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Spatial and Temporal Patterns of Waterbird Assemblages in Fragmented Wetlands of Southern Brazil

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Abstract.—Understanding the composition and abundance pattern of species across sites is a central question in community ecology. However, the structure of waterbird assemblages in fragmented wetlands has been poorly documented. We carried out twelve monthly censuses to describe the composition and abundance patterns in 42 wetland fragments and two lagoons in the coastal zone of Rio Grande do Sul, South Brazil. A total of 142,000 birds from 66 species, 18 families and 18 orders were recorded. Most species were either resident (29) or partial migrants (19). All migrant species (8 nearctic, 4 austral and 5 summer breeders) were recorded in small numbers and most of them were restricted to lagoons. The lagoons had more species (60) than the wetland fragments (55), even though the total fragment area (1,426 ha) was about twice the censused area in the lagoons (743 ha). Principal Coordinate Analysis revealed strong temporal and spatial gradients of abundance and composition that were similar in fragments and lagoons. The number of species varied among sites and showed no seasonal pattern. Abundances were higher in the wintering period (min. of 2,500 birds in March and max. of 23,000 in July) due to the increased abundance of Gruiformes and Anseriformes. The White-faced Whistling-duck (*Dendrocygna viduata*) and the Common Moorhen (*Gallinula chloropus*) were the most abundant and frequent species over the year, comprising together 69% of the total. The census captured 76% and 60% of the waterbird species listed for the region and the Rio Grande do Sul State, respectively. The study area shared more than 90% of the species with the nearby States and 76% with the Pantanal region. The beta-diversity among sites was 94% when only fragments are considered, and 38% when the lagoons are included in the calculation, showing that a great proportion of the waterbird richness at the landscape scale is accommodated as a beta component. The local abundance and composition of waterbird assemblages seemed to be affected by the interplay of several factors, including the rich regional pool of species, their wide range, the fragment area, the surrounding matrix and the presence of core refuges. A landscape perspective is essential on building sound conservation programs for waterbird assemblages. Received 16 October 2004, accepted 28 March 2005.

Key words.—Wildfowl, water birds, wetlands, fragmentation, richness, diversity, composition, abundance, beta diversity, turnover, seasonal pattern, temporal pattern, spatial pattern, ordination, principal coordinate analysis.

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Wetlands are important conservation sites due to the extensive food chain and rich biodiversity they support (Getzner 2002). However, the fast degradation of these ecosystems produces an urgent need for ecological studies to develop conservation programs. Almost half of the world's wetlands have disappeared in the last century due to agricultural and urban development (Shine and Klemm 1999). One of the main hydrological characteristics of South America is the existence of large wetlands (Neiff

2001). Approximately 95% of the inventoried wetlands in South America are in six countries, and Brazil has half of the total wetland area (Naranjo 1995). However, the Brazilian wetland inventory is not updated and it is restricted to only three scientific surveys (Maltchik 2003). South Brazil has approximately 3,441 wetlands and approximately 72% of them are smaller than 1 km² (Maltchik *et al.* 2003). This pattern is a consequence of strong habitat fragmentation due to agricultural expansion, especially rice

plantations (Gomes and Magalhães Júnior 2004). Conservative data indicate that approximately 90% of the wetlands in south Brazil have disappeared in the last century. Understanding the structure of aquatic communities in fragments and natural wetlands is a priority for biodiversity conservation strategies in south Brazil.

The State of Rio Grande do Sul and the Pantanal Region contain most of Brazil's wetland systems and waterbird diversity (Scott and Carbonell 1986). The Rio Grande do Sul State has 123 species in 20 families (Vélez 1997), corresponding to 14.8% of the world aquatic bird species (Rose and Scott 1994). Part of this diversity is explained by the fact that the State is part of important migratory route, including northern and southern migrants (Antas 1994; Belton 1994; Sick 1983). Nevertheless, the effects of wetland loss and fragmentation on the waterbird assemblages in south Brazil are unknown.

The process of habitat loss and fragmentation is a major cause of loss of species and changes in community structure (Diamond 1976). As the fragmentation proceeds, the remnants tend to become smaller and, at the same time, more isolated (Farina 1998; Sharpe *et al.* 1981; Wiens 1995). This process affects the movement of individuals through the landscape, and appears to select the species better adapted to the small, isolated wetlands (Brown and Dinsmore 1986; Fahrig and Merriam 1994; Fairbairn and Dinsmore 2001; Whited *et al.* 2000), thus reducing the local richness of species (alpha-diversity). On the other hand, the turnover of species among sites (beta-diversity) is expected to increase in fragmented landscapes due to isolation effects (Harrison 1997; Kneitel and Chase 2004; Moreno and Halffter 2001). The regional pool of species (gamma-diversity) is determined by alpha and beta components (Cody 1993) affected by habitat loss and fragmentation. Conversely, the regional species pool is also likely to be an important determinant of species richness in fragments (Caley and Schluter 1997).

The understanding of species composition and abundance patterns among sites is a central question in community ecology, but

is poorly documented for waterbirds in fragmented wetlands (Cox *et al.* 2000). This is particularly challenging because wetlands tend naturally to occur as disjoint patches of different sizes scattered in a matrix of upland habitats (Whited *et al.* 2000) and many wetland species need to use multiple sites to fulfill their need for resources (Boettcher *et al.* 1995; Gibbs 2000; Haig *et al.* 1998). Studies are particularly scarce on waterbirds and South American wetlands, where fragmentation is paramount (Caziani *et al.* 2001).

The aims of this paper are (1) to describe and compare the spatial and temporal patterns of richness, abundance and composition of waterbirds in a set of wetland fragments and natural lagoons and (2) to compare the species richness and assemblage composition with regional pools of species at landscape and regional scales. Our approach is an exploratory analysis to infer the underlying agents of pattern formation in a real landscape.

METHODS

Study Area and Design

The study area comprised a land section of 71,300 ha in the central portion of the coastal zone of Rio Grande do Sul (30°56'-30°22'S, 50°58'-50°22'W; Fig. 1), one of the regions with the highest concentration of wetlands in the state (Maltchik *et al.* 2003). The climate is subtropical, with mean annual temperature of 19°C and total annual rainfall of about 1,200 mm, evenly-distributed over the year. Rice plantations play a central role in regional economy (Gomes and Magalhães Júnior 2004). One main land use pattern dominates: a matrix of irrigated rice-fields and drained meadows in a roughly four-year rotation. Scattered in the landscape are remnants of wetlands and native forests, natural lagoons, man-made ponds and exotic *Eucalyptus* and pine plantations.

A complete low aerial photograph inventory (2000 m.a.s.l.) of the study area was made, obtaining about 250 oblique photographs at a 1:25,000 scale. A total of 212 wetland fragments were recognized and 50 were randomly selected for the study. The largest fragment and the two largest lagoons in the study area were added to the sample, making 53 sampling sites. Nine fragments were excluded either because they were drained or dry during the field sampling or because the poor quality of the aerial photographs. The final set comprised 44 sites. The Lagoa dos Gateados (2,000 ha) and the Lagoa da Reserva (1,500 ha) (Fig. 1) are large natural lagoons with extensive marginal wetlands representing the best available examples of non-fragmented wetlands and communities, used as reference sites. The lagoons and larger fragments are intensively used as water reservoirs for rice plantations and as sites for recreational or illegal fishing and hunting. Both large and small fragments are used as cattle's drinking sites.

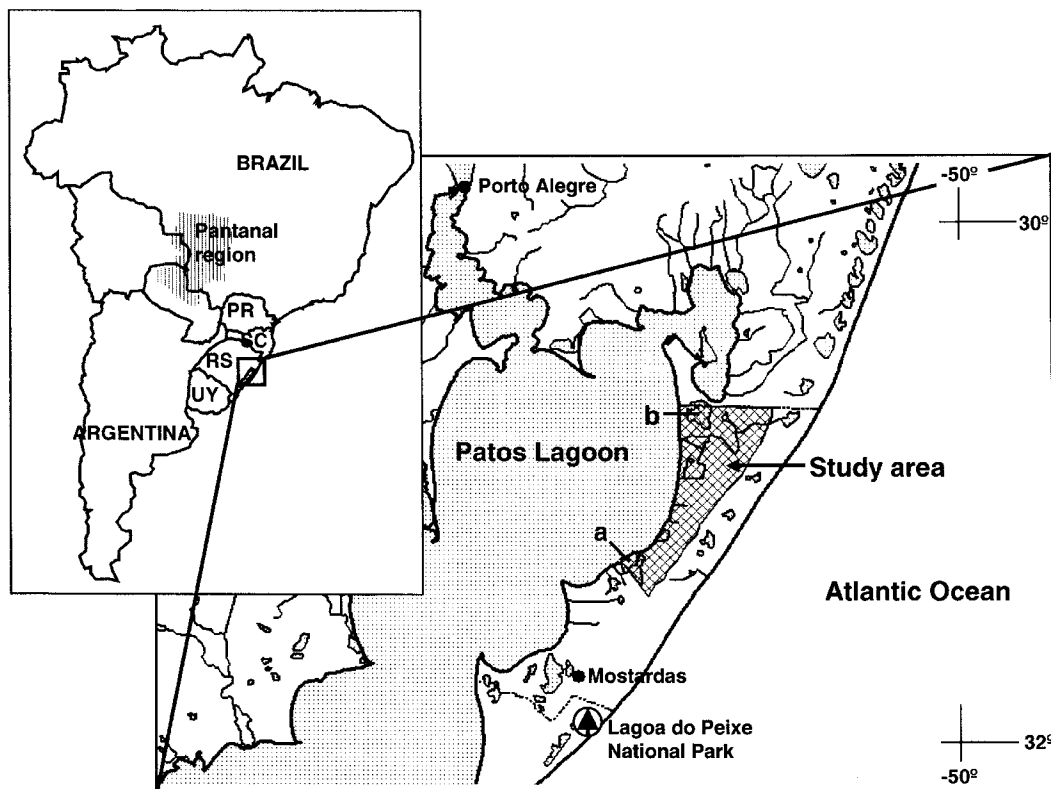


Figure 1. Study area (dashed) in the coastal zone of Rio Grande do Sul, South Brazil. Two natural lagoons—(a) Lagoa da Reserva and (b) Lagoa dos Gateados—and 42 wetland fragments were censused monthly over one year. RS—Rio Grande do Sul; SC—Santa Catarina; PR—Paraná; UY—Uruguay.

The area of the fragments was measured from aerial vertical photographs. The photographs were scanned with a resolution of 500 dpi, converted to RGB in the software Corel Draw 8® and exported to the SIG IDRISI 3.2.

Bird Census

Twelve monthly censuses were carried during 2003, each time changing the order of the site visits. The counts extended over the daylight period. We counted the whole area of the fragments and a section of the lagoons—395 ha of the Lagoa da Reserva and 345 ha of the Lagoa dos Gateados. At each site all birds were counted, so that the time effort was proportional to the size of the wetland. Large flocks were estimated in 10× or 100×, flushing the birds with rockets if necessary to count them in the air. Passerines and some secretive Rallidae were not considered because the counting method was not suitable.

The occurrence status of the species in Rio Grande do Sul was determined according to Bencke (2001) and Stotz *et al.* (1996) (see Appendix I). All species found were listed for inland freshwater wetlands in the coastal region of Rio Grande do Sul by Belton (1994).

Data Analysis

Species accumulation curves were built to assess if the 12-month sampling was sufficient to capture the true

number of species of the set of fragments and lagoons. For each site the Chao 1 index was employed to estimate the expected species richness. The Chao 1 is considered a robust procedure for richness estimation (Colwell and Coddington 1995; Walther and Martin 2001). The observed and estimated species richness for each site was obtained pooling the data of the twelve counts. The parameters and their standard deviations were calculated in the software ESTIMATES 5.0 (Colwell 1997).

Three Principal Coordinate Analyses—PCoA (Legendre and Legendre 1998) were carried out to describe spatial and temporal gradients of composition and abundance. Euclidian distances were computed between sampling sites, pooling the data of the twelve censuses on each fragment (spatial gradient in the fragments) and of the 42 fragments and the two lagoons in each census (temporal gradient in the fragments and in the lagoons). The counts were log-transformed. The PCoA generates an ordination based on a matrix of similarities between sampling sites, and includes an implicit transformation by centralization (Legendre and Legendre 1998). Only bird species appearing in at least three sample units were included in each analysis. The first axis of the spatial ordination was regressed against the area of the fragments. Ordinations were carried out in the software MULTIV 2.0 (Pillar 2000) and regressions in SPSS 12 (SPSS, Inc. 2003).

The species list for the studied area was compared with lists for the central coastal zone of Rio Grande do

Sul (the potential pool for the area), the nearby states in Brazil (Bencke 2001; Rosário 1996; Scherer-Neto 1980; Scherer-Neto and Straube 2001), the country (Comitê Brasileiro de Registros Ornitológicos 2004), the nearby countries (Azpiroz 2001; Narosky and Yzurieta 1989), the Brazilian Pantanal Region (Tubelis and Tomas 1999), Central Brazil and the Taim Ecological Station (Mähler *et al.* 1996) in the southern coastal zone of Rio Grande do Sul (the largest protected freshwater wetlands area in the region—32,000 ha). Marine species and secretive rallids were not considered in these analyses. The species richness was partitioned in the three components: alpha-diversity (local species richness), beta-diversity (the turnover of species) and gamma-diversity (regional pool of species). The partitioning was calculated as $\gamma = \alpha + \beta$ where α is the pooled number species of all sites (the landscape scale) or regions and β is the difference $\alpha = \gamma - \beta$. The parameter was calculated as $\beta = \sum_j (S_j - S_i)$ where q_j is the proportional area of the site j ; S_j is equal to γ ; and S_i is the number of species of the site i (Crist *et al.* 2003; Lande 1996). Therefore, three scales were considered: local scale (sites), landscape scale (study area), and regional scale (regions). The Lande's index weights the relative importance of each local assemblage on the regional assemblage, in our case the effect of the area of each fragment, lagoon or region.

RESULTS

The fragments differed in area by several orders of magnitude (Table 1) and most of them were small—50% were less than 10 ha, 90% smaller than 30 ha and only one was over 100 ha.

We recorded 142,000 birds belonging to 66 species, 18 families and 8 orders (Table 1). A total of 59% of the birds were found in the fragments. The families with the highest number of species and individuals were Ardeidae (9 spp.; 2,940 ind.), Anatidae (15 spp.; 73,000 ind.), Rallidae (8 spp.; 42,500 ind.) and Scolopacidae (7 spp.; 256 ind.) (Appendix I). There were eight nearctic and

four austral species, all in low numbers and seven were found only in the lagoons. Seven species were recorded for the first time in the peninsula region: Least Grebe (*Tachybaptus dominicus*), Rufescent Tiger Heron (*Tigrisoma lineatum*), Comb Duck (*Sarkidiornis melanotos*), Lake Duck (*Oxyura vittata*), Masked Duck (*Nomonyx dominicus*), Giant Wood-Rail (*Aramides ypecaha*) and the Purple Gallinule (*Porphyrula martinica*). The Lake Duck is considered a austral winter migrant in Rio Grande do Sul (Belton 1994; Bencke 2001), but the only record of the species was made in summer (December).

The White-faced Whistling-duck (*Dendrocygna viduata*) and the Common Moorhen (*Gallinula chloropus*) were the most abundant and frequent species all over the year, both in lagoons and fragments, corresponding together for 69% of the birds observed. Other frequent and abundant species were the White-faced Ibis (*Plegadis chihi*), Wattled Jacana (*Jacana jacana*), Brazilian Teal (*Amazonetta brasiliensis*), Great Egret (*Ardea alba*), Southern Screamer (*Chauna torquata*) and Whispering Ibis (*Phimosus infuscatus*). Several species showed a pattern of high abundance but low frequency of occurrence (White-winged Coot—*Fulica leucoptera*, Fulvous Whistling Duck—*Dendrocygna bicolor*, Rosy-billed Pochard—*Netta peposaca*, Masked Duck, Greater Yellowlegs—*Tringa melanoleuca*, Brown-hooded Gull—*Larus maculipennis* and Wood Stork—*Mycteria americana*). Few species tended to be widespread but not abundant, such as the Cocoi Heron (*Ardea cocoi*), Snowy Egret (*Egretta thula*), Limpkin (*Aramus guaranauna*), Maguari Stork (*Ciconia*

Table 1. Summary of the spatial and temporal patterns of species richness and abundance of waterbirds in 42 wetland fragments and two lagoons in the coastal zone of Rio Grande do Sul, Brazil.

	Total	Min	Max	Median	Mean	Chao 1
Area of fragments	1,426.0	0.1	145.2	8.8	16.3	
Area counted in the lagoons	743.0	348.0	395.0			
Richness in the fragments	55.0	3.0	40.0	16.5	18.6	55.1 ± 0.4
Richness in the lagoons	60.0	51.0	56.0	53.5	53.5	68.0 ± 11.7
Total richness for the year	66.0	34.0	49.0	39.5	40.2	66.7 ± 1.3
Abundance in the fragments	84,286.0	15.0	19,322.0	428.0	2,006.0	
Abundance in the lagoons	57,669.0	10,311.0	47,358.0			
Total abundance during the year	141,955.0	77.0	47,415.0	513.0		

maguari), South American Snipe (*Gallinago paraguaiiae*), Snail Kite (*Rostrhamus sociabilis*) and Long-winged Harrier (*Circus buffoni*).

Eleven species were found only in the lagoons and six only in the fragments, all with low abundance and frequency (Appendix I). Fourteen species were found only in lagoons or fragments greater than 300ha: the Least Grebe, Anhinga (*Anhinga anhinga*), Pinnated Bittern (*Botaurus pinnatus*), Rufescent Tiger Heron, Kelp Gull (*Larus dominicanus*), Masked Duck, Black-headed Duck (*Heteronetta atricapilla*), Coscoroba Swan (*Coscoroba coscoroba*), Black-necked Swan (*Cygnus melanocoryphus*), Black Skimmer (*Rhynchops niger*), Baird's Sandpiper (*Calidris bairdii*), Black-bellied Plover (*Pluvialis squatarola*), Solitary Sandpiper (*Tringa solitaria*) and the Ringed Kingfisher (*Chloroceryle amazona*).

The observed and estimated richness of the Chao1 index were about the same for the fragments and for the total census, but the estimated richness was higher than the observed richness for the lagoons (Table 1). More species were registered in the lagoons (60) than in the 42 fragments (55), even though the total area of the fragments was about twice the area of the lagoons studied. At each lagoon approximately the same number of species was found (56 in the Lagoa da Reserva and 51 in the Lagoa dos Gateados).

The number of species observed in the twelve censuses tended to reach an asymptote, suggesting that the effort employed was enough to record the true number of species in the study area (Fig. 2). The majority of species was recorded in the first census—64% in the fragments and 55% in the lagoons. The accumulation of species stabilized slower in the lagoons than in the fragments.

Ordinations of the twelve censuses carried out separately for lagoons and fragments showed a similar pattern of abundance and composition through the year (Fig. 4). The first and the second axes explained respectively 46% and 15% of the variance in the fragments and 45% and 14.9% in the lagoons. Abundances were higher in the wintering period due to the increased abundance of Gruiformes and Anseriformes. The concentration of wintering waterfowls

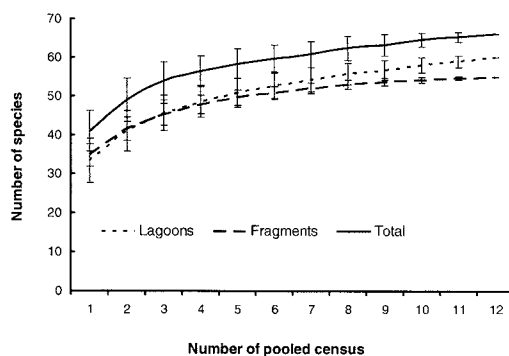


Figure 2. Smoothed species accumulation curves of waterbird assemblages of 42 wetland fragments and two lagoons in the coastal zone of Rio Grande do Sul, Brazil. Vertical bars show the standard deviation. Sample units are 12 monthly censuses.

was more pronounced in the fragments, but that of Galliformes was greater in the lagoons, particularly in the Lagoa da Reserva. The first axis separated summer and winter counts, while the second axis separated spring and autumn counts. The abundance of many species increased in winter (Neotropic Cormorant (*Phalacrocorax brasilianus*), Brazilian Teal, Common Moorhen, White-winged Coot, Coscoroba Swan, South American Snipe, Brown-hooded Gull, Silver Teal (*Anas versicolor*), the Pied-billed Grebe (*Podilymbus podiceps*), Rosy-billed Pochard, Spot-flanked Gallinule (*Gallinula melanops*) and White-tufted Grebe (*Rollandia rolland*), some were commoner in summer (Snowy Egret, Wood Stork, Collared Plover (*Charadrius collaris*), Striated Heron (*Butorides striatus*) and the Black Skimmer), several species were commoner in spring (Roseate Spoonbill (*Platalea ajaja*), Southern Screamer, Blackish Rail (*Pardirallus nigricans*), Rufescent Tiger Heron, Greater Yellowlegs, Pectoral Sandpiper (*Calidris melanotos*), Black-bellied Plover (*Pluvialis squatarola*), and two species were more common in autumn (Plumbeous Rail, *Pardirallus sanguinolentus* and Kelp Gull).

There was a strong gradient of abundance and composition across the sites, with all species associated with a single subset of large, species rich lagoons and fragments. The first two axis of the ordination of the 44 wetlands explained cumulatively 72% of the variation between sites. The lagoons were clearly sepa-

rated from the fragments (Fig. 3). When only the fragments were ordered (graph not shown), the first and second axis explained respectively 56% and 8% of the variation. In both cases, most of the species correlated with the first axis, all of them negatively. The species with low correlations ($r < 0.30$) were the uncommon ones, such as the Blackish Rail, Ringed Kingfisher and Little Blue Heron (*Egretta caerulea*). Thirty out of 50 species showed correlations greater than 0.70. The first axis was negatively related to the fragment areas ($R^2 = 0.46$; $F_{1,42} = 33.6$; $P < 0.001$).

The species richness at the landscape scale was high when compared to regional pools (Table 2). The census captured respectively 76% and 60% of the species listed for the central coastal zone and for the State of the Rio Grande do Sul. The study area also shares more than 90% of the species with the nearby States and 76% with the Pantanal region. The beta-diversity among sites was 94% (52 species) when only fragments are considered, and 38% (25 species) when the lagoons are included in the calculation. The regional beta-diversity was 38% (66 species).

DISCUSSION

The study was carried out in a single annual cycle, what could raise questions about the generality of the patterns found. The patterns are strong and consistent with other studies in Rio Grande do Sul, which also did not find a seasonal richness pattern (Accordi 2003; Vélez 1997). Moreover, the observed richness

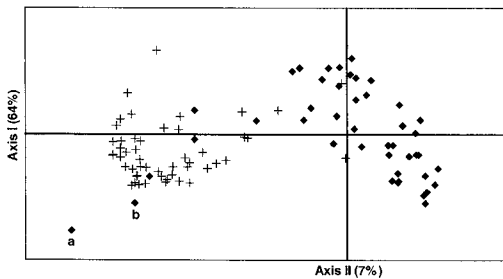


Figure 3. Ordination of 44 wetlands (diamonds) in the coastal zone of Rio Grande do Sul, South Brazil. Variables are the composition and abundance (log-transformed) of 43 waterbird species (crosses). a: Lagoa dos Gateados; b: Lagoa Reserva.

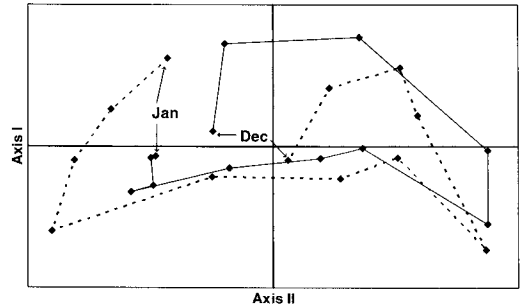


Figure 4. Ordination of 12 monthly censuses (diamonds) of waterbirds in 42 wetland fragments (continuous line) and two lagoons (dashed line) in the coastal zone of Rio Grande do Sul, Brazil. Variables are the composition and abundance (log-transformed) of 45 and 42 species, respectively. The arrows indicate the months along seasonal cycle.

is above the 80% threshold for comparative analyses (Colwell and Coddington 1995).

We found that large natural lagoons and sets of fragments have waterbird assemblages with similar seasonal patterns of species composition and abundance. The seasonal pattern corroborates the expected fluctuations due to movement and migration. The turnover between winter and summer migrants results in small seasonal variations in the number of species. Huge wintering aggregations are commonplace in waterbird communities in temperate regions (Kershaw and Cranswick 2003; Leopold 1949; Robertson and Cooke 1999). March, the month with the lowest abundance, was also the peak of the rice harvest in the region, suggesting a possible shift of habitat related to food availability. Several studies have shown that waterbirds occupy rice fields in a predictable pattern, related to the rice lifecycle (Colwell and Taft 2000; Czech and Parsons 2002; Day and Colwell 1998; Erwin 2002).

Our data showed that none of the waterbird species favored the small, isolated wetlands, as found in forest and grassland studies (Bellamy *et al.* 1996; Harrison 1997; Tscharrntke *et al.* 2002). In our study, all species correlated negatively with the first axis of the ordination, indicating that all respond to the fragmentation gradient in the same way. In small forest fragments, the edge effects favor some species, which is not the case in wetlands (Milsom *et al.* 2000; Pasitschniak-Arts

Table 2. Number of waterbird species in 44 wetlands in the Coastal Plain of Rio Grande do Sul and nearby regions.^{1,2}

Region	Land area ³ (km ²)	Richness ⁴	No. shared species ⁵
Study area	1.4	66	—
Taim Biological Station	3.2	77	58
RS—Peninsula	4,676.6	87	66
Rio Grande do Sul	281,749.0	111	66
Santa Catarina	95,346.0	100	61
Paraná	199,315.0	116	66
Pantanal	138,183.0	81	50
Brazil	8,547,403.0	142	66
Argentina	2,780,400.0	157	65
Uruguay	406,752.0	104	63

¹Marine species and secretive rallids were excluded from comparisons.

²See Methods for the list of references used.

³In the case of the study area, the land area is the total mapped satellite window. The sampling in the set of 44 wetlands, totaling 1,426 ha, is considered representative for the whole land area according to the accumulation of species.

⁴Total number of species. Equivalent to gamma or regional diversity in all cases except for the Taim Biological Station.

⁵Number of species shared with the study area.

et al. 1998). Area has been shown to be an important factor related to the gradient of species composition and abundance, as found in several other waterbird studies (Brown and Dinsmore 1986; Celada and Bogliani 1993; Paracuellos and Telleria 2004; Riffell *et al.* 2001). Several factors other than area have been associated with the abundance and richness of waterbirds, such as physicochemical conditions, food resources, vegetation cover and interspersions, and habitat and landscape configuration (Amezaga *et al.* 2002; Caziani *et al.* 2001; Elmberg *et al.* 1994; Fairbairn and Dinsmore 2001; Stickney *et al.* 2002). All these factors are probably implicated in the gradient found and deserve further attention.

The set of fragments had a waterbird assemblage similar to that found in the natural lagoons, but lacking a small number of uncommon species. The species absent in the fragments are either large-bodied (as the Anatidae), migratory (as the Charadriiformes) or naturally rare over their whole range (as the Ardeidae, Rallidae and the genus *Oxyura*) (Blake 1977). These traits have been associated with vulnerability to extinction (Bennett and Owens 1997). The small, isolated fragments may not provide adequate habitat for those species. However, it is possible that the absence of those uncommon species is simply a random placement effect (Coleman *et al.* 1982; Connor and McCoy 1979).

The study supports the idea that the richness and composition of waterbird species were strongly affected by fragmentation at the local (fragment) scale, but not at the landscape scale (the whole study area), where a greater portion of the species diversity is accommodated as a beta component. Partitioning the diversity in alpha and beta components demonstrated that a greater proportion of waterbird richness is unique to each site than found in studies with plants and insects (Crist *et al.* 2003; Gering *et al.* 2003; Summerville *et al.* 2003). The turnover of species was high (94%) among the fragments, but considerably lower when the lagoons were included in the analysis (38%). At the landscape scale, the species pool was still rich when compared to nearby regions or long-run inventories (Belton 1994). These findings suggest that the lagoons may be acting as core-areas (Hanski 1982) for the waterbirds, which use the fragments to complement or supplement their need for resources (Taylor *et al.* 1993). The rich regional pool of species could also be important in maintaining the landscape richness, through large scale movements across regions that share most of the species. Even though the importance of beta-diversity studies in regional conservation planning (Crist *et al.* 2003; Lande 1996; Veech *et al.* 2002), there are no empirical studies on the way regional

richness affects the number of species retained by fragments (Telleria *et al.* 2003).

The richness, abundance and composition of waterbird assemblages in fragmented landscapes seem to be affected by the interplay of several factors, including the regional pool of species (Gering *et al.* 2003; Telleria *et al.* 2003), their particular abundance and range patterns (Murray *et al.* 1999), the site and landscape structures, specially the area (Brown and Dinsmore 1986; Fairbairn and Dinsmore 2001), the presence of core refuges (Guillemain *et al.* 2002), and the influence of the surrounding matrix (Czech and Parsons 2002). Therefore, we suggest that a landscape perspective is essential for building sound conservation programs for waterbird assemblages (Caziani *et al.* 2001; Cox *et al.* 2000; Erwin 2002; Noss 1996).

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LITERATURE CITED

- Accordi, I. A. 2003. Estrutura espacial e sazonal da avifauna e considerações sobre a conservação de aves aquáticas em uma área úmida no Rio Grande do Sul, Brasil. Dissertation (Master in Ecology), Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.
- Amezaga, J. M., L. Santamaria and A. J. Green. 2002. Biotic wetland connectivity—supporting a new approach for wetland policy. *Acta Oecologica-International Journal of Ecology* 23: 213-222.
- Antas, P. T. Z. 1994. Migration and other movements among the lower Paraná river valley wetlands, Argentina, and the south Brazil/Pantanal wetlands. *Bird Conservation International* 4: 181-190.
- Azpiroz, A. B. 2001. Aves del Uruguay. Lista e introducción a su biología y conservación. Gupeca, Montevideo.
- Bellamy, P. E., S. A. Hinsley and I. Newton. 1996. Factors influencing bird species numbers in small woods in south-east England. *Journal of Applied Ecology* 33: 249-262.
- Belton, W. 1994. Aves do Rio Grande do Sul: Distribuição e Biologia. UNISINOS, São Leopoldo.
- Bencke, G. A. 2001. Lista de Referência das Aves do Rio Grande do Sul. Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre.
- Bennett, P. M. and I. P. F. Owens. 1997. Variation in extinction risk among birds: Chance or evolutionary predisposition? *Proceedings of the Royal Society of London Series B-Biological Sciences* 264: 401-408.
- Blake, J. G. 1977. *Manual of neotropical birds*. Univ. Chicago Press, Chicago.
- Boettcher, R., S. M. Haig and W. C. Bridges. 1995. Habitat-Related Factors Affecting the Distribution of Nonbreeding American Avocets in Coastal South-Carolina. *Condor* 97: 68-81.
- Brown, M. and J. J. Dinsmore. 1986. Implications of Marsh Size and Isolation for Marsh Bird Management. *Journal of Wildlife Management* 50: 392-397.
- Caley, M. J. and D. Schluter. 1997. The relationship between local and regional diversity. *Ecology* 78: 70-80.
- Caziani, S. M., E. J. Derlindati, A. Talamo, A. L. Sureda, C. E. Trucco and G. Nicolossi. 2001. Waterbird richness in Altiplano wetlands of northwestern Argentina. *Waterbirds* 24: 103-117.
- Celada, C. and G. Bogliani. 1993. Breeding Bird Communities in Fragmented Wetlands. *Bollettino di Zoologia* 60: 73-80.
- Cody, M. L. 1993. Bird diversity components within and between habitats in Australia. Pages 147-158 in *Species diversity in ecological communities: storical and geographical perspectives*. R. E. Ricklefs and D. Schluter (Eds.). University of Chicago Press, Chicago and London.
- Coleman, B. D., M. A. Mares, M. R. Willig and Y. H. Hsieh. 1982. Randomness, Area, and Species Richness. *Ecology* 63: 1121-1133.
- Colwell, M. A. and O. W. Taft. 2000. Waterbird communities in managed wetlands of varying water depth. *Waterbirds* 23: 45-55.
- Colwell, R. K. 1997. EstimateS 5: Statistical Estimation of Species Richness and Shared Species from Samples. Version 5.0.1. Department of Ecology and Evolutionary Biology, University of Connecticut.
- Colwell, R. K. and J. A. Coddington. 1995. Estimating terrestrial biodiversity through extrapolation. Pages 101-118 in *Biodiversity: Measurement and estimation*. D. L. Hawksworth (Eds.). Chapman & Hall, London.
- Comitê Brasileiro de Registros Ornitológicos. 2004. Listas de aves do Brasil. Available at <http://luzifgueiredo.sites.uol.com.br/cbro/listabr.htm>.
- Connor, E. F. and E. D. McCoy. 1979. Statistics and Biology of the Species-Area Relationship. *American Naturalist* 113: 791-833.
- Cox, R. R., D. H. Johnson, M. A. Johnson, R. E. Kirby, J. W. Nelson and R. E. Reynolds. 2000. Waterfowl research priorities in the northern Great Plains. *Wildlife Society Bulletin* 28: 558-564.
- Crist, T. O., J. A. Veech, J. C. Gering and K. S. Summer-ville. 2003. Partitioning species diversity across landscapes and regions: A hierarchical analysis of alpha, beta, and gamma diversity. *American Naturalist* 162: 734-743.
- Czech, H. A. and K. C. Parsons. 2002. Agricultural wetlands and waterbirds: A review. *Waterbirds* 25: 56-65.
- Day, J. H. and M. A. Colwell. 1998. Waterbird communities in rice fields subjected to different post-harvest treatments. *Colonial Waterbirds* 21: 185-197.
- Diamond, J. M. 1976. Island Biogeography and Conservation—Strategy and Limitations. *Science* 193: 1027-1029.
- Elmberg, J., P. Nummi, H. Poysa and K. Sjöberg. 1994. Relationships Between Species Number, Lake Size and Resource Diversity in Assemblages of Breeding Waterfowl. *Journal of Biogeography* 21: 75-84.

- Erwin, R. M. 2002. Integrated management of waterbirds: Beyond the conventional. *Waterbirds* 25: 5-12.
- Fahrig, L. and G. Merriam. 1994. Conservation of Fragmented Populations. *Conservation Biology* 8: 50-59.
- Fairbairn, S. E. and J. J. Dinsmore. 2001. Local and landscape-level influences on wetland bird communities of the prairie pothole region of Iowa, USA. *Wetlands* 21: 41-47.
- Farina, A. 1998. Principles and methods in landscape ecology. 1 Edition. Chapman & Hall, London.
- Gering, J. C., T. O. Crist and J. A. Veech. 2003. Additive partitioning of species diversity across multiple spatial scales: Implications for regional conservation of biodiversity. *Conservation Biology* 17: 488-499.
- Getzner, M. 2002. Investigating public decisions about protecting wetlands. *Journal of Environmental Management* 64: 237-246.
- Gibbs, J. P. 2000. Wetland loss and biodiversity conservation. *Conservation Biology* 14: 314-317.
- Gomes, A. d. S. and A. M. d. Magalhães Júnior. 2004. Arroz irrigado no Sul do Brasil. Embrapa, Pelotas.
- Guillemain, M., H. Fritz and P. Duncan. 2002. The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. *Biological Conservation* 103: 183-198.
- Haig, S. M., D. W. Mehlman and L. W. Oring. 1998. Avian movements and wetland connectivity in landscape conservation. *Conservation Biology* 12: 749-758.
- Hanski, I. 1982. Dynamics of Regional Distribution—the Core and Satellite Species Hypothesis. *Oikos* 38: 210-221.
- Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. *Ecology* 78: 1898-1906.
- Kershaw, M. and P. A. Granswick. 2003. Numbers of wintering waterbirds in Great Britain, 1994/1995-1998/1999: I. Wildfowl and selected waterbirds. *Biological Conservation* 111: 91-104.
- Kneitel, J. M. and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7: 69-80.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76: 5-13.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. Elsevier, New York.
- Leopold, A. 1949. *A sand county almanac and sketches from here and there*. Oxford University Press.
- Mähler, J. K., A. Kindel and E. A. I. Kindel. 1996. Lista comentada das espécies de aves da Estação Ecológica do Taim, Rio Grande do sul, BR. *Acta Biologica Leopoldensia* 18: 69-103.
- Maltchik, L. 2003. Three new wetlands inventories in Brazil. *Interciencia* 28: 421-423.
- Maltchik, L., E. Schneider, G. Becker and A. Escobar. 2003. Inventory of wetlands of Rio Grande do Sul (Brazil). *Pesquisas Botânica* 53: 89-100.
- Milsom, T. P., S. D. Langton, W. K. Parkin, S. Peel, J. D. Bishop, J. D. Hart and N. P. Moore. 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *Journal of Applied Ecology* 37: 706-727.
- Moreno, C. E. and G. Halffter. 2001. Spatial and temporal analysis of alpha, beta and gamma diversities of bats in a fragmented landscape. *Biodiversity and Conservation* 10: 367-382.
- Murray, B. R., B. L. Rice, D. A. Keith, P. J. Myerscough, J. Howell, A. G. Floyd, K. Mills and M. Westoby. 1999. Species in the tail of rank-abundance curves. *Ecology* 80: 1806-1816.
- Naranjo, L. G. 1995. An Evaluation of the First Inventory of South-American Wetlands. *Vegetatio* 118: 125-129.
- Narosky, T. and D. Yzurieta. 1989. *Birds of Argentina and Uruguay: a field guide*. Asociación Ornitológica del Plata, Buenos Aires.
- Noss, R. F. 1996. Conservation of biodiversity at the landscape scale. Pages 574-592 in *Biodiversity in managed landscapes: theory and practice*. R. C. Szaro and D. W. Johnston (Eds.). Oxford University Press, Oxford.
- Paracuellos, M. and J. L. Telleria. 2004. Factors affecting the distribution of a waterbird community: The role of habitat configuration and bird abundance. *Waterbirds* 27: 446-453.
- Pasitschniak-Arts, M., R. G. Clark and F. Messier. 1998. Duck nesting success in a fragmented prairie landscape: is edge effect important? *Biological Conservation* 85: 55-62.
- Pillar V. D. P. 2000. Multiv - Multivariate exploratory analysis, randomization testing and bootstrap resampling: User's Guide. Version 2.0. Universidade Federal do Rio Grande do Sul, Porto Alegre.
- Riffell, S. K., B. E. Keas and T. M. Burton. 2001. Area and habitat relationships of birds in Great Lakes coastal wet meadows. *Wetlands* 21: 492-507.
- Robertson, G. and F. Cooke. 1999. Winter philopatry in migratory waterfowl. *Auk* 116: 20-34.
- Rosário, L. A. 1996. As aves de Santa Catarina: Distribuição geográfica e meio ambiente. FATMA, Florianópolis.
- Rose, P. M. and D. A. Scott. 1994. Waterfowl population estimates. *International Waterfowl and Wetlands Research Bureau*, Cambridge.
- Scherer-Neto, P. 1980. *Aves do Paraná*. Zôo-Botânica Mário Nardelli, Rio de Janeiro.
- Scherer-Neto, P. and F. C. Straube. 2001. *Aves do Paraná*. História, lista anotada e bibliografia. Available at <http://www.ao.com.br/avesdo.htm>.
- Scott, D. and M. Carbonell. 1986. *Directorio de los Humedales de la Región Neotropical*. International Waterfowl and Wetlands Research Bureau and International Union for the Conservation of Nature, Slimbridge and Gland.
- Sharpe, D. M., F. W. Stearns, R. L. Burgess and W. C. Johnson. 1981. Spatio-temporal patterns of forest ecosystems in man-dominated landscape. Pages 109-116 in *Perspectives in Landscape Ecology*. S. P. Tjallingii and A. A. de Veers (Eds.). PUDOC, Wageningen, The Netherlands.
- Shine, C. and C. Klemm. 1999. Wetlands, water and the law: Using law to advance wetland conservation and wise use. IUCN, Gland.
- Sick, H. 1983. *Migrações de aves na América do Sul Continental*. Instituto Brasileiro de Desenvolvimento Florestal, Ministério da Agricultura, Brasília.
- SPSS, Inc. 2003. *SPSS for Windows Release 12.0.1 Standard Version*. Version 10.0.1 (27 Oct 1999). SPSS, Inc., Chicago.
- Stickney, A. A., B. A. Anderson, R. J. Ritchie and J. G. King. 2002. Spatial distribution, habitat characteristics and nest-site selection by Tundra Swans on the Central Arctic Coastal Plain, northern Alaska. *Waterbirds* 25: 227-235.
- Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III and D. K. Moskovits. 1996. *Neotropical birds: Ecology and*

- Conservation. The University of Chicago Press, Chicago and London.
- Summerville, K. S., M. J. Boulware, J. A. Veech and T. O. Crist. 2003. Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forests of North America. *Conservation Biology* 17: 1045-1057.
- Taylor, P. D., L. Fahrig, K. Henein and G. Merriam. 1993. Connectivity Is A Vital Element of Landscape Structure. *Oikos* 68: 571-573.
- Telleria, J. L., R. Baquero and T. Santos. 2003. Effects of forest fragmentation on European birds: implications of regional differences in species richness. *Journal of Biogeography* 30: 621-628.
- Tscharntke, T., I. Steffan-Dewenter, A. Kruess and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications* 12: 354-363.
- Tubelis D. P. and W. M. Tomas. 1999. Lista atualizada das espécies de aves do Pantanal. Available at <http://www.bdt.fat.org.br/workshop/cerrado/br/contribuicao/avespantanal>.
- Veech, J. A., K. S. Summerville, T. O. Crist and J. C. Ger-
ing. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99: 3-9.
- Vélez, E. 1997. Estrutura das comunidades de aves aquáticas no complexo de áreas úmidas de Tapes e Arambaré, Planície Costeira do Rio Grande do Sul. Unpublished Dissertation (Master in Ecology), Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.
- Walther, B. A. and J. L. Martin. 2001. Species richness estimation of bird communities: how to control for sampling effort? *Ibis* 143: 413-419.
- Whited, D., S. Galatowitsch, J. R. Tester, K. Schik, R. Lehtinen and J. Husveth. 2000. The importance of local and regional factors in predicting effective conservation—Planning strategies for wetland bird communities in agricultural and urban landscapes. *Landscape and Urban Planning* 49: 49-65.
- Wiens, J. A. 1995. Habitat Fragmentation—Island V Landscape Perspectives on Bird Conservation. *Ibis* 137: S97-S104.

Appendix I. Waterbird assemblage of 44 wetlands in the coastal zone of Rio Grande do Sul, South Brazil.

Family/Species	Common name	Fragments		Lagoons		Status ³
		Frequency ¹	Abundance ²	Frequency ¹	Abundance ²	
Podicipedidae					20	RE
<i>Podiceps major</i>	Great Grebe	6	7	2	2	RE
<i>Tachybaptus dominicus</i>	Least Grebe	0	0	1	80	NP
<i>Podilymbus podiceps</i>	Pied-billed Grebe	21	53	2	41	AP
<i>Rollandia rolland</i>	White-tufted Grebe	4	39	2		
Phalacrocoracidae					800	AP
<i>Phalacrocorax brasilianus</i>	Neotropic Cormorant	19	264	2		
Anhingidae					4	NP
<i>Anhinga anhinga</i>	Anhinga	0	0	2		
Ardeidae					7	RE
<i>Syrigma sibilatrix</i>	Whistling Heron	20	41	2	1	SM
<i>Botaurus pinnatus</i>	Pinnated Bittern	2	2	1	28	SM
<i>Butorides striatus</i>	Striated Heron	12	24	2	0	RE
<i>Trigrisoma lineatum</i>	Rufescent Tiger Heron	1	2	0	139	AP
<i>Nycticorax nycticorax</i>	Black-crowned Night Heron	28	591	2	430	RE
<i>Ardea alba</i>	Great Egret	38	739	2	298	RE
<i>Ardea cocoi</i>	Cocoi Heron	29	200	2	181	RE
<i>Egretta thula</i>	Snowy Egret	33	253	2	1	VG
<i>Egretta caerulea</i>	Little Blue Heron	2	4	1		
Ciconiidae					132	SM
<i>Mycteria Americana</i>	Wood Stork	19	564	2	90	SM
<i>Ciconia maguari</i>	Maguari Stork	29	172	2		
Threskiornithidae					876	RE
<i>Phimosus infuscatus</i>	Whispering Ibis	36	413	2	5253	RE
<i>Plegadis chihi</i>	White-faced Ibis	35	2647	2	64	RE
<i>Theristicus caerulescens</i>	Plumbeous Ibis	9	35	2	154	RE
<i>Platalea ajaja</i>	Roseate Spoonbill	15	447	2		
Anhimidae					1221	RE
<i>Chauna torquata</i>	Southern Screamer	21	1202	2		
Anatidae					8422	AP
<i>Dendrocygna viduata</i>	White-faced Whistling Duck	34	51965	2	2068	NP
<i>Dendrocygna bicolor</i>	Fulvous Whistling Duck	13	2358	2	1054	RE
<i>Amazonetta brasiliensis</i>	Brazilian Teal	41	3754	2	103	AP
<i>Anas flavirostris</i>	Speckled Teal	17	241	2	29	AP
<i>Anas georgica</i>	Yellow-billed Pintail	1	4	2	240	AP
<i>Anas versicolor</i>	Silver Teal	18	157	2	3	AM
<i>Anas platalea</i>	Red Shoveler	0	0	1	712	AP
<i>Netta peposaca</i>	Rosy-billed Pochard	4	1368	2	14	AM
<i>Heteronetta atricapilla</i>	Black-headed Duck	0	0	1	13	AM
<i>Callonetta leucophrys</i>	Ringed Teal	6	19	2	277	AP
<i>Coscoroba coscoroba</i>	Coscoroba Swan	1	43	2	66	AP
<i>Cygnus melanocoryphus</i>	Black-necked Swan	0	0	2	0	RE
<i>Sarkidiornis melanotos</i>	Comb Duck	2	3	0	0	RE
<i>Nomonyx dominicus</i>	Masked Duck	2	91	0	20	RE
<i>Oxyura vittata</i>	Lake Duck	0	0	1	1	AM

¹Number of sites where a species was recorded.

²Total sums of counts over the twelve censuses.

³Status of occurrence in Rio Grande do Sul according to Belton (1994) and Bencke (2001). RE—resident; SM—summer migrant, nidifying in RS; VG—vagrant in RS; AM—austral migrant; NM—nearctic migrant; NP—resident, nearctic partial migrant; AP—resident, austral partial migrant.

Appendix I. (Continued) Waterbird assemblage of 44 wetlands in the coastal zone of Rio Grande do Sul, South Brazil.

Family/Species	Common name	Fragments		Lagoons		Status ³
		Frequency ¹	Abundance ²	Frequency ¹	Abundance ²	
Accipitridae						
<i>Rostrhamus sociabilis</i>	Snail Kite	13	93	2	70	AP
<i>Circus buffoni</i>	Long-winged Harrier	15	55	2	22	RE
Aramidae						
<i>Aramus guarauna</i>	Limpkin	25	164	2	236	RE
Rallidae						
<i>Pardirallus sanguinolentus</i>	Plumbeous Rail	9	21	1	3	RE
<i>Pardirallus nigricans</i>	Blackish Rail	3	7	0	0	RE
<i>Aramides ypecaha</i>	Giant Wood-Rail	12	27	2	29	RE
<i>Aramides saracura</i>	Slaty-breasted Wood-Rail	0	0	1	3	RE
<i>Gallinula melanops</i>	Spot-flanked Gallinule	13	41	2	29	RE
<i>Gallinula chloropus</i>	Common Moorhen	31	10737	2	26227	AP
<i>Porphyrio martinica</i>	Purple Gallinule	1	1	0	0	SM
<i>Fulica leucoptera</i>	Red-gartered Coot	11	674	2	4670	AP
Rynchopidae						
<i>Rhynchops niger</i>	Black Skimmer	3	4	2	10	AP
Jacanidae						
<i>Jacana jacana</i>	Wattled Jacana	38	3806	2	2509	RE
Recurvirostridae						
<i>Himantopus himantopus</i>	Black-winged Stilt	21	307	2	297	RE
Charadriidae						
<i>Charadrius collaris</i>	Collared Plover	4	57	1	17	RE
<i>Pluvialis dominica</i>	American Golden-Plover	7	62	2	28	NM
<i>Pluvialis squatarola</i>	Black-bellied Plover	0	0	2	10	NM
Scolopacidae						
<i>Tringa melanoleuca</i>	Greater Yellowlegs	4	54	2	70	NM
<i>Tringa flavipes</i>	Lesser Yellowlegs	1	14	2	7	NM
<i>Tringa solitaria</i>	Solitary Sandpiper	0	0	1	3	NM
<i>Gallinago paraguayia</i>	South American Snipe	21	56	2	22	AP
<i>Calidris melanotos</i>	Pectoral Sandpiper	1	9	2	9	NM
<i>Calidris canutus</i>	Red Knot	0	0	2	8	NM
<i>Calidris bairdii</i>	Baird's Sandpiper	0	0	1	4	NM
Laridae						
<i>Larus maculipennis</i>	Brown-hooded Gull	14	354	2	478	AP
<i>Larus dominicanus</i>	Kelp Gull	1	2	2	23	RE
<i>Sterna superciliosus</i>	Yellow-billed Tern	12	35	2	60	RE
Alcedinidae						
<i>Ceryle torquata</i>	Ringed Kingfisher	3	3	0	0	RE
<i>Chloroceryle amazona</i>	Amazon Kingfisher	1	1	1	1	RE

¹Number of sites where a species was recorded.

²Total sums of counts over the twelve censuses.

³Status of occurrence in Rio Grande do Sul according to Belton (1994) and Bencke (2001). RE—resident; SM—summer migrant, nidifying in RS; VG—vagrant in RS; AM—austral migrant; NM—nearctic migrant; NP—resident, nearctic partial migrant; AP—resident, austral partial migrant.