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Waterbird Assemblages and Habitat Characteristics in Wetlands: Influence of Temporal Variability on Species-Habitat Relationships

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Abstract.—Patterns of spatial and temporal variation in species richness, abundance and diversity were evaluated in eight wetlands in Central-South Chile in relation to nine wetland characteristics. Twenty-six bird species were recorded, among the most representative families were Rallidae, Ardeidae and Anatidae with five species each. Stepwise regression analyses identified wetland area and water level fluctuations as the most important variables determining bird abundance. Variations in species richness were explained by wetland area, shoreline length, vegetation cover and water-level fluctuations. Shoreline development, shoreline length and wetland area lower than one-meter depth were especially important in determining species diversity. Cluster analyses showed similar results. Shoreline length was an important feature influencing total species number, but simple regression analysis showed that the species area relationship occurs in wetlands too. This study concludes that species richness, bird abundance and diversity reach higher values in larger and structurally more heterogeneous wetlands, but with important seasonal dynamics in waterbirds. The relationships between habitat characteristics and community structure did not remain unchanged throughout the year, suggesting that the birds respond differently to one or another habitat characteristic depending on the season. These results show the need for wetland conservation in Chile, paying special attention to the largest and most heterogeneous wetlands to conserve the greatest species richness and bird abundance.
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Key words.—wetlands, species richness, abundance, habitat features, habitat structure, shoreline length, wetland area, seasonal dynamics, Chile.

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The importance of habitat structure and complexity to avian ecology has been widely documented (MacArthur 1961; MacArthur *et al.* 1962; Cody, 1981, 1985), and positive correlations between habitat cover, habitat area, species richness and local abundance have been found (MacArthur 1961; Venier and Fahrig 1996). However, much of this research has been conducted in terrestrial ecosystems; few studies have examined habitat relationships of wetland birds.

The relationship between habitat structure and wetland bird assemblages is centered on habitat extension effects on the community structure (Froneman *et al.* 2001; Riffell *et al.* 2001). Species richness, bird abundance and species guild have been positively correlated with wetland area and water surface area (Babbitt 2000). Other studies have related the bird abundance and species richness with water level fluctuations, productivity, cover of aquatic vegetation and habitat heterogeneity (Kaminski and Prince 1984; Edwards and Otis 1999). Notwithstanding data on the relationship between habitat and aquatic bird assemblage structure, it is unclear which factors are the most important. Correlations between habitat characteristics and species richness, abundance, diversity and composition indicate that bird assemblages in urban habitats respond to a complex combination of factors, as in natural habitats (Germaine *et al.* 1998). Most studies that have tried to determine habitat selection by aquatic birds disagree on which features are most important (Murkin *et al.* 1997), and seasonal influence on habitat relationships has been poorly investigated (Froneman *et al.* 2001). Some habitat characteristics may change over time (e.g., water depth level, vegetation cover, among others) and bird selection criteria might also change in response to these habitat changes (Riffel *et al.* 2001). Also, bird habitat requirements change seasonally due to nest or food utilization in breeding and non-breeding seasons (DuBowy 1988; Froneman *et al.* 2001).

Worldwide, wetland ecosystems are being altered and reduced at an increasing rate by human activities (Wilen 1989). Growing recognition of wetlands as important environments for birds, due to their habitat diversity and high productivity, have led to increasing concern about the impact of their loss (Dugan 1990). Unfortunately, despite the value of wetland biodiversity and the influence of some wetland attributes on species diversity, in Chile, wetlands are still declining locally and regionally as a result of human pressure (Parra *et al.* 1989).

Our paper evaluates the influence of structural features of lacustrine wetlands on species richness, abundance and composition of birds. It also aims to quantify the characteristics that are more important for waterbirds in these wetlands. We consider seasonal effects on the aforementioned potential relationships and evaluate the species area relationship. Information about these relationships will contribute to the development of a wetland management plan in Chile.

METHODS

Study Area

Eight urban wetlands of the Concepción-Talcahuano-San Pedro de la Paz metropolitan area were included in the study (Fig. 1). Six of these wetlands are located to the north of the BíoBío River, central-south Chile (Lo Méndez, Lo Galindo, Las Tres Pascualas, Verde, Redonda y Lo Custodio) and two on the south of the BíoBío River (Laguna Grande of San Pedro and Laguna Chica of San Pedro).

These wetlands all have fluvial origins and those located on the northern riverside of the BíoBío originated from an old bed depression of the BíoBío River. The southern riverside sites, Laguna Grande of San Pedro and Chica of San Pedro, originated from sand damming of two sub-river basins and subsequent watershed erosion and sedimentation (Cisternas 1999). The wetlands present a mixture of emergent aquatic vegetation and open water areas, differences in size, vegetation cover and structural heterogeneity of the habitat, among others.

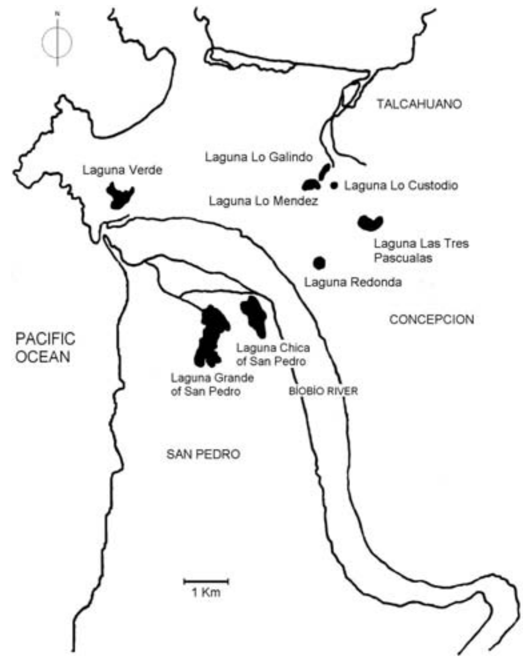

Figure 1. Study area, showing the eight wetlands of Concepción-Talcahuano-San Pedro metropolitan area.

Habitat Characteristics

Each wetland was surveyed once during each season in 2001 (autumn, winter, spring and summer). This was considered adequate to characterize changes in some features over the season. Nine physical and vegetation features were measured at each wetland: wetland area, open water area, total vegetation cover, vegetation heterogeneity (percentage cover of three major aquatic vegetation life forms, i.e. emergent, floating and submerged), wetland area shallower than one meter depth, vegetation cover and open water area ratio, shoreline length, shoreline development and water level fluctuation.

Wetland size, shoreline length, open water area, vegetation cover, vegetation heterogeneity, vegetation cover and open water area ratio were measured from aerial photos (1:5.000). These photographs were entered into a GIS program. Vegetation heterogeneity was evaluated for each wetland using the Shannon-Wiener Diversity Index (Krebs 1999), using the percentage cover of each vegetation group as abundance data. Shoreline development was calculated for each one of the wetlands based on the following equation (Margalef 1983):

$$D = \frac{S}{2\sqrt{a \times \pi}}$$

Where: D = Shoreline Development, S = Shoreline Length, a = Open Water Area

Surface of each wetland shallower than one meter depth was obtained from published material from previous studies on the same wetlands (Parra *et al.* 1989; Cisternas *et al.* 1999; Urrutia *et al.* 2000). Seasonal water level fluctuations were registered with a cm-marked sampling rod at fixed locations inside each wetland (Colwell and Taft 2000).

Bird Surveys

Studies were conducted seasonally from May 2000 (autumn, Southern Hemisphere) to March 2001 (summer, Southern Hemisphere). Bird counts were done between sunrise and 12:00 h and between 15:00 h and sunset, using binoculars (10×50). Surveys began near the wetland, where most of the surface area and edge was visible, and proceeded to identify and count all birds present (Bibby *et al.* 1993). The observer then walked around the perimeter of the wetland to flush and identify any unseen birds. Species composition, species richness and bird abundance were determined. To calculate species diversity (H') using the Shannon-Wiener index (Krebs 1999), information of the number of individuals of each species was used. Scientific names follow Araya *et al.* (1995). To determine temporal variation in waterbird presence and abundance in the wetlands, each wetland was counted three times during each season. Seasonal variation was detected by analyzing datasets from different seasons separately and comparing results.

Data Analyses

To classify wetlands on the basis of bird abundance, a cluster analysis, using the Euclidean distance similarity measure, was performed. Bird species composition was analyzed with cluster analyses using the percent disagreement method by unweighted pair-group method via arithmetic averages (UPGMA). To assess the statistical significance of observed clusters, bootstrap analyses on each cluster analysis with 5000 permutations on each original data matrix were performed following the methodology described by Jaksic and Medel (1990). To determine the relationship among nine wetland features (Table I) and bird abundances, ordination methods based on pair-wise similarity matrices were applied. The physical variables were transformed to Log (X+1) and normalized in order to compare variables with different unit measures (Clarke *et al.* 2005). The respective resemblance matrix was based on Euclidean Distance. Bird abundances at each wetland was standardized in respect to total abundance, to reduce eventual sampling effort biases, and square-root transformed to downweigh the influence of over-abundant taxa. For these variables, the resemblance matrix was based on the Bray Curtis index.

A principal component analysis (PCA) with centring and standardization of the variables was carried out in order to examine multivariate similarities among wetlands based on morphological and vegetational features. Standardization of variables in PCA allows for vary disparate variables to be compared (Gotelli and Ellison 2004).

Finally, to determine how environmental variables were related to bird abundances by wetland, we used the Biota-Environment matching (BIOENV) analysis (included in PRIMER v6.0; Clarke and Gorley 2005), with a permutation test (100 iterations) to test significance. This procedure uses a multiple regression approach to determine which environmental variables best explain the multivariate relationship of the bird assemblages.

Multiple regression analyses were done with log-transformed data. To determine the relationships between bird parameters and wetland characteristics (physical and vegetation attribute variables) for every season, separate stepwise multiple-regression analyses were done. Separate analyses were performed for each dependent variable (i.e. number of species, number of birds and species diversity) with all the predictor features (nine characteristics). A simple linear regression was used to test the species area relationship between species richness and wetland area.

RESULTS

Morphological and Vegetation Characteristics

Habitat characteristics varied among sites, and only some wetlands showed seasonal feature variations. Table 1 lists the wetland features measured. Spatial distribution of wetlands on the first and second axes of the PCA are plotted in Fig. 2a. Laguna Verde, Laguna Grande of San Pedro and Laguna Chica of San Pedro are separated along the first axis from all other wetlands. These are characterized by wetland size (area, open water area, shoreline length). The second axis mainly represents wetlands shape with shoreline development, vegetation cover and vegetation cover: open water area ratio. The PCA analysis using wetland characteristics is set out in Fig. 2b. First and second axes of the PCA explained 83% of the total variance and their eigenvalues were 4.46 and 2.97, respectively. Metrics that were related to the wetland size and shape attained the highest scores. Most of the metrics tended to follow the direction of Axis 1.

Bird Assemblages

Twenty six bird species were recorded at the eight wetlands during all seasons (Table 2). Throughout the year, the greatest number of species was recorded in Laguna Grande of San Pedro, Laguna Chica of San Pedro, and Laguna Verde. Bird abundance was highest at Laguna Grande of San Pedro, the largest wetland. Species diversity was the highest at Laguna Las Tres Pascualas, Laguna Lo Mendez, and Laguna Chica of San Pedro (Fig. 3).

Table 1. Morphological and vegetation features measured for eight wetlands in Concepción-Talcahuano-San Pedro metropolitan area during 2000/2001.

Wetland features	Redonda	Las Tres Pascualas	Lo Méndez	Lo Galindo	Lo Custodio	Grande Sn Pedro	Chica Sn Pedro	Verde
Lat. (S)	36°48’	36°48’	36°47’	36°47’	36°48’	36°51’	36°51’	36°47’
Long. (W)	73°04’	73°02’	73°03’	73°02’	73°02’	73°06’	73°05’	73°02’
Height (m.o. s. l.)	11	13	14	14	12	4	5	10
Maximal length (m)	208	431	351	494	80	2,500	1,900	340
Maximal width (m)	207	277	192	120	62	1,375	870	325
Shoreline length (m)	643	1,681	944	1,160	256	11,974	4,964	1,295 (S) 2,427 (W)
Wetland area (m^2)	29,275	77,642	44,880	40,313	3,420	2,018,344	519,231	126,806
Open water area (m^2)	28,488	65,620	38,105	38,398	3,278	1,923,603	513,273	27,036 (S) 44,121 (W)
Shoreline Development Index	1.08	1.85	1.36	1.67	1.26	2.43	1.95	2.22 (S) 6.01 (W)
Vegetation cover (%)	2.7	17.0	15.3	5.8	2.4	7.9	1.9	67.0
Water level fluctuation (m)	0.3	0.3	0.3	0.4	0.2	1.4	1.2	1.0

S: Summer; W: Winter.

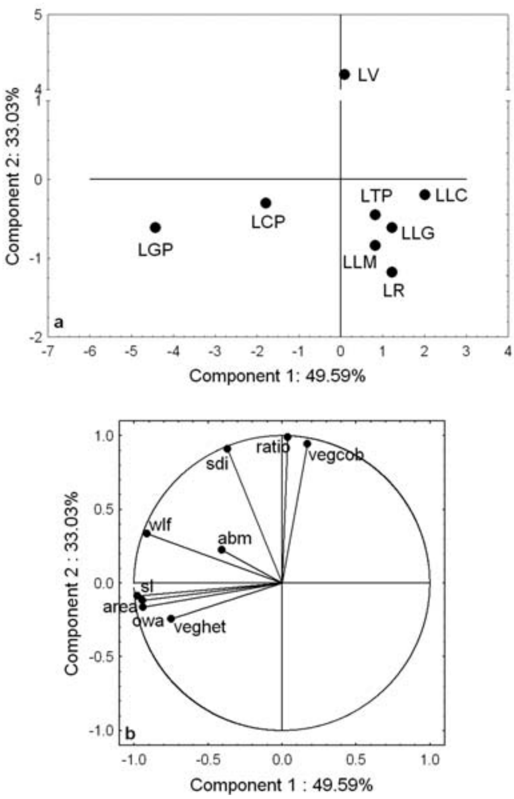

Figure 2a, b. Principal components analysis of studied wetlands (a), Principal components analysis of wetlands characteristics. LV: Laguna Verde; LGP: Laguna Grande of San Pedro; LCP: Laguna Chica of San Pedro; LTP: Laguna Tres Pascualas; LLG: Laguna Lo Galindo; LLM: Laguna Lo Méndez; LLC: Laguna Lo Custodio, and LR: Laguna Redonda, (b) Ordination of 9 wetland features on the first and second axes from PCA. Wetland features are labelled as follows: area: wetland area; owa: open water area; vegcov: vegetation cover; sl: shoreline length; wlf: water level fluctuation; sdi: shoreline development index; veghet: vegetation heterogeneity; abm: wetland area lower 1 meter depth; ratio: vegetation cover/open water area ratio.

Cluster analysis showed grouping of wetlands differing by 48% (critical value) in their species composition (Fig. 4), so clusters that differed by more than this value were considered significantly different ($P < 0.05$). The first cluster shared Passeriformes species associated with emergent vegetation (*Phleocryptes melanops* and *Tachuris rubrigastra*) and those that live in open water (e.g., *Fulica armillata* and *Phalacrocorax brasilianus*) in small wetlands with vast exposed areas that support only a few species. The second cluster showed a higher species number of Passeriformes and Anatidae. The cluster based on bird abundance revealed grouping of wetlands which differed by 49% of bird abundances. These wetlands supported smaller to medium assemblages of piscivorous and insectivorous birds such as *Phalacrocorax brasilianus* and *Cistothorus platensis* (Fig. 5).

Several patterns of waterbird composition and abundance emerge for these wetlands. Those with a bigger surface with high percentage of vegetation cover and vegetation heterogeneity have more species richness, examples being *Tachuris rubrigastra, Agelaius thilius* and *Cistothorus platensis.* Wading species and dabbling ducks increased on wetlands with a mixture of vegetated and exposed surface. On the other side, smaller wetlands with most exposed areas supported only a few bird species.

Bird Assemblages and Wetland Feature Relationships

The BIOENV analysis showed a total Rho value of 0.647, and this was statistically significant ($P < 0.04$). Three variables were selected as the best explaining bird abundance (total area, shoreline development index and vegetation heterogeneity). For this combination of variables the Rho value was equal to the total value (0.647).

Results of the stepwise multiple regression analysis for the autumn, winter, spring and summer seasons are summarized in Table 3. Only four environmental variables of the wetland complex (three structural and one vegetation characteristics) were significantly correlated with species richness (Table 3). In autumn and summer, species richness was best predicted by wetland area ($P < 0.014$ and $P < 0.012$, respectively). In the winter season shoreline length and vegetation cover best predicted species richness ($P < 0.006$). Water-level fluctuation was the best predictor in spring ($P < 0.007$). Total species richness was positively related principally with shoreline length ($P < 0.001$), but a species area relationship was also found (autumn $P < 0.05$; winter $P < 0.01$; spring $P <$

Table 2. Order, families, and waterbird species list recorded in eight wetlands in Concepción-Talcahuano-San Pedro metropolitan area during 2000/2001.

ORDER	FAMILY	SPECIES	COMMON NAME
Podicipediformes	Podicipedidae	*Rollandia rolland*	White-tufted Grebe
		Podiceps major	Great Grebe
		Podylimbus podiceps	Pied-billed Grebe
Pelecaniformes	Phalacrocoracidae	*Phalacrocorax brasilianus*	Olivaceus Cormorant
Ciconiiformes	Ardeidae	*Ixobrychus involucris*	Stripe-backed Bittern
		Ardea cocoi	White-necked Heron
		Casmerodius albus	Great Egret
		Egretta thula	Snowy Egret
		Nycticorax nycticorax	Black-crowned Night heron
Anseriformes	Anatidae	*Cygnus melanocoryphus*	Black-necked Swan
		Anas sibilatrix	Chiloe Wigeon
		Anas georgica	Yellow-billed Pintail
		Anas cyanoptera	Cinnamon Teal
		Netta peposaca	Rosy-billed Pochard
Gruiformes	Rallidae	*Pardirallus sanguinolentus*	Plumbeus Rail
		Gallinula melanops	Spot-flanked Gallinule
		Fulica armillata	Red-gartered Coot
		Fulica leucoptera	White-winged Coot
		Fulica rufifrons	Red-fronted Coot
Charadriiformes	Charadriidae	*Vanellus chilensis*	Southern Lapwing
Passeriformes	Troglodytidae	*Cistothorus platensis*	Grass Wren
Passeriformes	Furnariidae	*Cinclodes patagonicus*	Dark-bellied Cinclodes
		Phleocryptes melanops	Wren-like Rushbird
Passeriformes	Tyrannidae	*Hymenops perspicillatus*	Spectacled Tyrant
		Tachuris rubrigastra	Many-colored Rush-Tyrant
Passeriformes	Icteridae	*Agelaius thilius*	Yellow-winged Black-bird

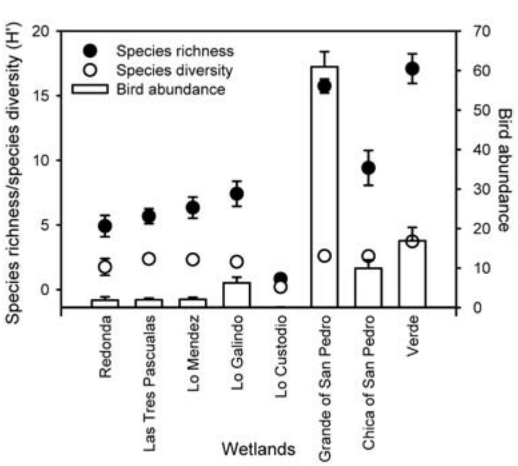

Figure 3. Species richness, species diversity (Shanon-Wiener Index) and waterbird abundance by wetland, with averages and S.D.s in the wetlands of the Concepción-Talcahuano-San Pedro metropolitan area during 2000/2001.

0.05; summer P < 0.05 and all season together P < 0.01) [Fig. 6]. Wetland area and shoreline length were the characteristics that best predicted species richness in these wetlands.

Four morphological wetland features were significantly correlated with bird abundance. In autumn, bird abundance was best predicted by wetland area (P < 0.002) and with water level fluctuation in winter (P < 0.003), spring (P < 0.002) and summer (P < 0.001). Water level fluctuation was the wetland characteristic that best predicted bird abundance. Change in species diversity was positively correlated with Shoreline Development Index in winter (P < 0.006) and with water-level fluctuation (P < 0.02) and vegetation heterogeneity with water/vegetation ratio (P < 0.04) in spring. There was seasonal variability in the habitat bird relationships. Some wetland features were more important to birds in winter whereas others had a stronger effect in spring or autumn.

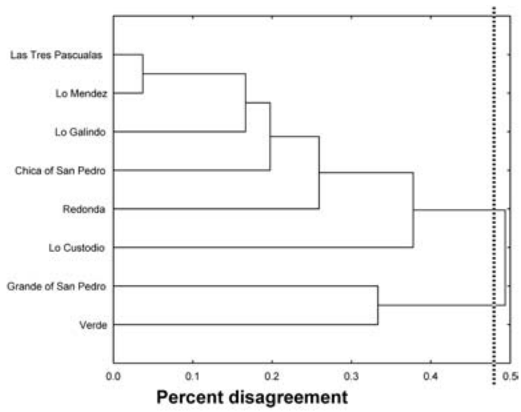

Figure 4. Cluster analysis based on bird species composition (presence-absence) of the eight wetlands of the Concepción-Talcahuano-San Pedro metropolitan area during 2000/2001. Vertical pointed line indicates critical value of significance (P < 0.05).

DISCUSSION

Wetland area, vegetation cover, and structural heterogeneity of the habitat were the most important features that affected wetland bird richness and abundance. Other studies conducted in wetland ecosystems have demonstrated the importance of habitat area and habitat heterogeneity (Svingen and Anderson 1998; Fairbairn and Dinsmore 2001; Riffel *et al.* 2001). Despite these results, distinct seasonal shifts in wetland features were important to the structure of bird assemblages. Hitherto, few studies have considered this variable, since most are restricted to short time periods or they do not separate the seasonal components in their analysis.

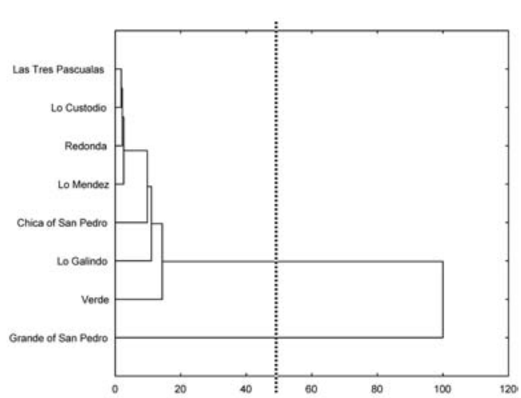

Figure 5. Cluster analysis based on bird abundance of the eight wetlands of the Concepción-Talcahuano-San Pedro metropolitan area during 2000/2001. Vertical pointed line indicates critical value of significance (P < 0.05).

Relationships among habitat and bird assemblages did not remain unchanged throughout the year, suggesting that birds responded differently to one or another habitat characteristic depending on the season. This was in agreement with the findings of Froneman *et al.* (2001) who recorded differences in relationships between habitat and community structure among seasons. According to Patterson (1976), Elmberg *et al.* (1993), the local abundance of food, water levels and habitat structure, are the most important factors associated to the spatio-temporal dynamics in many aquatic birds. (Brown and Dinsmore 1986; Brown *et al.* 1996). Considering that wetlands differ in their potential to provide habitat for wetland birds because species have contrasting life histories that influence the way that each interacts with the landscape (Naugle *et al.* 2001), our current understanding of what constitutes suitable wetland habitat and significant habitat characteristics for wetland birds must integrate the temporal effect.

Species richness and bird abundance increased with shoreline length and wetland size. Shoreline length presented a strong relationship with species number and abundance during autumn and winter, whereas during spring and summer, wetland area was the most influential. We found a strong relationship between species richness and area, and bigger wetlands supported a higher number of bird species. Additionally, we found that bird abundance was best predicted by water level fluctuation and wetland area (Ringelman and Longcore 1982; Froneman *et al.* 2001). According to Paszkowski and Tonn (2000), bigger wetlands can provide more microhabitats, thereby attracting a greater number of species. However, Hudson (1983), and Garay *et al.* (1991) showed that smaller wetlands maintained higher waterbird density and diversity than larger ones. In this context, the structural hetero-

Table 3. Habitat models using stepwise regression. Wetland features enter to analysis with P value < 0.05. area: wetland area; vegcov: vegetation cover; sl: shoreline length; wlf: water level fluctuation; sdi: shoreline development index; veghet: vegetation heterogeneity; abm: wetland area lower 1 meter depth; ratio: vegetation cover/open water area ratio.

Bird variables	Habitat model	R^2	P value
	AUTUMN		
Species richness	-0.987 + 0.38 × area	0.665	0.014
Bird abundance	-2.653 + 0.848 × area	0.815	0.002
Species diversity	0.021 + 0.820 × sdi	0.735	0.057
	WINTER		
Species richness	-1.60 + 0.701 × sl	0.825	0.020
	-1.78 + 0.719 × sl + 0.007 x vegcob	0.965	0.006
Bird abundance	1.175 + 1.898 × wlf	0.793	0.003
Species diversity	0.021 + 0.820 × sdi	0.738	0.006
	-0.557 + 0.571 × sdi + 0.202 x sl	0.891	0.045
	SPRING		
Species richness	1.073 + 0.935 × wlf	0.728	0.007
Bird abundance	1.812 + 1.905 × wlf	0.834	0.002
Species diversity	0.494 + 0.508 × wlf	0.623	0.020
	0.901 + 0.634 × veghet + 0.102 ratio	0.870	0.040
	SUMMER		
Species richness	-1,065 + 0,399 × area	0.681	0.012
Bird abundance	2,064 + 2,376 × wlf	0.852	0.001
Species diversity	-0.422 + 0.188 × abm	0.628	0.019
Total species richness	-0.744 + 0.548 × sl	0.761	0.005

geneity quantified by the shoreline development index and vegetation heterogeneity showed an important relationship with bird assemblages, but only in certain seasons. Shoreline length and shoreline development indices were considered as determinants of bird abundance, according to Hudson (1983), who suggested that in similar-sized wetlands, bird abundance will be higher in those that present more irregular perimeters since they offer longer shorelines, with more refuges.

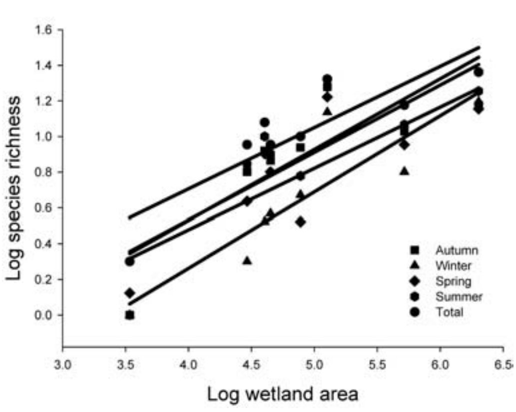

Figure 6. Species richness-area relationship using simple regression analyses on each season: autumn R^2: 0.813, P < 0.05; winter R^2: 0.890, P < 0.01; spring R^2: 0.801, P < 0.05; summer R^2: 0.826, P < 0.05 and total R^2: 0.871, P < 0.01.

In summary, species richness and bird abundance is fundamentally affected by attributes of wetland size. Assemblage complexity, measured by species diversity, appears affected more by heterogeneity in structural habitat. However, precise mechanisms driving habitat-wetland bird assemblages remain unclear and merit further investigation.

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