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Effect of habitat and landscape structure on waterbird abundance in wetlands of central Argentina

Pablo G. Brandolin · Pedro G. Blendinger

Abstract Determining the response of birds to local habitat characteristics and landscape structure is essential to understanding habitat selection and its consequences for the distribution of species. This study identified the influence of environmental factors as determinants of the waterbird assemblage composition in 39 wetlands in the Pampas of central Argentina. Multivariate analysis allowed the identification of environmental factors affecting the use of habitat by waterbird species, whose variable numbers were explained by local and landscape environmental factors. Interspecific variation in responses to changes in environmental factors shows that habitat selection occurs at a species-specific level, although species with similar ecological requirements tend to respond similarly to environmental heterogeneity. Plovers and flamingos were mostly associated with high salinity and the presence of a muddy shoreline and temporary ponds; ducks, herons and ibises were associated with vegetation abundance and decrease in salinity; piscivores and carnivorous species were associated with water depth. The small degree of overlap of habitat requirements between some species suggests a high level of specialization within waterbird assemblages. This knowledge can be used for the design of appropriate conservation and management strategies in central Argentina, where the alarming loss of wetlands requires management strategies that ensure the permanence of the greatest diversity of waterbirds.

Keywords Argentina · Canonical correspondence analysis · Waterbirds · Habitat requirements · Wetlands

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Introduction

Predicting species distributions from local habitat characteristics and landscape structure is a challenging task and is essential for understanding habitat selection and its consequences for the distribution of species (Githaiga-Mwicigi et al. 2002; Pearman 2002; Mayor et al. 2009). Factors such as biological interactions, structure of local vegetation, landscape features and historical effects determine habitat-specific relationships, suggesting that the processes that affect community composition operate simultaneously at different

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spatial scales (Wiens 1989; Cushman and McGarigal 2002; Pearman 2002; Martin and Blackburn 2012). The simultaneous study of factors operating at local and landscape levels can synthesize these perspectives and contribute to the understanding of community composition at the multi-scale level (Cornell and Karlson 1997).

Vegetation structure and landscape attributes influence local abundance and diversity of bird species (e.g., Naugle et al. 2000; Polis et al. 2004). Abiotic factors such as topography, geology and microclimate strongly interact with biotic and human processes, such as land use and disturbance regimes, resulting in complex spatial patterns of species occurrence and may have species-specific effects (Pearman 2002; Barbaro et al. 2007). It is well-known that habitat heterogeneity determines the spatial variation in the composition of terrestrial avifauna (e.g., MacArthur et al. 1962; Collins et al. 1982; Johnson et al. 1992; Titeux et al. 2004). The importance of habitat variation for the abundance and distribution of waterbirds is also well-known (Riffell et al. 2001; Weller 2004). For example, water depth strongly affects the use of wetlands by waterbirds, mainly because it influences the foraging ability of species which differ markedly in morphology and behavior (Vides Almonacid 1990; Ramesh and Ramachandran 2005; Bolduc and Afton 2008). Other factors, such as salinity and plant coverage and composition, can affect birds by influencing the use of foraging and nesting habitats (Takekawa et al. 2006; Ma et al. 2010).

Extensive areas of the central region of Argentina were originally characterized by systems of ponds patchily distributed across a grassland matrix. At present, agricultural activity has caused deep degradation and removal of the original natural habitats which has increased the fragmentation of wetlands and made of many of them disappear (Quirós et al. 2002; Brandolin et al. 2013). The diversity of wetlands found in these agroecosystems produces significant heterogeneity of habitats and resources for birds, providing sites available for stopover, resting, feeding, nesting and roosting for many waterbird species (Brandolin and Ávalos 2010). Habitat heterogeneity at the pond and landscape levels in southeastern Cordoba province (Argentina), coupled with its rich fauna of waterbirds, makes this region a propitious place to study the influence of environmental factors on the waterbird community.

The aim of this study was to describe the distribution and abundance of waterbirds in wetlands of central Argentina and to interpret the patterns observed in relation to variations in local habitat and landscape structure. We hypothesize that the presence of waterbirds in ponds is determined by the quality of the ponds as a source of resource for birds, defined by characteristics of the habitat at the local scale and by the structure of the landscape. Assuming that the quality of a wetland as habitat for waterbirds is positively associated with the availability of resources and environmental complexity and negatively with the intensity of degradation of habitat types that it contains, we expect that (1) bird species will make differential use of wetlands due to the presence of specific habitats generated by the characteristics of each pond, and that (2) responses will be more similar across species with similar ecological requirements than across the full pool of species. Finally, we discuss our results in the context of managing environmental conservation-oriented strategies for waterbird assemblages.

Materials and methods

Study area

The study was conducted in southeastern Cordoba province, Argentina, in an area of 19,606 km^2 in the transition between the Pampa eco-region and the Espinal eco-region (Fig. 1). The topography of this region is one of flat and occasionally undulating plains with some very low knolls. The climate is sub-humid and average annual rainfall is 700–800 mm, with a marked increase of more than 100 mm since the 1970s (Blarasin et al. 2005a). The elevation range is from 115 to 300 m above sea level. The study area forms part of the vast continental sedimentary basin of central and northeastern Argentina, which presents a significant development of wetland systems with ponds. In much of the region, drainage is endorheic or arheic, with periods of rainy years, with extensive and prolonged flooding, alternating with periods of low rainfall (Quirós et al. 2002).

The region has about 1900 ponds (of varying sizes), which add up to around 67,000 ha of waterlogged area (Brandolin et al. 2013). The lowest areas present permanent and temporary ponds, which are not thermally stratified except during very short periods.

Fig. 1 Location of the study area in Córdoba province, Argentina
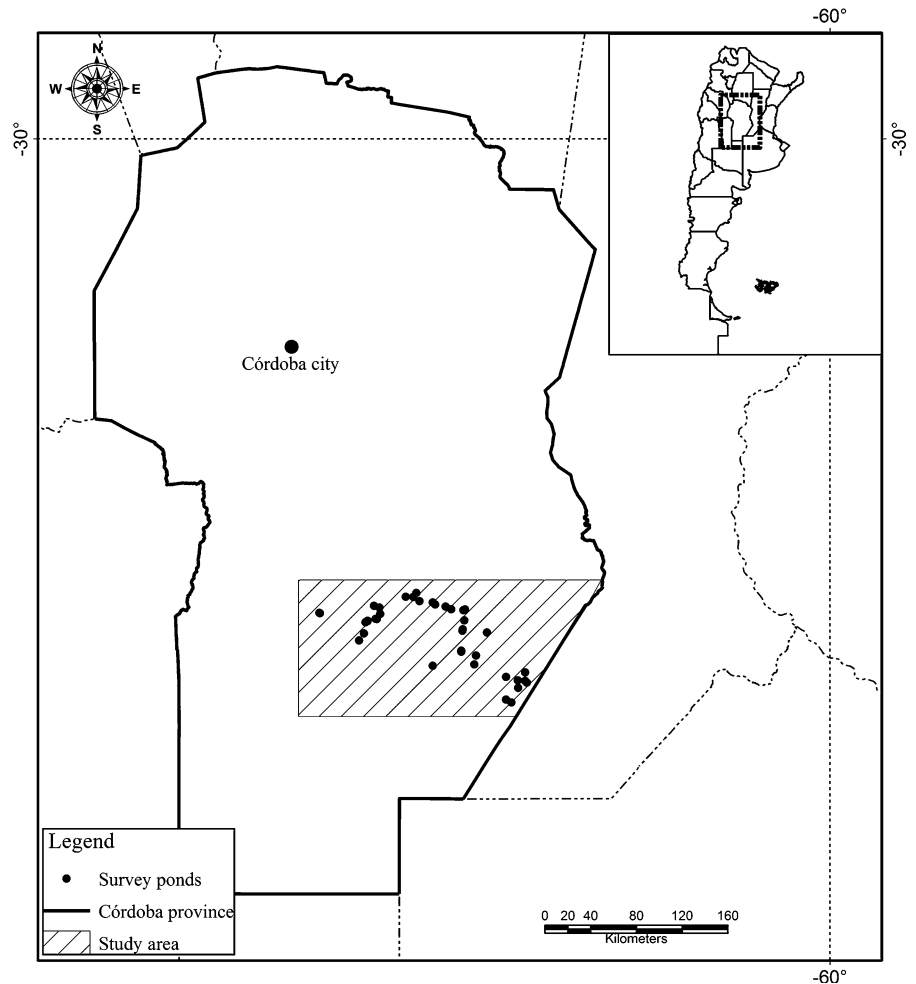
Depending on the salinity, they are classified as saline, subsaline, and in a few cases, freshwater ponds (Quirós et al. 2002). Aquatic environments in the study area can be grouped into classes on the basis of their origin: (1) ponds of aeolian origin associated with different types of dunes, which are elongated and egg-shaped in a NNE–SSW direction, closely associated with the local phreatic level; (2) ponds associated with deflation hollows, which are rounded or slightly egg-shaped, generally temporary and fed by rainwater or phreatic flow; (3) ponds of mixed (aeolian and tectonic) origin, which are rounded or sub-rounded without defined limits, fed by phreatic flow; and (4) ponds originating from rivers, that are half-moon shaped, sub-rounded or irregular, associated with many meanders, palaeo-riverbeds or palaeo-floodplains connected to rivers (Cantú and Degiovanni 1987).

Bird counts

Bird counts were undertaken in 39 ponds that represented the heterogeneity of the study area in terms of the environmental variables that we consider important for waterbirds. The ponds were selected through satellite images. All the ponds were surveyed repeatedly during all four seasons (winter, spring, summer and autumn) for three consecutive years (2007–2009). We used the method of surveys by visual encounters from point counts, following the recommendations of Bibby et al. (1998). These observation posts were strategically placed to get an unobstructed view of the chosen water body. The number of sites per pond varied in relation to the area and accessibility, with the number of posts required covering as much of the area of the pond as possible (Kissling 2004). The area

sampled from each position varied, extending up to 300 m from the observer (i.e., the distance at which a species was correctly recognized).

Observations were made with 8 × 40 binoculars and a 45× zoomed spotting scope. For each observation, we made a complete scan of the area to be sampled, identifying and counting all aquatic birds seen and heard, starting the count as soon as we arrived at the place so as to record birds flying away due to our presence. When the number of individuals of a species was too high (>100 individuals), we used the field telescope, and counted the number of individuals in the field of view; then we extrapolated that number to the total group according to the number of fields needed to complete the group (Bibby et al. 1998). In ponds with abundant emergent vegetation, the observation period was on average twice as long, in order to compensate for the difficulties in detecting birds due to reduced visibility. Coot species (Red-gartered, Red-fronted and White-winged Coots) were grouped into one morphospecies (*Fulica* spp.) due to the difficulty in identifying each species at long distances. Similarly, Gray-hooded and Brown-hooded Gulls were grouped as *Chroicocephalus* spp. due to the difficulty of differentiating the species in winter plumage. Species recorded in less than 10 % of wetlands surveyed over the entire study period were excluded from the analysis.

Environmental variables

The wetlands were characterized by 15 local and landscape variables considered potentially important for habitat use and local distribution of waterbirds because they are related to bird species biology (feeding, nesting, resting, cover from predators) (Table 1). To measure the variables:—total area (ha), perimeter (km), index of irregularity of the shoreline (following Wetzel 1975) and the number and area of ponds surrounding the sampled pond within a 10-km radius—we used a specific method based on a non-supervised classification of satellite images (for detailed methodology see Brandolin et al. 2013). In each pond, we measured the physicochemical variables:—conductivity (mS) and pH—using a combined digital tester. We took water samples from the surface, preserved them at cold temperatures and then transported them to the laboratory for measurement protocol according to specialists (Martinez de Fabricius

pers. comm.). The obtained values were corrected to standard temperature and pressure values (1 atm and 25 °C). To measure water depth, we drew a transect from the shoreline to the center of the pond, taking a measurement with a graduated scale every five meters. Hydroperiod, shoreline features (muddy, vegetated or modified) and the degree of disturbance were recorded via direct field observations. Vegetation cover was estimated through high quality images satellite of each pond (Google Earth). Although pond size and number fluctuate seasonally, they showed no great variation throughout the sampling period and due to the limited availability of satellite imagery to measure these seasonal fluctuations, the variables:—area, perimeter and shape—were calculated for each sampling year according to the availability of satellite images. The variables:—conductivity, pH and depth—were estimated for each census, whereas the variables:—pond hydroperiod, vegetation, type of shoreline, connectivity and disturbances—were calculated only once for the entire sampling period.

Analysis

As a first step, we built a correlation matrix among all variables and discarded those with high collinearity ($r > 0.7$). Since area x perimeter, area x shape and shape x perimeter had high collinearity, only area was retained in the analysis. To determine the appropriate multivariate ordination technique for our study, we conducted an exploratory analysis of the relationship between waterbird species abundances and environmental variables (Lepŝ and Smilauer 2003). Given the high gradient value (measure of beta diversity in community composition) in the first ordination axis for species (2.52 and 7.64, respectively), we used a unimodal response model (Canonical Correspondence Analysis, CCA; ter Braak 1986). A CCA is a direct gradient analysis that calculates a set of ordination axes based primarily on a matrix of bird abundances for each sampling and pond. The axes in the CCA are restricted by a second matrix of environmental variables; thus, the method identifies gradients in the bird community which can be directly attributed to the change in habitat characteristics (Palmer 1993). Since we focused on the scaling of distances among species for this analysis, the abundance data of species were log-transformed. In the CCA, we used an automatic forward selection of environmental variables.

Table 1 Description of local and landscape level variables used to characterize the wetlands of southeastern Cordoba province, Argentina

Variable	Description
Area (AREA)	Total pond area (ha)
Conductivity (CONDUC)	Electrical conductivity (µS) of pond water at 25 °C
Ph (pH)	pH values of pond water
Perimeter (PERIM)	Length (km) of the shoreline of each pond
Shape (SHAPE)	Wetzel's (1975) irregularity index of the shoreline: Shape = Perimeter/circumference of a circle of equal area
Depth (DEPTH)	Mean depth (cm) of the measurement transect from the observation site to the center of the pond
Hydroperiod (PERMA)	The length of time the pond holds water (permanent or temporary)
Internal vegetation (INTVEG)	Area covered by emerging vegetation in the interior of the pond. Categorical variable: none (0 %), small (1–50 %), large (>50 %)
Edge vegetation (EDGVEG)	Pond edge area covered by emerging vegetation. Categorical variable: none (0 %), small (1–50 %), large (51–99 %), all (100 %)
Muddy coast to 50 m (MUDDY50)	Presence of muddy coasts within a 50-m radius from the shoreline
Grassland to 50 m (GRASS50)	Presence of natural grasslands on coasts within a 50-m radius from the shoreline
Modified to 50 m (MODIF50)	Presence of modified coastline by human activity (dump, agriculture, constructions) within 50-m from the shoreline
Connectivity by ponds (CONNEC1)	Number of water bodies greater than 5 ha within a 10-km buffer area surrounding the sampled pond
Connectivity by area (CONNEC2)	Accumulated area of wetlands greater than 5 ha within a 10-km buffer area surrounding the sampled pond
Disturbances (DISTUR)	Ranking of disturbances according to the combination of the frequency of occurrence (rare/common) and degree (mild/severe). The presence of disturbances ranges from 1 (rare and mild) to 4 (common and severe); its absence corresponds to 0

Codes in text are shown in parentheses

Variables were added to the model in order of the greatest additional contribution to total variation explained. Only significant variables (Monte Carlo permutation test, $p < 0.05$) were included in the model. A Monte Carlo test with 999 permutations was then applied to evaluate the significance of the CCA axes (Palmer 1993) (Electronic Supplementary Material; ESM1).

We conducted separated CCAs with warm season (spring + summer) and cold season (autumn + winter) data to explore whether there was seasonal variation in the relationship between species abundance and environmental variables. In the warm season the relationships found were very similar to those obtained with pooled data, but in the cold season there were variations in the strength of the relationships; the relationships were much weaker in this season but with a similar distribution of species. Because we did not find strong seasonal differences (Electronic Supplementary Material; ESM2) we performed analyses with all data pooled.

For the graphical interpretation of the CCA, the arrows represent the direction of change of each variable through the CCA ordination, where the value of the variable increases in the direction of the arrow, the length of the arrow indicates the relative importance of the variable and the angle between the arrow and the axes indicates the degree of correlation with the ordination axes. The arrows can be interpreted as secondary axes and can therefore help interpret the distribution of species in relation to environmental gradients (Kent and Coker 1992). Thus, arrows in the same direction as a species with less than 90° angle (positive or negative) are considered as "positive

relations" between species and variables; angles of around 90° are considered "neutral relationships"; and angles greater than 90° (positive or negative) as "negative relationships". Additionally, to facilitate the visualization of the distribution of species along gradients generated by the CCA we made a cluster analysis based on the Group Average method with euclidean distance, using the scores of the first two axes of CCA (adapted from Russell et al. 2014).

Results

We conducted 250 counts and recorded 60 waterbird species belonging to 8 orders and 14 families, of which 29 species were recorded in 10 % or more of the wetlands surveyed over the study period (Table 2). The most frequently represented families were Anatidae and Scolopacidae, with 14 and 8 species, respectively. A total of 278,797 waterbirds were observed with a mean of 1115.18 birds per count. Wilson's Phalarope (*Phalaropus tricolor*, N = 50,096), Cattle Egret (*Bubulcus ibis*, N = 40,316), White-faced Ibis (*Plegadis chihi*, N = 33,083), Red Shoveler (*Anas platalea*, N = 23,898) and Chilean Flamingo (*Phoenicopterus chilensis*, N = 19,121), taken together, comprised 50 % of all birds counted. Each of the remaining species individually accounted for less than 5 % of the total. The abundance of waterbirds during surveys on different wetlands varied widely between species (Table 2).

The CCA model was composed of 12 variables used in the analyses. Only the variable CONNEC2 was not significant for the model. The four significant CCA axes (p = 0.001 for the four axes combined) explained 16.9 % of the total variance in the abundance of waterbird species (Table 3). The first two canonical axes explained 60.3 % of the variance in the abundance of waterbird species due to environmental variables (Table 3).

Species were more or less uniformly distributed along the environmental gradients defined by the first two canonical axes (Fig. 2). The first axis showed a contrast between species associated with presence of muddy shoreline, high conductivity, low vegetation and less connected wetlands and those that occurred predominantly in less saline wetlands with abundant vegetation and more connected wetlands. The second

axis displayed predominantly a gradient of water depth variability, wetland area and the condition of the wetland to be permanent or stationary (Fig. 2).

We observed that related species with similar ecological requirements (not necessarily related phylogenetically) tend to respond similarly to the environmental heterogeneity. This is seen in the abundances of a few species which were more closely associated positively with particular environmental variables: Chilean Flamingo and Wilson's Phalarope with MUDDY50 and CONDUC; Silvery Grebe (*Podiceps occipitalis*) and Coscoroba Swan (*Coscoroba coscoroba*) with AREA, DEPTH and PERMA; Great Grebe (*Podiceps major*) and Neotropic Cormorant (*Phalacrocorax brasilianus*) with DEPTH; Plumbeous Rail (*Pardirallus sanguinolentus*) and Cinnamon Teal (*Anas cyanoptera*) with INTVEG. Conversely, Pectoral Sandpiper (*Calidris melanotos*) was associated negatively with DEPTH and PERMA. Briefly, in general waders (e.g., plovers and flamingos) had a negative correlation with axis 1, which is associated with high conductivity and the presence of muddy shorelines. This species also had a negative correlation with axis 2 and more associated with temporary ponds. Duck, herons and ibis species were positively correlated with axis 1 and were associated with vegetation abundance and decrease in conductivity. For axis 2, the tendency was a positive association for open water piscivores and carnivorous species with pond depth (e.g., Neotropic Cormorant, Cocoi Heron, Snowy-crowned Tern) and a negative association for mainly herbivorous species (e.g., common gallinule, other coots and most of the ducks) (Fig. 2).

Cluster analysis revealed two outstanding clustering levels (Fig. 3), showing three main clusters of species (Main Group, hereafter MG) at 0.8 similarity distance, and seven secondary groups (hereafter SG 1–7) at a distance of 0.5. Secondary groups differed in terms of species-specific relationships with environmental variables (Table 4) and grouping species with similar ecological requirements. One main cluster included a single group (SG1) of 2 species, positively associated with depth of the pond and hydroperiod (Table 4). Other main cluster included two groups of birds mostly related positively to internal and edge vegetation or negatively to muddy shoreline and

Table 2 Percentage of occurrence and total abundance of bird species recorded in 39 ponds sampled in central Argentina

Family/scientific name	Common name	Code	% Occurrence	Abundance
ANHIMIDAE				
Chauna torquata	Southern Screamer	CHATOR	5.6	25
ANATIDAE				
Dendrocygna bicolor	Fulvous Whistling-Duck	DENBIC	4.8	393
Dendrocygna viduata	White-faced Whistling-Duck	DENVID	32.4	4843
Cygnus melancoryphus	Black-necked Swan	CYGMEL	7.6	280
Coscoroba coscoroba	Coscoroba Swan	COSCOS	50.4	3234
Anas sibilatrix	Chiloe Wigeon	ANASIB	2.8	26
Anas flavirostris	Yellow-billed Teal	ANAFLA	76.8	877
Anas georgica	Yellow-billed Pintail	ANAGEO	58.4	2739
Anas bahamensis	White-cheeked Pintail	ANABAH	71.6	8878
Anas versicolor	Silver Teal	ANAVER	46.0	1190
Anas cyanoptera	Cinnamon Teal	ANACYA	16.4	157
Anas platalea	Red Shoveler	ANAPLA	76.8	23,898
Netta peposaca	Rosy-billed Pochard	NETPEP	27.6	1194
Heteronetta atricapilla	Black-headed Duck	HETATR	19.6	1204
Oxyura vittata	Lake Duck	OXYVIT	50.4	5329
PODICIPEDIDAE				
Rollandia rolland	White-tufted Grebe	ROLROL	44.8	1366
Podilymbus podiceps	Pied-billed Grebe	PODPOD	5.6	17
Podiceps major	Great Grebe	PODMAJ	18.0	419
Podiceps occipitalis	Silvery Grebe	PODOCC	32.4	5264
PHOENICOPTERIDAE				
Phoenicopterus chilensis	Chilean Flamingo	PHOCHI	38.0	19,121
Phoenicoparrus andinus	Andean Flamingo	PHOAND	2.8	135
CICONIIDAE				
Ciconia maguari	Maguari Stork	CICMAG	16.0	204
Mycteria americana	Wood Stork	MYCAME	0.8	9
PHALACROCORACIDAE				
Phalacrocorax brasilianus	Neotropic Cormorant	PHABRA	16.0	1185
ARDEIDAE				
Nycticorax nycticorax	Black-crowned Night-Heron	NYCNYC	6.4	30
Bubulcus ibis	Cattle Egret	BUBIBI	5.6	40,316
Ardea cocoi	Cocoi Heron	ARDCOC	8.0	135
Ardea alba	Great Egret	ARDALB	16.4	117
Syrigma sibilatrix	Whistling Heron	SYRSIB	5.6	37
Egretta thula	Snowy Egret	EGRTHU	17.2	268
THRESKIORNITHIDAE				
Plegadis chihi	White-faced Ibis	PLECHI	38.4	33,083
Phimosus infuscatus	Bare-faced Ibis	PHIINF	1.2	9
Theristicus caudatus	Buff-necked Ibis	THECAU	0.4	2
Platalea ajaja	Roseate Spoonbill	PLAAJA	4.0	86
ARAMIDAE				
Aramus guarauna	Limpkin	ARAGUA	3.6	13

Table 2 continued

Family/scientific name	Common name	Code	% Occurrence	Abundance
RALLIDAE				
Pardirallus sanguinolentus	Plumbeous Rail	PARSAN	10.4	62
Gallinula galeata	Common Gallinule	GALGAL	1.6	4
Gallinula melanops	Spot-flanked Gallinule	GALMEL	1.6	5
Fulica spp.[a]		FULSPP	68.8	17,167
CHARADRIIDAE				
Pluvialis dominica	American Golden-Plover	PLUDOM	1.2	25
Vanellus chilensis	Southern Lapwing	VANCHI	70.8	3676
Charadrius collaris	Collared Plover	CHACOL	2.0	9
Charadrius falklandicus	Two-banded Plover	CHAFAL	0.8	23
RECURVIROSTRIDAE				
Himantopus mexicanus	Black-necked Stilt	HIMMEX	75.6	10,420
SCOLOPACIDAE				
Limosa haemastica	Hudsonian Godwit	LIMHAE	4.4	229
Tringa melanoleuca	Greater Yellowlegs	TRIMEL	23.2	518
Tringa flavipes	Lesser Yellowlegs	TRIFLA	37.2	1803
Calidris fuscicollis	White-rumped Sandpiper	CALFUS	7.2	14,003
Calidris bairdii	Baird's Sandpiper	CALBAI	4.4	531
Calidris melanotos	Pectoral Sandpiper	CALMEL	11.2	1134
Calidris himantopus	Stilt Sandpiper	CALHIM	4.0	5971
Phalaropus tricolor	Wilson's Phalarope	PHATRI	16.0	50,096
ROSTRATULIDAE				
Nycticryphes semicollaris	South American Painted-snipe	NYCSEM	1.2	8
LARIDAE				
Chroicocephalus spp.[b]		CHRSPP	45.6	15,721
Larus dominicanus	Kelp Gull	LARDOM	6.8	1257
Gelochelidon nilotica	Gull-billed Tern	GEONIL	2.8	28
Sterna trudeaui	Snowy-crowned Tern	STETRU	2.8	19

The species' code is formed with the first three letters of the genus and the first the letters of the specific epithet. Classification follows Remsen et al. (2013)

[a] Includes White-winged Coot (*Fulica leucoptera*), Red-gartered Coot (*Fulica armillata*) and Red-fronted Coot (*Fulica rufifrons*)

[b] Includes Brown-hooded Gull (*Chroicocephalus maculipennis*) and Gray-Hooded Gull (*Chroicocephalus cirrocephalus*)

Table 3 Summary of the canonical correspondence analysis (CCA) between the abundance of waterbird species and the measured environmental variables

Axes	1	2	3	4	Total variance inertia
Eigenvalues	0.15	0.08	0.04	0.03	1.86
Species-environment correlations	0.77	0.72	0.53	0.63	
Cumulative percentage variance					
Of species data	8.1	12.7	15.2	16.9	
Of species-environment	38.3	60.3	71.9	80.1	
Sum of all canonical eigenvalues				0.39	

conductivity (Table 4); SG2 with 4 species and SG3 which was the most diverse group including 11 species. The remaining main cluster mostly included birds positively associated with muddy shoreline and conductivity or negatively to depth of the pond (Table 4). It included four groups; SG4 with 2 species;

Fig. 2 Plot of the first two axes of the canonical correspondence analysis (CCA) ordination between waterbird species and environmental variables in wetlands of southeastern Córdoba province, Argentina. See Table 2 for acronyms of species

Fig. 3 Cluster representing the similarity amongst waterbird species in the space defined by the first two axes of the ordination between waterbird species and environmental variables. *MG (1–3)* indicate main clusters of species at 0.8 similarity distance and *SG (1–7)* indicate secondary groups at a distance of 0.5

SG5 with 4 species; SG6 with 1 species and SG7 with 5 species.

Discussion

Wetlands are critical for many waterbird species mainly due to their high primary productivity. This productivity leads to a high availability of resources which in turn favours the coexistence of many species (Weller 2004; Gatto et al. 2008). In turn, a high heterogeneity and variety of resources is determined by the variability in physical and biotic factors among ponds, such as conductivity, water depth, presence of muddy shoreline and internal vegetation. Waterbirds in wetlands of central Argentina make different uses of ponds according to the presence of specific habitat types, showing species-specific responses more similar among species with similar ecological requirements than across the regional pool of waterbird species.

Table 4 Summary of the main relationships between the abundance of waterbird species pooled in seven groups defined in a cluster analysis and 13 environmental variables determined with a canonical correspondence analysis

Group of species	Positive relation	Neutral relation	Negative relation
SG1	Depth; Perma; Grass50	Area; Muddy50; Conduc; pH; Connec1; IntVeg; EdgVeg; Modif50; Distur	
SG2	Connec2; IntVeg; EdgVeg; Modif50; Distur	Perma; Depth; Grass50; Connec1	Conduc; pH; Muddy50; Area
SG3	Connec1; IntVeg; EdgVeg; Modif50; Distur	Perma; Depth[a]; Grass50	Conduc; pH; Muddy50; Area
SG4	Conduc; pH; Muddy50	Area; Perma; Depth; Grass50	Connec1; IntVeg; EdgVeg; Modif50; Distur
SG5	pH; Area; Perma; Depth	Muddy50; Conduc; Modif50; Distur; Connec1	IntVeg; EdgVeg
SG6	Conduc; pH; Muddy50; Area; Perma	Depth; Grass50	Connec1; IntVeg; EdgVeg; Modif50; Distur
SG7		IntVeg; EdgVeg; Modif50; Distur	Area; Perma; Depth; Grass50; Connec1

Group names (SG 1–7) according to Fig. 3

[a] With the exception of *Oxyura vittata* (OXYVIT) whose relationship with depth was positive

Habitat conditions are important to understand the use of wetlands by waterbird species (King et al. 2010). For example, water depth affects foraging efficiency (Holm and Burger 2002). Water depth is influential mainly because it determines access to foraging sites by birds with different morphological traits such as a long neck and legs (Velasquez 1992; Elphick and Oring 1998; Colwell and Taft 2000; Isola et al. 2002; Ma et al. 2010). Diving birds (e.g., Great Grebe and Neotropic Cormorant) require deep waters and their foraging habitat is limited by the minimum water depth at which they dive (Ma et al. 2010). For wading birds foraging in the water column (e.g., Lake Duck), locomotion becomes slower in deep waters due to increased water resistance and hunting efficiency decreases because prey can escape vertically (Gawlik 2002). The observed strong positive or negative relationships with water depth showed by several bird species emphasize the importance of this environmental factor in determining habitat use by waterbirds. In the wetlands of central Argentina, the high heterogeneity in water depth of the ponds generates diverse habitat types that contribute to the diversity of bird assemblages.

Water salinity also strongly affects the abundance and composition of waterbird assemblages. Salt water is harmful to many continental waterbirds, since ingesting high concentration of salts can cause loss of body weight by dehydration (Purdue and Haines 1977; Hannam et al. 2003). Salt also reduces the waterproofing of feathers, by increasing the energy cost of thermoregulation (Ma et al. 2010). Moreover, salinity affects the composition of plant and invertebrate species in a wetland and thus further indirectly affects the use of ponds as foraging sites by birds (Takekawa et al. 2006). In contrast, some bird species may benefit from increased levels of salinity. In this study, flamingos and Wilson's Phalaropes were associated with ponds of high salinity, a favorable habitat for invertebrates (mainly ostracods and crustaceans such as *Artemia* sp.) that constitute and important part of their diet (Brandolin and Ávalos 2010). In turn, the combination of factors such as depth and salinity influence the development of aquatic vegetation, with certain levels of salinity and saturation being essential to vegetation growth. In this work, herbivorous waterbirds (e.g., coots, ducks) select ponds with low salinity and a higher quality of food due to the presence of vegetation.

The permanent edge and the interior vegetation (mainly *Schoenoplectus californicus* and *Typha* sp.) were important factor explaining the abundance of wading birds and ducks in the wetlands of central Argentina. Many waterbirds exploiting wetland vegetation also need open water areas to land, swim and feed, but different species respond to different ratios of

vegetation cover versus open water (Blanco 1999). The structure of aquatic vegetation directly influences the habitat use by birds (Bancroft et al. 2002) because it increases habitat heterogeneity (Naugle et al. 2000) and food availability via a higher amount of seeds, leaves, tubers and rhizomes (Ma et al. 2010). Furthermore, aquatic vegetation is an important habitat component since it provides shelter from predators and severe climatic conditions, as well as materials and sites for nesting. All these factors create complex relationships that make vegetated ponds particularly important habitats for birds and therefore require special care when planning conservation strategies.

Landscape context influences the species richness, abundance and persistence of waterbird populations (Dunning et al. 1992; Riffell et al. 2003; Elphick 2008). The main processes that favor the presence of waterbirds are linked to the complementation of resources among ponds, through the supplementation of scarce resources and local movement between ponds (Dunning et al. 1992). For example, the species richness of a pond can increase with the number of adjacent ponds because this stabilizes the availability of resources (e.g., food) in highly variable systems (Riffell et al. 2003). Furthermore, a higher level of connectivity between wetlands enables them to function as corridors between sites with habitat suitable for waterbird species. Waterbirds are extremely mobile and often commute daily among feeding sites and roosting areas or breeding colonies; many species move among sites within seasons, both locally and regionally, and seasonally migrate long distances (Elphick 2008). In the Pampas of central Argentina, species like shorebirds and flamingos showed a negative relationship with the connectivity variables, which suggests that birds with higher dispersive power are less affected by changes in the landscape connectivity and use more dispersed ponds. In contrast, more connected landscapes favored the abundance of less mobile species like coots and rails. The observed variation in the response of different species to changes in the landscape shows that different processes affect habitat selection at a species-specific level, although phylogenetically related species, and species with similar ecological requirements, tended to respond similarly to the environmental heterogeneity. Similarly, Elphick (2008) found between-taxa differences in both landscape features important for the presence of species and in the spatial scales at which these relationships occur.

Management implications

Wetland management aimed at preserving habitats for waterbirds must be based on specific knowledge of regional bird communities (Ma et al. 2010). The environmental requirements relevant for each species must be take into account in designing conservation strategies and management policies (Liordos 2010). For example, the relationship between depth and waterbird has served as the basis for the management of wetlands throughout the world (Bolduc and Afton 2008). To ensure the permanence of the diverse life forms adapted to the different environmental conditions displayed in the wetlands of central Argentina, management plans need to be implemented at the regional level, addressing conservation and the restoration of a heterogeneous landscape (integrating public and private lands). The maintenance of the environmental conditions of the larger ponds would favor increasing species richness of waterbirds because these water bodies generally have a high diversity of habitats (such as shoreline diversity and water depth variation). In turn, some wading birds would benefit from a plan to enrich the edges of the ponds with native vegetation, at the same time this has direct and indirect effects on wave action, to stabilize the shoreline, prevent erosion and benefit waterbirds that use this native vegetation. Besides, increased erosion by wind and water and hydrological changes as a result of canalization works resulting from the intensification of agricultural land use in the Pampas (Brandolin et al. 2013) tend to accelerate the deposition of sediments in wetlands (Cantero et al. 1998; Blarasin et al. 2005b). It would therefore also be necessary to include provisions in the management of wetlands to force actions to mitigate and control sedimentation, so as to avoid clogging and loss of depth, which strongly affects birds using areas of open and deep water.

Despite Argentina having been a contracting party to the Ramsar Convention on Wetlands of International Importance since 1991, the wetlands of central Argentina do not have any specific legal protection or planning requirements with respect to water use. Moreover, the advance of the agricultural frontier in the region has led to an alarming loss of wetlands (Brandolin et al. 2013). The absence of a management plan that includes natural components for the landscape highlights the urgent need of preserving the

remaining wetlands and their associated biodiversity. However, the protection of isolated wetlands (e.g., natural reserves) with low environmental heterogeneity does not guarantee the conservation of the full regional pool of waterbird species. Management of nomadic wildlife, such as waterbirds, requires conservation strategies that progress from the classical model of conventional reserves to the creation of networks of protected areas (Margules and Pressey 2000). Waterbirds move in complex patterns, often associated with highly fluctuating resources, so therefore conservation strategies for these species may differ fundamentally from those targeting more sedentary species and require new approaches in conservation planning (Runge et al. 2014). In these circumstances, management decisions including only local effects are inappropriate for the conservation of waterbirds (Roshier et al. 2002). If the requirements of waterbirds are at a greater scale (complex of wetlands) than is usually sought in the management of these habitats, then the value for conservation of individual wetlands cannot be measured in isolation from the wetlands mosaic in which they are located (Roshier et al. 2002). Therefore, a schedule of conservation of waterbirds from central Argentina requires the combined action of protecting selected wetlands representative of the diversity of regional habitats and the urgent implementation of management actions at the regional scale.

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