Marine Biology Research

ISSN: 1745-1000 (Print) 1745-1019 (Online) Journal homepage: http://www.tandfonline.com/loi/smar20

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To cite this article: Rafael Antunes Dias, Giovanni Nachtigall Maurício & Leandro Bugoni (2017) Birds of the Patos Lagoon Estuary and adjacent coastal waters, southern Brazil: species assemblages and conservation implications, Marine Biology Research, 13:1, 108-120, DOI: 10.1080/17451000.2016.1209525

To link to this article: http://dx.doi.org/10.1080/17451000.2016.1209525

MARINE BIOLOGY RESEARCH, 2017
VOL. 13, NO. 1, 108–120
http://dx.doi.org/10.1080/17451000.2016.1209525

ORIGINAL ARTICLE

Birds of the Patos Lagoon Estuary and adjacent coastal waters, southern Brazil: species assemblages and conservation implications

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ABSTRACT
Estuarine avifauna is usually diverse, with marked differences along the limnetic to marine gradient and strong influences from physical factors such as salinity, habitat heterogeneity and tidal regime. Here we describe the composition of the avifauna of the Patos Lagoon Estuary and adjacent marine beaches and waters, in southern Brazil, identify the main environmental factors determining variations in species richness along the limnetic-marine gradient, evaluate changes in species composition along this gradient, and discuss the role of the estuary for bird conservation. Overall, 268 bird species were detected at eight sites along the estuary. Despite similar observed richness in spring–summer (247 species) and autumn–winter (244), there was a strong seasonal influence in bird composition due to migrants. Estimated species richness at 94% coverage of sites ranged from 9 to 194.66. Species richness decreased markedly towards the lower estuary, with the single variable 'distance from the upper estuary', accounting for the most plausible model. The number of threatened species recorded per site was larger in the lower estuary due the predominance of seabirds and shorebirds on red lists. While the lower estuary holds key feeding and roosting areas for seabirds and shorebirds, the upper estuary harbours more species, mainly forest passerines and waterbirds. Our findings confirm that estuarine gradients strongly influence avian diversity and highlight the importance of estuaries for the conservation of birds, especially migratory sea and shorebirds, and resident saltmarsh-dependent species.

ARTICLE HISTORY
Received 6 January 2016
Accepted 27 May 2016
Published online 9 September 2016

RESPONSIBLE EDITOR
Franz Uiblein

KEYWORDS
Estuarine gradient; seabirds; shorebirds; waterbirds

Introduction

Estuaries are extremely productive environments, where nutrients and feeding opportunities are abundant (Day Jr et al. 2013). Estuaries are typically a mosaic of habitats such as sand and mud flats, beaches and banks, mangroves and/or saltmarshes, among others (Day Jr et al. 2013). This heterogeneity creates favourable habitats for roosting and feeding of a range of birds, especially wetland species with varied adaptations for foraging (Weller 1999; Takekawa et al. 2001). Such a scenario makes estuaries important areas for rich and abundant bird assemblages.

Estuaries are rarely the focus of avian assemblage studies, and comparisons among estuarine bird faunas are suboptimal at best. In the Seine Estuary, 250 bird species were found (Dauvin & Desroy 2005). Most species were migratory shorebirds (Charadrii), as expected for a megatidal estuary with over 11 m of variation in water level (Levoy et al. 2000). On the US Atlantic coast, a 158 ha tidal pond/salt marsh complex harboured 131 species, with higher abundance of waterfowl, gulls, shorebirds and songbirds (Reinert & Mello 1995). At another extreme, ponds previously exploited for salt production and adjacent wetlands in San Francisco Bay are home to 53 species of waterbirds from six foraging guilds (Takekawa et al. 2001). In South Africa, four intermittently open estuaries had richness values between 25 and 54 species, with a strong influence at the mouth on the abundance and the predominance of feeding guilds (Terörde & Turpie 2013). In coastal lagoons which function as intermittently open estuaries in south-eastern Brazil, water depth and vegetation, but not lagoon area, influenced avian guilds (Tavares et al. 2015).

Overall, studies have shown that very high salinities negatively affect bird richness, at least for some guilds (Halse et al. 1993; Takekawa et al. 2006; Tavares et al. 2015). The pattern of increased richness towards

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The supplementary material for this article (Tables SI–SIII) is available at http://dx.doi.org/10.1080/17451000.2016.1209525

freshwater zones was also found in the Seine Estuary for benthos, plankton and fish (Dauvin & Desroy 2005). Despite difficulties in comparing avian communities among estuaries, bird assemblages are expected to include both marine and inland elements along a marine-limnetic gradient.

The Patos Lagoon Estuary (PLE) drains a catchment area of 201,626 km^2 in the southernmost Brazilian state of Rio Grande do Sul and neighbouring Uruguay (Seeliger & Odebrecht 1997). This region is a biogeographic crossroads both on land and sea, lying on a tropical forest–temperate grassland transition and influenced by the western boundary currents of the South-western Atlantic Subtropical Convergence, the northward Malvinas/Falkland and southward Brazilian Currents (Seeliger & Odebrecht 1997). The catchment area harbours a diverse avifauna from three Zoogeographic Provinces (Stotz et al. 1996), a myriad of broadly distributed taxa (Belton 1984, 1985), and migratory birds from at least three landbird migration systems (Joseph 1997) and a series of seabird migration systems (Vooren 1997a). The PLE is considered a BirdLife International 'Important Bird Area' (Bencke et al. 2006) due to the presence of threatened species and important congregations of some shorebirds. The estuary has also been designated as a 'highly important priority area for conservation, sustainable use and benefit sharing of the Brazilian biodiversity' (MMA 2007).

The noteworthy avifauna of the PLE was observed early by sailors who named the lagoon as 'Patos' (= ducks in Portuguese), probably referring to flocks of black-necked swans *Cygnus melancoryphus* (Molina, 1782), which gather in the summer to feed on seagrass *Ruppia maritima* Linnaeus in shallow bays (Copertino & Seeliger 2010). The first mention of the avifauna of the region was made by naturalists such as von Ihering (1885, 1887, 1899, 2003), who reported the exploitation of eggs, meat and feathers of swans, spoonbills, gulls, terns and other waterbirds obtained from estuarine breeding grounds. Subsequently, museum collectors such as Emil Kaempfer secured specimens from the region, but the results were only partially published (Naumburg 1937, 1939). Up to the present time, the articles of William Belton (particularly the 1984 and 1985 contributions) on the birds of Rio Grande do Sul constitute the bulk of the knowledge on bird species composition in the estuary. Studies carried out solely in the estuary and surrounding environments began in the 1980s–1990s and focused mostly on descriptions of avifauna and the assessments of seasonal occurrence (Vooren & Chiaradia 1990; Vooren 1997a, 1997b; Dias & Maurício 1998). The twenty-first century spawned a series of contributions focusing on seasonal patterns (e.g. Bugoni & Vooren 2005; Barquete et al. 2008b), breeding biology (Gianuca et al. 2011) and trophic ecology of coastal seabirds (Bugoni & Vooren 2004; Naves & Vooren 2006; Barquete et al. 2008a; Silva-Costa & Bugoni 2013) and estuarine breeding of egrets, herons and spoonbills (Gianuca et al. 2012; Britto & Bugoni 2015; Faria et al. 2016).

A broader picture of the spatial distribution of avian assemblages in the estuary and the environmental factors affecting diversity are still lacking. In this paper, we deal with the bird fauna in the PLE and adjacent areas from a broad ecological perspective. Specifically, we aimed to answer the following questions: (1) What is the bird composition in the PLE and adjacent coastal waters? (2) To what extent do environmental factors influence avian diversity in the estuary? (3) Are there any important changes in bird species composition within the estuary? Based on such questions and patterns found in estuaries elsewhere, we hypothesize that (a) species richness will be lower in sites located in the lower portions of the estuary that are under a stronger marine influence; (b) species richness will be larger in sites that are larger, have larger habitat heterogeneity and are located in the upper portions of the estuary; and (c) sites located in the same position along the estuarine gradient will share more species.

Methods

Study area

The southern Brazilian PLE covers 971 km^2 from the Ponta da Feitoria to its mouth in the Atlantic Ocean (Asmus 1997) (Figure 1). Islands, channels and shallow bays are characteristic of the lower reaches of this permanently open estuary, which is connected to the ocean through a 20×0.5–3 km channel (Asmus 1997). Two jetties c. 3.5 km long stabilize the mouth of the estuary. Sediments are predominantly sandy in shallow areas and silty clay in the channels (Calliari 1997); the flow and level of water are primarily influenced by winds and rainfall, as the tidal amplitude at the coast is small (0.47 m, Möller et al. 2001). Narrow sandy beaches, banks, saltmarshes, and mud and sand flats occur along the margins. North and south of the mouth of PLE marine sandy beaches are bounded by coastal dunes. The climate is temperate-warm; lowest and highest mean annual temperatures range from 13 to 24°C; annual precipitation ranges from 1200 to 1500 mm and is regularly distributed throughout the year (Klein 1997). Evaporation is highest in the summer and a water deficit may occur

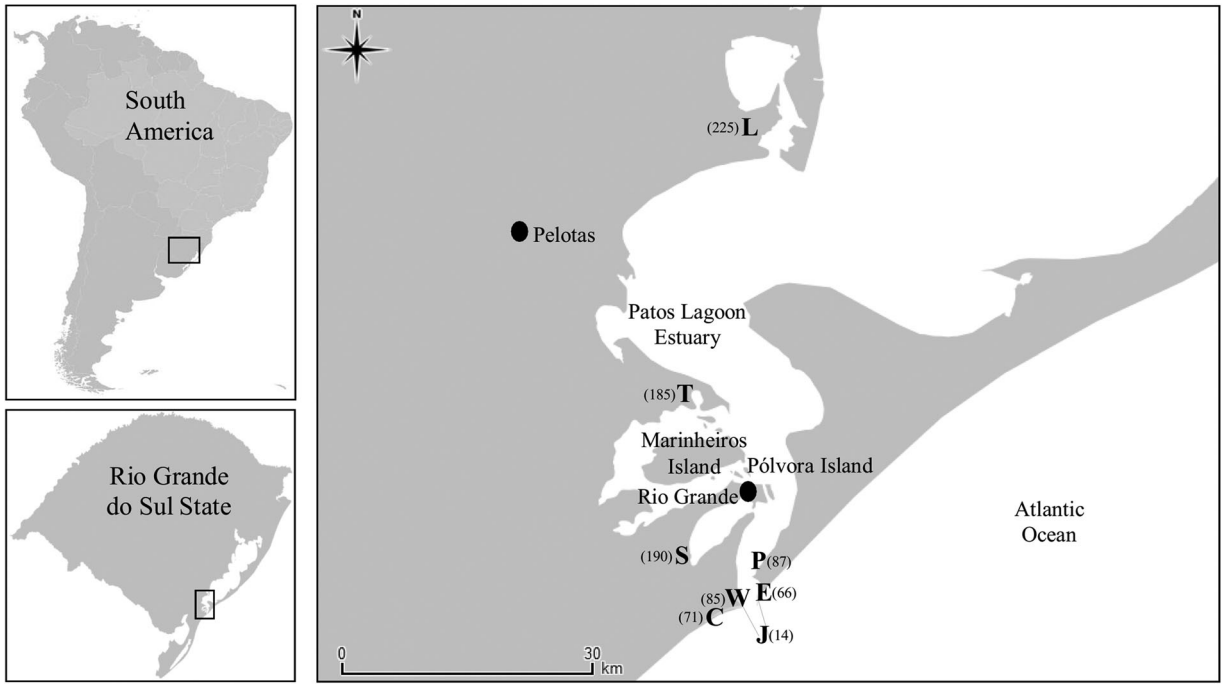

Figure 1. Map of the Lagoa dos Patos Estuary, southern Brazil, showing studied sites. L – Lagoa Pequena; T – Ilha da Torotama; S – Saco da Mangueira; P – Ponta dos Pescadores; E – base of the eastern jetty; W – base of the western jetty; J – coastal waters along the jetties; C – marine beach north of Cassino seaside resort. Values in parentheses are observed richnesses at sampled sites.

in dry summers (Klein 1997). Thus, salinity in the estuary is, in general, higher in the summer–autumn, especially when south-eastern and south-western winds prevail (Möller et al. 2001).

The estuary is situated in a matrix of grasslands, small forest patches, freshwater marshes, agriculture and urbanization. *Ruppia maritima* and floating matts of macroalgae grow in permanently flooded shallow areas (Seeliger 1997a, 1997b). Saltmarshes are covered by *Spartina* spp., *Scirpus* spp. and *Juncus* spp. (Costa 1997). Freshwater marshes are covered by tall stands of *Schoenoplectus californicus* (C. A. Mey.) Soják, *Scirpus giganteus* Kunth, *Typha* sp. and a variety of other aquatic and semiaquatic herbs in more open situations. Coastal dunes are covered mainly by *Blutaparon portulacoides* (A. St-Hil.) Mears and *Panicum racemosum* (P. Beauv.) Spreng. (Gianuca 1997). Grasslands are dominated by Poaceae, Asteraceae and Cyperaceae. Forests are 4–20 m tall and usually form long, narrow patches, with large *Ficus organensis* (Miq.) Miq. trees and *Syagrus romanzoffiana* (Cham.) Glassman palms.

Sampling procedures

We surveyed birds in eight wetland sites spanning the entire estuarine gradient, including coastal waters at the mouth of the estuary (Figure 1). These and other sites were sampled for different purposes in previous projects, so we only used data from sites with large seasonal effort and broad spatial coverage (> 17 surveys per site) in this contribution. Birds were sampled along linear transects. Transect length and number varied according to the area of the site (Table SI, supplementary material). Surveys were repeated with varying intensity among sites, but in all cases surveys covered all seasons of the year and all habitat types available at a given site (Table SI). All surveys were performed by at least one of us to minimize bias related to species identification. We listed all birds we saw or heard up to about 200 m from the central line of the transect. Individuals in flight were included only if foraging or displaying over the transect, or if moving between habitats located within the site. Species using coastal waters at the mouth of the estuary were sampled from the western jetty. Since our goal was to survey birds using open waters, we only included in the analysis species observed on the surface of the water or feeding on it in low flight, but not roosting on the jetty.

Data analyses and premises

We used coverage-based rarefaction and extrapolation (Chao & Jost 2012) to estimate and compare species richness between sites. This approach enables the

comparison of unbiased species richness of a set of communities based on samples of equal completeness measured by sample coverage (Chao & Jost 2012). Richness was extrapolated to double the smallest reference sample size. The 95% confidence intervals of the coverage-based rarefaction/extrapolation curves were constructed based on a bootstrap method with 100 replications. If the confidence intervals do not overlap for any fixed sample coverage less than or equal to the base coverage, significant differences at a level of 5% among the expected species richnesses are guaranteed (Chao & Jost 2012). We considered a list of species present on a given visit to a given site as a sampling unit. This analysis was carried out using iNEXT (Hsieh et al. 2013).

We used linear models to assess how characteristics of sites influence species richness along the estuarine gradient. Due to differences in sampling effort, we used the estimated rarefaction/prediction richness function for the lowest estimated rarefaction/prediction sample coverage function (Chao & Jost 2012) for each site as the response variable. We defined three predictor variables: the area of each site, the heterogeneity of habitats within each site, and the distance of each site to the upper limit of the estuary. Each set of analyses comprised eight distinct simple and multiple regression models (including a null model). We followed an information-theoretic approach to select models and used the second order Akaike Information Criterion (AIC_c) to measure model plausibility (Burnham & Anderson 2002). Analyses were carried out in R (R Core Team 2015), with the use of the *MuMIn* package (Bartón 2015).

The area and distances of each site to the upper limit of the estuary (i.e. Ponta da Feitoria) were measured using high-resolution satellite imagery available at Google Earth Pro (2015). Limits of the Lagoa Pequena were roughly traced according to MMA (2007) and the remaining estuarine sites according to Costa (1997). Limits of the marine beach south of the mouth of the estuary stretched 4.6 km from the base of the western jetty to the Cassino seaside resort. Limits of coastal waters at the mouth of the estuary corresponded to the area between the jetties plus a 200 m section towards the ocean. We used satellite images to delimit and measure the area of eight natural and two anthropogenic habitat types at each site: forest, grassland, freshwater marsh, saltmarsh, sand dune, sandy beach, inner water bodies (lagoons, channels), open water (200 m section of marine or estuarine waters measured from the margin of the site), agriculture and urbanization. The total area of sampled sites ranged from 0.53 to 194.46 km^2 (Table SI). Sites located in the upper reaches of the estuary were larger and had a larger cover of forest, grassland and freshwater marsh. Saltmarshes were proportionally larger at Ilha da Torotama and Saco da Mangueira, covering more than half of these sites. The area of vegetation classes declined towards the mouth of the estuary. We then built a data matrix of the total area (in km^2) of these habitat types per site and subjected it to Principal Components Analysis. We extracted the first principal component and used it as a reduced set of orthogonal explanatory variables expressing habitat heterogeneity at sites.

We used correspondence analysis (CA) to explore relationships between avifaunal composition and sites. Due to the marked influence of seasonality on the local avifauna (Belton 1984, 1985), we ran separate analyses for the spring–summer and autumn–winter periods. In the graphic output of the CAs we identified the main habitat of some groups of species in order to illustrate the influence of habitat preferences on avian composition between sampling units. The CAs were carried out on Multiv 2.63b statistical software (Pillar 2007).

Taxonomy and nomenclature follow Piacentini et al. (2015). Global, national and state of threat status follow IUCN (2015), MMA (2014) and Rio Grande do Sul (2014), respectively. Endemism follows Stotz et al. (1996). Habitat use is in accordance with Belton (1984, 1985) and BirdLife International (2015). Status of occurrence follows Belton (1984, 1985), Maurício et al. (2013) and our own unpublished data.

Results

We recorded 268 species of birds in the PLE, representing 65 avian families (Table SII). *Chroicocephalus maculipennis* (Lichtenstein, 1823) and *Nannopterum brasilianus* (Gmelin, 1789) had the highest incidence values, being recorded in 95% and 88% of all visits. In the spring–summer we detected 247 species and in the autumn–winter 244 species. Roughly 73% of the avifauna are breeding residents (Table SII). Twenty-one species are visitors that breed elsewhere in the southern hemisphere, while other 25 breed in the northern hemisphere. We recorded 17 Atlantic Forest and four Pampas endemics (Table SIII). Ten species are threatened with extinction in regional, national and global assessments (Table SIII). One to seven threatened species were recorded at sites, with larger values being recorded in the lower estuary. An additional 15 species are 'near-threatened'.

Observed species richness was highest at Lagoa Pequena, with 225 species, and lowest in coastal

Table I. Values of the estimated rarefaction/prediction sample coverage function (Chao & Jost 2012) and of the estimated rarefaction/prediction richness function for each site (with 95% bootstrap confidence lower and upper limits) for the lowest estimated rarefaction/prediction sample coverage function.

	Observed richness	Estimated richness[a]	Sample coverage estimator	Estimated richness[b]	Lower CI[b]	Upper CI[b]
Lagoa Pequena	225	237.65	1.00	194.66	189.59	199.73
Ilha da Torotama	185	190.09	0.99	146.96	144.14	149.78
Saco da Mangueira	190	185.20	0.98	149.94	142.32	151.55
Ponta dos Pescadores	87	92.72	0.99	69.29	66.18	72.41
Base of the eastern jetty	66	72.02	0.98	57.05	52.41	61.68
Base of the western jetty	85	86.71	0.97	74.26	69.45	79.07
Marine beach	71	73.60	0.94	73.60	64.18	83.02
Coastal waters	14	14.64	0.97	9.00	8.27	9.74

[a]Extrapolated to double the smallest reference sample size.
[b]At 94% coverage.

waters along the jetties, with 14 species. The estimated sample coverage ranged from 0.94 to 1.00, while estimated richness (at 94% coverage) ranged from 194.66 to 9.00. Estimated richness was larger at Lagoa Pequena and lowest in coastal waters (Table I, Figure 2). Ilha da Torotama and Saco da Mangueira displayed similar values of estimated species richness. Sites located at the mouth of the estuary also had similar values of species richness among themselves.

Of our full set of models assessing the effects of environmental descriptors upon estimated species richness, the one with distance from the upper limit of the estuary as single predictor variable was the most plausible, with an AIC_c weight of 0.64 (Table II).

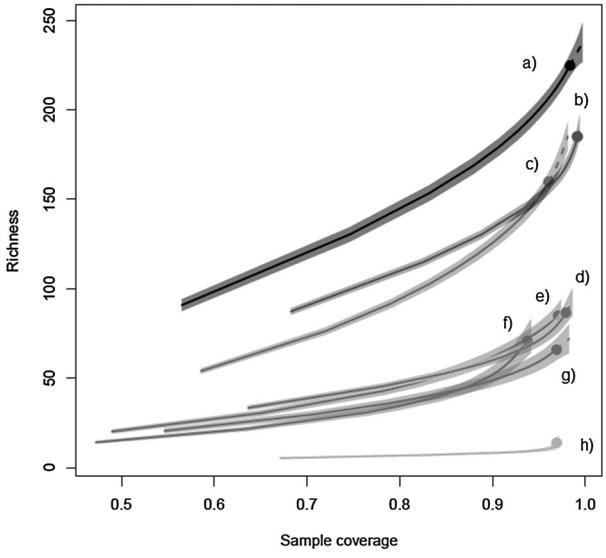

Figure 2. Coverage-based rarefaction and extrapolation sampling curves for birds at eight sites in the Patos Lagoon Estuary. Reference samples are indicated by solid dots. Curves were extrapolated to double the smallest reference sample size. Shaded areas indicate 95% confidence intervals. Sites: (a) Lagoa Pequena; (b) Saco da Mangueira; (c) Ilha da Torotama; (d) Ponta dos Pescadores; (e) base of the western jetty; (f) marine beach; (g) base of the eastern jetty; (h) coastal waters.

The first two axes of the CA ordinations explained 21.7% and 18.5% of the variation in sampling units and species composition in the spring–summer and autumn–winter, respectively (Figure 3). In both periods, sites were ordered following the estuarine gradient along the first axis, with coastal waters at one extreme and Lagoa Pequena at the other. Sites from the mouth of the estuary, including the marine beach and coastal waters, formed a distinct group in both analyses. Sampling units from Saco da Mangueira and Ilha da Torotama formed a second group near the origin of the ordination. Although a few sampling units from Lagoa Pequena grouped with the latter, most formed a distinct series in the upper right quadrant of the ordinations.

Waterbirds (Anseriformes, Ciconiiformes, Pelecaniformes and Gruiformes) were mostly related with sampling units from Ilha da Torotama, Saco da Mangueira and Lagoa Pequena (Figure 4a,b). Most of these species were associated with wetlands, both open marshes with floating and small emergent plants and dense stands of tall, emergent Cyperaceae. The few species of this group found at the mouth of the estuary were rallids such as *Pardirallus sanguinolentus* (Swainson, 1838) and *Porzana spiloptera* Durnford, 1877 that inhabit dense vegetation in saltmarshes.

Podicipediformes, Procellariiformes, Suliformes and Charadriiformes were mostly related with sites at the mouth of the estuary (Figure 4c,d). These birds were largely associated with tidal flats and lagoon margins, as well as sandy beaches along the estuarine channel and the adjacent ocean. Species that forage in the ocean and rest on the beach such as terns, gulls and skimmers were also associated with these sites. Pelagic species and open-water birds such as *Podicephorus major* (Boddaert, 1783) and *N. brasilianus* were more frequent in marine and estuarine waters at the mouth of the estuary in the autumn–winter (Figure 4d).

Arboreal and shrub-dependent passerines were largely related with sampling units from Ilha da

Table II. Models evaluating the effects of area, distance to the upper limit of the estuary, and habitat diversity upon estimated species richness of birds at eight sites in the Lagoa do Patos Estuary, southern Brazil.

Intercept	Area	Distance	Habitat	K	log(λ)	AIC_c	w_i
208.70	–	−2.70	–	3	−39.00	90.00	0.64
74.00	0.68	–	–	3	−40.00	93.00	0.13
96.80	–	–	1.50	3	−41.00	93.00	0.10
96.80	–	–	–	2	−44.00	94.00	0.08
420.30	−1.19	−6.90	–	4	−37.00	96.00	0.03
318.50	–	−5.40	−1.70	4	−38.00	97.00	0.02
8.80	2.61	–	−4.30	4	−40.00	101.00	0.00
675.90	−5.18	−9.90	7.00	5	−36.00	113.00	0.00

Models are ordered from the most (lowest AIC_c value) to the least plausible. The regression coefficients, number of parameters (K), maximized log-likelihood function (log(λ)), Akaike's Second-Order Information Criterion (AIC_c) and AIC_c weights (w_i) for each model are provided.

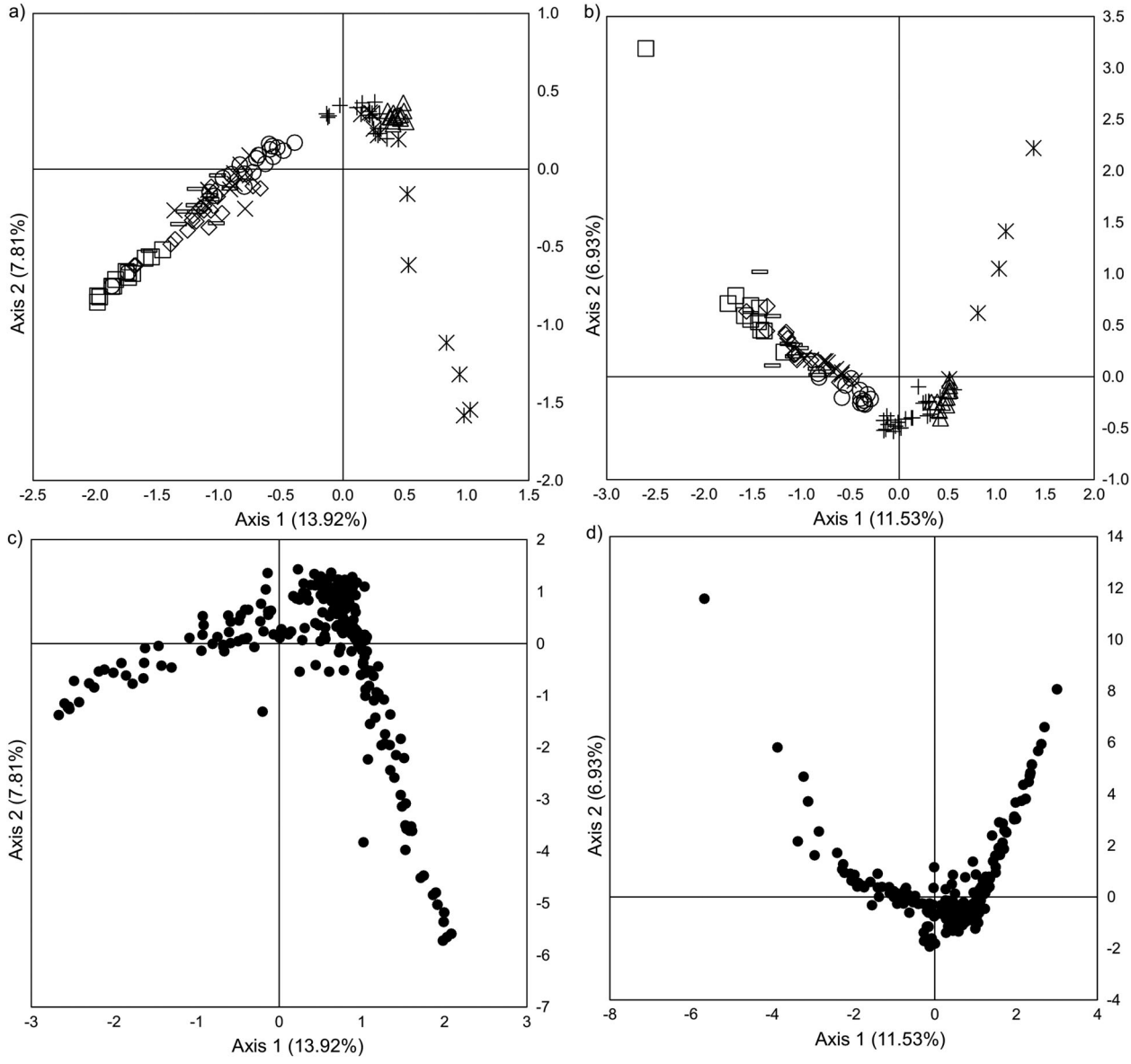

Figure 3. Correspondence analysis showing relationships between sampling units (a,b) and avifaunal composition (c,d) at eight sites in the Patos Lagoon Estuary. Separate analyses were carried out for the spring–summer (a,c) and autumn–winter (b,d). Note differences in the values of axes between panels. Lagoa Pequena – asterisk; Ilha da Torotama – triangle; Saco da Mangueira – cross; Ponta dos Pescadores – X; base of the eastern jetty – dash; base of the western jetty – circle; marine beach – diamond; coastal waters – square.

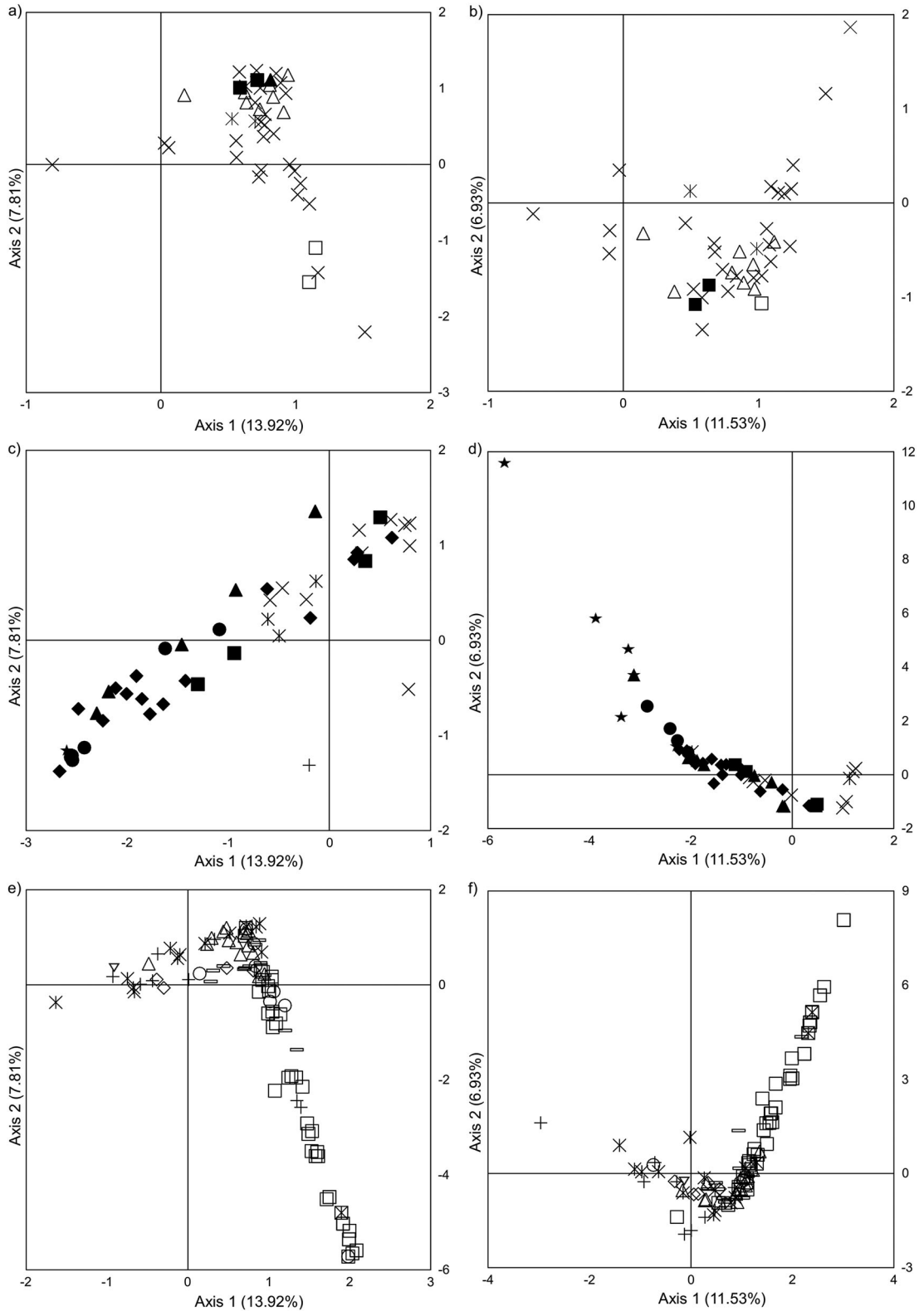

Figure 4. Selected groups of species in the correspondence analysis showing habitat-use in the Patos Lagoon Estuary. (a) Anseriformes, Ciconiiformes, Pelecaniformes and Gruiformes – spring–summer, (b) autumn–winter; (c) Podicipediformes, Procellariiformes, Suliformes and Charadriiformes – spring–summer, (d) autumn–winter; (e) Passeriformes – spring–summer, (f) autumn–winter. Note differences in the values of axes between panels. Habitat types: forest – open square; parkland and savanna – dash; shrubland and thicket – open circle; grassland – asterisk; dense wetland – open triangle; open wetland – X; open water – filled square; tidal flats and lagoon margins – filled triangle; sandy shore – filled diamond; marine littoral and beach – filled circle; pelagic – star; aerial – cross; generalist – open diamond; urban – inverted open triangle.

Torotama, Saco da Mangueira and especially Lagoa Pequena (Figure 4e,f). Forest-related Passeriformes tended to be more frequent in the spring–summer (Figure 4f). Passerines found in sites at the estuarine mouth were grassland and other open-vegetation taxa or aerial-feeding swallows.

Discussion

Avifauna of the Lagoa dos Patos Estuary

The avifauna of the estuary comprised 40.5% of the 661 species and 75.6% of the 86 bird families represented in the state of Rio Grande do Sul (Bencke et al. 2010). Although it is beyond the scope of our work to provide a thorough bird inventory for the estuary, at least 30 additional species are known for the region (Maurício & Dias 1996, 2000; Dias & Maurício 2002; Gianuca 2007; Dias et al. 2010; Gianuca et al. 2012; author's unpublished data, 2016). Thus, the total number of species in the area is over 300. Roughly 40% of bird families in the estuary are aquatic and semiaquatic. The remaining 39 bird families are essentially terrestrial, although some species of a few families (e.g. Furnariidae, Tyrannidae and Icteridae) are marsh-dwellers.

Species endemic to one of two Zoogeographic Provinces were recorded in the estuary (Stotz et al. 1996). Pampas endemics were more broadly distributed, especially because of the association of *Larus atlanticus* Olrog, 1958 and *Spartonoica maluroides* (d'Orbigny & Lafresnaye, 1837) with saltmarshes (Bencke et al. 2003). Atlantic Forest endemics, on the other hand, were recorded solely at forested sites.

Variation in species richness and composition along the estuary

Variation in estimated species richness along the estuarine gradient was related to a single predictor variable – distance from the upper limit of the estuary – suggesting that the ocean plays an overwhelming role in driving avian species richness. Sites at the mouth of the estuary are under strong marine influence, and stress from abiotic features such as salinity, wave action, tidal regimes and strong winds may limit the occurrence of terrestrial organisms such as birds. Salinity is one of the main oceanic-related drivers of diversity in estuaries, negatively affecting species richness of various organisms, including birds (Halse et al. 1993; Dauvin & Desroy 2005; Takekawa et al. 2006; Tavares et al. 2015). In our study area, salinity may indirectly affect avian diversity by limiting food items consumed by birds, as well as influencing habitat quality and availability by inhibiting plant development (Bemvenuti 1997). Salinity also affects birds directly by reducing reproductive success and physiological performance, especially in species lacking morphological, physiological and behavioural mechanisms that maintain osmoregulatory balance (Holmes & Phillips 1985; Gutiérrez 2014). In fact, nearly all aquatic birds inhabiting sites at the mouth of the estuary and adjacent to it belong to groups that display adaptations for salt excretion (Holmes & Phillips 1985; Gutiérrez 2014). These species, especially pelagic birds, rarely enter the estuary, apart from a few stray individuals occasionally found in the Patos Lagoon (Belton 1984).

Distance from the ocean may affect species richness in other ways, such as influencing the landscape of estuarine wetlands (Shriver et al. 2004). Sites near the mouth of the PLE are smaller and geologically younger than the innermost portions (Calliari 1997) and have not been fully colonized by vegetation, especially trees, which form tri-dimensional, complex habitats that harbour more niches and consequently species. The three uppermost sites in the estuary are also in contact with extensive grassland and freshwater marsh areas, with a large species-pool from where dispersing individuals may colonize estuarine margins. The presence of some typical/obligate forest bird families exclusively at Lagoa Pequena (Cracidae, Trogonidae, Conopophagidae, Dendrocolaptidae, Pipridae, Tityridae and Cotingidae) may be linked to riparian forest corridors that connect this site to the forests of Serra dos Tapes, a formerly continuous forest block that constitutes the southern limit of the Atlantic Forest (Maurício & Dias 2001).

Main breaks in species composition were found between the mouth of the estuary and the three uppermost sites, with some sampling units from Lagoa Pequena forming another distinct group. However, delimitations are not clear-cut because many species were shared between adjacent sites. The fact that sites were ordered according to their position in the estuary further highlights the importance of the estuarine gradient in driving avian diversity. Differences in habitat may explain large-scale variations in composition across sites, as demonstrated in adjacent grasslands, dunes and marine beaches (Gianuca et al. 2013). Species restricted to specific sectors of the estuary are forest passerines and freshwater marsh waterbirds characteristic of the uppermost sites, and seabirds and coastal shorebirds typical of the sandy beaches, sand and mud flats, and open waters of the estuarine mouth and adjacencies.

Bird composition in the estuary is also influenced by seasonal variations in conditions and resources. The most outstanding difference was the occurrence of pelagic seabirds in the ocean and at some sites at the mouth of the estuary during the austral autumn and winter. Pelagic seabirds nest during the austral spring and summer in southern latitudes and migrate towards our study area during the non-breeding season (Vooren 1997a). A few species of the South American Cool, Temperate Migration System (Joseph 1997) also follow this pattern, namely *Charadrius modestus* Lichtenstein, 1823, *L. atlanticus* and some Passeriformes. Another important migratory component in the estuary are passerines of the Temperate–Tropical Migration System (Joseph 1997). These species breed in southern Brazil and adjacent countries during the austral spring and summer, and migrate in autumn/winter to the tropical latitudes of South America (Belton 1985). Migratory passerines are largely associated with forests and open vegetation with trees and were typical of the three uppermost sites, especially Lagoa Pequena. Species that breed in the northern hemisphere and spend the austral spring and summer in South America (the Pan New World Migration System), such as some plovers, most scolopacids, *Sterna hirundo* Linnaeus, 1758, and some swallows (Belton 1984, 1985; Joseph 1997), were largely associated with the estuarine mouth.

Threats

Current threats to estuarine habitats include urban and industrial expansion, pollution, fires, poorly managed livestock grazing (Bencke et al. 2006; Tagliani & Asmus 2011) and recently, wind energy development. The port in Rio Grande is one of the largest in Brazil and harbours an expanding complex of industrial and naval facilities, with concomitant planned and unplanned urban development. The expansion of these agents has eliminated portions of wetlands in the lower PLE (Bencke et al. 2006), despite the existence of an environmental agenda for the sustainable use and development of the estuary (Tagliani & Asmus 2011). Increasing tourism in the estuary mouth and especially on adjacent marine beaches displaces feeding and roosting migratory birds. As demonstrated in our study, the heavily urbanized areas in the lower estuary are those holding more threatened species and requiring immediate attention in terms of conservation.

Conservation

Despite the century-old recognition of the importance of the PLE for birds (Ihering 1885, 1887, 1899, 2003), conservation-driven studies are limited. Lanctot et al. (2002) highlighted Ilha da Torotama as one of the most important staging areas in Brazil for *Calidris subruficollis* (Vieillot, 1819), while Dias et al. (2011) summarized the importance of the estuary for 22 Nearctic migrants. The recognition of the estuary as a conservation priority for birds is based on the occurrence of globally threatened and 'near-threatened' species (*L. atlanticus*, *P. spiloptera*, *S. maluroides*) and concentrations of *C. subruficollis* (Bencke et al. 2006; MMA 2007).

The increase in the number of threatened birds in the lower estuary is in line with global patterns demonstrating declines in seabird and shorebird populations (Croxall et al. 2012; BirdLife International 2015). Our data confirm that the estuary is a regular wintering area for *L. atlanticus* and *C. subruficollis*, two globally 'near-threatened' migratory birds (Lanctot et al. 2002; Bencke et al. 2006). Our results further highlight the importance of the estuary for *P. spiloptera*, which was found at half of our study sites, including Ilha da Torotama and Saco da Mangueira with extensive portions of saltmarsh habitat. On the other hand, the globally threatened *Procellaria aequinoctialis* Linnaeus, 1758 and *Xolmis dominicanus* (Vieillot, 1823) are only of marginal occurrence in the estuary. The two uppermost sites are important hunting areas for the regionally threatened *Circus cinereus* Vieillot, 1816, and sandy beaches at the mouth of the estuary and the adjacent ocean host large numbers of *Calidris canutus* (Linnaeus, 1758) and regionally threatened terns (Vooren & Chiaradia 1990; Bugoni & Vooren 2005).

Paradoxally, the only protected areas in the region, Pontal da Barra (65 ha private reserve), Lagoa Verde (510 ha municipal environmental protection area), and Molhe Leste (30 ha municipal wildlife reserve) are small, poorly implemented and of 'sustainable use' i.e. a type of reserve managed for biodiversity conservation and human sustainable activities. Full implementation of these reserves and inclusion of measures to ensure protection of threatened species in their management plans are badly needed. Establishment of protected areas in the extensive and nearly pristine saltmarshes of Lagoa Pequena and Ilha da Torotama, and increasing the area protected by the Molhe Leste and Lagoa Verde reserves to fully encompass saltmarshes, mudflats and beaches, would benefit threatened birds in the PLE.

A largely neglected aspect is the synergic importance of the PLE and other nearby areas regularly used by coastal birds. Among these is the Lagoa do Peixe National Park, a Ramsar site of international importance that comprises high-quality estuarine

habitats situated only 70 km north-east of PLE (Bencke et al. 2006). Both PLE and Lagoa do Peixe should be considered part of a larger network of sites relevant for shorebird conservation in south-eastern South America; treating each of these sites in isolation when planning broad scale development programmes is, at best, temerarious.

Apart from harbouring threatened species and large concentrations of birds, the high avian diversity in the estuary poses additional challenges and opportunities for conservation. As we have demonstrated, conservation of the regional diversity of the PLE can only be met if key sites across the entire estuarine gradient are protected, a goal that at first hand seems difficult to achieve. However, since many estuarine environments, including salt and freshwater wetlands, lagoon margins, and forests, are protected under Brazilian environmental law, simple practices such as law enforcement and environmental education campaigns could contribute to the conservation of key bird habitats without the necessity of creating a large number of protected areas. Furthermore, identifying and supporting environment-friendly activities such as birdwatching, organic farming and extensive livestock ranching in grasslands may increase income for local communities and raise awareness towards conservation.

Another important argument in promoting bird conservation in the PLE refers to the role that estuarine and marine birds have in providing key ecosystem services (Sekercioglu 2006). Studies in the PLE demonstrated that waterbirds regionally connect marine, estuarine, limnetic and even terrestrial environments by transporting energy and matter between them (Bugoni & Vooren 2004; Barquete et al. 2008a; Britto & Bugoni 2015; Faria et al. 2016). The abundance of long-distance migrants suggests that this linkage may span a substantial portion of the western hemisphere, which further highlights the importance of avian conservation in the PLE.

Conclusions

We demonstrated that the PLE holds a rich and diverse avifauna, including resident, migratory and Pampas/Atlantic Forest endemic species, some of which are threatened with extinction at multiple levels. Differences in species richness, composition and distribution of threatened species between the upper and lower estuary are largely related to the estuarine gradient and possibly with variations in habitat. We confirmed the importance of the estuary for the conservation of aquatic birds and the inefficiency of current protection measures. Adequate management and conservation of avian assemblages will only be achieved if differences in diversity within the estuary are taken into account, and if the regional and global importance of the PLE for birds is recognized.

Acknowledgements

We are grateful to many students and colleagues who took part in field sampling, particularly Rejane Both. The authors are also in debt with Suzana C. Barros and Jocarlos G. Alberton for support with the database, and Suzana P. Martins for providing the map. Vinicius A. G. Bastazini kindly helped with analytical aspects.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

LB has a fellowship from the Brazilian CNPq – Conselho Nacional de Desenvolvimento Científico e Tecnológico (PQ 310550/2015-7).

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