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Migratory flows and foraging habitat selection by shorebirds along the northeastern coast of Brazil: The case of Baía de Todos os Santos

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ABSTRACT

Large numbers of Nearctic shorebirds migrate and winter along the coast of northeastern Brazil, but there is little information on their migratory flows, foraging ecology, and on the structure of the species assemblages that they form with resident shorebirds. We studied these issues on intertidal flats of Baía de Todos os Santos (Bahia), the second largest bay in Brazil. During a full year cycle we carried out weekly bird counts in an intertidal area of 280 ha divided in sectors, where we also measured environmental parameters. The analyses of weekly counts resulted in a detailed phenology of use of the area by shorebirds. Five species were resident and ten were Nearctic migrants. Several of the latter had clear peaks in numbers in March and October, revealing the use of the bay as a stopover during both the north-bound and south-bound migration flows. A canonical correspondence analysis of the relationship between environmental parameters and bird numbers indicated that the foraging bird assemblage could be divided into five main groups, occupying distinct ecological gradients in the study area. The most important factors driving this structure were invertebrate prey abundance, percentage of fine sediments, area of mangrove cover and distance to channels. Our findings imply that maintenance of the diversity of intertidal habitats in this bay is crucial to satisfy the particular habitat requirements of resident and migrant shorebirds using the northeastern coastal regions of Brazil.

1. Introduction

Many Charadriidae and Scolopacidae shorebirds are highly migratory and depend on a network of wintering and migration stopover sites to complete their annual cycles (Morrison, 1984; Myers et al., 1987). During their temporary stay at these key sites, they spend a considerable amount of time feeding, recovering from migration and storing reserves for the next stage of their cycles (Myers et al., 1987; IWSG, 2003; Morrison et al., 2007).

The coasts of South America include important wintering and stopover grounds for more than 2.9 million migratory Nearctic Charadriidae and Scolopacidae, and many of these birds spend over half of their lives in these areas (Morrison and Ross, 1989). Although Nearctic shorebird flows are relatively well known in North America, their migratory connectivity with South America and the migratory flows within this continent are incompletely known and understood (Antas, 1983; Morrison and Myers, 1987; Myers et al., 1987; Morrison and Ross, 1989).

Migrant nearctic-breeding shorebirds are receiving increasing attention from researchers and conservationists, partly because adequate feeding and resting sites are limited and many are being affected by human activities (Bildstein et al., 1991), potentially compromising the survival of many shorebird populations (Myers et al., 1987; Morrison et al., 2001; Baker et al., 2004). Studies on seasonal abundance, migratory flows and habitat use, analyzed in relation to local environmental characteristics, are crucial for the adequate management of these areas and for shorebird conservation (Granadeiro et al., 2007).

The vast coast of Brazil is important for wintering and stopover of Nearctic shorebirds in South America (Morrison, 1984; Morrison and Myers, 1987; Morrison and Ross, 1989; Serrano, 2008), especially for the large species (Morrison and Ross, 1989). The major fluxes of shorebirds in the country are along interior flyways (Central Brazil and Central Amazonian/Pantanal flyways), used by

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birds coming from the Guianas to reach the south of the continent (Antas, 1983; Morrison and Ross, 1989). The north and south coasts of Brazil (primarily Maranhão and Rio Grande do Sul, respectively) are very important wintering regions, and are part of the Western Hemispheric Shorebirds Network (Antas, 1983; Morrison and Ross, 1989; Serrano, 2008). In the last ten years, seasonal surveys in the NE Atlantic coast of Brazil (5° S–15° S) revealed a significant number of shorebird wintering grounds along the Atlantic migratory flyway (Azevedo Júnior et al., 2001; Larrazábal et al., 2002; Tellino-Júnior et al., 2003; Lyra-Neves et al., 2004; Cabral et al., 2006; Barbieri, 2007; Barbieri and Hvenegaard, 2008). These sites have been recognized as important for the conservation of Nearctic and Neotropical shorebirds in Brazil (de Luca et al., 2006), but there is a lack of knowledge about the migratory flows and the phenology of each shorebird species within these flyways of the Western Hemisphere (Morrison and Myers, 1987).

In their stopover and wintering sites, different shorebirds exhibit specific ecological requirements, often occupying distinct foraging microhabitats as a function of the habitat characteristics (Granadeiro et al., 2004; 2007; Kober and Bairlein, 2009). Among the factors known to influence habitat use by shorebirds are the availability and distribution of prey (Hicklin and Smith, 1984; Kalejta and Hockey, 1994), sediment characteristics (Granadeiro et al., 2004; 2007; Kober and Bairlein, 2009), proximity to forested areas (Kober, 2004; Pomeroy, 2006; Yasué, 2006) and channels (Lourenço et al., 2005), and the presence of human activities (Navedo and Masero, 2007). Most of this information has been obtained in studies carried out in North America and Europe, as comparatively little research on shorebird ecology has been done in the Neotropics. This is a major constraint because the factors that influence habitat choice by shorebirds in the tropics are not necessarily the same as in the temperate zones. For example, mangroves border many intertidal areas in South America, potentially affecting their use by shorebirds in several ways (Kober, 2004; Kober and Bairlein, 2009), an issue unique to tropical regions.

In the 1980s Baía de Todos os Santos bay (state of Bahia, northeastern coast of Brazil), was identified as a wintering and stopover ground for Nearctic shorebirds that migrate to South America (Antas, 1983; Morrison and Myers, 1987; Morrison and Ross, 1989). This is the second largest bay in the country and harbors thousands of migrating shorebirds (Morrison and Ross, 1989), but detailed information on species richness, seasonal abundance and intertidal use is not available. Baía de Todos os Santos is characterized by an extensive intertidal area with a variable granulometric composition, associated with a mosaic of mangroves, drainage and river channels, and smaller areas of sandy beaches (Cirano and Lessa, 2007). The diversity of physical and biological conditions found in this bay is typical of many wetlands in the NE Atlantic coast of Brazil used by shorebirds assemblages (Antas, 1983), and hence represents a good general model to investigate shorebird distribution relative to environmental factors, habitat use and species-specific requirements.

In this study we investigated the seasonal variation in abundance of shorebirds (Charadriidae and Scolopacidae) in an intertidal region on the western coast of Baía de Todos os Santos, and interpreted their distribution in relation to environmental variables and to the distribution of Ciconiiformes. More specifically we (1) determined which migratory Charadriidae and Scolopacidae use the region as a stopover during migration and for wintering; (2) documented whether Ciconiiformes species have the same habitat preferences of migratory and resident Charadriiformes; (3) investigated the environmental variables that influence the use of the intertidal zone by foraging birds; and (4) examined the structuring of shorebird species assemblages in relation to their ecological requirements.

2. Material and methods

2.1. Study area

Baía de Todos os Santos covers an area of 1,223 km^2 (Fig. 1), with a mean depth of 9.8 m (Cirano and Lessa, 2007). The intertidal area of the bay covers 210 km^2 and is composed of sandy-clay sediments, often in conjunction with mangroves (Cirano and Lessa, 2007). The tides are semidiurnal and the amplitudes range from 0.9 to 3.1 in neap and spring tides respectively (http://www.cptec.inpe.br). In 1999, this bay was designated as an environmental protection area to preserve the mangroves and fauna therein, especially the migratory avifauna (State Decree n° 7.595, Bahia, Brazil).

The study area covers 280 ha of intertidal sediment flats, and is located on the western coast of the bay (12°46'S, 38°43'W), in the municipality of Saubara. We chose this study site because it has

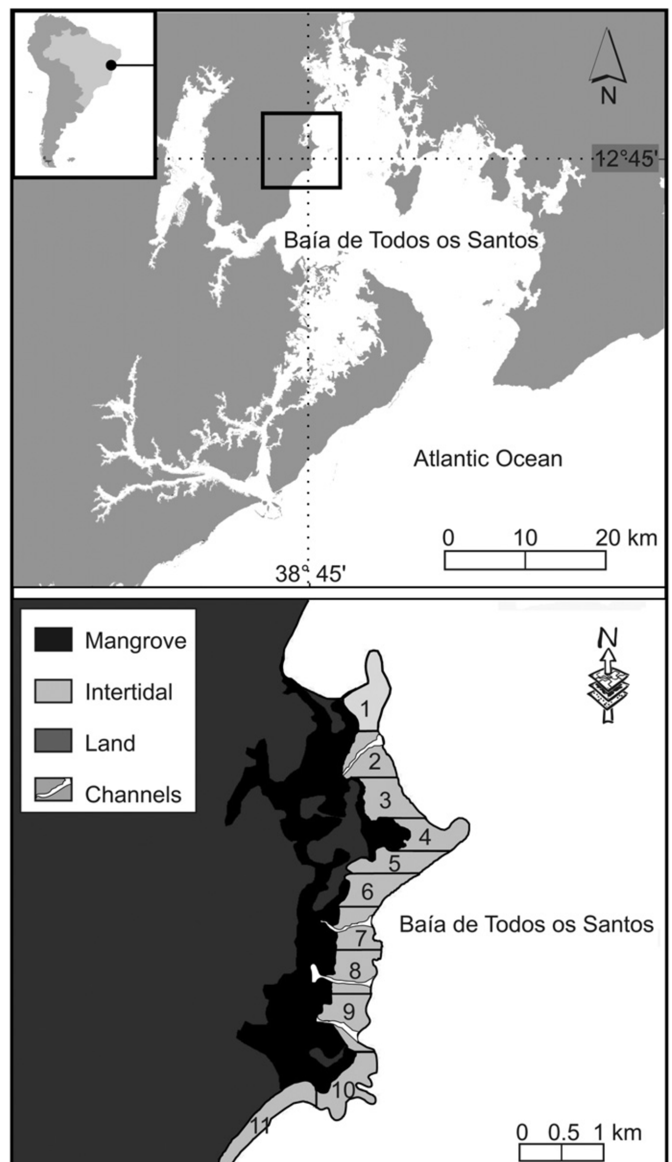

Fig. 1. Top: Baía de Todos os Santos, Brazil, and study site (black square). Bottom: detail of the study area showing the 11 sectors in the intertidal flat during low tide.

a relatively low anthropic activity, harbors numerous foraging shorebirds, and includes a wide range of physical conditions.

2.2. Bird censuses

The study area was divided into 11 contiguous sectors ($\sim$25 ha each) using natural landmarks, semi-permanent landmarks (wooden stakes) and a GPS (Fig. 1). Weekly bird censuses were conducted for 2 h after low tide in all the sectors from January to December 2007. All foraging birds were counted by the same observer, from fixed observation sites in the mangrove adjacent to each sector. The observer moved between these sites along trails inside the mangrove to avoid bird disturbance.

2.3. Seasonal abundance in study sectors

Weekly census data were used to describe the variation in bird species abundance over the year. Data were smoothed using a moving average (2 weekly censuses) to aid the interpretation of the trends. The borders of the sectors were digitized in a Geographic Information System (GIS, ArcView 3.2, ESRI, 1999), using as a reference a low tide satellite image (CBER-2, http://www.cbers.inpe.br). We calculated the area of each sector and converted the bird counts to density (birds 10 ha^{-1}). Counts were split into two periods, (austral) summer and winter, based on the very clear seasonal variation in the number of several species (see Results).

2.4. Environmental variables

To analyze bird distribution we considered the following environmental variables: density of traditional shellfishers, density of potential prey, percentage of fine sediments, mangrove cover, and distance to drainage or river channels.

2.4.1. Shellfishers

During the counts, we recorded the number of individuals collecting shellfish in each sector, as a proxy of anthropic activity, and expressed it as individuals ha^{-1}.

2.4.2. Prey density

We carried out twice-monthly sediment sampling between September and December 2007 (core: 10 $\times$ 10 $\times$ 10 cm) to assess the density of potential prey (macroinvertebrates) and percentage of fine sediments of each sector. The samples were collected along a transect perpendicular to the water line, at points located at 10 m, 110 m and 210 m from the upper limit of the sectors. We collected one sample to the right and one to the left of each point. The distance between these two samples varied from 2 to 16 m between the first and last collection day, to avoid sampling at the same exact site. Thus, on each day we collected six samples in each sector, totaling 528 samples over the entire period (48 samples in each sector). The sediment was sieved in the field through a 0.7 mm mesh and all benthic macroinvertebrates were counted. We calculated the mean density of animals (total n$^\circ$ of benthic macroinvertebrates/m^2) as an estimate of potential prey density in each sector. Mollusca, Crustacea and Polychaeta are abundant in the benthic macrofaunal assemblage in the west coast of the Baía de Todos os Santos (Barros et al., 2008), and represent an important part of the diet of most shorebirds in the Neotropics (e.g. Kober, 2004). All live invertebrates were immediately returned to their original sampling site. Larger animals (size >10 cm) and those that could easily escape during sampling (such as large Crustacea) were not sampled.

2.4.3. Percentage of fine sediments

A single sample (10 $\times$ 10 $\times$ 10 cm) was collected from each of the transect points (10, 110 and 210 m) to determine the percentage of fine sediments (i.e., sand, silt and clay <0.5 mm) predominant in each sector (adapted from Hicklin and Smith, 1984). This parameter was used to characterize the sediment composition of each sector. The sediments were separated by size using 4, 2, 1 and 0.5 mm mesh sieves, and then each sample was classified on a scale of 1–5 (adapted from Wentworth, 1922), as follows: (1) 81–100% of fine sediments; (2) 61–80% of fine sediments; (3) 41–60% of fine sediments; (4) 21–40% of fine sediments; and (5) 0–20% of fine sediments.

2.4.4. Mangrove cover and distance to channels

To estimate the extent of mangrove influence we measured the area of this habitat adjacent to each sector, in a 200-m buffer zone around its upper limit, using the GIS. We also calculated the minimum distance (m) between the rivers or drainage channels and the center of each sector. These variables were selected because they are known to potentially influence the distribution of foraging shorebirds in tidal areas (proximity to channels: Lourenço et al., 2005; forest cover: Yasué, 2006).

2.5. Data analysis

We used Canonical Correspondence Analysis (CCA; ter Braak, 1986) to examine the association between bird species and environmental variables. This analysis results in ordination axes constrained to be maximally correlated to a set of environmental predictors. The scores of species and environmental variables can then be represented jointly in the space defined by these axes to summarize the relationships between them. Analysis of the axes allows the assessment of which variables best explain species distribution (ter Braak, 1986; Palmer, 1993). Before CCA analysis, bird densities were transformed (square root) to attenuate the discrepancies between very abundant and rare species. Environmental variables were also centered and scaled to unit variance to remove arbitrariness from the different measurement units (ter Braak, 1986; Palmer, 1993). We checked collinearity among variables using a correlation coefficient and found that all correlations were lower than 0.63. Therefore, we kept all initial variables for analysis.

We used UPGMA (Unweighted Pair Group Method with Arithmetic Mean Algorithm; Gauch, 1982) cluster analysis on the scores of the first three axes of the CCA to identify the species grouping along the gradients generated by the CCA. For a description of the microhabitat used by each of these groupings we calculated the weighted mean of species density for each environmental variable (Gauch, 1982; ter Braak and Verndonschot, 1995). The weighted mean was calculated using the following formula: Weighted mean $= \Sigma$ (Var$_j$ Dsp$_i$)/Σ (Dsp$_i$), where: Var$_j$ = measure of the environmental variable in sector j (varying from 1 to 11); Dsp$_i$ = species density i of the cluster. For CCA, we used the vegan package (Oksanen et al., 2009) running under the R statistical software, version 2.9.0 (R Development Core Team, 2009).

3. Results

3.1. Seasonal variation of shorebirds

Ten species of shorebirds (Charadriiformes) regularly foraged in the study area: Black-bellied plover (*Pluvialis squatarola*), Semipalmated plover (*Charadrius semipalmatus*), Wilson's plover (*Charadrius wilsonia*) and Collared plover (*Charadrius collaris*) [Charadriidae], Whimbrel (*Numenius phaeopus*), Spotted sandpiper

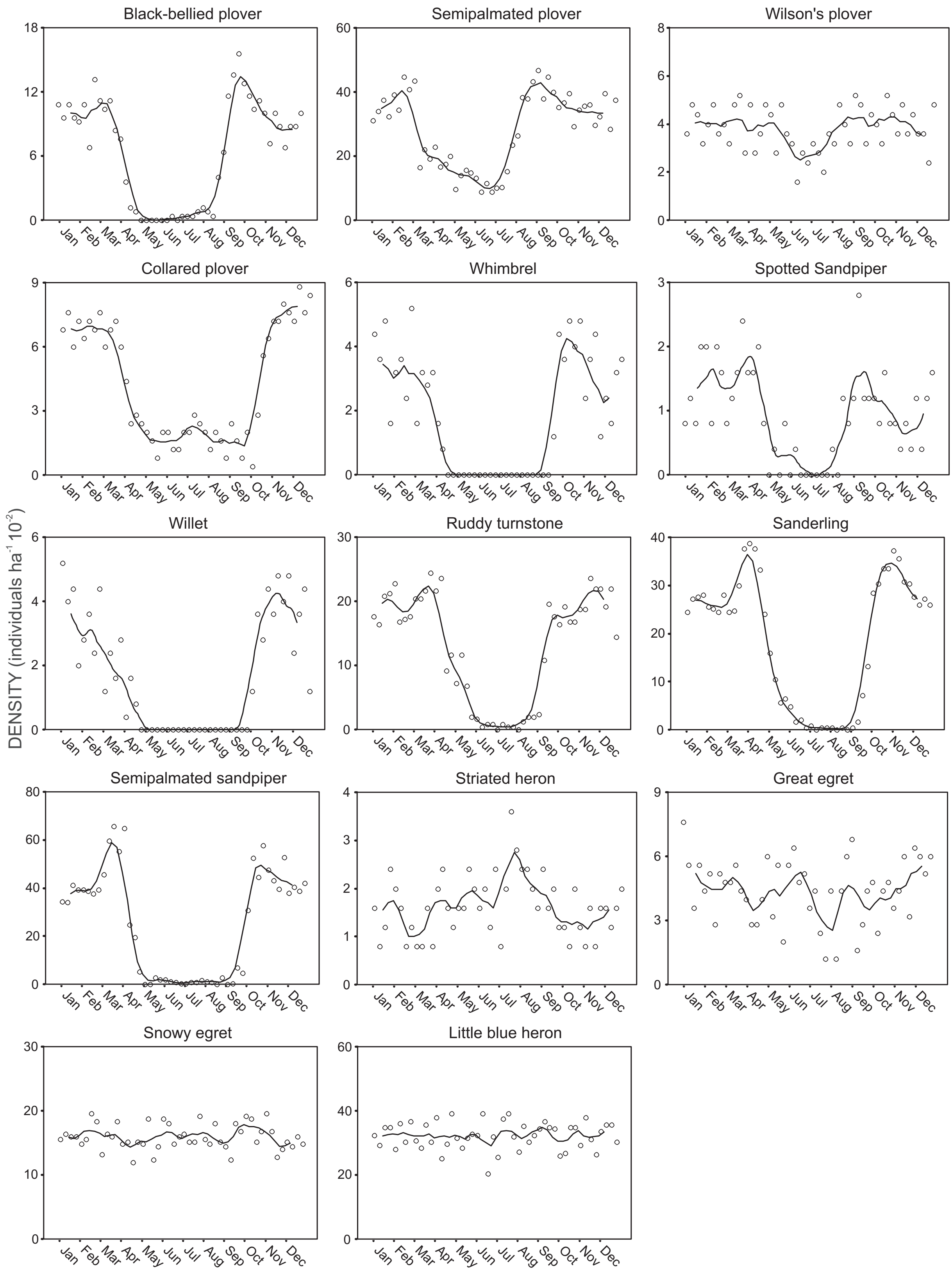

Fig. 2. Seasonal variation in density of foraging shorebirds Charadriidae, Scolopacidae and Ciconiiformes in an intertidal flat associated with mangrove in Baía de Todos os Santos, Brazil. The points are based on weekly counts in 2007. The lines represent 5-count moving averages.

(*Actitis macularius*), Willet (*Tringa semipalmata*), Ruddy turnstone (*Arenaria interpres*), Sanderling (*Calidris alba*) and Semipalmated sandpiper (*Calidris pusilla*) [Scolopacidae]. Most of these species are migrants that are away from Baía de Todos os Santos between approximately mid-April and mid-October (Fig. 2, Table 1). Maximum numbers of birds (approximately 430 individuals) were recorded in March and October, during the northward and southward migratory passages. There was little variation in the numbers of Wilson's plover over the year. Semipalmated plover groups and Collared plover individuals were present year-round, but their numbers were reduced during the austral winter. Black-bellied plover, Whimbrel, Spotted sandpiper, Ruddy turnstone, Sanderling and Semipalmated sandpiper only occasionally occurred in the area during the winter (Fig. 2). Two Short-billed dowitcher (*Limnodromus griseus*) individuals, one White-rumped sandpiper (*Calidris fuscicollis*) and five Least sandpiper (*Calidris minutilla*) were also observed foraging in the study area in 2007, but were excluded from the analysis. In addition to these Charadriiformes, four Ciconiiformes used the intertidal area over the year for foraging: Striated heron (*Butorides striata*), Great egret (*Ardea alba*), Snowy egret (*Egretta thula*) and Little blue heron (*Egretta caerulea*). The total numbers of birds counted was 23439 in 52 weekly censuses, of which 15462 were counted between the 2nd fortnight of October and the 1st fortnight of April and 7977 counted between the 2nd fortnight of April and the 1st fortnight of October.

3.2. Association between species and environmental variables

The first three canonical axes of the CCA explained almost all the variance (99.62%; Table 2), and separated the species into two large groups: (a) Ciconiiformes and Spotted sandpiper (Charadriiformes, Scolopacidae); and (b) the remaining Charadriiformes (Fig. 3). This separation was related mainly to percentage of fine sediments and invertebrate prey density and, to a lesser extent, mangrove cover and distance to channels (see below).

Cluster analysis of the species scores in the first three CCA axes allowed further segregation into five main species groups (Fig. 3), which exhibited distinct preferences relative to the environmental variables (Table 3, Fig. 4). Group 1 contained only the Ruddy turnstone, associated to coarser sediments (i.e., $<$40% of fine sediments), with high invertebrate prey density and far from channels. Group 2 contained the Black-bellied plover, Semipalmated plover, Wilson's plover and Collared plover (Charadriidae). This group was also associated with coarse sediments, relatively high prey abundance and located far from channels. Group 3 included the Whimbrel, Willet, Sanderling and Semipalmated sandpiper (Scolopacidae), and preferred substrates between 40% and 60% of fine sediments and high prey density, but relatively near channels. This was the group most associated to areas used by shellfishers. Group 4 contained the Spotted sandpiper (Scolopacidae) and Striated heron (Ardeidae), and was associated to areas with relatively ample mangrove cover and substrates with $>$40% of fine sediments. Finally, group 5, which included the Little blue heron, Snowy egret and Great egret (Ardeidae) preferred areas with greater mangrove cover, substrates with $>$60% of fine sediments, located near channels, and was apparently affected by the presence of shellfishers.

Table 1
Densities of foraging Charadriiformes and Ciconiiformes in the study area, at Baía de Todos os Santos, Brazil. The values shown are averages (birds per 100 ha ± SD) of weekly censuses conducted in 2007.

Order	Family	Species	Summer[a] ($N = 24$)	Winter[b] ($N = 24$)
Charadriiformes	Charadriidae	Black-bellied plover	0.89 ± 0.14	0.18 ± 0.29
		Semipalmated plover	2.99 ± 0.62	2.01 ± 1.19
		Wilson's plover	0.36 ± 0.06	0.31 ± 0.06
		Collared plover	0.62 ± 0.10	0.17 ± 0.07
	Scolopacidae	Whimbrel	0.29 ± 0.05	0.08 ± 0.10
		Spotted sandpiper	0.10 ± 0.05	0.05 ± 0.06
		Willet	0.30 ± 0.01	0.03 ± 0.07
		Ruddy turnstone	1.76 ± 0.21	0.48 ± 0.61
		Sanderling	2.57 ± 0.35	0.61 ± 0.94
		Semipalmated sandpiper	3.9 ± 0.75	0.29 ± 0.54
Ciconiiformes	Ardeidae	Striated heron	0.12 ± 0.04	0.17 ± 0.06
		Great egret	0.04 ± 0.10	0.35 ± 0.14
		Snowy egret	1.43 ± 0.17	1.40 ± 0.19
		Little blue heron	2.90 ± 0.31	2.91 ± 0.43

[a] Between 2nd fortnight of October and 1st fortnight of April.
[b] Between 2nd fortnight of April and 1st fortnight of October.

4. Discussion

4.1. Seasonal variations of birds in the intertidal area

Our data confirm the importance of the intertidal zone of the western coast of the Baía de Todos os Santos as a foraging area for Nearctic shorebirds during their stay in South America, mainly from September to March. This area is also important for resident populations such as Wilson's plover, Striated heron, Great egret, Snowy egret and Little blue heron. It is clear, however, that the number of birds that use the entire extension of Baía de Todos os Santos is much higher than what we report here, given that our censuses covered only a small portion of the large intertidal area of the bay (see Cirano and Lessa, 2007).

The Atlantic Ocean Flyway is used by many coastal species of Nearctic Charadriidae and Scolopacidae, and includes almost the entire coast of Brazil, from the mouth of the Amazon River (1° N) to the state of Rio Grande do Sul (34° S). However, it has been suggested that some birds avoid going all the way around the NE coast of Brazil by using an overland shortcut, the Northeastern variation of Atlantic Ocean Flyway (Antas, 1983), which connects the north coast of Brazil to Baía de Todos os Santos. Thus, this bay is probably a key area of convergence of two flyways during the southward migration, and possibly an important stopover for individuals that use both the coastal and overland flyways in their migration to southern South America (Antas, 1983; Morrison and Myers, 1987).

The weekly frequency of our censuses allowed us to detect and accurately time the migratory flows of shorebirds in Baía de Todos os Santos, including the passage of stopover birds. The results clearly show brief peaks of abundance of Nearctic species in September–October (southward migration) and again in February–March (northward migration). This corroborates the idea that Baía de Todos os Santos is an important stopover during southward migration, as suggested by Antas (1983) and Morrison and Myers (1987), and indicates that it is also important during the northward migration. In a review of census data and anecdotal observations, Morrison (1984) suggested that northward and southward routes may differ in southern Brazil, with northward routes being further inland. However, the author emphasized that the higher water level of the wetlands could provide unsuitable habitats for shorebirds during the northward migration and that more studies are necessary to establish the migration routes in this region. The

Table 2
Summary statistics of the canonical correspondence analysis (sum of all eigenvalues = 0.1946).

	Axis I	Axis II	Axis III
Eigenvalues	0.1673	0.0188	0.0077
Cumulative % variance	85.99	95.68	99.62
Species/environment correlations	0.925	0.692	0.814
Intersect correlation of environmental variables with axis			
Prey density (invertebrates)	0.83	0.21	−0.46
Shellfisher density	0.45	0.38	−0.28
Mangrove cover	−0.61	0.15	−0.59
Distance to channels	0.72	−0.32	0.46
Percentage of fine sediments	0.86	−0.48	0.17

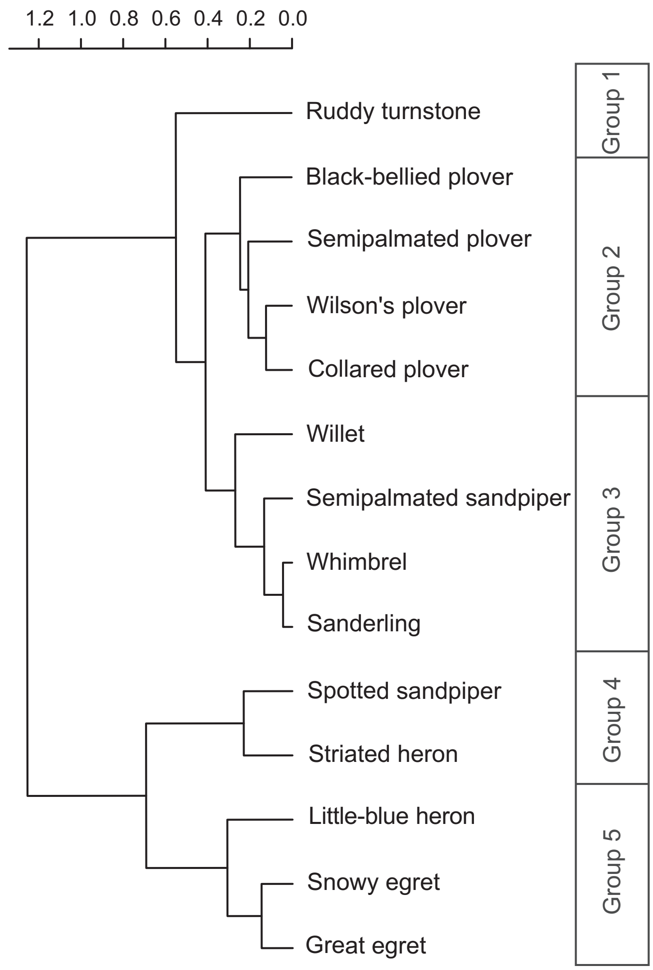

Fig. 3. Dendrogram based on Euclidean distances, representing the similarities among species in the space defined by the three first axes of the Canonical Correspondence Analysis (CCA).

peaks of abundance of Nearctic shorebirds observed at Baía de Todos os Santos suggest that the coastal route between north-eastern and southern sites may be an important flyway within Brazil in both south-bound and north-bound migration flows.

The Nearctic Semipalmated plover, Semipalmated sandpiper and Sanderling were the most abundant species in the intertidal study area during the southern summer. The same has been observed in other regions of the northeastern coast of Brazil (Tellino-Júnior et al., 2003; Cabral et al., 2006; Barbieri and Hvenegaard, 2008). Our data also confirm previous reports (Antas, 1983) that the Baía de Todos os Santos is an important foraging zone for less abundant Nearctic species, such as Whimbrel, Willet and Spotted sandpiper.

Not all Nearctic migrants leave the bay at the end of the southern summer, and our winter counts regularly registered dozens of Semipalmated plover and a few individuals of Black-bellied plover, Semipalmated sandpiper, Ruddy turnstone and Sanderling. These individuals were in wintering plumage (V. O. Lunardi, personal observation) and most likely were not physiologically prepared to fly back to their areas of origin (Tellino-Júnior et al., 2003; Cabral et al., 2006; Barbieri and Hvenegaard, 2008).

The numbers of Collared plover also varied seasonally, with a pattern similar to that of Nearctic species. Its numbers were highest from mid-October to mid-April, and lowest during May and September. This Neotropical species is commonly found in other coastal areas in Brazil, but with peaks of abundance that differ from

Table 3
Summary of the environmental characteristics (weighted means) in the areas of occurrence of each group of species at intertidal flats of Baía de Todos os Santos, Brazil.

Environmental variables	Group 1 Ruddy turnstone	Group 2 Black-bellied plover, Semipalmated plover, Wilson's plover, Collared plover	Group 3 Willet, Semipalmated sandpiper, Whimbrel, Sanderling	Group 4 Spotted sandpiper, Striated heron	Group 5 Little blue heron, Snowy egret, Great egret	Total (average of the 11 sectors)
Invertebrate (ind m^{-2} 10^{-2})	14.4	14.2	14.3	13.3	11.9	13.3
Percentage of fine sediments (scale 1–5)	3.5	3.2	2.9	2.6	1.9	2.9
Mangrove cover (ha)	31.5	31.8	34.2	37.9	43.8	33.4
Shellfishers (ind ha^{-1})	3.5	3.8	4.3	2.8	1.0	2.6
Channels distance (m)	2452.4	2225.1	1530.4	1537.3	847.9	1986.4

those that we observed in Baía de Todos os Santos. In southern Brazil it is more frequent between May and August (Vooren and Chiaradia, 1990; Barbieri and Pinna, 2005), in the north between January and August (Rodrigues and Lopes, 1997), and in the northeast the abundance patterns vary among sites (Tellino-Júnior et al., 2003; Cabral et al., 2006; Barbieri, 2007; Barbieri and Hvenegaard, 2008). Given that periods of higher abundance of Collared plovers in the southern coast of Brazil are roughly the opposite of those observed in Baía de Todos os Santos (northeastern Brazil), it is likely that there is also an annual migration route between these regions for this Neotropical shorebird.

Wilson's plover was the only Charadriiforme that did not show a clear pattern of seasonal variation in numbers. Most individuals of this species on the coast of Brazil are Nearctic migrants, but a resident population, which includes individuals in Mangue Seco, in the north of Baía de Todos os Santos, has been described as a new subspecies (*C. w. brasiliensis*), based on its plumage and reproduction (Grantsau and Lima, 2008). The relative stability of the numbers counted throughout the year, associated with evidence of reproduction in the area (Lunardi and Macedo, 2010), suggests that at least part of the population foraging in the study site belongs to the resident subspecies.

4.2. Species association and the influence of environmental variables

We found that percentage of fine sediments, invertebrate prey density, mangrove cover and distance to channels seem to drive the selection of foraging habitats by shorebirds in the area. All these environmental variables have been reported as potentially relevant for shorebirds in other geographic regions. Sediment characteristics is one of the most frequently cited variables (Goss-Custard and Yates, 1992; Yates et al., 1993; Granadeiro et al., 2007; Kober and Bairlein, 2009), and its importance may partly derive from the varying degrees of penetrability and moisture that are often related to the way in which different species search for prey (Myers et al., 1980; Granadeiro et al., 2004; Santos et al., 2010). It is also known that invertebrate density in the substrate may be directly related to foraging suitability of some shorebird species, mainly the Scolopacidae (Hicklin and Smith, 1984; Colwell and Landrum, 1993; Yates et al., 1993; Kalejta and Hockey, 1994; Butler et al., 2001). Finally, other recent studies also reported the influence of mangrove cover (Kober, 2004; Kober and Bairlein, 2009) and mudflat channels (Lourenço et al., 2005) on habitat use by shorebirds.

A substantial part of the variation in our data derived from the occupation of very specific habitats by the two main species clusters: one containing most of the Charadriiformes and the other the Ciconiiformes and a single Scolopacidae. This clear niche separation between resident Ciconiiformes and migratory Charadriiformes was also reported in a community of coastal birds in northern Brazil by Kober (2004), and explained by differences in seasonality, habitat and diets. These three aspects were also important in the spatial structuring of the bird assemblage in Baía de Todos os Santos. The group of Charadriiformes is mostly migratory and selected habitats with higher invertebrate abundance in the substrate. On the other hand, the Ciconiiformes are residents, often associated with mangroves and channels (see Results), where they

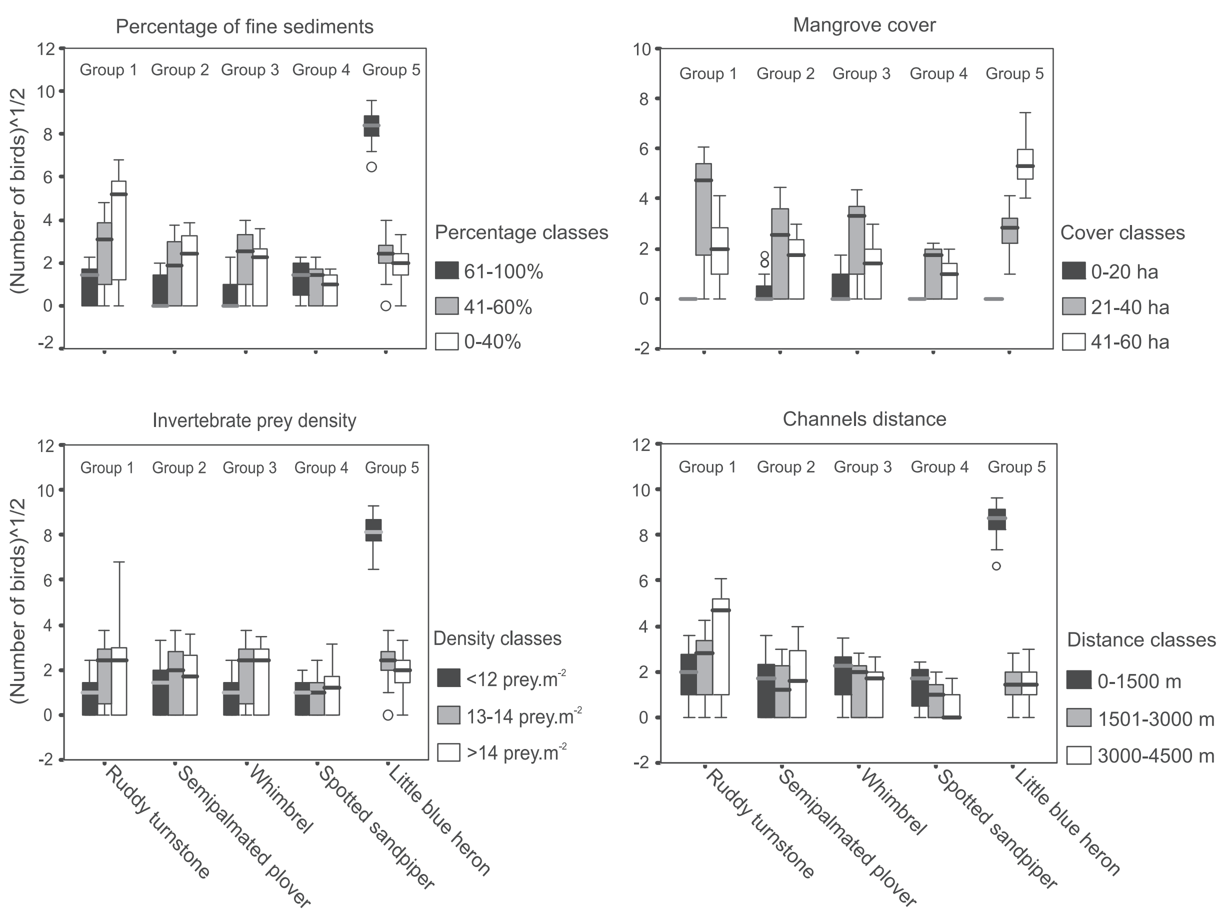

Fig. 4. Boxplots (median, interquartile range, minimum, maximum and outliers) of 52 weekly counts of five bird species (square root-transformed) in relation to the main driving environmental variables identified by the (three axes of the) CCA.

prey mostly on fishes along the channels and mangrove crabs (*Uca* spp.) at low tide (V. O. Lunardi, personal observation; see also Miranda and Collazo, 1997). Because of the rapid fleeing behavior of the fishes and *Uca* crabs, they were not found in the prey sampling (see Methods). This dependence on non-sampled prey explains why the Ciconiiformes species had lower densities in sites with higher invertebrate abundance. The association of the Scolopacidae Spotted sandpiper with the Ciconiiformes may result from the strong association of this species with channels and mangroves, a pattern that has also been reported for other Neotropical areas (Bolster and Robinson, 1990; Willis, 1994; Kober, 2004). The fact that the majority of shorebird species avoided the proximity to the ample mangrove areas could be explained by the higher risk of predation around these areas (see Whitfield, 2003; Kober, 2004; Pomeroy, 2006; Yasué, 2006).

Distribution within these two main species clusters shows slight species segregation in the five groups. The first group, composed solely of the Ruddy turnstone, preferred areas with coarser sediments located far from channels. This is partially consistent with previous observation in the Tagus estuary, Portugal, where this species is also closely associated with areas containing coarser sediments, although there it tends to be near channels (Granadeiro et al., 2004; 2007). The second (Charadriidae) and third groups (Scolopacidae), taxonomically distinct, were distributed along a gradient of two environmental variables, sediment type and distance to channels. Charadriidae are essentially visual foragers, whereas Scolopacidae are mainly tactile foragers. The characteristics of substrate and its moisture level may then exert an unequal influence on the detection and capture of prey by these two types of foragers (Kalejta and Hockey, 1994). Thus, it is to be expected that Charadriidae and Scolopacidae have different substrate foraging preferences (Myers et al., 1980; Granadeiro et al., 2007). Sediment characteristics and its moisture level could also determine prey distribution, thus indirectly influencing the distribution of the birds (Quammen, 1982; Hicklin and Smith, 1984; Kalejta and Hockey, 1994; Kober and Bairlein, 2009). Detailed studies on bird diet, prey distribution and sediment analysis are required to provide more information on foraging microhabitat preference in Charadriidae and Scolopacidae at Baía de Todos os Santos.

Shellfishing is an important subsistence activity that has been practiced by the community of this region for more than 400 years (Sousa, 1851), and in some regions it is known to cause detrimental effects on shorebird foraging in the intertidal areas (Navedo and Masero, 2007; Dias et al., 2008). However, the intensity of shellfishing in this intertidal area did not seem to disturb foraging birds, given that there was apparently no negative effect upon habitat occupation of most species of Charadriiformes (see also Yasué, 2006; Dias et al., 2008). However, our data do not entirely rule out the possibility of a negative impact of shellfishing disturbance, especially on Ciconiiformes. Other types of threats, however, seem to be much more critical for the shorebirds in the coast of Baía de Todos os Santos, particularly the urban and industrial developments, the contamination of invertebrates by heavy metals in one of the main rivers that drains into this bay (Hatje et al., 2006), and the contamination of sediments and mangroves by petroleum compounds (Celino et al., 2008). Regular monitoring of key tidal areas in Baía de Todos os Santos seems an advisable measure to monitor variations in shorebird numbers due to these potentially severe threats.

5. Conclusion

This study provided the first detailed description of seasonal abundance of migratory shorebirds (Charadriiformes) using the intertidal area of Baía de Todos os Santos, and of the timing of migratory flows of these birds along the coast of Brazil. Our analyses identified key factors that influence the distribution of these species and how they use the area, compared with the resident wading birds (Ciconiiformes). We found that the intertidal area is an important foraging ground for both resident and migratory shorebirds, which suggests that maintaining the diversity of intertidal habitats is crucial to meet the specific requirements of each species. Because of threats posed by the existing human activities and development in Baía de Todos os Santos, a high importance must be given to the region by favoring the conservation of foraging areas and reconciling bird occupation with that of the human communities.

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