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Complementary use of a wetland and its surrounding landscape by waterbirds in south-central Chile

Uso complementario de un humedal y su paisaje circundante por aves acuáticas en el centro sur de Chile

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ABSTRACT

Waterbirds are one of the most conspicuous components of wetlands, and are frequently proposed as bioindicators of the state of these ecosystems. However, the mobility of waterbirds allows them to make complementary use of resources found beyond the limits of permanent wetlands. Therefore, understanding the relationships between the conditions of waterbodies and waterbird populations, requires a landscape-level approach. The objective of this study was to assess the complementary use of a permanent wetland (estuary) and its surrounding landscape by a waterbird community in Central Chile. During three years, we seasonally censused the waterbird populations present at the estuary of the Carampangue river (128 ha) and, in addition, estimated the abundance of the same species in the surrounding landscape (3,952 ha) through 71 point-count stations. A total of 69 species of birds were recorded in the estuary, and 51 species in the surrounding landscape. The strong negative temporal correlations between the populations at the estuary and landscape are indirect evidence for a complementary use of the two systems, mostly driven by seasonal flooding in agricultural land. The seasonal use of landscape resources was more marked among Anseriformes and grebes. Using generalized additive models (GAM), we observed that the percentage of flooded area and non-flooded prairies were among the most important predictors of landscape use by most species. Our results reinforce the need to expand the assessment of waterbird populations beyond waterbodies, including neighboring habitats of potential usefulness for this group of birds.

Keywords: ephemeral wetlands, estuary, flooding, prairies.

RESUMEN

Las aves acuáticas son uno de los componentes más conspicuos de los humedales, y con frecuencia se proponen como bioindicadores del estado de estos ecosistemas. Sin embargo, la movilidad de las aves acuáticas les permite hacer un uso complementario de los recursos que se encuentran más allá de los límites de los humedales permanentes. Por lo tanto, comprender las relaciones entre las condiciones de los cuerpos de agua y las poblaciones de aves acuáticas requiere un enfoque a nivel de paisaje. El objetivo de este estudio fue evaluar el uso complementario de un humedal permanente (estuario) y su paisaje circundante por parte de una comunidad de aves acuáticas en Chile Central. Durante tres años, se censó estacionalmente las poblaciones de aves acuáticas presentes en el estuario del río Carampangue (128 ha) y, además, se estimó la abundancia de las mismas especies en el paisaje circundante (3.952 ha) a través de 71 estaciones de conteo puntual. Se registraron un total de 69 especies de aves en el estuario y 51 especies en el paisaje circundante. Las fuertes correlaciones temporales negativas entre las poblaciones en el estuario y el paisaje son evidencia indirecta de un uso complementario de los dos sistemas, impulsado principalmente por inundaciones estacionales en tierras agrícolas. El uso estacional de los recursos del paisaje fue más marcado entre anseriformes y zambullidores. Usando modelos aditivos generalizados (GAM), se observó que el porcentaje de área inundada y praderas no inundadas se encontraban entre los predictores más importantes del uso del paisaje por parte de la mayoría de las especies. Nuestros resultados refuerzan la necesidad de ampliar la evaluación de las poblaciones de aves acuáticas más allá de los cuerpos de agua, incluidos los hábitats vecinos de utilidad potencial para este grupo de aves.

Palabras claves: estuario, humedales temporales, inundación, praderas.

INTRODUCTION

The high productivity of wetlands makes these sites highly important foraging areas for waterbirds (Chatterjee *et al.* 2020), allowing several species to coexist using similar resources (Weller 1999). Large numbers of resident and migratory waterbirds aggregate in wetlands, forming bird communities that are highly diverse in terms of species richness and habitat requirements (Żmihorski *et al.* 2016).

Although the abundance and dynamics of waterbird populations are strongly related to attributes of wetlands such as size and depth (Josens *et al.* 2009), water quality (Mukherjee & Borad 2001), the aquatic plant community (Gayet *et al.* 2012), and the abundance of other animals (Green & Elmberg 2014), among others, there is a significant body of evidence pointing to an important effect of the characteristics of the landscape that surrounds such bodies of water. For example, many species of waterbirds, especially waterfowl such as dabbling ducks and geese (Herbert *et al.* 2021, Fox & Madsen 2017, Baldassarre 1984), visit agricultural lands and prairies to take advantage of the resources in those areas, either as supplementary foraging habitat (Navarro-Ramos *et al.* 2024, Ando *et al.* 2022, Moulton *et al.* 2022, MacMillan *et al.* 2004, Baldassarre 1984), or for roosting and/or nesting (Brides *et al.* 2021, Walker *et al.* 2013, Duncan, 1987). Even, many long-distance migrant waterbirds use seasonal flooded areas as stopovers during their journeys (Uden *et al.* 2015, Alabanese & Davis 2013, Skagen *et al.* 2008). The ability of birds to make a supplementary use of resources present in different landscape patches may improve the persistence of their populations (Dunning *et al.* 1992).

Hydrological fluctuations can lead to changes in the availability of habitat for birds in the landscape, affecting their abundance and accessibility to resources (Chen *et al.* 2022, Lorenzón *et al.* 2019). Waterbirds react rapidly to changes in the landscape (Ali *et al.* 2016), dispersing immediately once floods have occurred (Poiani 2006). These movements respond mainly to the search and use of new available resources (de Almeida *et al.* 2016). Species adapted to these temporary habitats benefit from nutrient enrichment, fish and invertebrates reproductive events, and nesting sites (Junk & Wantzen 2006, Poiani, 2006). In this way, waterbirds aggregate and disperse seasonally in response to fluctuating resources and life history needs (Cumming *et al.* 2012).

Because of the ephemeral nature of temporary wet areas, the species that use them also depend on upland habitats as well as nearby permanent aquatic ecosystems (Smith *et al.* 2019). The vagility of some species of waterbirds allows them to move regularly between neighboring wetlands and also between these wetlands and the surrounding landscape (Obernuefemann *et al.* 2013). The ability of birds to use the surrounding landscape as complementary habitat is a function of the species' dependence on permanent waterbodies (Acuña *et al.* 2019). While some species depend on waterbodies for almost all their activities, others can be seen regularly using the surrounding landscape for their activities (Herring *et al.* 2021, English *et al.* 2017).

The strong relationship between waterbird populations and wetland attributes not only provide the ecological basis for their management and conservation (Tavares *et al.* 2015), but also point to an important role of waterbird populations as bioindicators of wetland ecosystems (Amat & Green 2010). However, a potential limitation to the correct monitoring of waterbird populations lies in the fact that, traditionally, they have been assessed through censuses, usually restricted to a fixed area (i.e. the limits of a wetland). This wetland-centered approach imposes a potential bias on our understanding of waterbird population dynamics as it misses the portion of the populations that might be located outside permanent waterbodies (Haig *et al.* 1998).

The estuarine wetlands present in the coastal plains of Central Chile concentrate large numbers of many resident and migratory waterbird species (Thomson *et al.* 2020, Acuña *et al.* 2019, Estades & Vukasovic 2013). While resident species are potentially able to interact with the surrounding landscape throughout the year, most long-distance migrants will be in the region only during the austral Summer (Estades & Vukasovic 2013). This study seeks to answer whether there are relevant differences between migratory and resident waterbirds in their use of the surrounding landscape in Central Chile. Such knowledge would be of importance in guiding conservation actions for either group of species. We hypothesized that a large proportion of the waterbird species in the region use regularly the surrounding landscape, but that this use is modulated by seasonal flooding and the migratory pattern of birds. In particular, we predict that most of the activity of waterbirds in the landscape surrounding permanent wetlands is done by resident species. In contrast, long-distance migrants that visit the country during the austral summer, will be restricted to the permanent wetlands due to the limited flooded area in the landscape in summer months.

In addition, if birds are making a complementary and or supplementary use (sensu Dunning *et al.* 1992) of the landscape, we expect to see a negative temporal correlation between the number of individuals of a species in the estuary and in the landscape, reflecting the redistribution of birds between the two systems.

Therefore, the aims of this study are to i) describe the use by waterbirds of the landscape surrounding an estuary in Central Chile, ii) determine the temporal correlation between the abundances of waterbirds populations in both systems, and iii) examine the influence of habitat characteristics on the abundance and presence of waterbirds in the landscape.

METHODS

Study area

The study was carried out in the area of influence of the Carampangue river estuary (37° 14'S 73°17'W) , located near the city of Arauco, Biobío Region, Chile. The region, with a marked seasonality and oceanic- influenced temperate climate (Amigo & Ramírez 1998, Hajek & Di Castri 1975), is characterized by coastal plains, predominantly natural pastures destined for extensive livestock grazing (Oberdorfer 1960). Most non-floodable areas are covered with exotic pine plantations (*Pinus radiata* D. Don). The studied area covers the estuarine area (128.7 ha) and most of the Carampangue river basin, reaching an effective sampling area of 3,952 ha of flat pastures, including a proportion (~30 %) of seasonally flooded areas and excluding pine plantations and constructed areas (Fig. 1).

Habitat mapping

Habitat maps were prepared for the maximum and minimum situations of flooded land in the study area. Using georeferenced high-detail aerial photography obtained through an unmanned aerial vehicle, we characterized the seasonal variability of the habitat. Between 9:30 and 16:00 on days without rain, we used an Inspire 1 V.2 drone (DJI, China), at a flight height of 250 m to obtain images of the study area. This height was considered to optimize flight hours, and does not cause disturbance to the birds since at that height it is practically imperceptible (McEvoy *et al.* 2016). An overlap of 60 % in the horizontal axis and 30 % overlap in the forward axis were considered. To create the orthomosaic, the Agisoft Photoscan Professional v1.1.0.1976 software was used (Agisoft, Russia). The digitalization of the landscape elements was carried out manually using the ArcMap 10.2 software (ESRI 2011). The land cover classes were grouped into general categories, such as urban (roads and buildings), trees, low woody vegetation, prairies and marshes. In the estuarine area, we also distinguished sand banks and shores from mudflats or vegetated areas subject to tidal flooding. The water category included different water bodies, such as rivers, lagoons and temporarily flooded areas. Distance to the closest waterbody for every sampling point was get by calculating the Euclidean distance in a raster analysis of the Spatial Analyst Tools (ESRI 2011).

Bird surveys

We conducted bird surveys between August 2016 and April 2019, using different approaches for the estuarine zone and the surrounding landscape, mainly to account for difference in detectability likely to occur along the seasons. At the estuary of the Carampangue river we conducted eight census campaigns per year (2 campaigns x 4 seasons). Each campaign consisted of four complete censuses, involving two days and two censuses per day, one during the morning (starting at 08:00 am) and another in the afternoon (starting at 14:00 pm). In each census, all birds present in the 128.7 ha of estuary waters, shores and river banks were counted. For this purpose, three observation stations were established (Fig. 1), from which the birds were counted by a trained observer, supported by an assistant, using a 60-40X spotting scope (Swarovski, Austria). In addition to the census data, during the same period of time we surveyed the landscape four times per year, in the months of February, May, August and October. In three consecutive days, from dawn to 17:00 pm, we obtained information on the abundance of waterbirds in the surrounding agricultural matrix. In order to produce density estimates, we established a total of 71 sampling points, with a mean surveyed area of 4.02 ha (0.78 ha; 11.81 ha). The location of these points sought to maximize the coverage of different habitats conditions and to optimize commuting time between points. Because the habitat conditions for waterbirds around each sampling point varied, for every visit we estimated the percentage of flooded area visible from the point.

The counts considered all waterbirds and seabirds present in the surveyed area. Birds flying were only considered when they were clearly moving within the surveyed area (following Estades & Vukasovic 2013). At each point, a single experienced observer (RFT) carried out 10 min surveys, considering a 300 m of maximum observation distance and using 8x43 binoculars (Pentax DCF ED) for the observation and identification of birds. Vocalizations were also considered for bird identification and counts. To evaluate differences in the use of the environments, all recorded individuals were classified as performing of five activity categories: resting, foraging, bathing, breeding and other (modified from Crook *et al.* 2009). Bird names follow taxonomic classification of the South American Classification Committee (SACC) (Remsen *et al.* 2023).

Statistical analysis

In order to compare the census and point count data, we transformed the latter into absolute abundances by multiplying the average density (ind/ha) of each species by the total area of the floodable landscape (3,952 ha).

We used cross-correlations (Leaver *et al.* 1974) to examine the temporal relationships between the abundance for every species at both the estuary and the landscape. Before the analyses we detrended both data series to meet the assumptions of cross-correlation test (Dean & Dunsmuir 2016). Because censuses and point counts were conducted at different weeks during each the season, we conducted a linear interpolation of every time series in order to produce an abundance estimate for every month of the year (Meijering 2002).

In order to understand the changes in abundance in the landscape matrix, we looked for the most plausible generalised additive models explaining species abundance, which, according to a preliminary analysis, required the use of zero-inflated hurdle location-scale model with Poisson distribution for most of the species. One linear predictor was used for controlling the probability of presence and another for controlling the mean, given the presence of the species (Wood & Wood 2015). We used a backward selection approach from a saturated model based on Akaike information criterion AIC (Zuur *et al.* 2009), which included variables describing the surveyed areain a 250 m radius, such as percentage of waterbodies, prairies and marshes, percentage of the sampled area flooded at the moment of sampling, etc. (Table 1). The interaction between the percentage of prairies and percentage of flooded area in the census point, which represents areas that include prairie habitats that are partially flooded, was also included. Time to High tide as a variable was estimated using the time at the count and the tides chart provided by the Chilean Navy authority as an online source (https://tablademareas.com/cl/biobio/arauco). We included smoothing functions for Month for within-year variability. In the linear predictor that controls for the probability of presence, prairies, flooded and their interaction was also included. We controlled for pseudo replication by including Point as random effect. We used the mgcv R package version 1.8-35 (Wood & Wood 2015) to run all the generalised additive models and for the model selection process to check for multicolinearity, not allowing values greater than 0.66. All statistical analyses considered a level of significance of $\alpha = 0.05$ and were conducted in the R platform (R Core Team 2020).

In order to avoid any aberrant result, models were run only for species with a minimum frequency of two counts per year and in three different sampling units, making a total of 18 sightings (Hecht & Zitzmann 2021, Zuur *et al.* 2009).

Table 1. Ranges of values for habitat descriptor variables obtained through ArcMap 10 and observer estimation. Time to High-tide is measured as fraction of a day. Water level is a three level categorical variable (1: low, 2: medium, 3: high). Percentage of different land covers in the 250 m buffer around sampling points. / Rangos de valores para variables descriptoras de hábitat obtenidos a través de ArcMap 10.2 y estimación del observador. El tiempo hasta la marea alta se mide como fracción de un día. El nivel del agua es una variable categórica de tres niveles (1: bajo, 2: medio, 3: alto). Porcentaje de diferentes coberturas terrestres en la zona buffer de 250 m alrededor de los puntos de muestreo.

	Estuary						Matrix					
	Dry			Wet			Dry			Wet		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Distance to Water Body (m)	4.0	18.8	38.7	8.7	26.2	130.0	0.0	50.4	469.9	0.0	193.6	1329.1
Time to High Tide (day)	0.1	0.2	0.2	0.0	0.1	0.4	0.1	0.2	0.5	0.0	0.1	0.4
Waterlevel	1.0	1.9	2.0	1.0	2.3	3.0	1.0	1.0	2.0	1.0	1.6	3.0
% flooded	0.0	60.0	90.0	5.0	69.7	100.0	0.0	2.0	85.0	0.0	20.8	90.0
% Urban	0.0	0.3	1.7	0.0	0.3	1.7	0.0	12.1	57.8	0.0	12.1	57.8
% Road	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.7	14.5	0.0	4.7	14.5
% Woodland	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.5	73.0	0.0	9.8	73.0
% Prairy	0.8	14.2	26.7	0.3	13.9	26.5	12.3	55.9	92.5	10.1	39.1	65.2
% Beach	0.0	14.5	36.8	0.0	15.0	37.6	0.0	0.1	4.0	0.0	0.0	4.4
% Mudflat	8.1	16.1	35.5	0.9	16.1	36.3	0.0	0.1	10.1	0.0	0.1	10.1
% Vegas	11.5	20.8	31.3	0.2	14.5	33.2	0.0	4.9	28.0	0.0	2.0	23.6
% Shrubs	5.2	19.7	37.0	5.5	17.3	38.9	0.0	3.7	37.2	0.0	2.1	21.8
% Treeless Hill	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	13.4	0.0	0.3	13.6
% Water	9.4	14.4	18.4	10.7	22.4	38.3	0.0	2.7	27.9	0.0	26.8	58.1
% Agriculture	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	30.8	0.0	3.0	23.0

RESULTS

A total of 72 species from six orders were recorded in the Carampangue estuary and the surrounding landscape during the three years study. In the estuary area we recorded 69 species, including 25 shore and marine species, and in the agricultural landscape only 51 species were detected (Table 2). A large proportion of resident waterbird species (78 %) was recorded using the flooded agricultural landscape. Only four migrant species, three (33 %) of boreal breeders and one (50 %) of neotropical migrant species used the flooded landscape.

The habitat characteristics of the study area varied greatly for waterbird species throughout the year, with two observed extremes in spring (October) and summer (February). During February (dry season) the estuary and its surrounding landscape reached an area of 251 ha categorized as waterbodies, comprised of 111 independent flooded patches. On the other hand, during the wet season 827 flooded patches were identified, reaching a total of 1,404 ha (Fig. 1).

Cross-correlations for species abundance at the estuary and the landscape showed different patterns in the use of these habitats. For many species there was a clear negative correlation between their numbers in the landscape and those at the estuary, mostly resident species, such as grebes, ducks and coots (Fig. 2). However, other species, such as Cocoi Heron (*Ardea cocoi*), Great Egret (*Ardea alba*), and Coscoroba Swan (*Coscoroba coscoroba*), and some migrant species, such as Lesser Yellowlegs (*Tringa flavipes*) and Spectacled Tyrant (*Hymenops perspicillatus*), showed a clear positive cross-correlation in their abundance in both areas.

Table 2. Mean population size (± SE) for waterbird species recorded at the Carampangue estuary and its surrounding landscape at different seasons through 3 years of study (2016-2019). Cross-correlations among species abundances in estuary and landscape, showing the time lag corresponding to the largest correlation. Rare species or with few sighting in one season (9) are not appearing. Migratory status: A for austral migrants wintering in Central Chile and breeding in Southern South America; B for boreal migrants; N for neotropical migrants, species that migrate within the neotropics; and R for Residents in South Central Chile (although some species may engage in short distance movements). / Tamaño medio de la población (± SE) de las especies de aves acuáticas registradas en el estuario de Carampangue y su paisaje circundante en diferentes estaciones durante los 3 años de estudio (2016-2019). Correlaciones cruzadas entre las abundancias de especies en el estuario y el paisaje, mostrando el desfase temporal correspondiente a la mayor correlación. No aparecen especies raras o con pocos avistamientos en una temporada (9). Estatus migratorio: A para migrantes australes que pasan el invierno en el centro de Chile y se reproducen en el sur de América del Sur; B para migrantes boreales; N para migrantes neotropicales, especies que migran dentro del neotrópico; y R para Residentes en el centro sur de Chile (aunque algunas especies pueden realizar desplazamientos de corta distancia).

		Estuary				Landscape				Cross-correlation	
Species	**Migratory status**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Lag (months)**	**R**
Podicipediformes											
White-tufted Grebe (*Rollandia rolland*)	R	9.3 ± 3.8	3.8 ± 4.3	0.1 ± 0.3	5.1 ± 3.8	25.3 ± 12.3	48.0 ± 49.5	12.6 ± 12.6	8.6 ± 7.4	2	-0.84
Silvery Grebe (*Podiceps occipitalis*)	R	5.9 ± 8.0	8.5 ± 12.5	5.4 ± 12.3	1.0 ± 2.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Pied-billed Grebe (*Podilymbus podiceps*)	R	2.5 ± 1.5	1.4 ± 1.5	0 ± 0	0.5 ± 0.6	17.0 ± 29.4	167.5 ± 91.1	66.8 ± 56.2	8.4 ± 7.3	2	-0.95
Great Grebe (*Podiceps major*)	R					4.2 ± 7.3	0 ± 0	0 ± 0	21.8 ± 15.7		
Pelecaniformes											
Peruvian pelican (*Pelecanus thagus*)	R	216.0 ± 123.2	69.8 ± 105.4	15.5 ± 16.5	2.9 ± 3.8	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Neotropic Cormorant (*Phalacrocorax brasilianus*)	R	637.9 ± 296.8	383.5 ± 176.2	249.2 ± 122.4	321.0 ± 312.0	46.3 ± 28.9	21.6 ± 26.9	50.0 ± 24.7	46.6 ± 35.2	-2	-0.57
Great Egret (*Ardea alba*)	R	13.0 ± 8.3	4.8 ± 4.3	1.2 ± 1.8	4.5 ± 2.5	42.4 ± 29.5	127.0 ± 14.8	67.0 ± 32.2	38.9 ± 13.4	-2	0.80
Cocoi Heron (*Ardea cocoi*)	R	1.3 ± 0.6	1.0 ± 0.9	0.1 ± 0.3	0.9 ± 1.4	0 ± 0	8.8 ± 7.6	4.1 ± 7.2	12.6 ± 12.4	1	0.58
Snowy Egret (*Egretta thula*)	R	12.3 ± 7.1	7.7 ± 7.3	1.1 ± 1.2	4.7 ± 3.6	8.4 ± 7.3	215.8 ± 104.2	209.0 ± 13.5	38.9 ± 13.8	1	-0.86
Cattle Egret (*Bubulcus ibis*)	R	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.2	258.8 ± 118.2	191.3 ± 119.8	247.2 ± 95.2	203.5 ± 66.5	0	-1
Black-crowned Night-Heron (*Nycticorax nycticorax*)	R	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	12.5 ± 12.4	8.3 ± 14.4		
White-faced Ibis (*Plegadis chihi*)	R	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.2	4.2 ± 7.3	34.9 ± 27.1	96.4 ± 72.6	4.1 ± 7.2	0	1

Continuation Table 2.

		Estuary				Landscape				Cross-correlation	
Species	**Migratory status**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Lag (months)**	**R**
Black-faced Ibis (*Theristicus melanopis*)	R	0 ± 0	0 ± 0	0.2 ± 0.8	0 ± 0	8.3 ± 14.4	22.0 ± 20.3	29.2 ± 7.0	17.2 ± 14.9	0	-1
Anseriformes											
Coscoroba Swan (*Coscoroba coscoroba*)	R	9 ± 6.8	7.4 ± 4.4	7.0 ± 7.0	8.2 ± 5.1	0 ± 0	30.8 ± 20.7	16.7 ± 7.1	0 ± 0	0	0.86
Black-necked Swan (*Cygnus melanocoryphus*)	R	2.4 ± 2.0	1.3 ± 1.4	0.5 ± 1	2.4 ± 3.5	17.0 ± 29.4	96.2 ± 19.3	41.6 ± 40.0	4.1 ± 7.2	1	-0.85
Yellow-billed Pintail (*Anas georgica*)	R	110.5 ± 147.1	73.2 ± 34.6	67.2 ± 55.8	159.3 ± 43.1	59.5 ± 70.2	667.7 ± 220.4	485.3 ± 200.2	8.7 ± 7.5	0	-0.93
Yellow-billed Teal (*Anas flavirostris*)	R	17.0 ± 11.7	5.5 ± 6.1	1.5 ± 2.2	14.8 ± 16.4	50.5 ± 33.0	329.3 ± 152.5	155.1 ± 97.0	29.5 ± 28.4	1	-0.56
White-cheeked Pintail (*Anas bahamensis*)	R	0.2 ± 0.4	0 ± 0	0 ± 0	0.1 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Chiloe Wigeon (*Mareca sibilatrix*)	R	1.8 ± 3.1	7.5 ± 6.1	3.8 ± 3.8	3.0 ± 3.4	12.6 ± 12.7	74.3 ± 19.2	37.5 ± 21.4	0 ± 0	0	-0.79
Cinnamon Teal (*Spatula cyanoptera*)	R	2.1 ± 1.9	1.0 ± 1.8	0.4 ± 0.6	2.4 ± 2.7	8.5 ± 14.7	91.9 ± 56.9	62.7 ± 0.5	0 ± 0	0	-0.86
Red Shoveler (*Spatula platalea*)	R	1.4 ± 2.6	0.5 ± 0.6	0.3 ± 0.8	2.0 ± 2.0	0 ± 0	13.0 ± 22.6	0 ± 0	0 ± 0	0	-0.77
Lake Duck (*Oxyura vittata*)	R	0.1 ± 0.2	0 ± 0	0 ± 0	0.1 ± 0.2	4.1 ± 7.2	0 ± 0	0 ± 0	0 ± 0	0	-0.98
Domestic duck (*Anas platyrynchos f. domestica*)	R	0 ± 0	0.1 ± 0.3	0.3 ± 0.4	0 ± 0	12.6 ± 12.7	34.9 ± 14.5	25.0 ± 12.3	0 ± 0		
Gruiformes											
Plumbeous Rail (*Pardirallus sanguinolentus*)	R	0.7 ± 0.9	0.1 ± 0.3	0.5 ± 0.7	1.0 ± 0.7	8.3 ± 14.4	30.9 ± 20.7	16.6 ± 28.8	8.9 ± 15.4	-1	-0.69
Spot-flanked Gallinule (*Porphyriops melanops*)	R	0.1 ± 0.3	0.1 ± 0.2	0 ± 0	0 ± 0	46.6 ± 7.3	61.0 ± 61.8	37.6 ± 0.3	21.8 ± 15.7	4	-0.78
White-winged Coot (*Fulica leucoptera*)	R	1.4 ± 1.4	3.5 ± 6.4	0 ± 0	0.42 ± 0.9	42.2 ± 32.0	226.7 ± 186.7	229.8 ± 24.1	17.3 ± 8.0	2	-0.82
Red-gartered Coot (*Fulica armillata*)	R	19.1 ± 19.2	10.5 ± 13.7	1.9 ± 3.3	3.67 ± 5.8	29.6 ± 19.4	327.1 ± 249.4	58.7 ± 40.6	8.7 ± 7.5	2	-0.63
Red-fronted Coot (*Fulica rufifrons*)	R	0.1 ± 0.2	0 ± 0	0 ± 0	0.1 ± 0.2	8.5 ± 7.4	12.9 ± 12.9	4.2 ± 7.3	0 ± 0	3	-0.64

Continuation Table 2.

		Estuary				Landscape				Cross-correlation	
Species	**Migratory status**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Lag (months)**	**R**
Charadriiformes											
Southern Lapwing (*Vanellus chilensis*)	R	45.0 ± 42.4	36.9 ± 18.3	61.5 ± 31.4	131.0 ± 39.8	2638.2 ± 338.4	3426.5 ± 431.3	2846.2± 456.46	1824.4 ± 642.0	3	-0.86
White-necked Stilt (*Himantopus mexicanus*)	R	64.6 ± 19.5	27.3 ± 34.1	10.0 ± 14.2	28.5 ± 18.7	21.2 ± 36.8	118.6 ± 36.5	91.5 ± 100.8	12.9 ± 22.4	2	0.62
Collared Plover (*Charadrius collaris*)	A	1.0 ± 1.5	3.3 ± 2.0	3.0 ± 3.4	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Two-banded Plover (*Charadrius falcklandicus*)	A	1.0 ± 2.5	4.2 ± 5.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Rufous-chested Dotterel (*Charadrius modestus*)	A	3.0 ± 4.3	14.0 ± 7.1	0.2 ± 0.8	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
American Oystercatcher (*Haematopus palliatus*)	R	282.0 ± 78.7	161.8 ± 57.6	66.2 ± 25.5	89.7 ± 27.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Greater Yellowlegs (*Tringa melanoleuca*)	B	1.8 ± 1.4	0.4 ± 1.1	3.5 ± 4.1	13.9 ± 6.6	0 ± 0	0 ± 0	4.1 ± 7.2	0 ± 0	0	-1
Lesser Yellowlegs (*Tringa flavipes*)	B	9.5 ± 10.4	0 ± 0	26.7 ± 27.6	33.0 ± 27.14	0 ± 0	0 ± 0	29.1 ± 50.4	0 ± 0	-1	0.76
Willet (*Tringa semipalmata*)	B	0 ± 0	0.1 ± 0.5	0 ± 0	0.1 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Whimbrel (*Numenius phaeopus*)	B	26.9 ± 25.8	57.2 ± 68.1	63.3 ± 41.6	139.5 ± 168.3	0 ± 0	30.9 ± 27.7	62.6 ± 12.0	8.7 ± 7.5	-2	-0.60
Hudsonian Godwit (*Limosa haemastica*)	B	1.4 ± 4.2	2 ± 6.9	0 ± 0	0.5 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Ruddy Turnstone (*Arenaria interpres*)		0 ± 0	0 ± 0	0.5 ± 1.73	0.1 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Sanderling (*Calidris alba*)	B	7.5 ± 19.9	7.1 ± 15.4	52.3 ± 56.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Baird's Sandpiper (*Calidris bairdii*)	B	0 ± 0	0.1 ± 0.3	7 ± 7.9	0.2 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Magellanic Snipe (*Gallinago magellanica*)	R	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4.2 ± 7.3	8.7 ± 15.1	20.9 ± 7.3	0 ± 0		
Kelp Gull (*Larus dominicanus*)	R	1157.6 ± 611.9	817.8 ± 669.3	471.5 ± 331	383.3 ± 196.7	0 ± 0	173.5 ± 223.6	58.5 ± 56.3	13.0 ± 13.3	4	0.74
Grey Gull (*Leucophaeus modestus*)	R	37.9 ± 48.1	41.8 ± 42.5	29.1 ± 39.6	1.3 ± 2.7	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Franklin's Gull (*Leucophaeus pipixcan*)	B	1427.2 ± 2495.9	0 ± 0	14.0 ± 40.6	1528.4 ± 992.5	0 ± 0	0 ± 0	0 ± 0	0 ± 0		

Continuation Table 2.

		Estuary				Landscape				Cross-correlation	
Species	**Migratory status**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Lag (months)**	**R**
Brown-hooded Gull (*Chroicocephalus maculipennis*)	R	2532.7 ± 2388.0	510.0 ± 1042.5	3.0 ± 2.9	67.8 ± 77.0	4.2 ± 7.3	149.7 ± 83.2	58.5 ± 19.1	8.7 ± 7.5	-2	-0.85
South American Tern (*Sterna hirundinacea*)	A	466.0 ± 589.5	409.9 ± 250.1	76.9 ± 93.5	0.5 ± 1.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Snowy-crowned Tern (*Sterna trudeaui*)	R	8.3 ± 6.5	1.6 ± 1.3	0.6 ± 0.6	1.0 ± 1.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Inca Tern (*Larosterna inca*)	R	0.1 ± 0.3	0.8 ± 1.0	1.1 ± 3.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Elegant Tern (*Thalasseus elegans*)	B	128.5 ± 258.7	0 ± 0	1.5 ± 4.5	99.2 ± 127.0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Black Skimmer (*Rynchops niger*)	N	15.4 ± 32.8	41.4 ± 94.6	0 ± 0	18.4 ± 49.0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Passeriformes											
Bar-winged Cinclodes (*Cinclodes fuscus*)	R	0.4 ± 0.6	0.1 ± 0.39	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Spectacled Tyrant (*Hymenops perspicillata*)	N	0 ± 0	0 ± 0	0.2 ± 0.4	0.9 ± 0.7	0 ± 0	0 ± 0	12.6 ± 21.9	8.9 ± 15.4	0	0.94
Austral Negrito (*Lessonia rufa*)	R	2.2 ± 0.9	1 ± 0.7	4.3 ± 1.3	2.7 ± 2.0	0 ± 0	0 ± 0	4.1 ± 7.2	0 ± 0	0	0.99
Grass Wren (*Cistothorus platensis*)	N	0.1 ± 0.2	0 ± 0	0 ± 0	0.1 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Correndera pipit (*Anthus correndera*)	R	0.7 ± 1.0	0.5 ± 0.6	0.5 ± 0.5	0.5 ± 1.0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Yellow-winged Blackbird (*Agelaius thilius*)	R	4.8 ± 6.2	1.4 ± 2.1	0.1 ± 0.2	0.5 ± 1	8.5 ± 14.7	0 ± 0	16.91 ± 29.2	4.4 ± 7.7	0	-0.75

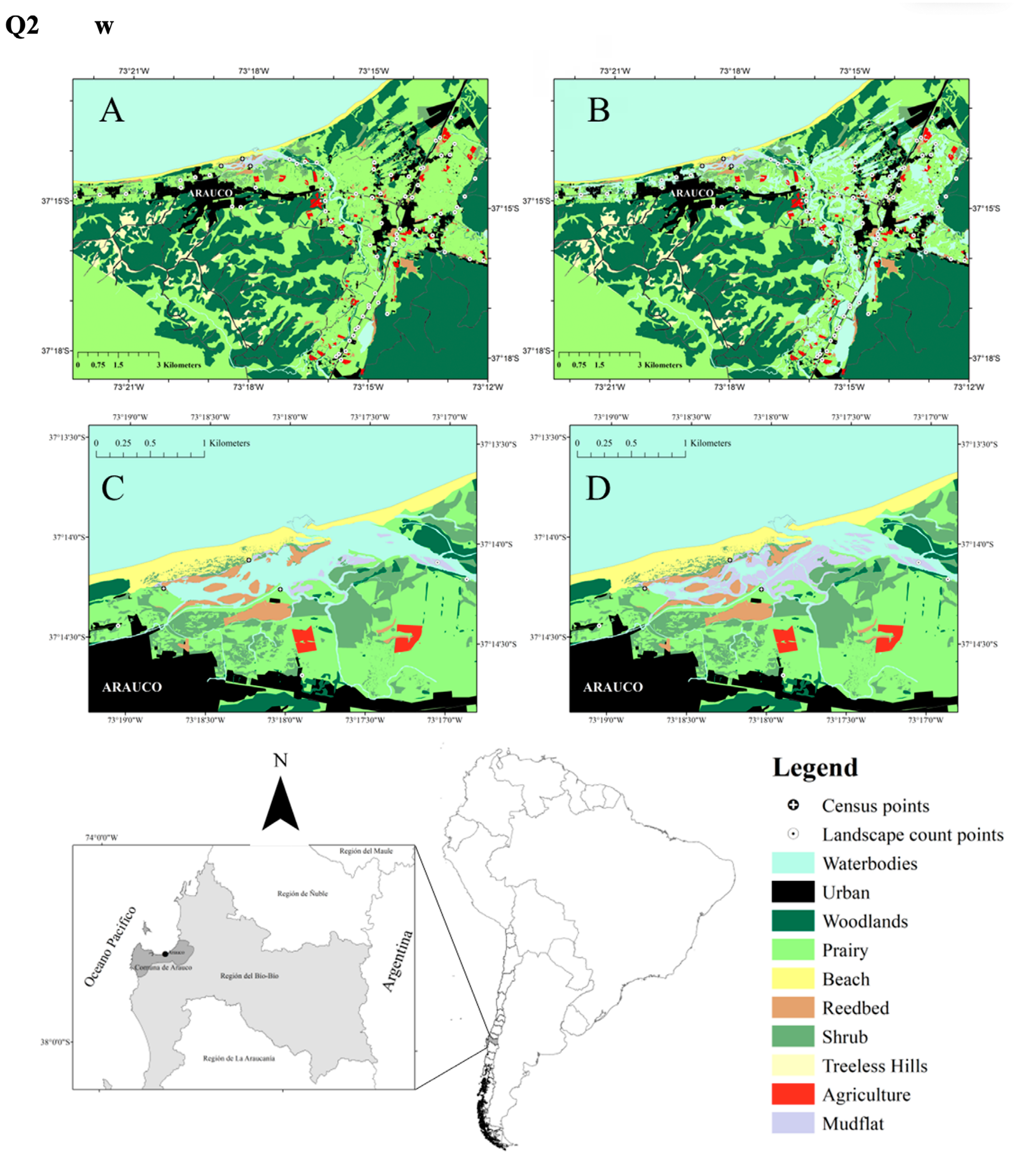

Figure 1. Description of the study area in terms of general land cover categories. A. Study area at the peak of the dry season (February). B. Study area at the peak of the wet season (October). C. Detailed image for the estuarine zone during the low-tide, and D during the high-tide. / Descripción del área de estudio en términos de categorías generales de cobertura del suelo. A. Área de estudio en el pico de la estación seca (febrero). B. Área de estudio en el pico de la temporada de lluvias (octubre). C. Imagen detallada de la zona estuarina durante la marea baja y D durante la marea alta.

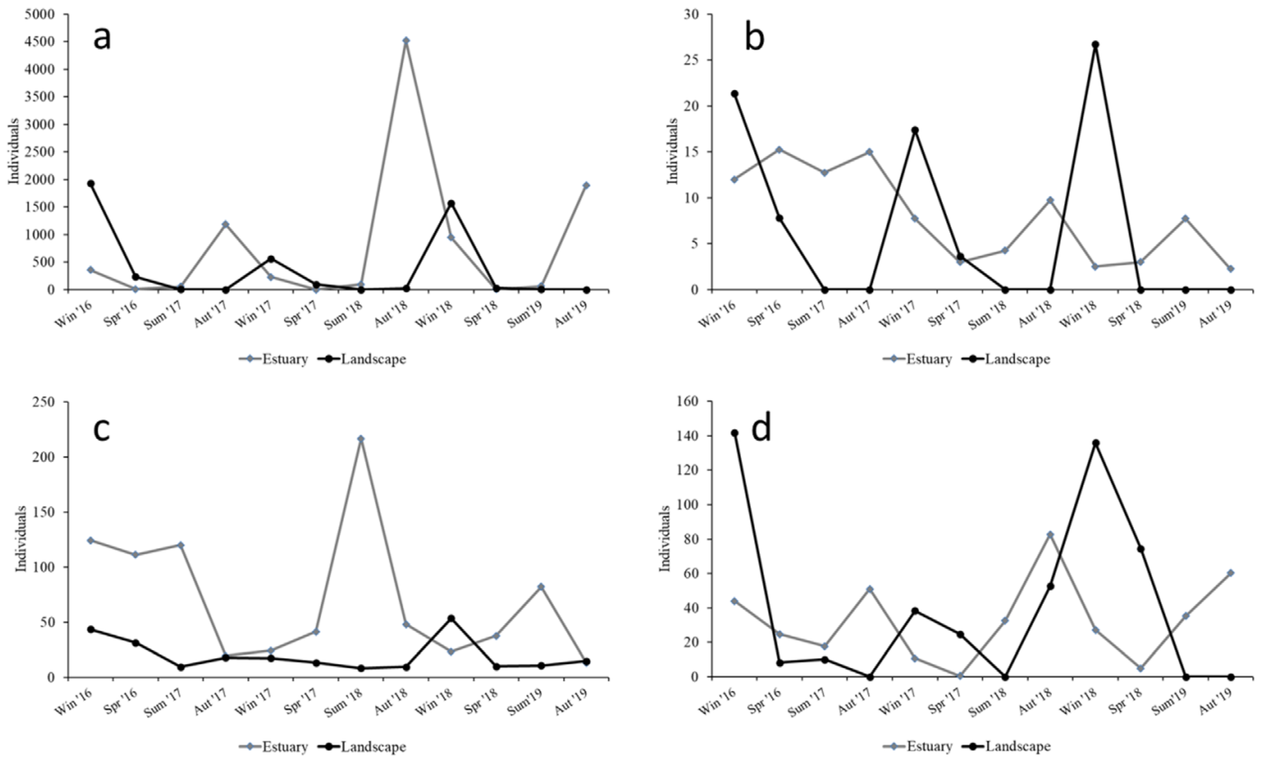

Figure 2. Population sizes estimated for A. Brown-hooded Gull (*Chroicocephalus maculipennis*). B. Coscoroba Swan (*Coscoroba coscoroba*). C. Whimbrel (*Numenius phaeopus*), and D. White-necked Stilt (*Himantopus mexicanus*). Bird numbers at the estuary area and the estimated abundance for the surrounding landscape. / Tamaños de población estimados para A. Gaviota Cahuil (*Chroicocephalus maculipennis*). B. Cisne Coscoroba (*Coscoroba coscoroba*). C. Zarapito (*Numenius phaeopus*), y D. Perrito (*Himantopus mexicanus*). Número de aves en el área del estuario y la abundancia estimada para el paisaje circundante.

Models explaining birds' use of the agricultural landscape were fitted for only 19 species due to low number of records (Table 3). To avoid any possible highly uncertain estimated smooth functions and parameters, we ran models for species with more than 18 counts. For most of the analyzed species the percentage of flooded area in the landscape was important in explaining the species presence and abundance. Prairies in the sampled area positively explained the presence and abundance of many resident species. The interaction term between prairies and flooded explained the presence of Whimbrel (*Numenius phaeopus*) and the abundance of Yellow-billed Teal (*Anas flavirostris*) and White-necked Stilt (*Himantopus mexicanus*). The percentage of water bodies in the 250 m radius of each sampling point was important in explaining the abundance of White-winged Coot (*Fulica leucoptera*) and the White-necked Stilt. Cattle Egret (*Bubulcus ibis*) was the only species for which the distance to waterbodies was statistically significant, with a negative effect on its abundance. During the flooded period, there was an increase in the records of birds feeding and roosting while, at the same time, the proportion of species recorded in those activities also increases (Table 4). Reproduction associated activities were also seen more frequently and for more species during that time. Many species that build floating nest take advantage of the flooded landscape during the early months of the springtime.

Table 3. Results from selected GAM models explaining bird use of the surrounding landscape of the Carampangue estuary. Model fitting achieved by maximum likelihood. Showing linear predictors for the abundance (count model) and presence (binomial model) models for the species. Models' goodness-of-fit are presented through Deviance explained. / Resultados de modelos GAM seleccionados que explican el uso del paisaje circundante al estuario de Carampangue por parte de las aves. Ajuste del modelo logrado por máxima verosimilitud. Mostrando predictores lineales para la abundancia (modelo de conteo) y presencia (modelo binomial) para las especies. La bondad de ajuste de los modelos se presenta a través de la desviación explicada.

Species	Fixed effects of count model											
	DWB		Time to High Tide		Flooded		Prairy		Marsh		Water	
	B	p	β	p	β	p	β	p	β	p	β	p
Black-necked Swan					-0.066	0.034			-0.387	0.432		
Cattle Egret	-0.001	0.018			0.011	0.066	0.032	0.003	0.057	0.023		
Snowy Egret												
Great Egret												
Brown-headed Gull												
Kelp Gull											0.022	0.119
Cinnamon Teal	0.000	0.638	5.890	0.187	-0.021	0.186	-0.003	0.886				
Yellow-billed Teal					0.080	<0.001	0.083	0.002				
Yellow-billed Pintail					0.013	<0.001						
Chiloe Wigeon	0.002	0.244	-6.59	0.349					0.382	0.344		
White-necked Stilt	-0.002	0.033	4.350	0.157	0.048	0.009	0.030	0.330			-0.063	0.017
Pied-billed Grebe												
Southern Lapwing *					5.53e-3	0.010	0.011	<0.001				
White-winged Coot	-0.001	0.169	2.043	0.233			0.031	0.013			0.047	0.001
Red-gartered Coot			4.496	0.001					-0.056	0.221		
Spot-flanked Gallinule **	-2.8-4	0.172			0.012	0.487					0.057	<0.001
Neotropic Cormorant	-0.005	0.302			0.022	0.045					0.044	0.254
Whimbrel							0.055	0.281				

DWB: Distance to nearest water body; flooded: percentage of area flooded in 250 m radius; Prairy: percentage of area of prairies in 250 m radius; Marsh: percentage of area of marshes in 250 m radius; Water: percentage of area of water bodies in 250 m radius; EDF: effective degree of freedom, it reflects the degree of non-linearity of the curve (edf = 1 is equivalent to a linear relationship, 1 < edf ≤ 2 is weakly non-linear relationship, edf > 2 is a highly non-linear relationship). DevExpl: Deviance explained.

*Model fitted under a negative binomial distribution; **Zero-inflated GAM model Poisson with only a linear predictor.

Continuation Table 3.

Species	Fixed effects of count model		Randomeffect		Fixed effects of binomial model						Randomeffect		DevExpl
	Flooded x Prairy		Month		Flooded		Prairy		Flooded x Prairy		Point		
	β	p	edf	p	β	p	β	p	β	p	edf	p	%
Black-necked Swan			2.658	0.25	0.006	<0.001	0.034	0.146			21.52	<0.001	59.8
Cattle Egret			1.76	0.09	-0.009	0.354	-0.001	0.805	3.0e-4	0.102	36.54	<0.001	11.5
Snowy Egret			1.84	0.23							33.42	<0.001	11.5
Great Egret			1.01	0.56	0.024	<0.001					23.05	<0.001	25.2
Brown-headed Gull			1.80	0.66							13.25	0.021	8.97
Kelp Gull			1.00	0.61	0.025	<0.0001					13.37	0.052	12.6
Cinnamon Teal			1.85	0.17	0.052	<0.001	-0.002	0.896			18.90	<0.001	47.7
Yellow-billed Teal	-0.001	<0.001	1.83	0.02	0.041	<0.001					21.57	<0.001	29.5
Yellow-billed Pintail			1.98	0.19	0.044	<0.001	0.004	0.522			30.71	<0.001	27.5
Chiloe Wigeon			1.40	0.79	0.055	<0.001	0.028	0.188			15.13	0.001	54.5
White-necked Stilt	-0.001	0.009	1.00	0.41	0.035	<0.001					25.86	<0.001	38.8
Pied-billed Grebe			1.66	0.62							34.98	<0.001	26.1
Southern Lapwing *	-2.1e-4	<0.001	2.83	<0.001									10.8
White-winged Coot			1.00	0.06	0.049	<0.001					33.64	<0.001	49.3
Red-gartered Coot			2.47	0.04	0.053	<0.001					20.20	<0.001	41.6
Spot-flanked Gallinule **			1.00	0.08									70.1
Neotropic Cormorant			1.00	0.19							29.29	<0.001	49.5
Whimbrel			1.00	0.37	-0.037	0.108	-0.091	0.030	0.002	0.003	21.33	<0.001	39.8

DWB: Distance to nearest water body; flooded: percentage of area flooded in 250 m radius; Prairy: percentage of area of prairies in 250 m radius; Marsh: percentage of area of marshes in 250 m radius; Water: percentage of area of water bodies in 250 m radius; EDF: effective degree of freedom, it reflects the degree of non-linearity of the curve (edf = 1 is equivalent to a linear relationship, 1 < edf ≤ 2 is weakly non-linear relationship, edf > 2 is a highly non-linear relationship). DevExpl: Deviance explained.

*Model fitted under a negative binomial distribution; **Zero-inflated GAM model Poisson with only a linear predictor.

Table 4. Bird diurnal activities observed in the landscape during the wet and dry seasons (years 2016-2019). Proportion of individuals recorded feeding, roosting, bathing or birds engaged in reproductive activities, such as courting, copulating, nesting, or caring for chicks. / Actividades diurnas de aves observadas en el paisaje durante las estaciones húmeda y seca (años 2016-2019). Proporción de individuos registrados alimentándose, descansando, bañándose o participando en actividades reproductivas, tales como cortejar, copular, anidar o cuidar polluelos.

	Dry				Wet			
Species	**Feed**	**Rest**	**Bath**	**Breed**	**Feed**	**Rest**	**Bath**	**Breed**
White-tufted Grebe	0.0	0.0	0.0	0.0	52.4	28.6	4.8	0.0
Pied-billed Grebe	0.0	50.0	0.0	0.0	25.8	56.1	0.0	3.0
Great Grebe	0.0	100.0	0.0	0.0	40.0	20.0	20.0	0.0
Neotropic Cormorant	0.0	22.2	0.0	0.0	9.4	59.4	0.0	0.0
Great Egret	16.7	16.7	0.0	0.0	41.3	44.4	0.0	0.0
Snowy Egret	60.0	0.0	0.0	0.0	37.3	47.5	0.0	0.0
Cocoi Heron	0.0	0.0	0.0	33.3	0.0	40.0	0.0	40.0
Cattle Egret	30.8	15.4	0.0	0.0	46.9	43.0	0.0	0.0
Black-crowned Night-Heron	0.0	50.0	0.0	0.0	0.0	75.0	0.0	0.0
White-faced Ibis	0.0	100.0	0.0	0.0	59.5	24.3	0.0	0.0
Black-faced Ibis	100.0	0.0	0.0	0.0	47.1	29.4	0.0	0.0
Coscoroba Swan					36.4	63.6	0.0	0.0
Black-necked Swan	0.0	0.0	100.0	0.0	36.6	43.9	0.0	0.0
Yellow-billed Pintail	0.0	0.0	0.0	0.0	13.3	66.9	1.9	0.9
Yellow-billedTeal	33.3	50.0	0.0	0.0	14.0	69.3	2.0	0.0
White-cheeked Pintail					0.0	0.0	0.0	0.0
Chiloe Wigeon					21.2	63.6	3.0	0.0
Cinnamon Teal					21.4	64.3	4.8	0.0
Red Shoveler					0.0	80.0	0.0	0.0
Lake Duck					0.0	100.0	0.0	0.0
Domestic duck					21.1	57.9	0.0	0.0
Plumbeous Rail					17.6	41.2	5.9	0.0
Spot-flanked Gallinule	50.0	50.0	0.0	0.0	28.0	44.0	2.0	2.0
White-winged Coot	0.0	100.0	0.0	0.0	50.0	31.9	2.1	3.5
Red-gartered Coot	0.0	100.0	0.0	0.0	26.9	57.7	0.0	3.8
Red-fronted Coot					33.3	50.0	0.0	0.0
Southern Lapwing	38.4	37.4	0.3	0.0	30.6	55.2	0.2	1.6
White-necked Stilt	0.0	0.0	0.0	0.0	51.7	40.0	0.0	3.3
Greater Yellowlegs					50.0	50.0	0.0	0.0
Lesser Yellowlegs					77.8	22.2	0.0	0.0
Whimbrel	0.0	100.0	0.0	0.0	33.3	45.8	0.0	0.0
Magellanic Snipe					0.0	0.0	0.0	0.0
Kelp Gull	0.0	100.0	0.0	0.0	16.1	71.0	1.6	0.0
Brown-hooded Gull	0.0	0.0	0.0	0.0	25.0	66.1	0.0	0.0
Spectacled Tyrant					40.0	40.0	0.0	0.0
Austral Negrito					100.0	0.0	0.0	0.0
Yellow-winged Blackbird					0.0	57.1	0.0	0.0
Average	15.0	40.5	4.6	1.5	29.8	47.3	1.3	1.6
Proportion of species	20.6	41.2	5.9	2.9	61.2	69.4	22.4	16.3

DISCUSSION

Most of the waterbirds present in the Carampangue river estuary were also recorded in the surrounding pastures. As predicted, most long-distance migrants did not use the surrounding landscape, likely because by the time in which these species visit the study region, most of the terrain has already dried up. Species such as whimbrels and Franklin's gulls (*Leucophaeus pipixcan*), are known to use agricultural fields for feeding (Burger *et al.* 2010), but resources offered in the studied landscape for these migrant species might not be as attractive as alternatives.

We also observed that for many species that made an important use of the landscape, there was a significant negative cross-correlation between the population sizes at the estuary and the landscape, suggesting a redistribution of individuals between these two systems throughout the year (Acuña *et al.* 2019) Although our data only provides indirect evidence of the movement of birds, a tracking study of gps-tagged Yellow-billed Pintails carried out by us in the area (authors, unpublished data) confirms the supplementary use of these two habitats by this species.

For a large proportion of the species the population sizes in the agricultural landscape increased during the winter and spring seasons, when flooding reaches its highest level. In the case of waterfowl, this variation can reach 6 to10 times the population sizes observed in summer (Table 2). In seasonal wetlands, many populations of waterfowl find resources and habitat conditions necessary to support their processes. Waterbirds benefit from using alternative sites to feed and reproduce during the flood season (Sebastián-González *et al.* 2010). Regarding trophic resources, the seasonal flooding triggers a pulse of primary productivity (Acuña *et al.* 2019, Wantzen *et al.* 2008) that has repercussions through the trophic chain. Most of these fields are grazing prairies, and the flooding events help to incorporate nutrients and accumulate organic matter in the soils, making these sites richer and productives (Wantzen *et al.* 2008, Junk & Wantzen 2006). Herbivorous species, such as coots, Black-necked Swan (*Cygnus melancopryphus*), Coscoroba swan and Chiloe wigeons (*Mareca sibilatrix*), take advantage of the germination and growth of aquatic and terrestrial plants. However, most species of waterfowl are predators, taking advantage of the fact that seasonal wetlands are used by aquatic insects and various species of amphibians to mate and reproduce (Smith *et al.* 2019). Species such as ibises were more abundant in the landscape than in the estuary itself. Resources offered by agricultural landscapes also attract seabird species, such as Kelp Gulls (*Larus dominicanus*) and Brown-hooded Gulls (*Chroicocephalus maculipennis*), both species known by using a great variety of food resources (Ludynia *et al.* 2005, Ghys & Favero 2004). Similarly, the offer of suitable nesting sites, which are enhanced by seasonal trophic resources and by the isolation caused by flooding of fields, attracts a significant number of bird species to nest in these environments (Wantzen *et al.* 2008, Poiani 2006). Nesting in seasonal wetlands at this study site has been recorded for Red-gartered coot (*Fulica armillata*), White-winged coot, Pied-billed Grebe (*Podilymbus podiceps*), Spot-flanked gallinule (*Porphyriops melanops*), and Yellow-billed Pintail (*Anas georgica*), as well as Southern Lapwing (*Vanellus chilensis*) and White-necked Stilt in nearby uplands, and Cocoi Heron in tall trees (R. Thomson *pers. obs*.). On the other hand, in the area of the estuary and its shores, we only recorded the reproduction of Coscoroba Swan, American Oystercatcher (*Haematopus palliatus*) and Southern Lapwing (I. Núñez *pers. comm*.). The latter supports the idea that seasonal wetlands, through the recruitment of new individuals, may contribute significantly to the maintenance of waterbird populations in the study region.

Areas of the landscape that are not flooded also play an important role for some species of waterbirds. These zones serve as a refuge for animals that are not strictly aquatic but that exploit the Aquatic-Terrestrial transition zone (Wantzen *et al.* 2008). Many species of waterfowl find roosting sites in non-flooded areas and some species, as previously mentioned Southern Lapwing and White-necked Stilt, nest on the ground (Walker *et al.* 2013). At the same time, the mosaic of flooded and non-flooded areas allows the peasant economy to remain productive in these seasons, providing valuable habitat for livestock (Kirby *et al.* 2002). However, the simultaneous use by birds and livestock of these areas generates a conflict in itself, due tothe trampling of nests and general disturbance of the breeding habitat (Buckley *et al.* 2022, Musitelli *et al.* 2016), developing a kind of ecological trap for the birds (Shydlovskyy & Kuzyo 2016). Despite its popularity worldwide, this issue has not been formally addressed in the study region.

As the waters recede, birds that are mostly swimmers leave the landscape and find refuge in permanent wetlands (Poiani 2006). In our study, this process can be easily seen in some species of ducks, where their abundance in the landscape was considerably reduced or disappeared, while their numbers steadily increase in the Carampangue river estuary (Table 2) (Fig. 3). In addition, individuals were found to make daily visits to the estuary from seasonal wetlands. Red-Gartered Coots probably perform similar daily movements as a function of the tides that influence the available habitat in the estuarine lagoon, as the model predicting their abundance in the landscape included a variable related to the time of the high tide in the estuary (Table 3).

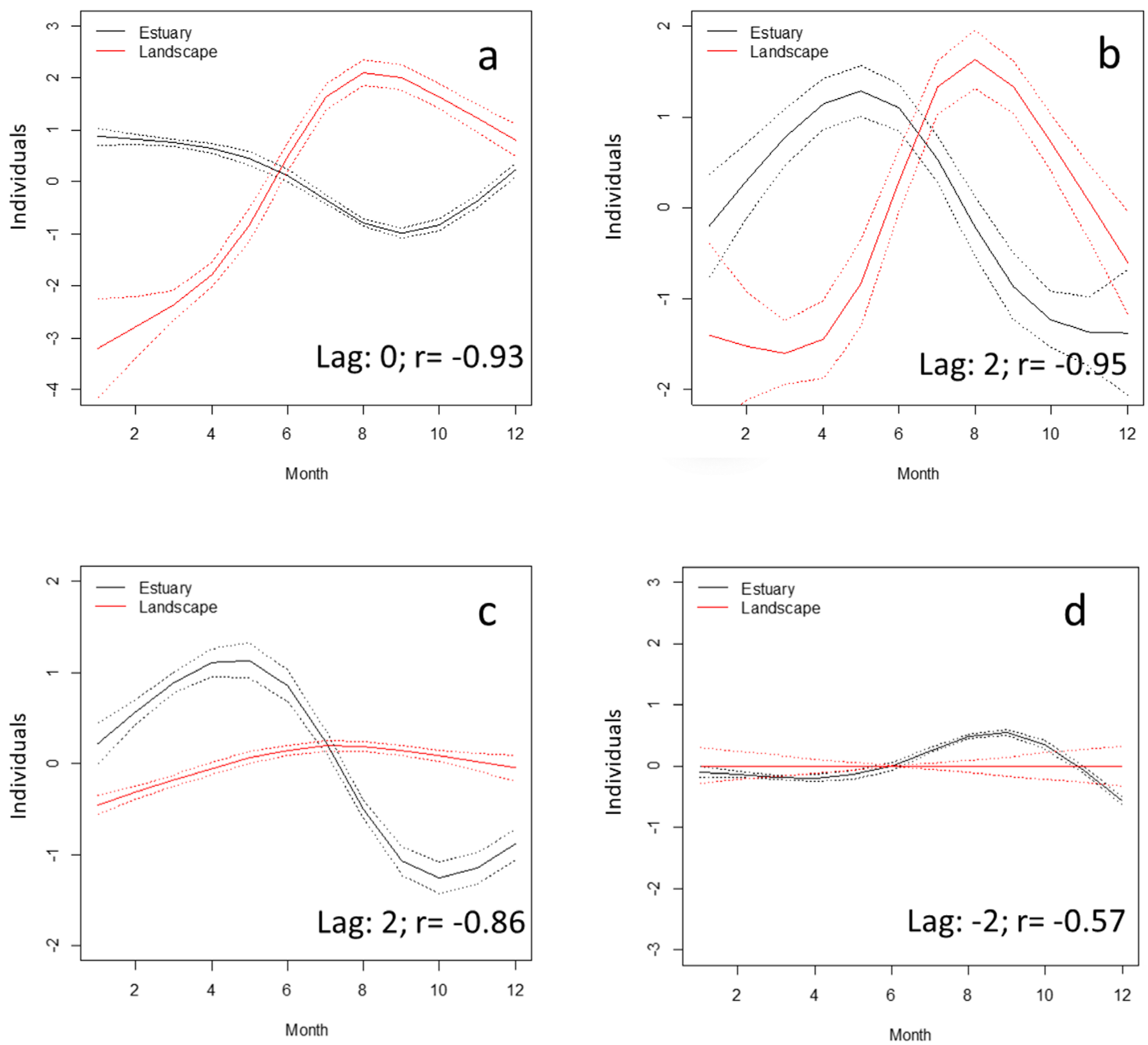

Figure 3. Modelled monthly population size around the mean (± SE) for A. Yellow-billed Pintail (Anas georgica). B. Pied-billed Grebe (*Podilymbus podiceps*). C. Southern Lapwing (*Vanellus chilensis*), and D. Neotropic Cormorant (Phalacrocorax brasilianus) for the estuary area and the surrounding landscape. / Tamaño de población mensual modelado alrededor de la media (± SE) para A. Yeco (*Phalacrocorax brasilianus*). B. Picurio(*Podilymbus podiceps*). C. Queltehue (*Vanellus chilensis*) y D. Pato Jergón Grande (*Anas georgica*) para el área del estuario y el paisaje circundante.

The results of the models presented in Table 3 evidently agree with the life-history descriptions for the species, and confirm our field observations. In general, the models show that within the landscape the characteristics of the sampled sites would well explain the presence of the species, with the random effects (point) statistically significant for most of them, although this does not occur much in the case of the species abundance. For most waterbirds, both their presence and their abundance are explained by the percentage of flooded land in the sampled area (Table 3). Species known to be adapted to terrestrial activities, such as Cattle Egret, Southern Lapwing, White-winged Coot, Yellow-billed Teal, and Yellow-billed Pintail (Jaramillo *et al.* 2003), their presence or abundance depend on the availability of a percentage of non-flooded prairies.

It is possible that our data might have been affected by between season changes in species detectability. We recognize two factors that could alter the species detectability during our study; these are the vegetation growth and the degree of flooding. Vegetation growth in height in some areas of landscape would decrease the ability of the observer to detect birds. In a completely different way, the level of flooding would act on the detectability of some species. Some species, such as Magellanic Snipe, are displaced to high areas by the rise in the water level, allowing the observer to see several individuals in non-flooded areas (R. Thomson *pers. obs.*). The recess of waters pull out some species from flooded reedbeds (Cumming *et al.* 2012), such as Spot-flanked Gallinule or Red-Fronted Coot (*Fulica rufifrons*) in this study for example.

Our results highlight the need for an integral landscape habitat assessment. Population estimates based only on traditional censuses may provide an incomplete picture of the situation of many species, likely underestimating the real numbers and obscuring regional population trends, i.e. in UK the Dispersed Waterbird Survey estimates exceed by more than 50 % for eight species when compared to Wetland Bird Survey (WeBS) (Jackson *et al.* 2006) Bird diversity conservation requires a comprehensive understanding of the bird-environment relationship throughout the year (Newton 1998). Thus, it is important to incorporate in waterbird assessments the nearby land and wetlands that populations of interest can use (Acuña *et al.* 2019), which has increasing local relevance when land use changes are evaluated (Pellet & Cornejo 2021). Finally, seasonal wetlands, or floodplains, are among the most threatened ecosystems worldwide due to the alteration of hydrological dynamics (Lorenzón *et al.* 2019), such as the drainage of fields for agriculture and urbanization (Pauchard *et al.* 2006). The conservation of waterfowl populations may also require active measures carried out in the surrounding landscape of protected permanent wetlands.

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REFERENCES

Acuña, M.P., Vukasovic, M.A., Hernández, H.J., Acuña, T.A., Estades, C.F. 2019. Effects of the surrounding landscape on waterbird populations in estuarine ecosystems of central Chile. Wetland Ecology and Management 27: 295-310.

Albanese, G., Davis, C.A. 2013. Broad-scale relationships between shorebirds and landscapes in the Southern Great Plains. Auk 130: 88-97.

Ali, E., Ismahan, H., Moussa, H. 2016. Diversity patterns and seasonal variation of the waterbird community in Mediterranean wetlands of Northeastern Algeria. Zoology and Ecology 26:85-92.

Ando, H., Ikeno, S., Narita, A., Komura, T., Takada, A., Isagi, Y., Oguma, H., Inoue, T., Takenaka, A. 2022. Temporal and interspecific dietary variation in wintering ducks in agricultural landscapes. Molecular Ecology 32(23): 6405-6417.

Amat, J.A., Green, A.J. 2010. Waterbirds as Bioindicators of Environmental Conditions. En: Hurford, C., Schneider, M., Cowx, I. (Eds) Conservation Monitoring in Freshwater Habitats: 45-52. Springer, Dordrecht.

Amigo, J., Ramírez, C. 1998. A bioclimatic classification of Chile: woodland communities in the temperate zone. Plant Ecology. 136: 9-26.

Baldassarre, G.A., Bolen, E.G. 1984. Field-feeding ecology of waterfowl wintering on the southern high plains of Texas. Journal of Wildlife Management 48: 63-71.

Brides, K., Wood, K. A., Hall, C., Burke, B., M[c]elwaine, G., Einarsson, O., Rees, E. C. 2021. The Icelandic Whooper Swan Cygnus cygnus population: current status and long-term (1986-2020) trends in its numbers and distribution. Wildfowl 71(71): 29-57.

Buckley, B.R., Lituma, C.M., Keyser, P.D., Holcomb, E.D., Smith, R., Morgan, J. J., Applegate, R.D. 2022. Effects of grazing strategy on facultative grassland bird nesting on native grassland pastures of the Mid-South USA. PeerJ 10: e13968.

Burger J., Gochfeld, M., Ridgely, R. 2010. Migratory behavior of Franklin's gulls (*Larus pipixcan*) in Peru. Journal of Energy Power Engineering 2: 143-147.

Chen, S., Zhang, Y., Xu, C., Cao, L., Huang, Z.Y., Li, C., Chen, B.J.W., Lu, C., Xu, W., Song, Y., De Boer, W.F. 2022. Neighbourhood threats: landscape context and anthropogenic changes can trigger waterbird population collapse. Landscape Ecology 37(12): 3141-3158.

Chatterjee, A., Adhikari, S., Pal, S., Mukhopadhyay, S.K. 2020. Foraging guild structure and niche characteristics of waterbirds wintering in selected sub-Himalayan wetlands of India. Ecological Indicators 108: 105693.

Crook, S.L., Conway, W.C., Mason, C.D., Kraai, K.J. 2009. Winter time-activity budgets of diving ducks on eastern Texas reservoirs. Waterbirds 32(4): 548-558.

Cumming, G.S., Paxton, M., King, J., Beuster, H. 2012. Foraging guild membership explains variation in waterbird responses to the hydrological regime of an arid-region flood-pulse river in Namibia. Freshwater Biology 57: 1202-1213.

De Almeida, B.A., Silva, C.B., Gimenes, M.R., Dos Anjos, L. 2016. Waterbirds in a floodplain: influence of spatial and environmental factors through time. Revista Brasileira de Ornitologia 24: 314-322.

Dean, R.T., Dunsmuir, W.T. 2016. Dangers and uses of cross-correlation in analyzing time series in perception, performance, movement, and neuroscience: The importance of constructing transfer function autoregressive models. Behavior Research Methods 48: 783-802.

Duncan, D.C. 1987. Nest-site distribution and overland brood movements of northern pintails in Alberta. Journal of Wildlife Management51(4): 716-723.

Dunning, J.B., Danielson, B.J., Pulliam, H.R. 1992. Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65: 169-175.

English, M.D., Robertson, G.J., Peck, L.E., Mallory, M.L. 2017. Agricultural food resources and the foraging ecologies of American black ducks (*Anas rubripes*) and mallards (*Anas platyrhynchos*) at the northern limits of their winter ranges. Urban Ecosystems 20: 1311-1318.

ESRI. 2011. ArcGIS Desktop Release 10. Environmental Systems Research Institute, Redlands, CA.

Estades, C.F., Vukasovic, M.A. 2013. Waterbird population dynamics in estuarine wetlands of Central Chile. Ornitologia Neotropical 24: 67-83.

Fox, A.D., Madsen, J. 2017. Threatened species to super-abundance: The unexpected international implications of successful goose conservation. Ambio 46: 179-187.

Gayet, G., Croce, N., Grillas, P., Nourry, C., Deschamps, C., Du Rau, P.D. 2012. Expected and unexpected effects of waterbirds on Mediterranean aquatic plants. Aquatic Botany 103: 98-105.

Green, A.J., Elmberg, J. 2014. Ecosystem services provided by waterbirds. Biological Reviews 89(1): 105-122.

Ghys, M., Favero, M. 2004. Espectro trófico de la gaviota capucho café (*Larus maculipennis*) en agroecosistemas del sudeste de la provincia de Buenos Aires, Argentina. Ornitologia Neotropical 15: 493-500.

Haig, S.M., Mehlman, D.W., Oring, L.W. 1998. Avian movements and wetland connectivity in landscape conservation. Conservation Biology 12: 749-758.

Hajek, E., Di Castri, F. 1975. Bioclimatografía de Chile. Editorial Universidad Católica de Chile, Santiago.

Hecht, M., Zitzmann, S. 2021. Sample size recommendations for continuous-time models: Compensating shorter time series with larger numbers of persons and vice versa. Structural Equation Modelling 28(2): 229-236.

Herbert, J.A., Chakraborty, A., Naylor, L.W., Krementz, D.G. 2021. Habitat associations of wintering dabbling ducks in the Arkansas Mississippi Alluvial Valley: implications for waterfowl management beyond the mallard. Wildlife Biology 2021(1): 1-10.

Herring, M.W., Robinson, W.A., Zander, K.K., Garnett, S.T. 2021. Increasing water-use efficiency in rice fields threatens an endangered waterbird. Agriculture, Ecosystems & Environment 322: 107638.

Jackson, S.F., Austin, G.E., Armitage, M.J.S. 2006. Surveying waterbirds away from major waterbodies: implications for waterbird population estimates in Great Britain. Bird study 53: 105-111.

Jaramillo, A., Burke, P., Beadle, D. 2003. Field guide to the birds of Chile: including the Antarctic Peninsula, the Falkland Islands and South Georgia. Christopher Helm, London.

Josens, M.L., Haydee, E.A., Favero, M. 2009. Seasonal variability of waterbird assemblages in relationship to habitat characteristics in a Pampas wetland. Waterbirds 32(4): 523-530.

Junk, W.J., Wantzen, K.M. 2006. Flood pulsing and the development and maintenance of biodiversity in floodplains. En: Batzer, D.P., Sharitz, R.R. (Eds) Ecology of freshwater and estuarine wetlands: 407-435.University of California Press, Berkeley.

Kirby, D.R., Krabbenhoft, K.D., Sedivec, K.K., Dekeyser, E.S. 2002. Wetlands in northern plains prairies: benefitting wildlife and livestock. Rangel 24: 22-25.

Leaver, R.H., Thomas, T.R. 1974. Analysis and presentation of experimental results. Macmillan.

Lorenzón, R.E., Beltzer, A.H., Olguin, P.F., León, E.J., Sovrano, L.V., Antoniazzi, C.E., Ronchi Virgolini, A.L. 2019. Temporal variation of bird assemblages in dynamic fluvial wetlands: seasonality and influence of water level and habitat availability. Revista de Biología Tropical 67: 1131-1145.

Ludynia, K., Garthe, S., Luna-Jorquera, G. 2005. Seasonal and regional variation in the diet of the kelp gull in northern Chile. Waterbirds 28: 359-365.

Macmillan, D., Hanley, N., Daw, M. 2004. Costs and benefits of wild goose conservation in Scotland. Biological Conservation 119: 475-485.

McEvoy, J.F., Hall, G.P., McDonald, P.G. 2016. Evaluation of unmanned aerial vehicle shape, flight path and camera type for waterfowl surveys: disturbance effects and species recognition. PeerJ 4: e1831.

Meijering, E. 2002. A chronology of interpolation: from ancient astronomy to modern signal and image processing. Proceedings of the IEEE 90: 319-342.

Moulton, C.E., Carlisle, J.D., Knetter, S.J., Brenner, K., Cavallaro, R.A. 2022. Importance of flood irrigation for foraging colonial waterbirds. The Journal of Wildlife Management 86(7): e22288.

Mukherjee, A., Borad, C.K. 2001. Effects of waterbirds on water quality. Hydrobiologia 464(1-3): 201-205.

Musitelli, F., Romano, A., Møller, A.P., Ambrosini, R. 2016. Effects of livestock farming on birds of rural areas in Europe. Biodiversity and conservation 25: 615-631.

Navarro-Ramos, M.J., Van Leeuwen, C.H., Olsson, C., Elmberg, J., Månsson, J., Martín-Vélez, V., Lovas-Kiss, Á., Green, A.J. 2024. Seed dispersal between aquatic and agricultural habitats by greylag geese. Agriculture, Ecosystems & Environment 359: 108741.

Newton, I. 1998. Population limitation in birds. Academic Press, CA.

Oberdorfer, E. 1960. Pflanzensoziologische Studien in Chile - Ein Vergleichmit Europa. J. Cramer, Weinheim. 208 pp.

Obernuefemann, K.P., Collazo, J.A., Lyons, J.E. 2013. Local movements and wetland connectivity at a migratory stopover of Semipalmated sandpipers (*Calidris pusilla*) in the southeastern United States. Waterbirds 36(1): 63-76.

Pauchard, A., Aguayo, M., Peña, E., Urrutia, R. 2006. Multiple effects of urbanization on the biodiversity of developing countries: The case of a fast-growing metropolitan area (Concepción, Chile). Biological Conservation 127: 272-281.

Pellet, P., Cornejo, C. 2021. Las aves en la Región del Biobío (Chile): su riqueza, composición y distribución. Gayana 85(1): 55-77.

Poiani, A. 2006. Effects of floods on distribution and reproduction of aquatic birds. Advances in Ecological Research 39: 63-83.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. Version 3.4. R Foundation for Statistical Computing. Vienna, Austria.

Remsen, J.V., Jr., Areta, J.I., Bonaccorso, E., Claramunt, S., Del-Rio, G., Jaramillo, A., Lane, D.F., Robbins, M.B., Stiles, F.G., Zimmer, K.J. 2023. A classification of the bird species of South America. Version November 27, 2023. Museum of Natural Science, Louisiana State University. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm

Sebastián-González, E., Sánchez-Zapata, J.A., Botella, F. 2010. Agricultural ponds as alternative habitat for waterbirds: spatial and temporal patterns of abundance and management strategies. European Journal of Wildlife Research 56: 11-20.

Shydlovskyy, I., Kuzyo, H. 2016. Anthropogenic or ecological trap: what is causing the population decline of the Lapwing *Vanellus vanellus* in Western Ukraine? The Ring 38(1): 43-55.

Skagen, S.K., Granfors, D.A., Melcher, C.P. 2008. On determining the significance of ephemeral continental wetlands to north American migratory shorebirds. Auk 125: 20-29

Smith, L.L., Subalusky, A.L., Atkinson, C.L., Earl, J.E., Mushet, D.M., Scott, D.E., Lance, S.L., Johnson, S.A. 2019. Biological connectivity of seasonally ponded wetlands across spatial and temporal scales. Journal of the American Water Resource Association 55: 334-353.

Tavares, D.C., Guadagnin, D.L., De Moura, J.F., Siciliano, S., Merico, A. 2015. Environmental and anthropogenic factors structuring waterbird habitats of tropical coastal lagoons: implications for management. Biological Conservation 186: 12-21.

Thomson, R.F., Vukasovic, M.A., Estades, C.F. 2020. Estado de las poblaciones del Rayador (*Rynchops niger*) en Chile. Gayana 84: 144-151.

Thompson, W.L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 119: 18-25.

Uden, D.R., Allen, C.R., Bishop, A.A., Grosse, R., Jorgensen, C.F., Lagrange, T.G., Stutheit, R.G., Vrtiska, M.P. 2015. Predictions of future ephemeral springtime waterbird stopover habitat availability under global change. Ecosphere 6. https://doi.org/10.1890/ES15-00256.1

Walker, J., Rotella, J.J., Schmidt, J.H., Loesch, C.R., Reynolds, R.E., Lindberg, M.S., Ringelman, J.K., Stephens, S.E. 2013. Distribution of duck broods relative to habitat characteristics in the Prairie Pothole Region. Journal of Wildlife Management 77: 392-404.

Wantzen, K.M., Junk, W.J., Rothhaupt, K.-O., 2008. An extension of the floodpulse concept (FPC) for lakes. En: Wantzen, K.M., Rothhaupt, K.-O., Mörtl, M., Cantonati, M., Tóth, L.G., Fischer, P. (Eds) Ecological Effects of Water-Level Fluctuations in Lakes: 151-170. Springer Netherlands, Dordrecht.

Weller, M.W. 1999. Wetland birds: habitat resources and conservation implications. Cambridge University Press.

Wood, S., Wood, M.S. 2015. Package ‘mgcv’. In R Package Version 1: 729.

Żmihorski, M., Pärt, T., Gustafson, T., Berg, Å. 2016. Effects of water level and grassland management on alpha and beta diversity of birds in restored wetlands. Journal of Applied Ecology 53: 587-595.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

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