egret	*Egretta thula*	White-faced Whistling-Duck	*Dendrocygna viduata*
Cattle Egret	*Bubulcus ibis*	Black-bellied Whistling-Duck	*Dendrocygna autumnalis*
Striated Heron	*Butorides striatus*	Muscovy Duck	*Cairina moschata*
Black-crowned Night-Heron	*Nycticorax nycticorax*	White-cheeked Pintail	*Anas bahamensis*
Bare-faced Ibis	*Phimosus infuscatus*	Silver Teal	*Anas versicolor*
White-faced Ibis	*Plegadis chihi*	Red Shoveler	*Anas platalea*

(Table 2. Cont.)

English Name	Scientific Name	English Name	Scientific Name
Ringed Teal	*Callonetta leucophrys*	Black-necked Stilt	*Himantopus mexicanus*
Rosy-billed Pochard	*Netta peposaca*	Wattled Jacana	*Jacana jacana*
Brazilian Duck	*Amazonetta brasiliensis*	South American Snipe	*Gallinago paraguaiae*
Giant Wood-Rail	*Aramides ypecaha*	Large-billed Tern	*Phaetusa simplex*
Purple Gallinule	*Porphyrula martinica*	Yellow-billed Tern	*Sterna superciliaris*
Common Moorhen	*Gallinula chloropus*	Black Skimmer	*Rynchops niger*
White-winged Coot	*Fulica leucoptera*	Ringed Kingfisher	*Ceryle torquata*
Limpkin	*Aramus guarauna*	Amazon Kingfisher	*Chloroceryle amazona*
Southern Lapwing	*Vanellus chilensis*	Green Kingfisher	*Chloroceryle americana*
Collared Plover	*Charadrius collaris*		

BAHIA DE ASUNCION

Seasonal variation. Forty-two species of resident waterbirds were recorded at the Bahía de Asunción. Although all three species of kingfishers were recorded, they were not censused. Of 17 species observed during 10 or more censuses (>20% of censuses), the abundance of all 17 was negatively correlated with water levels at the Bahía de Asunción (Table 3). None was positively correlated with water levels. The abundance of all 10 species recorded during 5-9 censuses (10-20% of censuses) appeared to be greater during periods of low water (Table 3).

The temporal variation in abundance of most species recorded during five or more counts is presented in Figs. 3-6. Data for the Southern Lapwing, Collared Plover, Black-necked Stilt and Wattled Jacana were presented in Hayes and Fox (1991), and are not repeated here. In apparent contrast with most waterbirds, the duck species tended to be most abundant in fall and spring.

Eleven species of waterbirds were observed during less than five censuses: Least Grebe, Pied-billed Grebe, Anhinga, Jabiru, Southern Screamer, Fulvous Whistling-Duck, Muscovy Duck, White-cheeked Pintail, Red Shoveler, Giant Wood-Rail, Common Moorhen and South American Snipe. Of these, only the Anhinga and Southern Screamer were seen during high water levels.

The abundance of all 17 species of waterbirds recorded during 10 or more censuses varied during different habitat conditions.

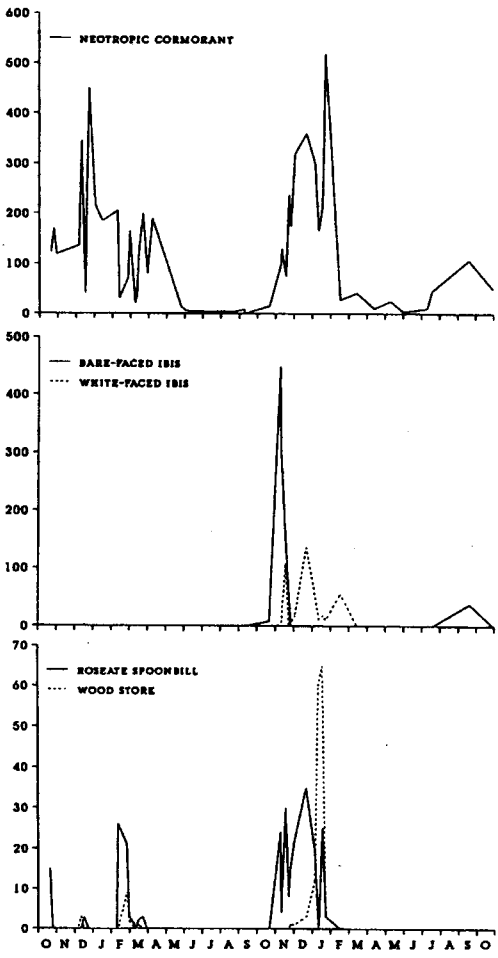

Figure 3. Abundance (y-axis) of Neotropic Cormorant, Bare-faced Ibis, White-faced Ibis, Roseate Spoonbill and Wood Stork at the Bahía de Asunción from October 1987 to October 1989 (x-axis).

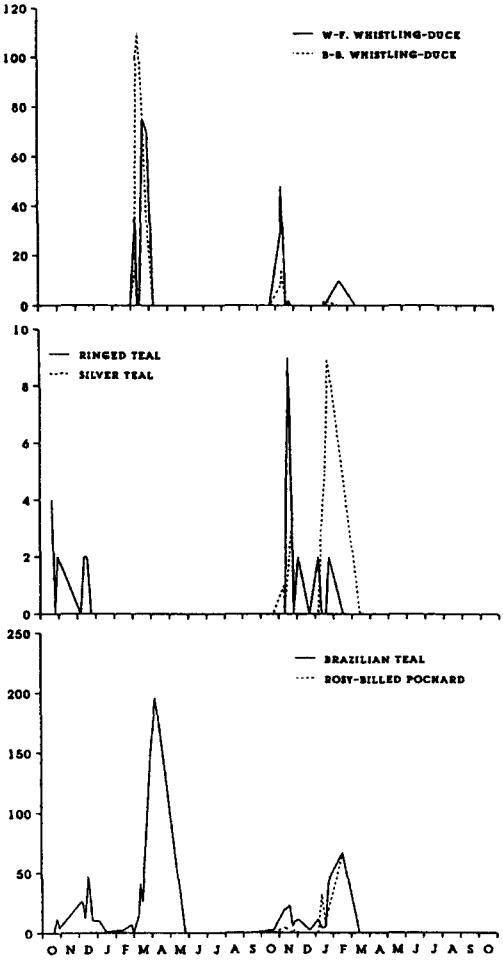

Figure 4. Abundance (y-axis) of six species of ducks (Anatidae) at the Bahía de Asunción from October 1987 to October 1989 (x-axis).

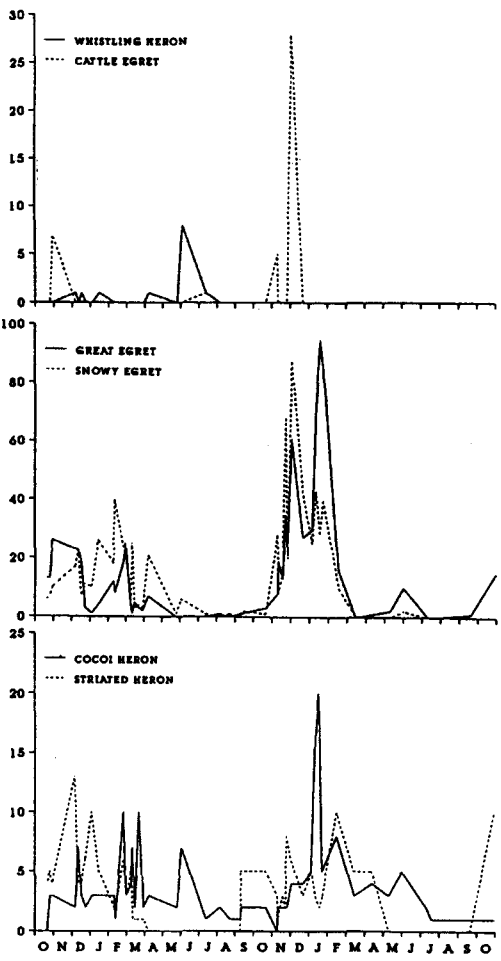

Figure 5. Abundance (y-axis) of six species of herons (Ardeidae) at the Bahía de Asunción from October 1987 to October 1989 (x-axis).

All were more common during periods when land was exposed (water level <400 cm; usually November-March) than during periods of high water (usually April-October; Table 3).When land was exposed, only the Large-billed Tern was significantly more common when the water was rising (GRASS condition), and none was more common when the water was receding (MUD condition; Table 3).

Interannual variation. The abundance of several species of waterbirds differed between the austral summers of 1987-1988 (n = 19) and 1988-1989 (n = 12). Of the 17 species observed during 10 or more censuses (>20 % of censuses), only the Yellow-billed Tern was more common during the summer of 1987-1988 ($U = 53.5$, $P < 0.01$). Six species were more common during the summer of 1988-1989: Great Egret ($U = 31.5$, $P < 0.001$), Snowy Egret ($U = 44$, $P < 0.01$), White-faced Ibis ($U = 0$, $P < 0.001$), Roseate Spoonbill ($U = 45$, $P < 0.01$), Limpkin ($U = 60$, $P < 0.01$) and Black-necked Stilt ($U = 6$, $P < 0.001$). The abundance of 10 spe-

cies did not vary between the summers of 1987-1988 and 1988-1989: Neotropic Cormorant ($U = 79.5, P > 0.15$), Brazilian Duck ($U = 113.5, P = 1.0$), Cocoi Heron ($U = 97.5$, $P > 0.50$), Striated Heron ($U = 111.5$, $P > 0.90$), Wood Stork ($U = 67.5$, $P > 0.05$), Southern Lapwing ($U = 111.0$, $P > 0.90$), Collared Plover ($U = 104.5$, $P > 0.70$), Wattled Jacana ($U = 73$, $P > 0.10$), Large-billed Tern ($U = 67$, $P > 0.05$) and Black Skimmer ($U = 106$, $P > 0.75$).

Of the species observed during 5-10 censuses, the Whistling Heron was recorded only during the summer of 1987-1988, and the Bare-faced Ibis, Silver Teal and Rosy-billed Pochard were recorded only during the summer of 1988-1989; the Cattle Egret, White-faced Whistling-Duck, Black-bellied Whistling Duck, Ringed Teal, Purple Gallinule and White-winged Coot were recorded during both summers.

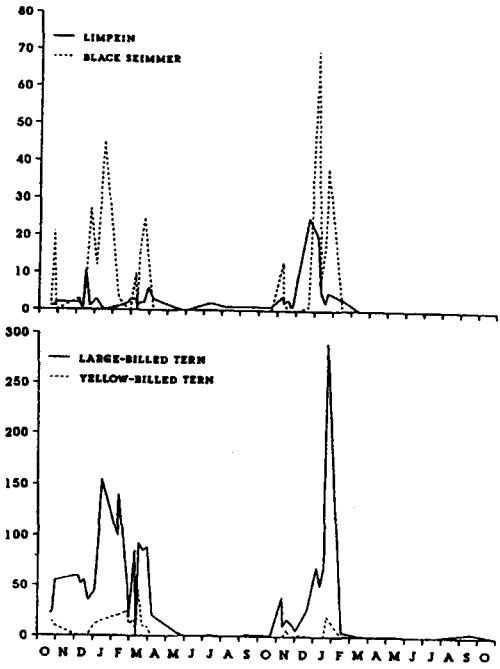

Figure 6. Abundance (y-axis) of Limpkin, Black Skimmer, Large-billed Tern and Yellow-billed Tern at the Bahía de Asunción from October 1987 to October 1989 (x-axis).

PARAGUAY RIVER

Seasonal variation. Thirty-eight species of waterbirds were recorded during this study (Table 4). Of 21 species with sufficient data for statistical analysis (observed during >20% of 10 min count periods; n = 291), the abundance of 18 (86%) varied seasonally, with three being most common during the August census, 10 during October and five during January (Table 4; includes both Snowy and Cattle Egrets, whose data were combined because of difficulty in identification from a distance). None was most common in June, when water levels were highest.

Geographical variation. Because the number of 10 min count periods in each sector varied during the four censuses ($X^2 = 27.1, df = 9, P < 0.002$), tests for geographical variation in abundance were computed for each census and for all censuses combined. When all censuses were combined, geographical variation in abundance was documented for 11 species, with three species being most abundant in sector 3 and eight in sector 4; none was most abundant in sectors 1 or 2 (Table 5; see sectors in Fig.2). Of these 11 species, tests during each census revealed significantly higher densities in sectors 3 or 4 during one or more censuses for each species, with only two exceptions: Great Egret densities were greatest in sector 2 during the August census ($H = 12.7$, $P < 0.01$), and Wood Stork densities did not vary geographically during any single census.

The abundance of several species which did not vary geographically when all data were combined did vary significantly during one or two censuses (Table 5). Southern Screamer densities were greatest in sector 2 during the June census; Snowy/Cattle Egret densities were greatest in sector 4 during the June census and in sector 1 during the January census; and Wattled Jacana densities were greatest in sector 3 during the August census (Table 5).

Table 3. Correlation coefficients (r_s) between abundance and water level, mean number of individuals/census during different habitat conditions, and results of statistical tests comparing means during different habitat conditions (M = mud, G = grass and W = water) for 27 species of waterbirds observed during five or more counts at the Bahía de Asunción. Statistical tests are given only for species observed during 10 or more censuses.

Species	r_s	Birds / Count			MxGxW	MxG
		Mud	Grass	Water	*H*	*U*
Neotropic Cormorant	-0.733***	190.7	170.4	21.6	25.48***	98.0
Whistling Heron	—	0.1	0.2	0.6	—	—
Cocoi Heron	-0.382**	2.6	5.7	2.4	9.79**	61.0
Great Egret	-0.816***	23.5	21.7	2.2	24.71***	68.5
Snowy Egret	-0.764***	27.7	19.3	0.9	30.27***	101.5
Cattle Egret	—	3.3	0.1	0.1	—	—
Striated Heron	-0.612***	4.7	3.7	1.9	8.67*	90.0
Bare-faced Ibis	—	79.9	0.0	2.9	—	—
White-faced Ibis	-0.473**	23.7	7.8	0.0	11.03**	82.5
Roseate Spoonbill	-0.591***	12.8	5.6	0.0	15.52***	78.0
Wood Stork	-0.588***	0.7	8.0	0.0	7.35**	102.0
White-faced Whistling-Duck	—	6.7	10.0	0.0	—	—
Black-bellied Whistling-Duck	—	1.8	17.4	0.0	—	—
Silver Teal	—	0.7	1.2	0.0	—	—
Ringed Teal	—	1.9	0.3	0.0	—	—
Rosy-billed Pochard	—	1.0	6.5	0.0	—	—
Brazilian Duck	-0.524***	12.0	37.9	0.1	27.96***	95.0
Purple Gallinule	—	0.1	0.3	0.0	—	—
White-winged Coot	—	0.0	1.6	0.0	—	—
Limpkin	-0.523***	4.2	3.9	0.4	20.42***	95.0
Southern Lapwing	-0.757***	13.0	18.8	0.5	32.64***	67.0
Collared Plover	-0.683***	26.3	67.6	0.0	32.72***	56.5
Black-necked Stilt	-0.476**	50.2	35.0	1.5	14.10***	101.0
Wattled Jacana	-0.648***	22.0	29.1	4.1	28.25***	73.5
Large-billed Tern	-0.619***	28.0	76.9	0.8	30.72***	50.5#
Yellow-billed Tern	-0.299*	3.9	10.6	0.1	12.16**	78.0
Black Skimmer	-0.387**	3.5	15.5	0.0	19.86***	61.5
Number of censuses	—	12	19	16	—	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, # $P < 0.0167$

DISCUSSION

Seasonal variation. Virtually all species of waterbirds at the Bahía de Asunción were most common during periods of low water. This is hardly surprising given that most of these species usually forage in relatively open areas while wading in shallow water. Lower water levels expose a larger surface area of potential feeding habitat, and also concentrate prey (e.g., fish) in smaller areas where they may be more easily captured and, in the case of dessicating ponds, may not be able to escape. The large areas of land exposed during low water also provide birds with nesting or resting areas; this was especially apparent for the Neotropic Cormorant, Large-billed Tern, Yellow-billed Tern and Black Skimmer. The greater abundance of duck species during fall and spring suggest seasonal movements along the river, but may simply coincide with periods of optimal foraging conditions for these birds.

The greater abundance of the Large-

Table 4. Linear densities of waterbirds along the Paraguay River during different seasons. A plus sign (+) indicates that the species was observed during the census, but not during a 10 min count period. Statistical comparisons (Kruskal–Wallis tests) between months are given only for species observed during > 20% of 10 min count periods (n = 291).

	Birds/10 km				
Species	**June**	**Aug.**	**Oct.**	**Jan.**	***H***
Pied-billed Grebe	—	—	—	0.1	—
Neotropic Cormorant	2.8	45.6	305.0	67.8	133.6***
Anhinga	1.6	3.4	9.0	1.2	117.1***
Rufescent Tiger-Heron	0.1	0.1	0.5	—	—
Whistling Heron	+	1.1	—	0.2	—
Cocoi Heron	6.6	4.9	22.2	17.7	82.0***
Great Egret	8.1	13.0	133.1	4.6	106.5***
Snowy/Cattle Egret	3.9	9.6	84.1	2.4	102.8***
Striated Heron	0.2	0.2	3.0	0.3	10.3*
Black-crowned Night-Heron	1.0	—	1.2	+	—
Bare-faced Ibis	0.9	0.8	5.9	—	81.6***
White-faced Ibis	—	—	—	11.8	—
Plumbeous Ibis	—	—	0.2	+	—
Buff-necked Ibis	0.2	0.1	+	—	—
Roseate Spoonbill	—	—	2.4	0.1	41.4***
Jabiru	+	0.2	1.0	1.5	11.3*
Wood Stork	—	—	0.3	7.9	45.0***
Maguari Stork	0.3	0.3	2.6	3.2	19.0***
Southern Screamer	1.7	1.2	1.5	1.4	4.2
White-faced Whistling-Duck	—	—	4.8	0.5	—
Black-bellied Whistling-Duck	—	—	8.0	1.1	—
Muscovy Duck	+	0.1	0.2	0.2	—
Ringed Teal	—	0.2	—	—	—
Rosy-billed Pochard	0.1	—	—	—	—
Brazilian Duck	—	0.3	0.2	—	—
Unidentified duck	—	—	1.4	0.3	—
White-winged Coot	—	0.1	—	—	—
Limpkin	0.4	0.5	0.6	0.3	5.4
Southern Lapwing	0.7	2.9	1.8	0.4	16.7***
Collared Plover	—	0.1	—	—	—
Black-necked Stilt	0.1	0.4	0.1	0.5	—
Wattled Jacana	1.0	2.9	0.2	0.3	9.5*
Large-billed Tern	0.1	0.6	4.4	28.7	61.2***
Yellow-billed Tern	0.1	1.9	19.1	25.3	43.0***
Black Skimmer	0.4	0.5	18.3	11.0	14.1**
Ringed Kingfisher	1.7	4.8	3.1	0.9	20.2***
Amazon Kingfisher	0.6	0.5	0.9	0.4	7.1
Green Kingfisher	0.3	—	0.1	0.1	—
Number of 10 min counts	58	68	78	87	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

billed Tern during periods when the water was rising and the Bahía de Asunción was dominated by a grass substrate, as well as along the Paraguay River in January, may coincide with periods of optimal foraging conditions or may be related to nesting activities (e.g., postbreeding dispersal from their breeding colonies).

Along the Paraguay River, many species of waterbirds were most abundant in October, even though water levels were lower (but rising) in January. As with the Bahía de Asunción, extensive mudflats were exposed along the river's banks in October, whereas tall grasses covered the same areas in January. The Wood Stork, Maguari Stork and Jabiru, all of which prefer feeding in tall grass marshes rather than mudflats, were

Table 5. Mean number of birds per 10 min count period along four geographical sectors of the Paraguay River. Unless stated otherwise, data during all censuses are combined. Only species observed during > 20% of count periods (n = 291) are included.

Species	1	2	3	4	*H*
Neotropic Cormorant	18.7	19.9	24.6	110.5	27.0***
Anhinga	0.3	0.6	1.7	1.0	8.6*
Cocoi Heron	1.8	1.9	4.4	8.8	57.5***
Great Egret	1.7	11.8	7.1	50.4	16.0**
Snowy/Cattle Egret	2.7	3.4	3.5	2.3	3.2
June census	1.0	1.3	0.0	4.0	17.8***
January census	1.1	0.3	0.4	0.3	9.9*
Striated Heron	< 0.1	< 0.1	0.1	2.9	59.1***
Bare-faced Ibis	0.4	1.2	11.5	0.0	15.6***
Roseate Spoonbill	0.1	0.2	0.2	0.0	2.7
Jabiru	< 0.1	< 0.1	0.5	0.0	23.4***
Wood Stork	0.5	< 0.1	0.5	2.9	17.4***
Maguari Stork	< 0.1	< 0.1	1.1	0.2	60.9
Southern Screamer	0.3	0.5	0.3	0.3	4.3
June census	0.2	0.9	0.2	0.0	10.7*
Limpkin	< 0.1	< 0.1	0.2	0.4	12.3**
Southern Lapwing	0.3	0.4	0.4	< 0.1	3.2
Wattled Jacana	0.1	< 0.1	0.6	0.2	5.9
August census	0.0	0.0	1.8	—	13.2**
Large-billed Tern	2.8	0.4	2.9	4.7	33.0***
Yellow-billed Tern	3.6	2.4	3.1	3.7	5.6
Black Skimmer	1.1	1.2	3.3	2.5	0.7
Ringed Kingfisher	0.1	0.8	0.7	1.0	17.4***
Amazon Kingfisher	< 0.1	0.1	0.1	0.4	6.1
Number of 10 min counts					
Combined censuses	74	99	98	20	
June census	25	16	15	2	
August census	19	24	25	0	
October census	12	33	27	6	
January census	18	26	31	12	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

most common along the river in January, as might be expected. The differences in waterbird densities along the river during October and January are probably due to differences in foraging conditions, but may be related to nesting activities. None of the waterbird species recorded during this study was observed nesting at the Bahía de Asunción, although some undoubtedly do. Nesting colonies of Large-billed Tern, Yellow-billed Tern and Black Skimmer were observed, but could not be examined, on sandbars farther north along the river.

Although South America possesses an abundance of freshwater wetlands (Scott and Carbonell 1986), little is known about the basic ecology of waterbirds in most of these areas, or even of seasonal changes in waterbird populations. Many wetlands of South America, including those associated with the Paraguay River, are subject to annual cycles of flooding and drying (e.g., Antas 1983, Kushlan *et al.* 1985, Hayes and Fox 1991, Bucher *et al.* 1993); in response to changing hydrological conditions, waterbirds must continually seek areas where foraging conditions are adequate. This study suggests that waterbirds appear most commonly along the Paraguay River during periods of low water, from November to March, and are present in low densities during periods of high water, from April to October. In contrast, many species of raptors appear to be most common during high water levels, and

may be attracted to prey concentrated in emergent vegetation when the river floods (Hayes 1991).

Exactly where the waterbirds go during periods of high water is unknown. Presumably they move to nearby wetlands away from the Paraguay River, such as in the Paraguayan Chaco to the west. However, there may also be seasonal movements upstream to the Pantanal of Brazil or beyond, downstream to the Pampas and coastal estuaries of Argentina, or eastward to coastal wetlands of southern Brazil and Uruguay (Antas 1994). Information is needed on seasonal changes in resident waterbird populations in wetlands away from the Paraguay River in order to better understand the movements of waterbird populations in the Paraguay River watershed.

Interannual variation. Interannual differences in abundance of waterbirds at the Bahía de Asunción likely reflect differences in precipitation and the availability of habitat elsewhere in the Paraguay River watershed during these two years. Because of a prolonged drought during the austral winter and spring of 1988, many wetland areas away from the Paraguay River dried up, possibly concentrating resident waterbirds in remaining wetlands associated with the river (Hayes and Fox 1991). This may explain why several species of waterbirds were more abundant during the austral summer of 1988-1989.

Geographical variation. The censuses along the Paraguay River indicate that the densities of many species are greatest in the northern sectors. This was especially apparent for the Neotropic Cormorant, Cocoi Heron and Great Egret. Although marshes and sandbars seem to be more extensive in these sectors, the waterbirds may be more concentrated simply because the river is narrower.

Conservation. The Paraguay River ecosystem is becoming increasingly degraded by a variety of anthropogenic factors. As a consequence of large-scale production of cash crops and biomass fuel production in the river's watershed, high concentrations of toxic compounds have contaminated the river and have been magnified within the tissues of fish and birds as the chemicals move up the food chain (see review by Alho *et al.* 1988). Mass mortalities of fish occur periodically, and undoubtedly have a negative impact on bird populations.

A more alarming threat is the proposed development of the Hidrovia navigation system along the Paraná and Paraguay rivers (Bucher *et al.* 1993). The plan envisions damming the upper Paraguay River to control flooding, dredging and channeling the river's course to enhance navigation, and diverting the river's water into the agricultural areas of the Chaco through irrigation canals. If implemented, the proposed Hidrovia projects will undoubtedly have a negative effect on most waterbird populations. Because bird populations are excellent indicators of environmental change (Morrison 1986), waterbird censuses along the Paraguay River should be conducted regularly in order to monitor the effects of chemical contamination and other changes due to the proposed Hidrovia waterway.

The data presented in earlier studies (Hayes *et al.* 1990, Hayes and Fox 1991) and in this paper indicate that the Bahía de Asunción is one of the most important areas along the Paraguay River for concentrations of resident and migratory waterbirds. Furthermore, its proximity to a large urban center, its increasingly contaminated condition, and its potential for recreational activities make it an ideal focal point for conservation and environmental education initiatives in Paraguay (Hayes 1989, Ramírez 1991). Because the northern bank of the bay is subject to inundation and is thus unsuitable for development (Hayes and Fox 1991), I recommend that the Paraguayan government declare the more pristine portions of the Bahía de Asunción a protected area and that steps be taken to prevent further contamination of the bay, clean up contaminated areas and punish offenders.

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