

Waterbird Response to Changes in Habitat Area and Diversity Generated by Rainfall in a SW Atlantic Coastal Lagoon

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Abstract.—The rainfall regime of the Pampas region of Argentina shows a long-term cyclic behavior that has increased in intensity over the historical mean during the last four decades. In this paper we explored the effects of changes in monthly cumulative rainfall on lagoon and riparian habitat, and, in turn on the wetland waterbird community. We also explored the responses of waterbird morphofunctional groups to fluctuation in water level and habitat diversity caused by the change in rainfall at the Mar Chiquita Coastal Lagoon, Argentina (37°32' to 37°45'S, 57°19' to 57°26'W). Analysis of satellite images shows that increases in rainfall increased wetland water surface, but reduced riparian habitat area and habitat diversity. Increases in water surface negatively affected the abundances and species richness of waterbirds; habitat diversity did not explain a significant portion of total waterbird variability. Shorebirds (i.e., yellowlegs, plover, sandpiper) were the most affected by reduction in mudflats and habitat diversity. Other waterbirds (i.e., long-legged wading birds, waterfowls) were affected by increases in water surface (ducks, swans, long-legged waterbirds and gulls), decrease in mudflat availability (long-legged waterbirds and gulls), and decrease in habitat diversity (ducks). Our results show that the inter-annual variability in the rainfall pattern influenced the presence and abundance of most waterbirds, and species richness and composition. Fluctuation in water depth *per se* is known to be a key factor for habitat use of many waterbirds, but habitat diversity also needs to be considered. Received 25 January 2007, accepted 27 June 2007.

Key words.—Argentina, flooding, habitat diversity, marsh, rainfall, remote sensing, shorebirds, waterbirds, water depth, wetland.

Waterbirds 30(4): 541-553, 2007

Waterbirds are an important component of wetland environments, with direct and indirect effects on these ecosystems (see Comin *et al.* 2000), however, interrelationships between waterbirds and these environments are still not well understood (Kushlan 1989; Colwell and Taft 2000). Topographically variable wetlands support more waterbird species due to the diversity of microhabitats, including exposed mudflats, emergent wetlands, and deep water (Colwell and Taft 2000). Changes in precipitation may affect water depth and spatial diversity in wetlands and influence the distribution of waterbirds (Vilina and Cofre 2000).

In central Argentina, “the Pampas”, rainfall regime shows a long-term cyclic behavior (Walter 1967) that, during the last four decades (1960-present), has increased in intensity over the annual historical mean (Viglizzo *et al.* 1995, 1997; Lucero and Rozas 2002).

Rainfall in the eastern portion of this region has increased from a yearly average of 751 mm from 1900-1950 (range 396-1,231 mm) to 934 mm from 1950-2004 (range 588-1,826 mm; Canepuccia 2005). This region is characterized by a flat landscape where heavy rains frequently cause flooding (Frenguelli 1950; Soriano *et al.* 1991) that affects wetland habitat availability and habitat diversity. This is of conservation concern given the high conservation value of wetlands for a large number of waterbird species in the Pampas region (e.g., Narosky and Di Giacomo 1993; Gómez and Toresani 1998).

In the East of Pampas region, Mar Chiquita coastal lagoon supports a large number of waterbirds. Then, an increase in rainfall that alters habitat area and diversity at a local scale may also affect the abundance and diversity of birds. Birds may move to other regions, when local conditions are not appro-

appropriate (e.g., Nearctic migratory shorebirds). Moreover, given that waterbirds do not breed in the study area (Martínez 2001), we do not expect a temporal lag response as a consequence of alteration in their breeding behavior (i.e., season change in egg/juvenile mortality). We expect immediate responses to environmental variations. Given these patterns, we explored the importance of hydrological variability in the abundance and diversity of waterbirds inhabiting a fluctuating wetland ecosystem. For this purpose, we analyzed 1) the effect of changes in monthly cumulative rainfall on availability of lagoon and associated riparian habitat, 2) their effects on the waterbird community including responses of waterbird morphofunctional groups to fluctuation in water level and habitat diversity.

METHODS

Study Area

Our study was carried out in the Mar Chiquita coastal lagoon (37°32' to 37°45'S, 57°19' to 57°26'W, Argentina; Fig. 1), one of the southernmost coastal lagoons along the Atlantic coast of South America (Fasano *et al.* 1982; Iribarne 2001). The area is a UNESCO Man and the Biosphere Reserve (Iribarne 2001) and an important wintering site for migratory shorebirds (e.g., Blanco *et al.* 1995; Palomo *et al.* 1999; Martínez 2001). The lagoon is shallow (mean depth = 0.4-0.6 m) with a one-m tidal range, a water surface of 46 km², and a watershed of about 10,000 km² (Fasano *et al.* 1982). The area is topographically variable and many species use the beaches for feeding and roosting, where they concentrate in large flocks (e.g., Palomo *et al.* 1999; Martínez 2001). Cordgrass (*Spartina densiflora*) is the dominant plant species in the low and middle marshes all around the lagoon (Isacch *et al.* 2006). The rainy season is from October to March (Fasano *et al.* 1982; Reta *et al.* 2001).

Waterbird Surveys

Bird species and number of individuals were surveyed in two sampling units (northern extreme at the mouth of channel 5, and at the mouth of the Sotelo creek; Fig. 1) by two observers. The sampling unit was a 600 × 200 m long transect parallel to the vegetated border of the lagoon (i.e., a sampling unit of twelve ha). At each unit, observers stopped at points to maximize observation and minimize disturbances, and counted all waterbirds observed. Different detection probabilities (see Nichols *et al.* 2000) were minimized by sampling birds within a relatively short distance (no more than 200 m); by comparing results from two observers, and by the fact that there were no visual obstructions and observed birds were relatively large (between 15 and 140 cm). In addition, smaller birds (i.e., shorebirds) could be easily recorded because they were usually near the coastline.

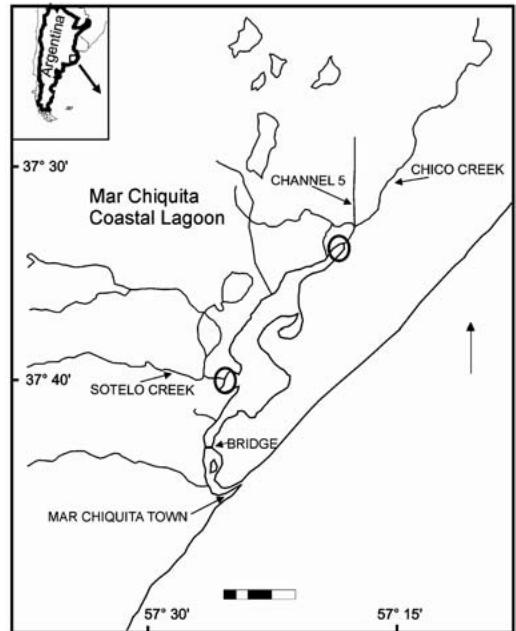


Figure 1. Map showing the study sites within Mar Chiquita coastal lagoon. The map in the upper left corner shows the location of Mar Chiquita Lagoon in the Argentina coast. Sampling sites are indicated by a circle (upper—northern extreme, lower—Sotelo Creek).

Each site was sampled every one or two months between October 1993 and March 1994 (N = 12), May 1997 and February 1998 (N = 12), and between May 2001 and February 2004 (N = 39). Bird surveys were not made under extreme weather conditions (windy and/or rainy days; Conner and Dickson 1980). Waterbirds, identified to species level, were placed in 'morphofunctional groups' based on taxonomic and morphologic similarities (Kushlan 1989; see Appendix 1).

Changes in Habitat Area

Habitat area and diversity were calculated using Landsat satellite images. The images analyzed were two from the ETM+ sensor (path-row 223-86: 19 August 2001, 9 December 2001) and six from the TM sensor (path-row 223-86: 25 March 1997, 6 October 1998, 11 January 2000, 16 February 2001, 3 February 2002; path-row 224-86: 24 March 2000). All images were geocoded to a UTM Gauss Kruger coordinate system using a first-order transformation and nearest neighbor re-sampling (Campbell 2002). The images were georeferenced by using points gathered in the field with GPS, and the root-mean squared error achieved was lower than one pixel (30 × 30 m). After that, all other images were re-sampled with points from the first image, and the root-mean squared error achieved was always <0.6 pixels.

To determine habitat areas from the images, a strip of lagoon coast including vegetation and mudflat/water habitats was selected (masking the uplands and areas always covered by water). Then, a supervised classification to the masked images was applied, selecting three classes: water, mudflat and vegetation, dominated by

Cordgrass (*Spartina densiflora*). For the classification procedure, a maximum-likelihood algorithm based on the probability density function associated with a particular training site signature was used (Richards 1986). After that, the spectral signature for each class was analyzed and confirmed that reflectance ranges were never superposed among classes in at least one band of Landsat (i.e., habitats were consistently separated). After having all these variables evaluated, the area of each of the three classes was determined.

Statistical Analyses

From bird counts, the abundance per sampling unit was estimated (i.e., per twelve ha), the number of individuals for eight morphofunctional groups (see Appendix 1), species richness, and species diversity by using a Shannon diversity index (Magurran 1988; $H' = -\sum p_i \log p_i$, where p_i is the proportion that the i th species contributes to the total number of birds). The area of the three habitat classes was determined from each satellite image and used to estimate habitat diversity using a Shannon diversity index (here p_i is the proportion that the i th habitat surface contributes to the total landscape surface). Simple linear regression (Zar 1996) was used to analyze relationships between surface of each habitat, habitat diversity, and changes in monthly rainfall. Rainfall data were obtained from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA), National Environmental Satellite, Data, and Information Service Office, National Climatic Data Center <http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html> from Mar del Plata city station (37°56'S; 57°35'W). This coastal city is located 25 km south from our study site.

Using a regression model (Neter *et al.* 1990) obtained between cumulative rainfall (30 d before satellite imagery) and the surface of each habitat estimated by means of satellite imagery ($N = 8$), the surface value of each habitat was estimated for days when birds were surveyed. The same analyses were made to assess the relationships among habitat diversity and habitat surface parameters, as independent variables, and waterbird responses related to their number, species richness and diversity, as dependent variables. However, given that waterbird abundances exhibit annual cycles of density, with greatest abundance during spring and summer (Filipello and López de Casenave 1993; Martínez 2001), the relationship between waterbird abundance and diversity, and habitat surface parameters for each season were analyzed. The independent variables were log transformed to comply with methodological assumptions (see Neter *et al.* 1990). Outliers were detected using the leverage methods (Neter *et al.* 1990). Given that the independent variables are strongly multicollinear, a forward-stepwise multiple regression was applied to discard redundant variables and to select the model with lower complexity and higher explanatory capability (Sokal and Rohlf 1995). Statistical significance was assessed using t -tests for partial correlation coefficients (Sokal and Rohlf 1995). To show and disentangle unique from shared contributions of two collinear independent variables (water surface and habitat diversity, see Figs. 4 and 5), the unique contribution of each one was determined. To do that, it was assumed that one of these variables is functionally more important than the other (Graham 2003). Moreover, as water surface had the highest R^2 value, it was assumed that it was function-

ally more important. To detect the effect of habitat diversity (Graham 2003), this variable was regressed against the water surface, replacing the less negligible variable (habitat diversity) with the residuals from the regression. Thus, subsequent regression analyses (residual regressions) with dependent variables were unbiased since the explanatory variables were no longer statistically collinear (Graham 2003).

RESULTS

Rainfall-Habitat Diversity Relationship

During 1993, 1997, and beginning of 2003, rainfall was similar to the average for the last 100 years (Fig. 2). However, rainfall was above average during 2001 and 2002 and lowest at the end of 2003 (Fig. 2). The regression model obtained between rainfall and the surface of each habitat estimated by means of satellite imagery shows a significant fit which allows to estimate the area of each habitat for the months that birds were surveyed. A positive relationship between rainfall and wetland water surface was found ($a = 2.82$ (0.03), $b = 0.002$ (<0.01), $r^2 = 0.83$, $F = 29.18$, $P < 0.001$, $N = 8$, Fig. 3a). As rainfall increase, more beach and mudflat areas were covered by water ($a = 2.71$ (0.52), $b = -0.02$ (0.05), $r^2 = 0.68$, $F = 12.93$, $P < 0.01$, $N = 8$, Fig. 3a) and there was a decrease in the surface of salt marsh area ($a = 3.12$ (0.02), $b = -0.001$ (<0.01), $r^2 = 0.83$, $F = 29.14$, $P < 0.001$, $N = 8$, Fig. 3a). A negative relationship between habitat diversity and rainfall was also found ($r^2 = 0.66$; $F = 11.69$, $P = 0.014$, $N = 8$, Fig. 3b).

Waterbird Responses to Rainfall

Eight thousands eight hundreds and ten waterbirds belonging to 44 species were observed, including primarily shorebirds (mainly *Tringa melanoleuca*, *T. flavipes*, *Himantopus melanurus*, *Limosa haemastica* and *Pluvialis dominica*; 27%), swans (*Cygnus melanocoryphus* and *Coscoroba coscoroba*; 13%), and coots (*Fulica armillata*, *F. leucoptera*, and *F. rufifrons*; 10%). Shorebirds were most abundant during spring and summer, swans most abundant during autumn, and coots during summer and autumn (Table 2).

During 1993 and 1997, when rainfall was not different from the average of the last 100

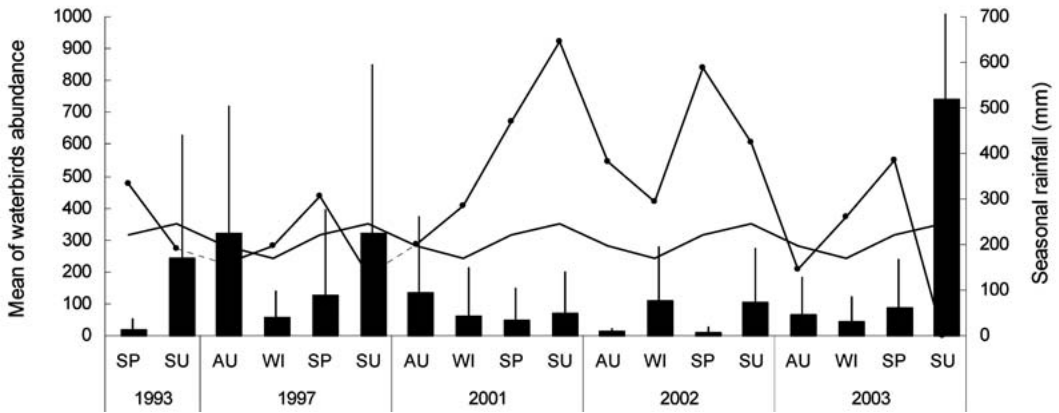


Figure 2. Total number of waterbirds (bars) and its SD (vertical bars), rainfalls by season (points connected by lines) during 1993, 1997 and 2001 to 2003, and the average of seasonal rainfalls from 1900 to 2003 in Mar Chiquita Lagoon, Argentina (line) (Canepuccia *et al.* 2005). AU: Autumn (21 March to 20 June), WI: Winter (21 June to 20 September), SP: Spring (21 September to 20 December), SU: Summer (21 December to 20 March). Samples numbers are the same as in Table 2.

y ($t_6 = -0.72$, $P > 0.5$), abundance of waterbirds was high, and was highest during summer 2003 when rainfall was lower than average. When rainfall increased and reached the highest values during 2001 and 2002, the number of waterbirds was lowest (Fig. 2). In general, forward-stepwise multiple regression showed a negative relationship among water surface and number of individuals (Fig. 4), richness (Fig. 5), and diversity of waterbirds for autumn ($R^2 = 0.87$, $F = 47.62$, $P < 0.01$, $N = 9$), spring ($R^2 = 0.50$, $F = 15.26$, $P < 0.01$, $N = 17$) and summer ($R^2 = 0.47$, $F = 15.92$, $P < 0.01$, $N = 20$). However, there was no relationship among water surface and number of individuals (Fig. 4), richness (Fig. 5), and diversity ($R^2 < 0.001$, $F = 0.01$, $P = 0.92$, $N = 16$) in winter. In the simple regression between residuals of habitat diversity and waterbirds richness, an outlier was detected in spring (4 December 2003) and other in summer (13 March 2002; leverage: $h_{ii} > 2 \sum h_i/n$, see Figs. 4 and 5). These outliers were excluded from the analysis because correspond to dates of high rainfall (>250 mm monthly). However, with or without these outliers, habitat diversity did not explain a significant portion of variability in waterbird richness after including water surface as a variable ($P > 0.05$, Fig. 5).

Waterbird morphofunctional groups differed in their responses to each habitat vari-

ation due to rainfall (Tables 1 and 2). Although some groups, such as ducks (in autumn), long-legged waterbirds (in spring), gulls and swans (in summer), declined in abundance in response to increase in water surface, others, such as cormorants, increased in abundance (in winter). In relation to increases in mudflat and beach surfaces, several groups such as long-legged waterbirds, shorebirds (in autumn), shorebirds (in spring) and gulls (in summer) increased. Shorebirds (in spring) and ducks (in summer) also increased in abundance in response to an increase in local habitat diversity (see Table 1, for more details see Table 2).

DISCUSSION

We found that rainfall was positively correlated with water surface, and negatively correlated with habitat diversity. Also water depth and habitat diversity changes due to rainfall, as well as the magnitude of these changes, are important factors influencing the abundance and diversity of most groups of waterbirds in this region.

In the Argentinean pampas, annual rainfall has increased during the past 40 y (Viglizzo *et al.* 1995). Our data show that the rainfall regime has a strong effect on landscape configuration. Although we assessed change

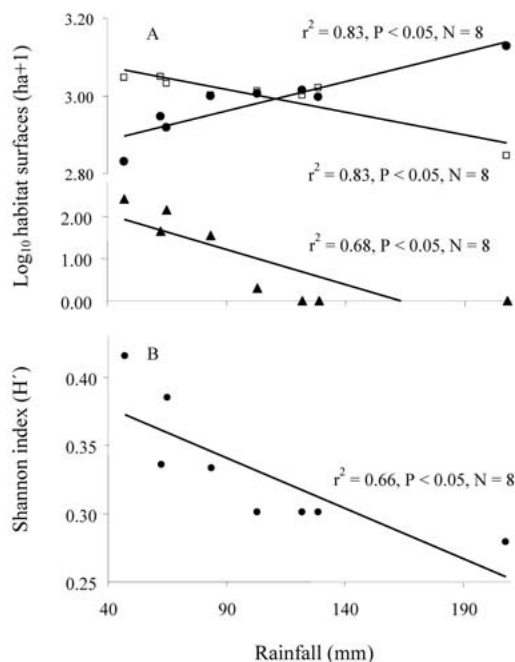


Figure 3. Relationship between cumulative seasonal rainfalls, and a) habitats surface obtained by satellite imagery (circles: water surface, square: salt-marsh surface, and triangles: mudflat surface); and b) habitat diversity (Shannon Index), in Mar Chiquita Lagoon, Argentina (Canepuccia *et al.* 2005).

in water surface, we believe that this parameter is related to water depth in this region. This is expected because the study area is located on a low lying coastal plain (Isla and Gaido 2001) where rainfall translates into changes in water levels that inundate the wetlands (Isla 1997). Fluctuation of water depth *per se*, is a key factor for many waterbirds (Kushlan *et al.* 1985; Kushlan 1989). The relationship between changes in water depth and habitat use by waterbirds is correlated with waterbird morphological features such as beak, neck (Poysa 1983), and leg length (Baker 1979). In wetlands elsewhere, the largest density and diversity of shorebirds and waterfowl occurred when wetlands average 15-20 cm depth (e.g., Californian wetlands, Colwell and Taft 2000). Few species used exclusively habitat deeper than 25 cm (Colwell and Taft 2000). Many species prefer to forage in habitat with less than ten cm depth (Fredrickson and Reid 1986).

The waterbirds habitat use as a response to water depth change appears to be the case of our study system, where greater waterbird abundance and diversity were recorded when the lagoon was at its lowest depth level. Furthermore, over a time span of a decade (i.e., our study), local diversity and number of waterbirds appear to be associated to physical factors like rainfall regime. This is a common pattern in highly stressed habitats (such as some estuarine environments), where physical factors (e.g., habitat diversity, coastal storms, waves, flow and rainfall regime) have an important role in determining community structure (e.g., Ross *et al.* 1985; Capone and Kushlan 1991). Moreover, changes in habitat diversity also may affect the diversity and abundance of waterbirds such as shorebirds and ducks. Habitat diversity influences community structure in a variety of environments, such as forest, grasslands and wetlands (e.g., Wiens 1974; Roth 1976; Colwell and Taft 2000). In our study, when water was shallow, the lagoon had a mosaic of mudflat with diverse microtopography, sand banks, surfacing polychaete reefs (see Schwindt *et al.* 2004), cordgrass areas, and shallow or deep water areas. However, the landscape became more homogeneous as rainfall increased, leaving only areas dominated by shallow and deep waters.

Shorebirds (Families Recuvirostridae, Charadriidae and Scolopacidae) were most affected by the increase in water depth. Shorebirds have relatively short legs (four to 20 cm), feed on benthic invertebrates in mudflats and shallow waters (Hayman *et al.* 1987; Escapa *et al.* 2004) and use dry beaches or other open areas without water to rest (Palomo *et al.* 1999; Martínez 2001). Primarily the increase in water depth results in mudflat flooding and the consequent drop in their availability. These changes should have direct effects on shorebird foraging and roosting habitat use (i.e., autumn). But when the mudflat is restricted, habitat diversity may play the most important role, affecting abundance of most shorebirds (i.e., spring and summer). The relationship between water depth and shorebird abundance has also been observed to be affected by tidal level (e.g., Burger *et al.* 1977), but in a short

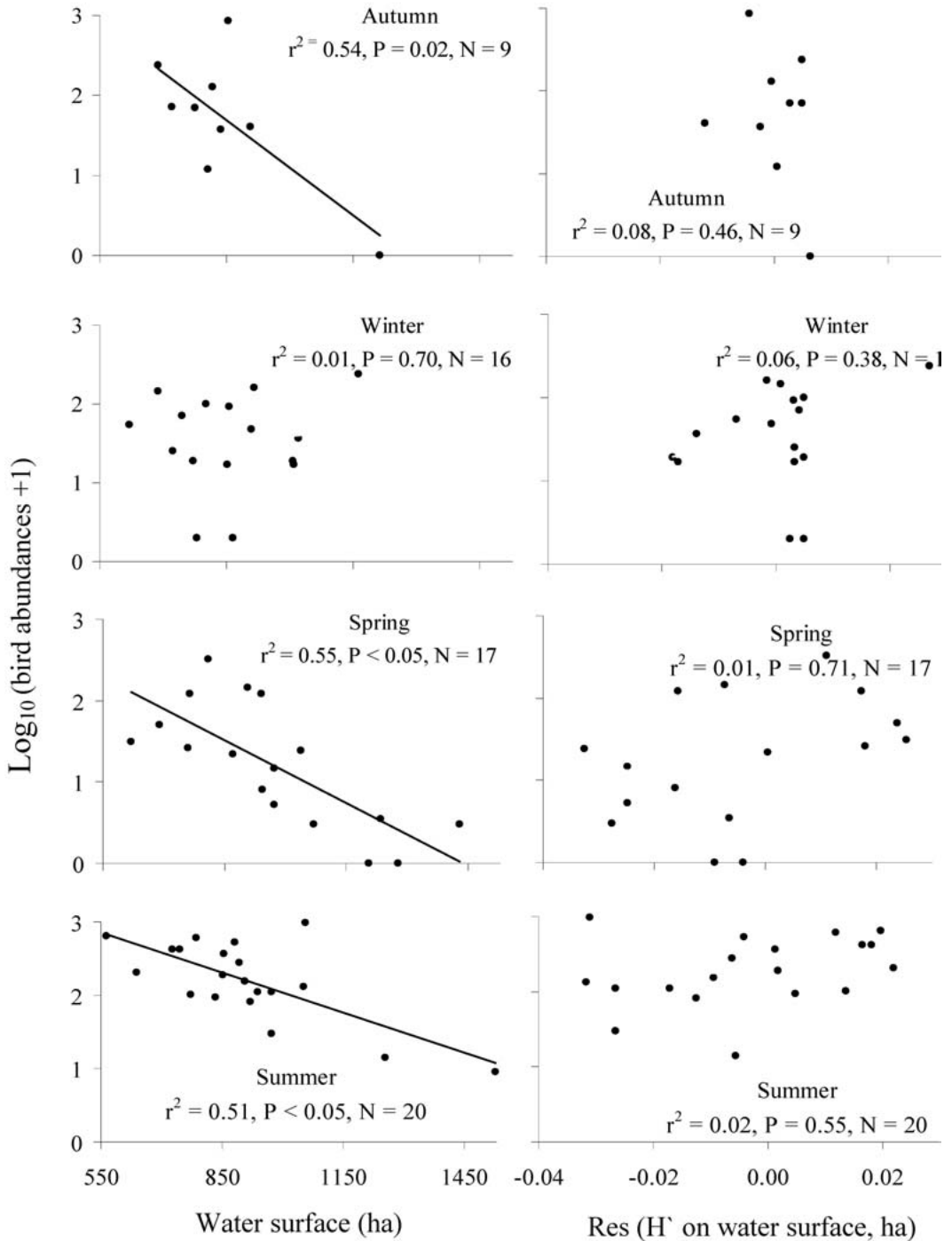


Figure 4. Waterbirds abundance in relation to water surface (left) and habitat diversity (right) when water surface remains statistically constant (Canepuccia *et al.* 2005). Res: residual of regression analyses.

term and with predictable effect. However, when the habitat is flooded by rainfall, the persistence of the change is longer, and thus

the effect on shorebirds should be larger. Most shorebird species in our study site are migratory (Nearctic and Patagonian mi-

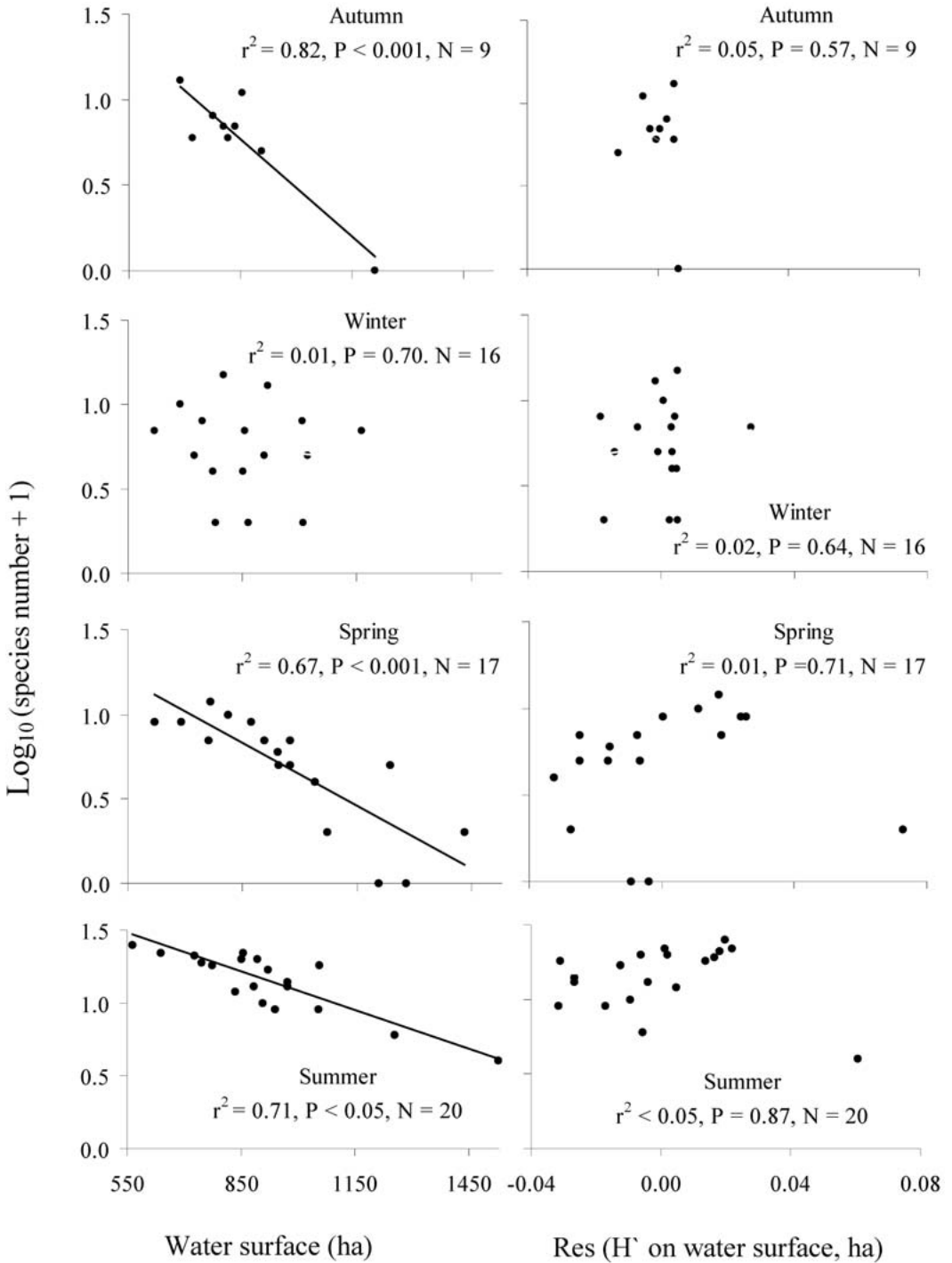


Figure 5. Richness of waterbirds in relation to water surface (left) and habitat diversity (right) with water surface held statistically constant (Canepuccia *et al.* 2005). Res: residual of regression analyses.

grants, see Appendix 1), using the site during the non-breeding period. Migratory shorebirds exploit resources seasonally mak-

ing them dependent on a specific sequence of sites essential for completing the annual cycles (Myers *et al.* 1987).

Table 1. Waterbirds responses to habitat area and habitat diversity change at Mar Chiquita obtained from forward stepwise multiple regression. R^2 : Multiple regression coefficients, b_n : partial regression coefficients for the variable included in the model, F: Fisher values, P: probability associated was indicated as significant: <0.05 or non-significant: n.s., N: samples number. Au: Autumn (21 Mar to 20 Jun), Wi: Winter (21 Jun to 20 Sep), Sp: Spring (21 Sep to 20 Dec), Su: Summer (21 Dec to 20 Mar).

Group/season	Habitat area (ha)			Habitat diversity (S')	R^2	F	P	N
	Water	Mudflat	Saltmarsh					
	b_1	B_2	b_3	b_4				
Ducks								
Au.	-0.002				0.52	6.46	<0.05	9
Wi.	-0.011		0.363	-25.740	0.28	1.57	n.s.	16
Sp.	-0.001				0.10	1.59	n.s.	17
Su.				8.807	0.42	13.10	<0.001	20
Long-legged waterbirds								
Au.		0.007			0.52	6.52	<0.05	9
Wi.	0.003			0.010	0.11	0.82	n.s.	16
Sp.	-0.002				0.38	7.85	<0.01	17
Su.	-0.001				0.39	10.03	<0.01	20
Shorebirds								
Au.		0.005			0.47	6.16	<0.05	9
Wi.	-0.005			-11.872	0.17	1.38	n.s.	16
Sp.		0.004		21.525	0.61	11.03	<0.01	17
Su.				13.053	0.43	12.74	<0.01	20
Grebes								
Au.								9
Wi.	-0.001	-0.002			0.13	0.94	n.s.	16
Sp.			-0.0004		0.14	2.43	n.s.	17
Su.		-0.001			0.07	1.26	n.s.	20
Gulls								
Au.		0.003			0.25	2.34	n.s.	9
Wi.	0.005			17.541	0.11	1.26	n.s.	16
Sp.								17
Su.	-0.002	0.001			0.48	7.81	<0.01	20
Swans								
Au.	-0.002				0.10	0.80	n.s.	9
Wi.								16
Sp.			0.001		0.04	0.69	n.s.	17
Su.	-0.002				0.20	4.26	<0.05	20
Coots								
Au.			0.006	-5.816	0.14	0.48	n.s.	9
Wi.				2.838	0.07	1.04	n.s.	16
Sp.			0.001		0.09	1.47	n.s.	17
Su.			0.001		0.06	1.20	n.s.	20
Cormorants								
Au.								9
Wi.	0.003				0.28	5.09	<0.05	16
Sp.			0.001		0.09	1.50	n.s.	17
Su.	-0.001				0.06	1.24	n.s.	20

Swimmers or long-legged waterbirds showed no morphological limitations to remain during flooding periods. Among them, long-legged waterbirds have generalized dietary habits and forage by wading in shallow

open marshes. These characteristics together with their morphofunctional characteristics (i.e., long legs and neck), allow them to utilize fluctuating wetlands (Kushlan 1981, 1989). Swimming species, such as waterfowl, used

Table 2. Mean number of individuals of morphofunctional groups of waterbirds and mean number of species and individuals, by season, in Mar Chiquita Lagoon, Argentina. Number of species are indicated between brackets (to the right of the group name) and the number of samples for each season are at the right of the season name. Au: Autumn (21 Mar to 20 Jun), Wi: Winter (21 Jun to 20 Sep), Sp: Spring (21 Sep to 20 Dec), Su: Summer (21 Dec to 20 Mar).

	Seasons																	
	1993			1997				2001				2002			2003			
	Sp(4)	Su(8)	Au(3)	Wi(4)	Sp(3)	Su(2)	Au(2)	Wi(5)	Sp(3)	Su(2)	Au(2)	Wi(3)	Sp(4)	Su(5)	Au(3)	Wi(4)	Sp(3)	Su(3)
Ducks (9)	1.5	25.3	4.7	3.3		1.0	16.5	3.6	13.0	5.0	5.0	22.0	1.0	5.6		9.7	3.3	75.3
Swans (2)		27.7	174.0	2.5	0.7	19.0	6.0	28.4				0.7		0.2		1.8	39.0	23.3
Long-legged wading birds (9)	0.5	10.4	23.3	23.3	25.7	23.0	80.5	7.2	8.7	21.5	1.0	16.7	1.5	12.0	2.0	1.5	2.0	37.3
Coots (3)	3.2	9.3	93.7	2.5		32.0			1.3	3.0	2.0			13.4	8.3	12.3	27.0	127.7
Gulls (4)		28.0	8.0	9.5		9.0	5.5	2.2				39.0	2.8	19.0		3.3	0.7	105.7
Cormorant (1)	0.4	1.5		2.8	2.0	0.5		19.0	6.0			19.7	2.0	8.4	1.7		2.0	8.0
Grebes (3)	0.4	0.3				1.5			0.7		3.0	2.3	0.5	1.8	2.7	0.8	0.7	
Shorebirds (11)	11.1	85.4	15.0	8.0	89.7	161.5	17.0	0.8	15.7			4.3		29.8	4.0	12.5	13.3	217.0
Number of individuals	17	241	319	56	125	319	136	62	48	70	11	108	8	106	66	43	89	740
Number of species	18	30	15	15	15	18	14	10	10	9	6	17	8	31	10	18	15	36

deeper zones lacking emergent vegetation. Coots and grebes fed in open waters, but remain near the mudflat and areas covered by grasslands used for nesting. Furthermore, increases in water depth still hamper access to benthos by some species, decrease access to free-living aquatic organisms (fishes, zooplankton) due to their higher dispersion (Kushlan 1976), and decrease roosting areas (banks and shallow waters). Indeed, benthic vegetation (i.e., *Ruppia maritima* in this area) is the main food resource for a large number of species, like the Coscoroba Swans, Black-necked Swans and ducks (Bortolus *et al.* 1998).

Predator species, like gulls, cormorants or grebes, may be affected by a decrease in water level that concentrates their food resources in small patches facilitating their capture (Kushlan 1976). Fluctuations in water depth also can restrict or allow avian habitat use through control of prey abundance and availability. In southern Florida wetlands, the abundance of fish and aquatic invertebrates increased during the deep-water season, but during the dry season, falling water levels increase their availability to long-legged wading birds by concentrating prey in dry seasonal pools (Kushlan 1989; Frederick and Ogden 2001). Long-legged wading birds take advantage of the abundant and available food supply to nest in the dry season (Hafner and Britton 1983; Frederick and Collopy 1989; Kushlan 1989; Frederick and Ogden 2001). Peaks in waterbird abundance observed at the end of 2003, after a prolonged rainy period (2001-2002, see Fig. 2) may support the hypothesis that this change in abundance was probably due to a peak in abundance or availability of prey. The negative relationship between gulls and mudflat availability could be explained by the exploitation by these birds of banks to rest and feed (see Martínez 2001). The lack of a relationship between bird abundance and rainfall during the austral winter may be due to changes in bird behavior during winter. However, it is more likely that it was due to the low number and diversity of waterbirds during this season (see Table 2).

In summary, we provide evidence that the inter-annual variability in the rainfall pat-

tern influences the presence and/or abundance of most waterbirds species. The fluctuation in water depth *per se* is a key factor for many waterbirds, but also changes in habitat diversity. Our results also provide evidence that in dynamic and stressed habitats, physical factors such as rainfall largely affect local communities (Ross *et al.* 1985; Capone and Kushlan 1991). Moreover, our results show an example of how large-scale processes like incremental changes in rainfall due to global climate change can affect local ecological events, such as the cycles of abundance and diversity of birds in wetlands.

ACKNOWLEDGMENTS

We thank to F. Isla for allowing us to use the image processing software Idrisi 32 and the Argentinean National Commission of Space Activities (CONAE) for providing the satellite images. We also thank M. S. Bo, C. De Francesco, L. Biondi, A. Koyuk, M. S. Fanjul and L. Cermelo for their field assistance and, A. Novaro and D. Blanco, for helpful comments of an early version of this manuscript. We thank K. A. Hobson, and an anonymous referee whose comments have greatly improved the manuscript. This project was partially supported by Universidad Nacional de Mar del Plata, Fundación Antorchas (13900-13), ANPCyT, CONICET (PIP 2851, all granted to O.I.). A. D. Canepuccia and J. P. Isacch were supported by Postdoctoral fellowships from the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET).

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Appendix 1. Waterbird species recorded in the study area grouped by morphofunctional similarity.

Ducks	Brown Pintail, <i>Anas georgica</i> , Vieillot 1816	Resident
	Southern Wigeon, <i>A. sibilatrix</i> , Poepping 1829	Resident
	Speckled Teal, <i>A. flavirostris</i> , Vieillot 1816	Resident
	Red Shoveler, <i>A. platalea</i> , Vieillot 1816	Resident
	Cinnamon Teal, <i>A. cyanoptera</i> , Vieillot 1816	Resident
	Silver Teal, <i>A. versicolor</i> , Vieillot 1816	Resident
	Lake Duck, <i>Oxyura vittata</i> , Philippi 1860	Resident
	White-faced Tree Duck, <i>Dendrocygna viduata</i> , Linnaeus 1766	Resident
	Rosy-billed Pochard, <i>Netta peposaca</i> , Vieillot 1816	Resident
Swans	Black-necked Swan, <i>Cygnus melanocoryphus</i> , Molina 1782	Resident
	Coscoroba Swan, <i>Coscoroba coscoroba</i> , Molina 1782	Resident
Long-legged wading birds	Maguari Stork, <i>Ciconia maguari</i> , Gmelin 1789	Resident
	Great Egret, <i>Egretta alba</i> , Gmelin 1789	Resident
	Snowy Egret, <i>E. thula</i> , Molina 1782	Resident
	Cattle Egret, <i>Bubulcus ibis</i> , Linnaeus 1758	Resident
	White-necked Heron, <i>Ardea cocoi</i> , Linnaeus 1766	Resident
	White-faced Ibis, <i>Plegadis chihi</i> , Vieillot 1817	Resident
	Roseate Heron, <i>Syrigma sibilatrix</i> , Temminck 1824	Resident
	Chilean Spoonbill, <i>Platalea ajaja</i> , Linnaeus 1758	Resident
	Whistling Flamingo, <i>Phoenicopterus chilensis</i> , Molina 1782	Resident
Grebes	Great Grebes, <i>Podiceps major</i> , Boddaert 1783	Resident
	White-tufted Grebe, <i>Rollandia Rolland</i> , Lesson 1828	Resident
	Pied-billed Grebe, <i>Podilymbus podiceps</i> , Lesson 1842	Resident
	Neotropical Cormorant, <i>Phalacrocorax olivaceus</i> , Gmelin 1789	Resident
Coots	Red-fronted Coot, <i>Fulica rufifrons</i> , Philippi and Landbeck 1861	Resident
	Red-gartered Coot, <i>F. armillata</i> , Vieillot 1817	Resident
	White-winged Coot, <i>F. leucoptera</i> , Vieillot 1817	Resident
Gulls	Kelp Gull, <i>Larus dominicanus</i> , Lichtenstein 1823	Resident
	Olrog's Gull, <i>L. atlanticus</i> , Olrog 1958	Winter visitant
	Brown-hooded Gull, <i>Chroicocephalus maculipennis</i> , Lichtenstein 1823	Resident
	Gray-hooded Gull, <i>C. cirrocephalus</i> , Vieillot 1818	Resident
Shorebirds	Greater Yellowlegs, <i>Tringa melanoleuca</i> , Gmelin 1789	Summer visitant
	Lesser Yellowlegs, <i>Tringa flavipes</i> , Gmelin 1789	Summer visitant
	Semipalmated Plover, <i>Charadrius semipalmatus</i> , Bonaparte 1825	Summer visitant
	Southern Lapwing, <i>Vanellus chilensis</i> , Wagler 1827	Resident
	South American Stilt, <i>Himantopus melanurus</i> , Vieillot 1817	Resident
	Stilt Sandpiper, <i>Micropalama himantopus</i> , Bonaparte 1826	Summer visitant
	Pectoral Sandpiper, <i>Calidris melanotos</i> , Vieillot 1819	Summer visitant
	Red Knot, <i>C. canutus</i> , Wilson 1813	Summer visitant
	White-rumped Sandpiper, <i>C. fuscicollis</i> , Vieillot 1819	Summer visitant
	Hudsonian Godwit, <i>Limosa haemastica</i> , Linnaeus 1758	Summer visitant
	American Golden Plover, <i>Pluvialis dominica</i> , Muller 1776	Summer visitant
Other species*	Snowy-crowned Tern, <i>Sterna trudeaui</i> , Audubon 1838	Resident
	Chimango Caracara, <i>Milvago chimango</i> , Vieillot 1816	Resident

*Species with low abundance, not included in the analysis by group.