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SEASONALITY, HABITAT USE, AND FLOCK SIZES OF SHOREBIRDS AT THE BAHÍA DE ASUNCIÓN, PARAGUAY

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ABSTRACT.—Twenty species of shorebirds were recorded during 47 censuses along the margins of the Paraguay River at the Bahía de Asunción, Paraguay, from 1987–1989. The numbers of most Nearctic migrants (15 species) were higher during boreal fall than during spring, presumably due to flooding of the Paraguay River basin during spring and summer; numbers of Neotropical residents (five species) peaked during December–March. The abundance of most shorebirds, especially Neotropical species, was correlated negatively with water level, an inverse measure of habitat availability. Interannual variation in abundance appeared to be related to local hydrological conditions. Each species differentially exploited a given habitat, providing evidence of habitat partitioning. Intraspecific flock sizes of most species were correlated with abundance and, by inference, seasonality and habitat availability. The evolution of Nearctic shorebird migration in the interior of South America appears to have been influenced by seasonal cycles of precipitation and the effects on habitat availability. *Received 19 Feb. 1991, accepted 20 June 1991.*

RESUMEN.—Se registraron 20 especies de playeros durante 47 censos a lo largo de los márgenes del río Paraguay en la bahía de Asunción, Paraguay, desde 1987 hasta 1989. La mayoría de migrantes neárticos (15 especies) alcanzaron números más altos durante el otoño boreal que durante la primavera, presumiblemente a causa de las inundaciones de la cuenca del río Paraguay durante la primavera y el verano; los residentes neotropicales (cinco especies) alcanzaron números más altos durante diciembre–marzo. La abundancia de la mayoría de playeros, especialmente los neotropicales, fue correlacionada negativamente con el nivel de agua, una medida inversa de disponibilidad de hábitat. La variación interanual en abundancia pareció estar relacionada con las condiciones hidrológicas locales. Cada especie explotó un cierto hábitat en una manera diferente, proveyendo evidencia de la partición de hábitat. Los tamaños de las bandadas intraespecíficas de la mayoría de las especies fueron correlacionados con abundancia y, por inferencia, estacionalidad y disponibilidad de hábitat. La evolución de migración por los playeros neárticos en el interior de Sudamérica parece haber afectado por ciclos estacionales de precipitación y los afectos sobre la disponibilidad de hábitat.

Although our knowledge of the distribution and abundance of Nearctic shorebird migrants along the coasts of South America is fairly extensive (Morrison and Ross 1989), studies of seasonality and habitat use of mixed assemblages of shorebirds in South America have been confined thus far

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to coastal areas in Peru (Hughes 1979, Duffy et al. 1981), Venezuela (McNeil 1970), Surinam (Spaans 1978), southern Brazil (Harrington et al. 1986, Vooren and Chiaradia 1990), Argentina (Myers and Myers 1979), and inland in central Venezuela (Thomas 1987) and eastern Peru (Bolster and Robinson 1990). There are no published quantitative studies of migrant shorebird populations from the interior of South America south of the Amazon basin.

On the basis of specimen records and anecdotal observations, Antas (1983) inferred that far fewer Nearctic shorebird migrants pass through the interior of South America during boreal spring migration than in autumn. This was thought to be related to differences in the quantity of precipitation during these periods and their effects on the hydrological basins. In most parts of central South America, rainfall is highest from November to March, thus flooding most river valleys when migrants are traveling northward toward their breeding grounds (Antas 1983). However, during the subsequent dry season, water levels fall rapidly along the major rivers and flooded lakes begin to dry up, thus creating a mosaic of mudflats, sandbars, and wet grasslands which collectively provide excellent habitat for southbound Nearctic shorebird migrants. The evolution of Nearctic shorebird migration in the interior of South America is thus postulated to have been influenced by seasonal cycles of precipitation and the resulting effects on habitat availability. However, there has been little quantitative evidence to support this hypothesis.

The status of Nearctic migrant shorebirds in the Republic of Paraguay, a land-locked country in south-central South America, was recently summarized by Hayes et al. (1990). Here we report the results of a two-year study on the seasonality and ecology of migrant and resident shorebirds at the Bahía de Asunción, Departamento Central, Paraguay. We focus on the differential seasonal use of the Bahía de Asunción by shorebirds and the effects of varying water levels on habitat availability, abundance, and flock sizes of shorebirds. We use our data to evaluate the hypothesis of Antas (1983) that Nearctic shorebird migration in the interior of South America has been influenced by seasonal cycles of precipitation and the effects on habitat availability.

STUDY AREA AND METHODS

Study area.—The Bahía de Asunción is a shallow bay of the Paraguay River situated along the northern outskirts of Asunción, the largest city in Paraguay (ca 800,000 residents). Roughly 4 km long and up to 2 km wide, the bay covers a variable surface area of 2–5 km^2. Because of the large amplitude of water level fluctuations along the Paraguay River, the width and depth of the bay vary greatly between seasons. However, day-to-day changes are small and usually unidirectional, with water level changes rarely exceeding 10 cm (Fig. 1;

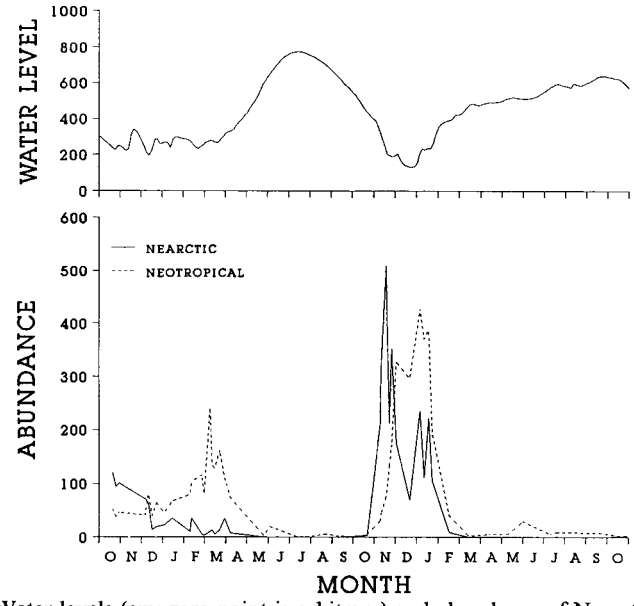

FIG. 1. Water levels (cm; zero point is arbitrary) and abundance of Nearctic and Neotropical shorebirds (all species combined for each group) at the Bahía de Asunción from October 1987 to October 1989.

unpubl. data). The southern and eastern banks of the bay are densely populated by humans, most of whom are poor squatters, and garbage is widely strewn in adjacent areas. The northern bank is lower in elevation and subject to inundation; it is inhabited by only a few families when water levels are low. Government buildings and a deep water port are located on both sides of the bay near its mouth at the western end. The bay is bordered on its northern and eastern edges by small patches of forest, several ponds, lagoons, marshes, and during periods of low water, extensive mudflats and fields.

Water levels at the Bahía de Asunción are usually highest during the dry season, from May to August, and lowest during the wet season, from November to January (Fig. 1). This results partly from the seasonal pattern of rainfall at the river's sources and partly from the inability of the river's drainage system to pass along immediately the large volumes of water it receives periodically in the form of precipitation (Anonymous 1985). Since 1978, flooding of the Paraguay River has reached unprecedented proportions, presumably due to the increased runoff of precipitation resulting from extensive deforestation in the river's watershed.

The widely fluctuating water levels of the Bahía de Asunción cause pronounced cyclical changes in the bay's physical appearance. During high water levels (>400 cm), much of the bay is under water with only the taller vegetation emerging above the surface. When the water recedes during the austral spring, the bay's emerging shoreline consists of bare mud. As the water continues to recede the upper shoreline dries out, and short grasses sprout, thus creating grassy fields except in several sandy or salty areas which remain barren. Sections of several lagoons transform into ponds as the water reaches its lowest levels; some ponds are choked with vegetation, whereas others continue to dry up and form large mudflats.

Grasses and sedges sprout along the water's edge when the water levels begin to rise again, eventually reaching a height of 0.5–1.0 m. When the water rises during the boreal spring, much of the shoreline transforms into a marsh, although several areas of bare soil still remain, especially at the upper levels of the bay. There is no published information on the limnology, botany, or invertebrate populations of the Bahía de Asunción.

Sampling methods.—From 20 October 1987 to 30 October 1989, we conducted 47 censuses of shorebirds at irregular intervals at the Bahía de Asunción. Up to five censuses were conducted each month except for November 1987 and June and August 1989; censuses were conducted more frequently during periods when shorebirds were common. During each census we covered the same areas of the bay on foot, rowboat, or by both methods. With the aid of 7× binoculars, we counted individual birds or estimated their numbers when in large flocks. All birds seen were counted, including those flying overhead; flying birds were identified either by their characteristic size and shape or, in the case of *Calidris* spp., by voice. Because of the highly variable amount of suitable shorebird habitat, we were unable to obtain densities based on the number of shorebirds per unit area. 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 shorebirds were present.

In addition to counting birds, we recorded data on water levels, intraspecific flock sizes (number of individuals in a cohesive flock with a maximum distance of three m between individuals) and the habitat used by foraging individuals of each species. Data on water levels at the Bahía de Asunción were obtained from the Dirección de Hidrografía y Navegación of the Armada Nacional; water levels were used as an inverse measure of habitat availability (i.e., high habitat availability during low water, low habitat availability during high water). Three distinctive habitats occurred along a dry-wet gradient: dry land, wet land, and shallow water. The taxonomy of shorebird species mentioned in the text follows the A.O.U. check-list (1983) and Altman and Swift (1989).

Statistical analyses.—Spearman rank correlation coefficients (r_s-statistic; Siegel 1956) were used to compare shorebird abundance (number of individuals per count for a given species) with water levels and flock sizes. Mann-Whitney *U*-tests (*U*-statistic; Siegel 1956) were used to compare seasonal differences in the abundance of shorebirds during the periods of October–December and January–March (using only counts when mud or grass flats were exposed, with water level <400 cm), the abundance of shorebirds between the winters of 1987–1988 and 1988–1989 (using same criteria), and the correlations of abundance and water level between Nearctic and Neotropical species. All statistical tests were computed with *Statistix* software (Heisey and Nimis 1985). All probability values are two-tailed, with $\alpha = 0.05$.

RESULTS

Seasonality.—Twenty species of shorebirds were recorded during this study. Of these, 10 species were regularly occurring (>50 individuals recorded during study period) Nearctic migrants: Lesser Golden-Plover (*Pluvialis dominica*), Greater Yellowlegs (*Tringa melanoleuca*), Lesser Yellowlegs (*T. flavipes*), Solitary Sandpiper (*T. solitaria*), Upland Sandpiper (*Bartramia longicauda*), Hudsonian Godwit (*Limosa haemastica*), White-rumped Sandpiper (*Calidris fuscicollis*), Pectoral Sandpiper (*C. melanotos*), Stilt Sandpiper (*C. himantopus*), and Buff-breasted Sandpiper (*Tryngites subruficollis*). Five species of Nearctic migrants were rarely

observed (< four individuals during study period): Black-bellied Plover (*P. squatarola*), Spotted Sandpiper (*Actitis macularia*), Red Knot (*C. canutus*), Least Sandpiper (*C. minutilla*), and Sanderling (*C. alba*); accounts of these species were given by Hayes et al. (1990). Four species of resident Neotropical shorebirds were recorded regularly: Southern Lapwing (*Vanellus chilensis*), Collared Plover (*Charadrius collaris*), Black-necked Stilt (*Himantopus mexicanus*) and Wattled Jacana (*Jacana jacana*). Only five South American Snipe (*Gallinago paraguaiae*), a fifth species of Neotropical shorebird, were recorded. The data used in the statistical analyses were restricted to the 14 species of regularly occurring shorebirds at the Bahía de Asunción.

Seven species of regularly occurring Nearctic migrants appeared most commonly during the period of October to December, either occurring in small numbers or absent during January to April, even though suitable habitat was available: Lesser Golden-Plover, Greater Yellowlegs, White-rumped Sandpiper, Stilt Sandpiper, Upland Sandpiper, Hudsonian Godwit and Buff-breasted Sandpiper (Fig. 2); statistical tests supported this observation for all species but the Upland Sandpiper and Stilt Sandpiper (Table 1). Three species of Nearctic migrants occurred in fair numbers throughout the boreal winter: Solitary Sandpiper, Lesser Yellowlegs, and Pectoral Sandpiper (Fig. 2; Table 1). The numbers of all four species of regularly occurring Neotropical residents increased slowly during the months of October and November and peaked during December to March (Fig. 2). Statistical tests indicated that the Southern Lapwing and Collared Plover were more common during the period of January to March (Table 1). In contrast with the resident species, maximum counts of all Nearctic shorebird migrants combined were roughly twice as high prior to December than afterwards, even when water levels remained low (<400 cm) through early April 1988 (Fig. 1).

Interannual variation.—The abundance of all Nearctic shorebirds combined was much greater during the boreal winter of 1988–1989 (N = 12) than during 1987–1988 (N = 19; $U = 21.0$, $P < 0.001$; see Fig. 1). This pattern held true for six species of Nearctic shorebirds: Lesser Golden-Plover ($U = 21.0$, $P < 0.001$), Greater Yellowlegs ($U = 24.5$, $P < 0.001$), Lesser Yellowlegs ($U = 18.0$, $P < 0.001$), Hudsonian Godwit ($U = 47.5$, $P < 0.01$), Pectoral Sandpiper ($U = 13.5$, $P < 0.001$), and Stilt Sandpiper (absent during 1987–1988, data insufficient for analysis; see Fig. 2). However, the abundance of four species of Nearctic shorebirds did not vary between 1987–1988 and 1988–1989: Solitary Sandpiper ($U = 109.5$, $P > 0.85$), Upland Sandpiper ($U = 93.0$, $P > 0.40$), White-rumped Sandpiper ($U = 79.5$, $P > 0.15$), and Buff-breasted Sandpiper ($U = 85.0$, $P > 0.20$). Of the Neotropical shorebird species, only the Black-necked Stilt was

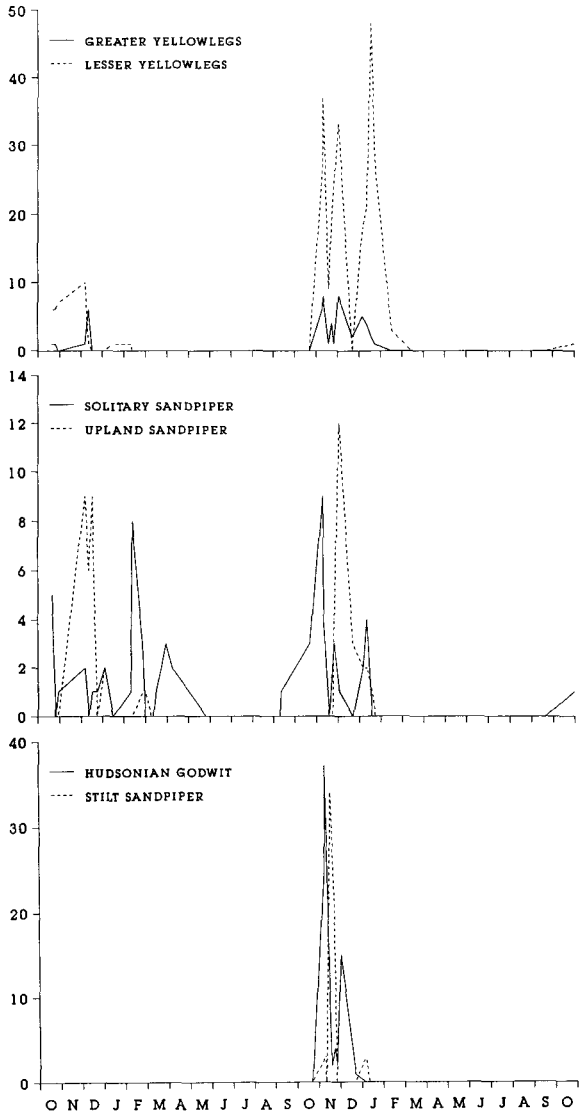

FIG. 2. Abundance (*y*-axis) of 14 species of shorebirds at the Bahía de Asunción from October 1987 to October 1989 (*x*-axis).

more abundant during the winter of 1988–1989 ($U = 6.0$, $P < 0.001$). The abundance of the other three species did not vary between 1987–1988 and 1988–1989: Southern Lapwing ($U = 111.0$, $P > 0.90$), Collared Plover ($U = 104.5$, $P > 0.70$), and Wattled Jacana ($U = 73.0$, $P > 0.10$;

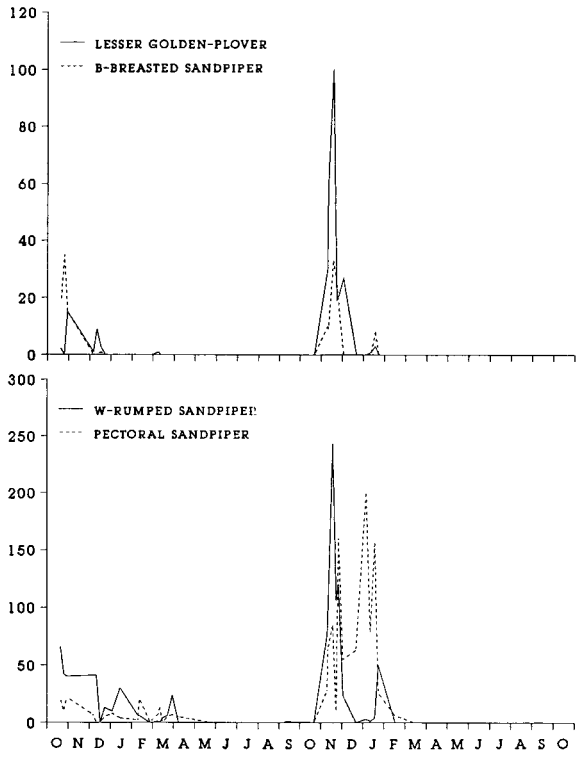

FIG. 2. Continued.

see Fig. 2). The abundance of all Neotropical shorebirds combined was greater during the winter of 1988–1989, but not quite significantly so ($U = 67.0$, $P = 0.059$; see Fig. 1).

Habitat use.—The abundance of all species of Neotropical shorebirds and five of the Nearctic migrant species was negatively correlated with water level (Table 1); i.e., the abundance of most species of shorebirds was directly proportional to the availability of habitat (exposed mudflats or fields). The correlation coefficients of resident species averaged higher than those of migrant species ($U = 2$, $P < 0.01$).

Although the 14 species of shorebirds overlapped greatly in their use of habitat, each species differentially exploited a given habitat along a dry-wet gradient (Fig. 3). The Wattled Jacana and Solitary Sandpiper appeared to overlap completely in habitat use (Fig. 3); however, the Wattled Jacana was the only species observed to forage on floating vegetation

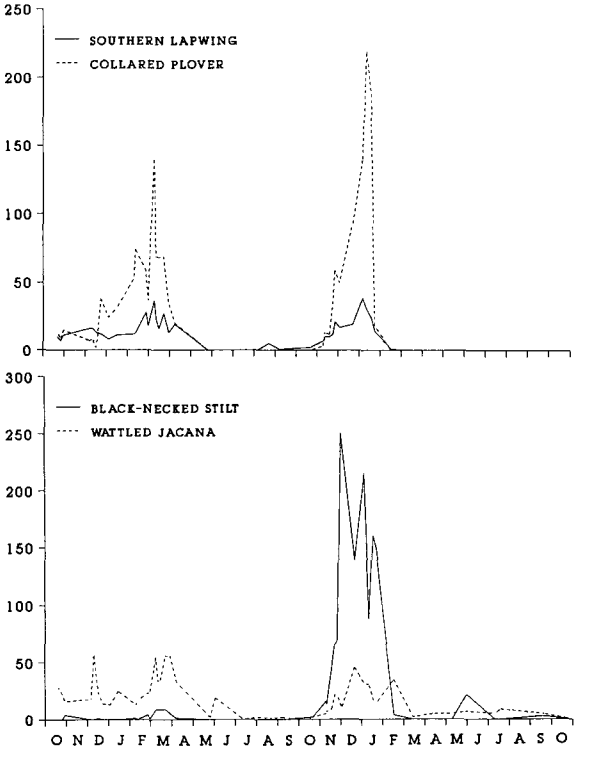

FIG. 2. Continued.

(used exclusively [100%] during periods of inundation but rarely [0.5%] when exposed land was available), a habitat not shown in Fig. 3.

Flock sizes.—Mean intraspecific flock sizes varied greatly between species, ranging from 1.3 birds/flock in the Solitary Sandpiper to 13.7 in the Black-necked Stilt (Table 2). Intraspecific flock sizes were correlated with abundance for all four Neotropical species, but only for half of the Nearctic migrant species (Table 2).

DISCUSSION

Seasonality.—This study demonstrates that many species of Nearctic shorebirds are absent or less abundant at the Bahía de Asunción during the boreal spring. Maximum counts of all Nearctic shorebird migrants combined were roughly twice as high prior to December than afterwards, even when water levels remained low through early April. Data from

TABLE 1

MEAN COUNTS OF SHOREBIRDS DURING PERIODS OF LOW WATER (<400 CM) DURING OCTOBER–DECEMBER (N = 14) AND JANUARY–MARCH (N = 16) WITH MANN-WHITNEY *U*-TEST COMPARING MEANS, AND SPEARMAN RANK CORRELATION COEFFICIENTS COMPARING SHOREBIRD ABUNDANCE WITH WATER LEVELS

Species	Oct.–Dec.	Jan.–Mar.	*U*	Water level r_s
Southern Lapwing	12.9	19.6	63.5*	−0.757***
Lesser Golden-Plover	20.5	0.3	32.0***	−0.267
Collared Plover	25.4	76.6	44.5**	−0.683***
Black-necked Stilt	43.1	41.4	106.5	−0.476**
Wattled Jacana	21.6	30.1	68.5	−0.648***
Greater Yellowlegs	2.8	0.8	51.5*	−0.374*
Lesser Yellowlegs	12.8	7.5	69.5	−0.376*
Solitary Sandpiper	2.1	1.6	98.5	−0.263
Upland Sandpiper	3.1	0.6	88.0	−0.319*
Hudsonian Godwit	6.1	0.0	56.0*	−0.093
White-rumped Sandpiper	64.6	9.1	37.5**	−0.509***
Pectoral Sandpiper	37.9	33.5	85.0	−0.638***
Stilt Sandpiper[a]	4.2	0.2	—	—
Buff-breasted Sandpiper	11.6	0.6	46.5**	−0.086

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
[a] Insufficient data (observed during only four censuses).

specimen records and observations from other areas in Paraguay indicate that most Nearctic shorebird species are less abundant during northbound migration even in areas away from the Paraguay River (Hayes et al. 1990; Hayes, unpubl. data).

The northbound route(s) used by these Nearctic migrants is unknown; most likely they either migrate northward along the Atlantic coast or fly nonstop through central South America until they reach the Carribean or Atlantic coasts or nearby inland areas (Antas 1983). Large concentrations of spring migrants have been reported along the Atlantic coast of southern Brazil (Harrington et al. 1986, Vooren and Chiaradia 1990) and in the interior of Venezuela (Thomas 1987). In contrast with Paraguay, the availability of habitat in the interior of Venezuela is apparently greater during boreal spring than during fall (Thomas 1987). The data from the Bahía de Asunción and elsewhere support the hypothesis of Antas (1983) that the evolution of migration by Nearctic shorebirds in the interior of South America has been influenced by seasonal cycles of precipitation and the resulting effects on habitat availability.

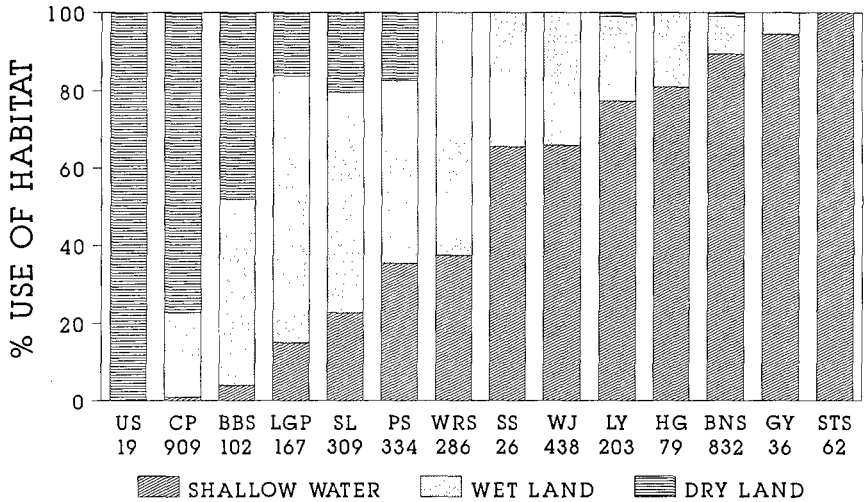

FIG. 3. Percent habitat use of shorebirds at the Bahía de Asunción, with N values below. US = Upland Sandpiper; CP = Collared Plover; BBS = Buff-breasted Sandpiper; LGP = Lesser Golden-Plover; SL = Southern Lapwing; PS = Pectoral Sandpiper; WRS = White-rumped Sandpiper; SS = Solitary Sandpiper; WJ = Wattled Jacana; LY = Lesser Yelowlegs; HG = Hudsonian Godwit; BNS = Black-necked Stilt; GY = Greater Yellowlegs; STS = Stilt Sandpiper.

The numbers of shorebirds occurring at the Bahía de Asunción and other areas in the interior of South America (e.g., Dott 1985, Thomas 1987, Bolster and Robinson 1990, Hayes et al. 1990) are small in comparison with the numbers reported along coastal areas (Morrison and Ross 1989). Although large numbers of migrant shorebirds apparently pass through the interior of South America, they are widely dispersed; there are no known "staging areas" (Myers 1983) in need of special protection.

Interannual variation.—The larger concentrations of shorebirds observed during the boreal winter of 1988–1989 do not appear to be related to the availability of habitat at the Bahía de Asunción, and no information is available on the abundance or availability of food resources. We suspect that the larger concentrations in 1988–1989 may have resulted from a lack of available habitat elsewhere in the Paraguay River watershed. Because of a long, extended drought during the autumn of 1988, many wetland areas away from the Paraguay River (e.g., in the Chaco) dried up (pers. obs.). If these wetlands host shorebird populations during normal years, then during a drought shorebirds might be expected to concentrate

TABLE 2

FLOCK SIZES OF REGULARLY OCCURRING SHOREBIRDS AT THE BAHIA DE ASUNCION WITH SPEARMAN RANK CORRELATION COEFFICIENTS COMPARING FLOCK SIZE WITH ABUNDANCE

Species	Flock Size				Abundance
	N	$\bar{x}$	SD	Range	r_s
Southern Lapwing	206	2.2	1.9	1–15	0.189*
Lesser Golden-Plover	49	5.2	7.9	1–50	0.155
Collared Plover	224	5.6	11.4	1–94	0.212*
Black-necked Stilt	82	13.7	24.5	1–174	0.301*
Wattled Jacana	185	3.7	4.3	1–32	0.216*
Greater Yellowlegs	29	1.7	1.4	1–7	0.560*
Lesser Yellowlegs	63	4.1	4.9	1–21	0.196
Solitary Sandpiper	43	1.3	1.0	1–5	0.566**
Upland Sandpiper	18	2.4	2.3	1–9	0.801**
Hudsonian Godwit	14	5.6	6.0	1–18	0.378
White-rumped Sandpiper	68	12.1	20.4	1–125	0.419**
Pectoral Sandpiper	144	5.8	11.7	1–120	0.255*
Stilt Sandpiper	9	6.9	6.6	2–22	0.271
Buff-breasted Sandpiper	36	4.8	3.9	1–17	0.229

* $P < 0.01$.
** $P < 0.001$.

in suitable habitat along the Paraguay River and larger bodies of water away from the river. Quantitative evidence supporting this hypothesis comes from a shorebird census conducted by Hayes (unpubl. data) at two small ponds and a flooded field (roughly 0.02 km^2) at Guarambaré, Departamento Central, an agricultural community situated about 9 km east of the Paraguay River and 28 km southeast of the Bahía de Asunción.

Habitat use.—The abundance of shorebirds at the Bahía de Asunción during a given year is clearly related to the availability of habitat, especially for Neotropical residents, as indicated by the correlations with water level. The lower correlation coefficients of Nearctic migrant species are indicative of their more transient appearance in Paraguay. Many species of migrants apparently winter farther south (Myers and Myers 1979, Morrison and Ross 1989) despite an abundance of suitable habitat at the Bahía de Asunción throughout the boreal winter. Although some species overlapped greatly in their habitat use, the differential use of habitats by each shorebird species along a dry-wet gradient provides evidence of habitat partitioning while at the Bahía de Asunción.

Flock sizes.—Burger and Gochfeld (1983) found that flock sizes of shorebirds were influenced by location, activity (roosting, foraging), date,

and environmental variables such as tide, cloud cover, temperature, and wind. The presence or absence of a predator also affects the sizes of shorebird flocks (Myers 1984). Our findings indicate that flock sizes of certain species are influenced by abundance and, by inference, seasonality and availability of habitat.

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