

Dietary relationships among Nearctic and Neotropical migratory shorebirds in a key coastal wetland of South America

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Abstract. Dietary requirements influence the structure of shorebird assemblages, and information on diet is a key to understanding why and when particular species of shorebird use an area and how competition for food might shape their geographical distributions. We describe the diet and patterns of use of food resources of four migratory shorebirds at Samborombón Bay, Argentina, one of the most important sites for shorebirds in the western hemisphere. The birds consumed items representing at least 15 taxa but only a few taxa comprised the main resources consumed. The four species of shorebird showed dietary flexibility influenced by season and tidal level. Co-occurring species showed complementary differentiation in two dimensions of their respective trophic niches (taxonomic composition, size-class). The greatest differences in taxonomic composition of the diet were between Red Knots, which fed mainly on molluscs, and the other three species, which fed mainly on polychaetes. Polychaete consumers that co-occurred during autumn (Hudsonian Godwit and White-rumped Sandpiper) focussed on different prey sizes. Alternatively, shorebirds that co-occurred during winter (Hudsonian Godwits and Two-banded Plovers) fed mainly on polychaete of similar size but showed differences in the taxonomic composition of their diets. Interspecific competition for food resources might shape the composition of the shorebird assemblage of our study area during the austral autumn and winter.

Additional keywords: Argentina, diet, molluscs, polychaetes, Samborombón Bay, trophic ecology.

Received 21 March 2015, accepted 24 July 2015, published online 17 September 2015

Introduction

The niches occupied by species are defined by multiple dimensions of physical and biological axes (Hutchinson 1957) but, in birds, the trophic dimension is of primary importance because the availability of food resources is one of the main factors limiting population sizes (Newton 2003). Food limitation is also one of the major ecological factors proposed to explain the evolution of migration (Cox 1968). Migratory behaviour allows birds to exploit resources in different regions at different times of the year (Newton 2008). From an evolutionary point of view, migration strategies may arise if the benefits of moving seasonally between regions are greater than the benefits of staying in one region (Lack 1968). There is considerable evidence to support the hypothesis that availability of food in wintering areas regulates populations of migratory birds (see Sherry *et al.* 2004). The availability of food during migration also plays a key role in the regulation of shorebird populations given that, for many species, large numbers of individuals are concentrated in a small

number of stopover sites, which they depend on to refuel and continue their migration (Myers 1983). In addition, food resources may play a key role in shaping local species assemblages through interspecific competition that influence species coexistence at a given site (Begon *et al.* 2006).

To ensure the continued availability of food resources for migratory shorebirds at stopover sites and in their wintering range, and thus preserve habitat quality for shorebirds, the dietary requirements of the species using these sites must be determined (Myers 1983). However, there is little information available for most stopover sites in South America compared with the wealth of information on shorebird dietary composition (e.g. Haramis *et al.* 2007) and the abundance of the predominant prey of shorebirds for many key sites in North America (e.g. Sweka *et al.* 2007). Samborombón Bay, in Buenos Aires Province, Argentina, is one of the most important sites for shorebirds in the Americas, with estimates of >100 000 shorebirds annually (WHSRNews 2012). Most of these are Nearctic migrants (from the Pan New World

Migration System; after Joseph 1997) that use the area as a wintering site in the austral summer and as a stopover site in the austral autumn (Morrison and Ross 1989; Vila *et al.* 1994). In the austral autumn, the shorebird assemblage is largely dominated by Nearctic migrants engaged in northbound migration, with Hudsonian Godwits (*Limosa haemastica*) and White-rumped Sandpipers (*Calidris fuscicollis*) the most abundant (median abundance $\sim 3\text{--}4\times$ greater than that of other Nearctic migrants; Martínez-Curci *et al.* 2015). During the austral winter, most Nearctic migrants leave for their breeding grounds in the northern hemisphere but some individuals, called over-summerers (after McNeil *et al.* 1994), arrest migration and remain in the area. Hudsonian Godwits and Red Knots (*Calidris canutus rufa*) are the most abundant Nearctic breeders that remain over the austral winter (Martínez-Curci *et al.* 2015). They join Neotropical migrants from the South American Cool Temperate Migration System (after Joseph 1997), which arrive at Samborombón Bay after breeding in the Patagonian region. The Two-banded Plover (*Charadrius falklandicus*) is the most abundant such migrant at this site (Martínez-Curci *et al.* 2015).

Despite the importance of Samborombón Bay for shorebird ecology and conservation in South America, there are large gaps in our knowledge of the area, including data on trophic ecology. Previous studies (Botto *et al.* 1998; Iribarne and Martínez 1999; Ieno 2000; Ieno *et al.* 2004; Ribeiro *et al.* 2004) have focussed on the austral summer and autumn and targeted some common Nearctic species, particularly species that consume crabs (Iribarne and Martínez 1999; Ribeiro *et al.* 2004). Conversely, the diets of some of the most abundant species, such as White-rumped Sandpipers and Two-banded Plovers (Martínez-Curci *et al.* 2015) have not been studied and there is also little information on shorebird trophic ecology in Samborombón Bay during the austral winter. Likewise, several important aspects of shorebird over-summering have not been studied. Although several studies have contributed to our understanding of over-summering, including the identification of possible mechanisms that trigger this behaviour (e.g. McNeil *et al.* 1994; Summers *et al.* 1995), the influence of exploitation competition among co-occurring species on patterns of over-summering has not, to our knowledge, been investigated.

In this study we focussed on the most abundant Nearctic and Neotropical migrants, including two over-summering species: the White-rumped Sandpiper, Hudsonian Godwit, Red Knot and Two-banded Plover. Other migratory shorebirds regularly present at Samborombón Bay (e.g. American Golden Plover (*Pluvialis dominica*), Grey Plover (*Pluvialis squatarola*), Ruddy Turnstone (*Arenaria interpres*) and Whimbrel (*Numenius phaeopus*)) were not included in our analyses because they are much less abundant than the four species studied (Martínez-Curci *et al.* 2015) and because their trophic relationships have been already described (Iribarne and Martínez 1999; Ribeiro *et al.* 2004). Our aim was to evaluate the role that food competition plays in shaping species assemblages at Samborombón Bay by assessing the degree of dietary similarity in co-occurring shorebirds residing in the area during the austral autumn – when virtually only Nearctic shorebirds were present – and winter – when Nearctic and Neotropical species (from both flyways) were present. Our specific objectives were: (1) to describe the diet and the breadth of trophic niche of the most abundant migratory shorebirds during

the austral autumn and winter; (2) to assess the influence of common use of food in assemblage composition and patterns of over-summering.

Methods

Study area

This study was conducted at the southern tip of Samborombón Bay, Buenos Aires Province, Argentina, between Punta Rasa and the port of San Clemente (Fig. 1). Tides are low-amplitude (<1.5 m) and semidiurnal. The estuarine shores are gently sloping and extensive; muddy intertidal flats are exposed during low tide (Isacch *et al.* 2006). The oceanic beaches have only narrow intertidal zones composed of fine sediments (Bértola and Morosi 1997) and are crossed by several tidal channels, which are frequently used by foraging shorebirds at high tide (N. S. Martínez-Curci, pers. obs.). The estuarine and oceanic beaches are both influenced by mesohaline waters but freshwater has a greater influence on the former and seawater on the latter.

Sampling and processing

Dietary composition was determined by analysis of faecal samples collected during the austral autumn (March–April) and winter (June–July) of 2012 from estuarine mudflats during low tide and oceanic beaches during high tide. To ensure samples were collected from target species, single-species flocks were targeted. In addition, only fresh faeces were collected. Thus, we avoided collecting older samples that might have corresponded to other species. Flocks of Hudsonian Godwits fed in estuarine habitats at low tide and faeces were obtained in autumn and winter ($n = 35$ for each season); White-rumped Sandpipers also fed in estuarine environments at low tide, but faeces were collected only during the austral autumn ($n = 35$) because the species was absent in winter. Neither of these species fed on the oceanic beaches at high tide and so no high-tide samples were collected. Red Knots fed in estuarine environments at low tide and on oceanic beaches at high tide, and faeces were collected in autumn and winter ($n = 140$: 35 for each tidal level and season). Two-banded Plovers had the same feeding patterns as Red Knots and were sampled in a similar fashion, except samples were collected only in winter ($n = 35$ for each tidal level). Collected faecal samples were stored individually in plastic bags and kept in a freezer (at -20°C) and were analysed later with a zoom stereo microscope (8–50 \times , Leica Wild M8, Leica Microsystems, Wetzlar, Germany).

Prey items were identified to the lowest taxonomic level possible through the analysis of remnants (Table 1). The identification process was aided by the use of a reference collection of benthic invertebrates from the study area, the use of identification guides (Orensanz and Estivariz 1971; Castellanos 1994) and consultation with specialists (G. Darrigran [Museo de La Plata, Universidad Nacional de La Plata]; M. González Castro and M. Cavalli [Universidad Nacional de Mar del Plata]; and L. Bala, S. Laurenti and L. Musmeci [Centro Nacional Patagónico]). For polychaetes, right and left mandibles were counted and the maximum count of either mandible was used as the minimum number of individuals present in faeces. In the case of the polychaete *Laeonereis culveri* (the most frequently consumed quantifiable prey item) the length of the mandibles found in faeces

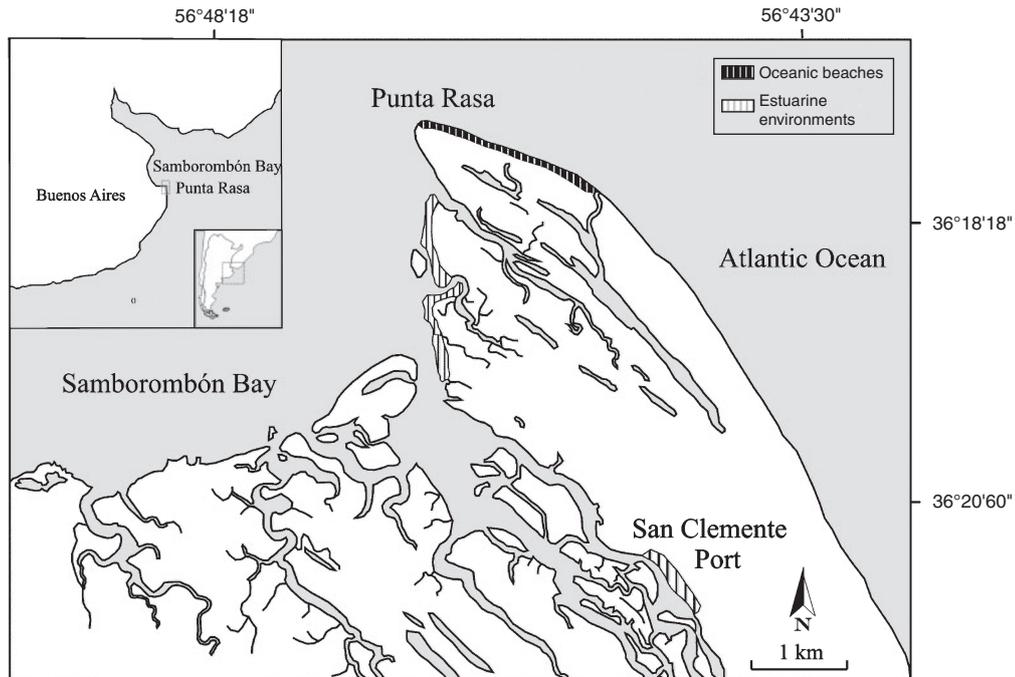


Fig. 1. The study area and location of the oceanic beaches and estuarine environments where faeces were collected. The insets show the location of Punta Rasa and Samborombón Bay in Buenos Aires province and southern South America.

were measured with a zoom stereo microscope (Leica Wild M8) with a graduated ocular to the nearest 0.01 mm.

Data analysis

Dietary composition was determined by combining data within a season (autumn, winter) and tidal level (low, high), and was expressed as relative frequency of occurrence of each prey type (F_o), calculated as the number of faeces in which the prey type was present divided by the total number of faecal samples. Prey items were pooled to the level of taxonomic class for subsequent analyses. The cumulative numbers of prey types were plotted against the number of faeces analysed for each shorebird species, season or tidal level. All curves reached an asymptote, which suggests adequate sample sizes for description and comparison of diet.

To measure breadth of trophic niche, Levins' standardised index $B_A = (B - 1) / (N - 1)$ (Hurlbert 1978) was calculated for each species in each season, where: $B = 1 / \sum p_j^2$ is Levins' measure of niche breadth; p_j^2 is the proportion of individuals using the resource state j ; and N is the number of possible resources of states. B_A can range from 0 to 1; values close to 0 identify species with specialised diets and those close to 1 are indicative of species with generalised diets.

Taxonomic differences in dietary composition between shorebird species were assessed with multivariate analysis of similarities (ANOSIM) and permutational analysis of variance (PERMANOVA), performed with PRIMER 6 and PERMANOVA+ (Clarke and Gorley 2006; Anderson *et al.* 2008). Because not all prey items were quantifiable (see Table 1 for details on quantifiable prey types), the data matrix was constructed using

presence–absence. Subsequent analyses were performed on a Bray–Curtis similarity matrix, with 9999 permutations. ANOSIM and PERMANOVA compared the similarities among samples within groups versus samples in different groups, and used permutations to obtain a probability associated with the null hypothesis of no differences among groups (Anderson 2001). One-way ANOSIM was used to test for differences in faecal composition for single factors (species, season, tidal level). When performed on a presence–absence data matrix, the R statistic of ANOSIM is a direct measure of the differences in taxonomic composition of faeces among different groups. Values close to 1 indicate very different faeces, whereas values close to 0 indicate small differences (Clarke 1993). This advantageous feature of the R -statistic was the main reason for selecting ANOSIM over one-way PERMANOVA for one-factor comparisons. ANOSIM, however, cannot incorporate interactions in a multifactorial design. This contrasts with the pseudo F -ratio statistic of PERMANOVA, which allows a direct additive partitioning of variation for complex models (Anderson 2001). Thus, a two-way PERMANOVA analysis was used to test for differences in Red Knot dietary composition between seasons and tidal levels as well as the interacting effect of both factors. Bonferroni corrected one-way ANOSIM tests were conducted for pairwise comparisons. Finally, the similarity percentage (SIMPER) routine (Clarke 1993) was used to examine the overall dissimilarities among faecal samples of different species, seasons and tidal levels and to assess the contribution of each prey class to this dissimilarity.

To determine the length of the polychaetes *Laeonereis culveri* that were consumed, a linear regression model for total body length as a function of mandible length was developed (body length = $92.61 \times (\text{mandible length})^{1.84}$; $R = 0.90$, $P < 0.01$,

Table 1. Frequency of occurrence of prey consumed by four shorebird species in the Punta Rasa area, Samborombón Bay, Argentina during the 2012 austral autumn and winter

Frequency of occurrence is shown as the number of faecal samples in which the prey type was present divided by the total number of faecal samples processed. Samples were collected at low tide (LT) and high tide (HT). Prey types are reported by taxonomic class and minimum taxonomic level recognised ($n = 35$ faecal samples for each seasonal and tidal category). The identified body parts of prey are listed; unique body parts used for quantification of prey are shown in italics. For the faecal samples of Hudsonian Godwit, the frequency of occurrence of the fish Mugiliformes and Clupeiformes could not be determined (ND)

Taxa	Body parts identified	Hudsonian Godwit		Red Knot				White-rumped Sandpiper	Two-banded Plover	
		Autumn	Winter	Autumn		Winter		Autumn	Winter	
		LT	LT	LT	HT	LT	HT	LT	LT	HT
Polychaeta		1	0.71	0.29	0.26	0.03	0.26	1	0.91	0.83
<i>Laonereis culveri</i>	<i>mandible</i>	1	0.29	0.11	0.03	0	0.11	0.97	0.74	0.46
<i>Neanthes succinea</i>	<i>mandible</i>	0.23	0.26	0.11	0	0	0.08	0.17	0.63	0.23
Undetermined	chaetae	0	0.34	0.11	0.23	0.03	0.11	0.03	0.14	0.34
Gastropoda		0	0.2	0.23	0.8	1	0.86	0	0.06	0.03
<i>Littoridina australis</i>	<i>apex, shell</i>	0	0.2	0.23	0.8	1	0.86	0	0.06	0.03
Bivalvia		0.06	0.31	0.86	0.43	0.4	0.63	0	0.37	0.06
<i>Macra</i> spp.	<i>hinge, shell</i>	0	0.08	0.17	0.14	0.17	0.43	0	0.09	0
<i>Mytella charruana</i>	<i>hinge, shell</i>	0.06	0.03	0.8	0.2	0.11	0.31	0	0	0
<i>Donax hanleyanus</i>	<i>hinge, shell</i>	0	0	0.03	0.09	0.09	0.03	0	0	0
<i>Tagellus plebeius</i>	<i>hinge, shell</i>	0	0.14	0.11	0	0	0.03	0	0.26	0
Undetermined		0	0.11	0.06	0.11	0.06	0.14	0	0.06	0.06
Ostracoda	<i>antennae, shell</i>	0.57	0.17	0.17	0.06	0.17	0.34	0.57	0.17	0
Malacostraca	<i>antennae, leg</i>	0.23	0.03	0	0	0.03	0	0.08	0.34	0
Amphipoda		0.2	0.03	0	0	0.03	0	0.03	0.34	0
Isopoda		0.11	0	0	0	0	0	0.03	0	0
Insecta		0.2	0	0	0.51	0.06	0.26	0.43	0.23	0.94
Curculionidae	<i>head, elytra</i>	0	0	0	0.26	0	0.2	0.14	0.17	0.8
Carabidae	<i>mandible, elytra</i>	0	0	0	0.03	0	0.06	0	0	0.03
Diptera	<i>wing, head</i>	0.03	0	0	0.09	0	0	0.06	0	0.06
Undetermined	<i>wing, appendage</i>	0.17	0.03	0	0.31	0.06	0.09	0.26	0.09	0.43
Arachnida	<i>leg</i>	0	0	0	0.06	0	0	0	0.03	0
Actinopterygii	<i>vertebrae, scale</i>	0	0.29	0	0	0	0	0	0	0.06
Mugiliformes	<i>scale</i>	0	ND	0	0	0	0	0	0	0
Clupeiformes	<i>scale</i>	0	ND	0	0	0	0	0	0	0.06
Undetermined		0.06	0.08	0	0.03	0	0	0.06	0	0.03

$n = 112$ polychaetes) using the reference collection previously mentioned. Differences in size (median, variance and distribution) of *L. culveri* consumed by different shorebird species were assessed through Kolmogorov–Smirnov tests using STATISTICA version 7.0 (StatSoft Inc. 2004).

Results

Dietary composition and trophic niche-breadth

The four species of shorebird consumed a wide variety of food types, but two prey types, polychaetes and molluscs, comprised the greatest frequency of occurrence (Fo). Hudsonian Godwits, White-rumped Sandpipers and Two-banded Plovers fed mainly on polychaetes, whereas Red Knots fed mainly on molluscs (gastropods and bivalves) (Fig. 2).

The trophic niche-breadth of Hudsonian Godwits was narrower during the austral autumn ($B_A = 0.26$) than in winter ($B_A = 0.40$), and dietary composition differed slightly between seasons (Fig. 2). For Hudsonian Godwits, 70% of the overall average dissimilarity (55.5%) was explained by a lower consumption of polychaetes and ostracods during winter, when the consumption of bivalves increased and items not consumed

during winter were also recorded, such as gastropods (mud snails *Littoridina* sp.) and fish (order Mugiliformes (probably *Mugil liza*) and order Clupeiformes (probably *Anchoa marinii* and *Engraulis anchoita*)) (Table 1). Polychaetes were, however, the main prey consumed in both seasons. The polychaetes eaten included two nereid species: *Laonereis culveri*, which was present in all autumn faecal samples (median 10 individuals/faeces, range 4–23, $n = 34$ faecal samples), and *Neanthes succinea*, which occurred less frequently (Fo = 0.23; Table 1) and in smaller numbers (median 2 individuals/faeces, range 1–5, $n = 6$ faecal samples). During winter the consumption of *L. culveri* decreased and individuals consumed were significantly smaller (median length 32.92 mm, $n = 42$ *L. culveri* individuals) than those eaten in autumn (median length 55.89 mm, $n = 372$ *L. culveri* individuals; Kolmogorov–Smirnov $D = 0.63$, $P < 0.01$; Fig. 3a, 3b).

White-rumped Sandpipers ($B_A = 0.27$) fed mostly on polychaetes and, to a lesser extent, on ostracods, insects and malacostracans (Fig. 2). *Laonereis culveri* was found in almost all faecal samples (median 6 individuals/faeces, range 1–24, $n = 32$), whereas *Neanthes succinea* occurred much less frequently (Table 1) and in smaller numbers (median 1 individual/faeces,

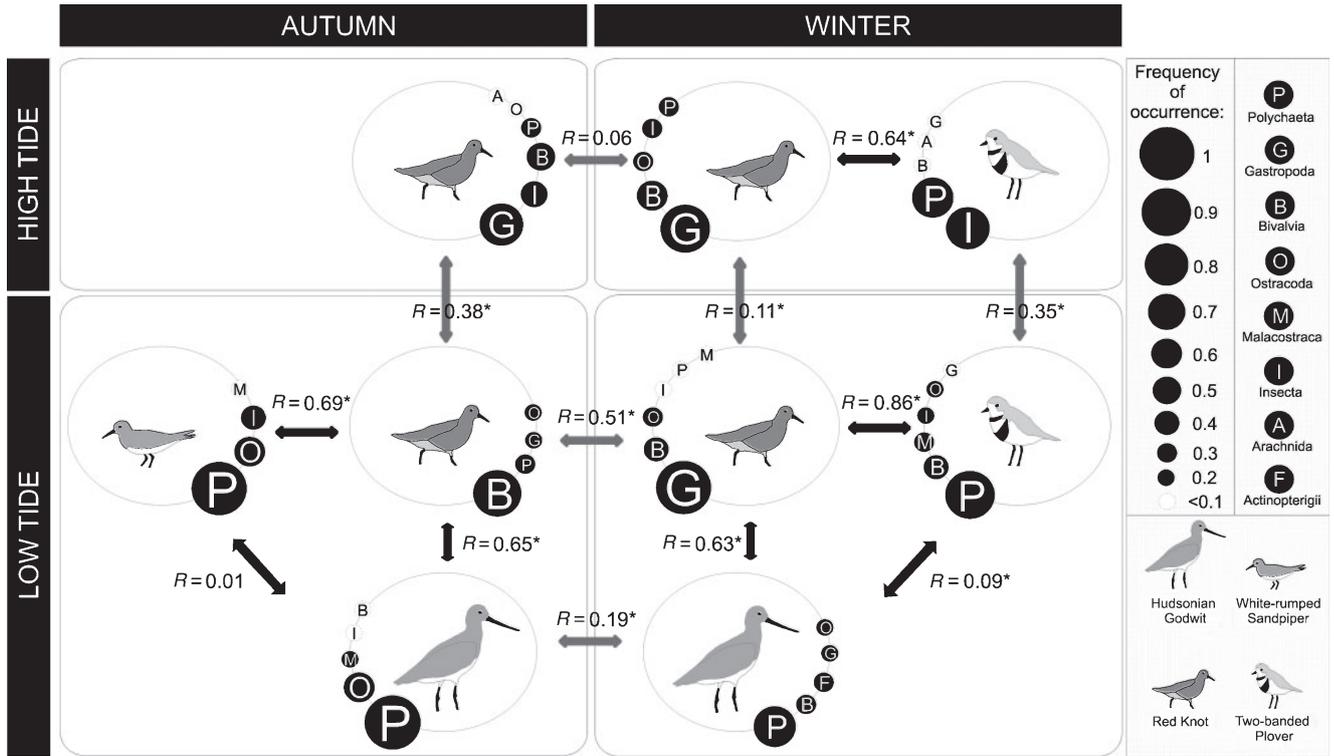


Fig. 2. Dietary composition, intraspecific differences (grey arrows) and interspecific differences (black arrows) as functions of season (autumn or winter) and tidal level (low or high) for four shorebird species (Hudsonian Godwit, Red Knot, White-rumped Sandpiper and Two-banded Plover) at Punta Rasa, Samborombón Bay, Argentina. The ANOSIM R -statistic (Clarke 1993), performed using presence-absence data, is a direct measure of differences in species composition in faeces; R values close to 0 indicate small differences and those close to 1 large differences; * = significance at $P \leq 0.01$.

range 1–2, $n=8$). White-rumped Sandpipers ate only small *L. culveri* (median length 20.83 mm; Fig. 3c).

The trophic niche-breadth of Red Knots was similar in austral autumn ($B_A=0.20$) and winter ($B_A=0.17$), and reflected a specialised diet based mainly on molluscs (Table 1). The taxonomic composition of Red Knot faeces differed between seasons (Permanova: $F_{1,139}=24.62$, $P<0.001$), tidal level ($F_{1,139}=13.02$, $P<0.001$) and the interaction of season and tide ($F_{1,139}=31.85$, $P<0.001$). The largest difference was observed between season at low tide, whereas we observed no seasonal differences at high tide (Fig. 2). At low tide, >70% of overall average dissimilarity (68.2%) between seasons was explained by differences in consumption of gastropods and bivalves, with the consumption of mud snails increasing and that of bivalves decreasing during winter (Table 1).

During autumn, Red Knots fed mostly on bivalves at low tide (particularly the Charrua Mussel (*Mytella charruana*); median 2 individuals/faeces, range 1–5, $n=24$ faecal samples), whereas at high tide they fed mainly on gastropods (median 4 individuals/faeces, range 2–7, $n=9$ faecal samples; Table 1). More than 90% of the overall average dissimilarity (68.2%) of the composition of faeces at both low and high tides was explained by high consumption of gastropods and insects at high tide and consumption of bivalves and ostracods at low tide.

During winter, gastropods (mud snails) comprised the most frequently occurring prey (Table 1) at both low tide (median 108 individuals/faeces, range 24–281, $n=34$ faecal samples) and high

tide (median 65 individuals/faeces, range 47–121, $n=12$ faecal samples). Most of the differences (90%) between composition of faeces between high and low tide (40% overall average dissimilarity) was a result of frequent consumption of bivalves, ostracods, insects and polychaetes at high tide.

Two-banded Plovers showed one of the broadest niche breaths ($B_A=0.35$) among the studied species. Dietary composition differed with tidal level (Fig. 2, overall average dissimilarity 52.9%), with >85% contributed by a higher consumption of insects at high tide and increased consumption of bivalves, polychaetes and Malacostraca at low tide. *Laonereis culveri* was the most frequently occurring polychaete at both low tide (median 4 individuals/faeces, range 1–18, $n=20$) and high tide (median 1 individual/faeces, range 1–13, $n=13$); median total length of these polychaetes was 32.26 mm ($n=143$ polychaetes, Fig. 3d.) and did not differ significantly between high and low tides (Kolmogorov–Smirnov $D=0.01$, $P>0.1$).

Dietary similarities among coexisting species

We found differences in the dietary composition of the three species that coexisted during the austral autumn – Red Knots, Hudsonian Godwits and White-rumped Sandpipers (ANOSIM: $R=0.46$, $P<0.01$) – and during the austral winter – Red Knots, Hudsonian Godwits and Two-banded Plovers (ANOSIM: $R=0.53$, $P<0.01$). In both autumn and winter, the diet of Red Knots differed from that of the other co-occurring species (Fig. 2). During the austral

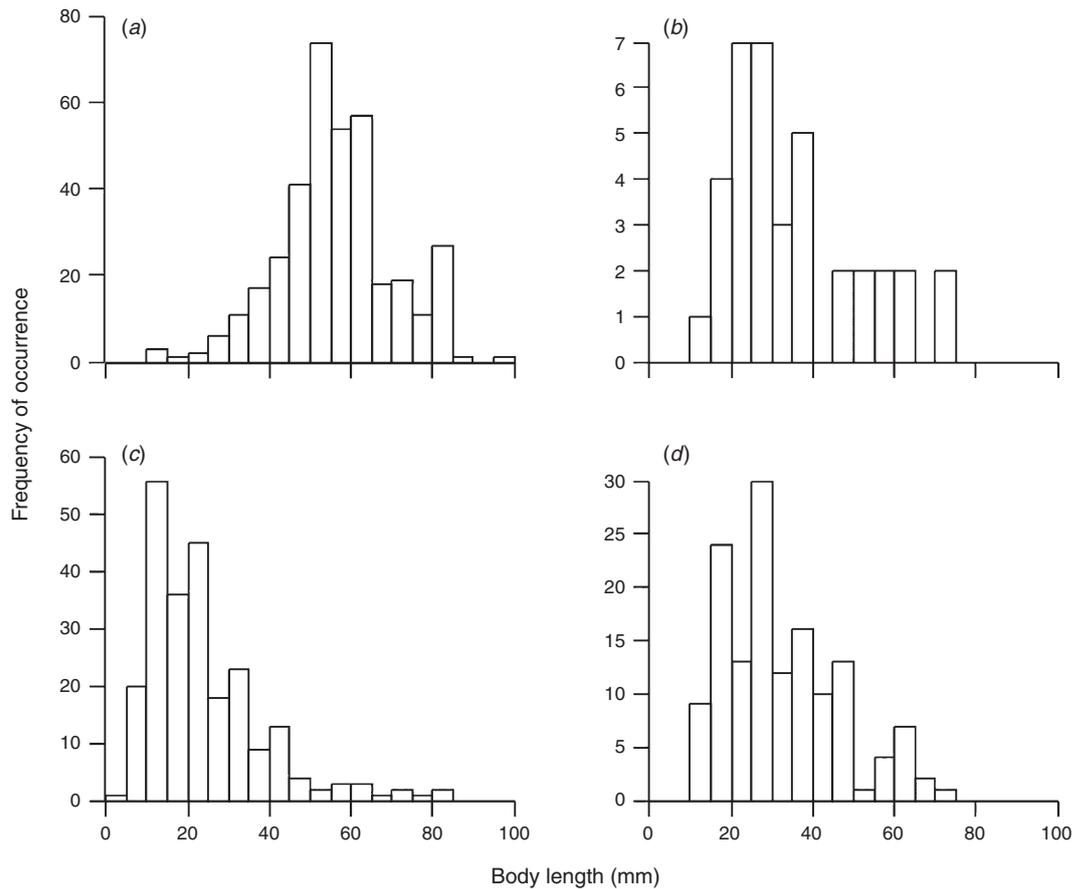


Fig. 3. Frequency of occurrence of different size-classes of the polychaete *Laeonereis culveri* found in (a–b) faeces of Hudsonian Godwits during (a) austral autumn and (b) winter; (c) faeces of White-rumped Sandpipers during austral autumn; and (d) faeces of Two-banded Plovers during austral winter.

autumn, Red Knots consumed mostly bivalves whereas Hudsonian Godwits and White-rumped Sandpipers consumed mostly polychaetes and ostracods (Tables 1 and 2). During the austral winter, the main difference between the diet of Red Knots and Hudsonian Godwits was greater consumption of gastropods and bivalves by Red Knots compared with greater numbers of polychaetes and fish by Hudsonian Godwits (Tables 1 and 2). Compared with the diet of Two-banded Plovers, at low tide Red Knots ate more gastropods and bivalves than the Plovers, whereas the Plovers ate more polychaetes (Tables 1 and 2). At high tide, the diet of Red Knots and Two-banded Plovers also differed (Fig. 2), with Red Knots consuming more gastropods and bivalves than the Plovers, and Plovers eating more insects and polychaetes than Red Knots (Tables 1 and 2).

Differences in dietary composition between consumers of polychaetes were less pronounced and showed complementary differentiation in two dimensions of their trophic niche. For a given pair of shorebird species, lack of differences in taxonomic composition of faeces was coupled with differences in size of prey and vice versa. For example, during the austral autumn, Hudsonian Godwits and White-rumped Sandpipers both fed primarily on *Laeonereis culveri* (Fig. 2) but the size of prey consumed differed. Hudsonian Godwits fed on larger *L. culveri* (Fig. 3a;

median length 55.95 mm, $n=372$ polychaetes) than White-rumped Sandpipers (Fig. 3c; median length 20.83 mm, $n=239$ polychaetes; Kolmogorov–Smirnov $D=0.78$, $P<0.01$). In contrast, during the austral winter, Hudsonian Godwits and Two-banded Plovers fed on *L. culveri* of similar size (Fig. 3b, 3d; Kolmogorov–Smirnov $D=0.13$, $P>0.10$) but the dietary composition of the two species differed (overall average dissimilarity 57.3%). In this case, most differences were driven by greater consumption of bivalves, polychaetes and malacostracans by Two-banded Plovers and greater consumption of fish by Hudsonian Godwits (Table 2).

Discussion

We found significant differences in the diet of four shorebird species that use Samborombón Bay during the austral autumn and winter. We also found evidence that the use of food resources by these four species may influence the structure of the shorebird community in the Bay. The four targeted species showed complementary differentiation (Begon *et al.* 2006) in two dimensions of their trophic niche – taxonomy and size-class of prey. Our results, combined with those of previous studies (Iribarne and Martínez 1999; Ribeiro *et al.* 2004), identify three groups of

Table 2. Overall average dissimilarities (%) and contribution of each prey type to overall dissimilarity (SIMPER analysis; Clarke 1993) between pairs of co-occurring shorebird species feeding during the austral autumn or winter at low (LT) or high tide (HT) in Samborombón Bay, Argentina

HuGo, Hudsonian Godwit; WrSa, White-rumped Sandpiper; ReKn, Red Knot; TbPl, Two-banded Plover

	Austral autumn		ReKn–WrSa LT	HuGo–TbPl LT	Austral winter		
	HuGo–WrSa LT	HuGo–ReKn LT			HuGo–ReKn LT	ReKn–TbPl LT	HT
Overall average dissimilarity (%)	31.68	77.97	80.05	57.28	83.72	89.35	78.03
Contribution to overall dissimilarity (%)							
Polychaeta	0	28.26	26.64	18.03	26.61	29.86	20.80
Gastropoda	0	7.45	7.08	8.75	33.29	33	26.90
Bivalvia	2.75	31.54	30.6	20.46	15.21	14.25	17.25
Ostracoda	39.50	18.47	18	10.94	8.13	6.71	9.11
Malacostraca	17.73	6.17	2.87	14.40	1.29	9.33	0
Insecta	33.13	6.47	13.20	8.28	1.47	6.28	23.17
Arachnida	0	0	0	0.88	0	0.57	0
Actinopterygii	0	0	0	15.37	11.63	0	2.06
Undetermined	6.88	1.64	1.60	2.88	2.12	0	0.70

shorebird at Samborombón Bay that differ in their major prey type: (1) species that mainly consume molluscs (Red Knot), (2) species that mainly eat polychaetes (Hudsonian Godwit, White-rumped Sandpiper and Two-banded Plover), and (3) species that primarily consume crabs (American Golden Plover, Grey Plover, Whimbrel, and Ruddy Turnstone). Within the species that primarily consume polychaetes we found differences in size of prey between the shorebird species. In addition, Iribarne and Martínez (1999) recorded differences between ages and sex among shorebird species that primarily consume crabs.

The diets of the Hudsonian Godwit and the Red Knot during the austral autumn at Samborombón Bay have been already described (Ieno 2000; Ieno *et al.* 2004). Our results, however, suggest the species consume a much broader prey spectrum than previously reported. For instance, although mud snails were virtually the only prey eaten by Red Knots in a previous study (Ieno *et al.* 2004), we identified, under the same environmental conditions (autumn low tide), five species of molluscs, being *Mytella charruana* (Mytilidae), the most frequently occurring prey items. These patterns correspond with data from other areas, which indicate that molluscs represent the main prey for this species (Van Gils & Wiersma 1996; Piersma *et al.* 1997). Because human harvesting of molluscs in South America has increased, especially of the Charrua Mussel, the range of which has declined significantly (Carranza *et al.* 2009), the dependence of Red Knots on molluscs is of conservation concern. Future strategies that aim to improve the status of this shorebird should consider management guidelines to guarantee healthy mussel populations.

Unlike the diet of the Red Knot, the diets of the species that primarily consume polychaetes are poorly known throughout their geographical ranges (David 1992; Piersma *et al.* 1997; Walker *et al.* 2011). Our data on the diet of the Hudsonian Godwit concur with those of Ieno (2000), that *Laonereis culveri* is the mostly frequently consumed species. However, in contrast to this study, in which no mandibles were found in 120 faeces samples analysed, we observed mandibles in almost all of the faeces samples and, based on these findings, were able to estimate the length of the *L. culveri* consumed. The little available information on the diet of the species that primarily consume polychaetes

(David 1992; Wiersma 1996; Walker *et al.* 2011) suggests a euryphagic diet. Euryphagic species have broad dietary flexibility, which allows the exploitation of variable resources. Such a characteristic, however, is generally only evident at a regional scale because, at any given site, these birds tend to focus on the most abundant prey (Skagen and Oman 1996). Our results are consistent with this idea since polychaete-consumer species were the most abundant shorebirds in the area and fed mainly on the most abundant benthic species (Martin *et al.* 2004). *L. culveri* can reach high densities in mixohaline sediments (Eliás 1992; Eliás and Ieno 1993) and at Samborombón Bay exhibits one of the highest levels of secondary production reported for any polychaete species worldwide, indicating a large transfer of biomass to upper trophic levels (Martin and Bastida 2006).

Demographic parameters of *L. culveri* at Samborombón Bay probably influence dietary patterns within the local shorebird community. This polychaete has two marked recruitment peaks that define austral spring and austral autumn cohorts. In autumn the population is composed of fully grown and small individuals (Martin and Bastida 2006). The different sizes of *L. culveri* found in the faeces of Hudsonian Godwits and White-rumped Sandpipers in autumn fit the size-pattern of the two polychaete cohorts. By austral winter, the population of the autumn cohort of *L. culveri* from the previous year declines naturally owing to the 15–17 month lifespan of the species. Even though an additional new autumn cohort is also present in winter, these individuals are very small (Martin and Bastida 2006) and are probably not profitable prey for shorebirds. The lack of a significant difference in the size of *L. culveri* consumed by Hudsonian Godwits and Two-banded Plovers during winter indicates both are probably feeding on the same cohort.

Our data suggest that polychaetes might be a limited food resource during the austral winter at Samborombón Bay. During winter, the diet of Hudsonian Godwits was characterised by a lower frequency of occurrence of polychaetes and a broader trophic niche-breadth than in autumn. This pattern is congruent with optimal foraging theory in so far as predators tend to specialise on a few highly profitable prey types when they are abundant but incorporate more prey types, even less-profitable

ones, when food resources become scarce (Pulliam 1985). The increased predation pressure on small polychaetes by Hudsonian Godwits and Two-banded Plovers during winter may explain the absence of over-summering White-rumped Sandpipers, which also rely on small *L. culveri* in their diet. Interspecific exploitation competition is difficult to confirm under natural conditions (Begon *et al.* 2006). We believe, however, it is one of the most plausible explanations for our observed patterns in shorebird community composition at this site.

Although faecal analysis as a means to describe shorebird diets provides precise information on trophic ecology and is widely used in shorebirds studies (e.g. Dekinga and Piersma 1993; Isacch *et al.* 2005), the approach has some limitations. One important caveat is the underestimation of soft-tissued prey items (Ralph *et al.* 1985). To our knowledge the only potential soft-tissue prey species that could be underestimated in our study is the jawless polychaete *Heteromastus similis*, which Botto *et al.* (1998) reported as prey of shorebirds at Samborombón. Our reference benthic collection, however, indicated that *L. culveri* was the dominant species whereas *H. similis* was present only in small numbers at our most important shorebird feeding sites. Thus, even though the relative importance of *H. similis* as shorebird prey may have been underestimated by us, it is not likely to be a significant prey item, at least during the austral autumn and winter when we conducted our study. New techniques, such as DNA barcoding, which allows some prey taxa to be identified in the absence of morphological evidence (King *et al.* 2008), may add additional insight to shorebird trophic ecology, especially when combined with more traditional methods.

Acknowledgements

We thank L. Bala, C. Bruni, M. Cavalli, G. Darrigran, S. Gennuso, M. González Castro, N. Lahsen, S. Laurenti, I. Martínez, M. Medina, L. Musmeci and T. Rolla for their assistance with field work and processing of faecal samples. We are grateful to Rick Lancot and an anonymous reviewer who significantly improved the manuscript. This work was supported by the Rufford Foundation, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Universidad Nacional de Mar del Plata (UNMdP). Centro Nacional Patagónico and UNMdP provided access to laboratory equipment. The Centro de Estudios de Recursos Costeros – Municipalidad de La Costa and the Organismo Provincial para el Desarrollo Sostenible provided accommodations and assistance in the study area.

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