Small- and large-scale effect of the SW Atlantic burrowing crab *Chasmagnathus granulatus* on habitat use by migratory shorebirds

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Abstract

Here we address the question of whether the presence of the burrowing crabs *Chasmagnathus granulatus* affects small- and large-scale habitat use by migrant shorebirds. This crab is the dominant species in soft bare sediments and vegetated intertidal areas along the SW Atlantic estuaries (southern Brazil 28°S to the northern Argentinean Patagonia 42°S). They generate very extensive burrow beds in soft bottom intertidal areas. Our information shows that this burrowing crab affects the small-scale habitat use by shorebirds, given that shorebirds never walk through the funnel-shaped entrances of burrows. Given that crab burrow entrances occupy up to 40% of the intertidal area, there is a large decrease of available shorebird habitat in crab beds, restricting their activity to the spaces between the burrows. The southern migratory shorebird *Charadrius falklandicus* maximize the use of these areas by foraging closer to the burrows than the other bird species. Neotropical migrants, such as *Calidris fuscicollis*, *Pluvialis squatarola* and *Tringa melanoleuca*, used foraging paths that tended to maximize the distance from burrows, especially the distance to larger burrows. A field experiment showed that this was not necessarily due to a decrease in the availability of polychaetes near the crab burrows. A combination of landscape measurements and satellite images showed that crab beds covered up to 40% of the intertidal area of the Mar Chiquita coastal lagoon (37°40′ S, Argentina), and nearly 100% of the intertidal area of the Bahia Blanca estuary (38°48′ –39°25′ S, Argentina). These two estuaries are located along the migratory flyway of Neotropical migratory shorebirds, but the Bahia Blanca estuary (area~110,000 ha) shows a much lower shorebird diversity than Mar Chiquita (area~4500 ha). The most common species in Bahia Blanca is the two-banded plover *C. falklandicus*, the species least affected by crabs at Mar Chiquita and which prefers to use high-density crab areas as foraging sites. The oystercatcher *Haematopus palliatus* was also most abundant in high-density crab areas, but they used these areas for resting. The abundances of preys varied during the study period and between the crab density areas, indicating that the use of these areas by birds is independent of crab density. However, burrowing

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crabs affect the depth distribution of polychaete and thus their availability to shorebirds. We suggest that this shorebirds–burrowing organism interaction could be generalized for other intertidal estuarine habitats.

1. Introduction

The choice of feeding areas by shorebirds in estuaries is influenced by several factors including sediment penetrability (Myers et al., 1980; Quammen, 1984; Mouritsen and Jensen, 1992) and prey availability (Bryant, 1979). A factor that has not received much attention is that intertidal mudflats are often strongly modified by the presence of organisms that affect the sediment (i.e., bioturbators). Those species are mainly burrowing crustaceans, such as thalassinidean shrimps in estuaries and bays from the northern hemisphere (e.g., Suchanek, 1985; Posey, 1986; Posey et al., 1991), or burrowing crabs in SW Atlantic estuarine mud flats (e.g., Iribarne et al., 1997; Botto and Iribarne, 2000). These bioturbators process large amounts of sediment (e.g., Branch and Pringle, 1987; Iribarne et al., 1997; Botto and Iribarne, 2000) and affect the sedimentary environment, usually by increasing water retention during low tide (especially in sediments with high contents of silt and clay; Rhoads and Young, 1970) and redistributing sediment particles (Levinton, 1989). As a result, they often determine the lateral and vertical distribution of other benthic species (Brenchley, 1981; Botto and Iribarne, 1999), which indirectly may affect shorebirds by altering their prey density and availability (Botto et al., 1998, 2000).

Estuarine intertidal flats from the southwestern Atlantic region (southern Brazil 28°S to northern Patagonia, Argentina 41°S) are stopover and wintering sites for several shorebird species that reproduce in North America and winter in South America (hereafter named Neotropical migrants). These species include the Red Knot (*Calidris canutus*), white-rumped sandpiper (*Calidris fuscicollis*), Hudsonian godwit (*Limosa haemastica*), greater yellowlegs (*Tringa melanoleuca*), lesser yellowlegs (*Tringa flavipes*), American golden plover (*Pluvialis dominica*) and black-bellied plover (*Pluvialis squatarola*) (e.g., Myers and Myers, 1979; Myers, 1980; Morrison and Ross, 1989; Botto et al., 1998). The two-banded plover *Charadrius falklandicus* is the only species that breeds in coastal Patagonia and winters in northern Argentina and Uruguay (Myers and Myers, 1979; Myers, 1980).

Intertidal flats and saltmarshes of the same region are dominated by the burrowing crab *Chasmagnathus granulatus* (Boschi, 1964; Capitoli et al., 1977, 1978; D'Incao et al., 1990; Spivak et al., 1994; Iribarne et al., 1997). This species inhabits the intertidal, from the soft bare sediment flats to areas vegetated by marsh plants (Boschi, 1964; Spivak et al., 1994; Iribarne et al., 1997; Bortolus and Iribarne, 1999) often generating extensive and dense (up 60 crab·m^{-2}) burrowing assemblages (Iribarne et al., 1997; Botto and Iribarne, 2000). Crabs excavate and maintain large (up to 7-cm diameter) semi-permanent open burrows (with an entrance that may reach 30 cm in diameter) that in the marsh area can extend up to 1 m into the sediment (Iribarne et al., 1997; Botto and Iribarne, 2000). They are one of the major habitat modifiers in SW Atlantic estuarine intertidal flats, and thus there is a potential for interfering with habitat selection and by migratory shorebirds (Botto et al., 2000).

A comparison between three nearby stopover estuarine environments in the SW Atlantic—Bahia Samborombon (35°30′–36°22′S), Mar Chiquita coastal lagoon (37°40′S) and Bahia Blanca (38°48′–39°25′S)—showed a surprisingly low diversity of shorebirds at the Bahia Blanca estuary (Botto et al., 1998), which is one of the largest intertidal mudflats in this region. The major difference between this site and the others appears to be the extremely large proportion of the intertidal area occupied by the burrowing crab *C. granulatus* (Botto et al., 1998). Indeed, a study performed at the Mar Chiquita coastal lagoon (Botto et al., 2000) showed that shorebirds species use the areas dominated by burrowing crabs differentially. *C. falklandicus* is the only species that spends all year in the southern hemisphere (Myers and Myers, 1979; Myers, 1980) and used the bioturbated areas more frequently than other bird species. Their prey capture

rate and feeding efficiency in these areas was also higher than *C. fuscicollis* and the yellowlegs *T. flavipes* and *T. melanoleuca* which were more common and efficient outside the burrow areas. Field experiments also showed that shorebirds do not affect polychaete density inside crab beds, but they reduce densities outside them (Palomo et al., 2003). This difference may be because sediments in crab beds remain wetter, softer and more homogeneous across the intertidal flats and throughout the tidal cycle than in areas without crabs (Palomo et al., 2003; Escapa et al., 2004). The vertical movement of infaunal organisms following during he tidal exposure/submergence cycle is greater in habitats without crabs. Prey organisms spend more of the time buried deeper in the sediment of crab beds, which decreases their availability to predators (Palomo et al., 2003; Escapa et al., 2004). Thus, several lines of evidence suggest that the pattern of low shorebird diversity at the Bahia Blanca estuary is the result of a crab–shorebirds interaction. To evaluate this general hypothesis is the main goal of this work.

At a local patch scale, migratory shorebirds use crab beds differentially (see Botto et al., 2000), but the actual mechanism is still not understood. Thus, one of the purposes of this study is to determine how size and density of crab burrows affect habitat use by local and migratory shorebirds at a small scale. To evaluate the hypothesis that differences in shorebird diversity between estuaries are the result of differences in the area covered by crab burrows (Botto et al., 2000), we compared this factor between Mar Chiquita coastal lagoon and the Bahia Blanca estuary. This was done using a combination of analysis of satellite images and field sampling. However, given that the previous study of shorebird habitat selection (Botto et al., 2000) was performed at the Mar Chiquita coastal lagoon, we repeated the study at Bahia Blanca estuary to evaluate if the pattern holds across estuaries.

2. Material and methods

2.1. Small-scale observations and experiments

A field study for the small-scale habitat use by shorebirds was performed at the Mar Chiquita coastal lagoon. This site is a microtidal (<1 m) body of brackish water (~4500 ha; i.e., Lanfredi et al., 1987;

Spivak et al., 1994) and characterized by mudflats and a large surrounding cordgrass (*Spartina densiflora*) marsh (Iribarne et al., 1997; Botto et al., 1998, 2000; Botto and Iribarne 2000). The burrowing crab *C. granulatus* is the numerically dominant macro-invertebrate in this area, being found in both the *S. densiflora* marsh and the bare mudflats (Spivak et al., 1994; Iribarne et al., 1997). The study site is a patchwork of crab beds and (located at the same intertidal level) without crabs (Botto and Iribarne, 2000).

2.1.1. Relationship between shorebird foraging paths and crab burrows

Each crab burrow is funnel-shaped with a large (up to 30-cm diameter), shallow (up to 5-cm depth) depression at the top and a smaller diameter (up to 7 cm diameter) burrow up to 50 cm deep in the mudflat; see Iribarne et al., 1997). Thus, the whole structure occupies a large surface area and if avoided by shorebirds the available foraging area will decrease. To determinate if shorebirds forage inside burrows, or just walk across them, the foraging path of at least 200 individuals of each species were followed for at least 10 m within the crab beds. A telescope (18×36) was used to identify species and to obtain information on their behavior. This was done by an observer standing at more than 30 m away. After shorebirds were identified to species, their foraging paths were identified by direct observation of their tracks in the sediment. Each time an individual walked between two adjacent burrows we measured the distance between its foraging path and the nearest burrow (a), and the distance between both burrows (b). Then a relative distance index, hereafter RDI, was obtained using the ratio a/b. On the assumption that crab burrows may affect the foraging path of different species differently, a Chi-squared analysis, hereafter χ^2 (Zar, 1999), of the distribution of the RDI was performed for all species pair combinations. By comparing the shape of distributions, this analysis allowed us to determine if some species avoided burrows more than others.

2.1.2. Experimental evaluation of the effect of burrow size on the foraging path of shorebirds

Since our results showed that shorebirds foraging paths tend to maximize the relative distance to burrows, a field experiment was performed to evaluate

if shorebird foraging paths are affected by different burrow sizes. An artificial crab bed (10×10 m) was constructed on a nearby mudflat, an area with very low crab density. Burrows were constructed using cores of 4- and 10-cm diameter, the range of sizes found in the natural crab bed (see Iribarne et al., 1997). The distribution of artificial burrows was homogeneous (spaced at 50 cm intervals) and alternating in sizes. At the next low tide, the foraging paths of different shorebird species were measured in relation to the burrows as described above. The results included foraging paths between burrows of equal and different sizes. Then, the frequency distribution of paths in relation to the distance between burrows of different sizes was calculated again using the RDI as described before. To determine whether shorebird burrow avoidance depended on their diameter, we examined the symmetry and kurtosis (Zar, 1999) of the frequency distribution generated by the RDI. In the case of burrows of different sizes, we evaluated symmetry (g_1; Zar, 1999). In the case of burrows of equal diameter, we also evaluated kurtosis (g_2; Zar, 1999) to see if shorebirds used the area between burrows differently. A platikurtic distribution indicates that birds used a wider path between burrows while a leptokurtic distribution indicates that they used a narrower path between burrows.

2.1.3. Relationship between crab burrows and shorebird infaunal prey

Shorebirds appears to avoid walking in or close to burrows, but the burrows may also affect the spatial distribution of their prey (i.e., polychaetes). To test this hypothesis, the density of polychaete fecal pellets on the surface (see Palomo and Iribarne, 2000) was measured at different distances (0–5, 5.1–10, 10.1–15 and 15.1–20 cm) from burrows (sampling unit of 5×5 cm). These fecal pellets belong to *Laeonereis acuta*, the dominant intertidal polychaete in this region (Palomo and Iribarne, 2000; Gutierrez et al., 2000; Botto and Iribarne, 2000), and given their correlation with individual density (see Palomo and Iribarne, 2000) were used as a surrogate of polychaete spatial distribution. Samples were also taken in three directions: (a) sediment mound (see Fig. 3), (b) sides (right and left from the axis between the sediment mound and the opposite side) and (c) opposite to the mound (see Botto and

Iribarne, 2000 for description). The null hypothesis of no difference was evaluated with a two-way (distance and direction) ANOVA test (Zar, 1999). The data were transformed when necessary to comply with the assumptions of the test.

Polychaete fecal pellet densities were also measured with the same methodology to test whether artificial burrows have a similar effect on shorebirds to natural crab burrows, and if they also affect the distribution of the infauna. To evaluate the null hypothesis of no effect on polychaete distribution the density of organisms from infaunal samples were evaluated with a one-way ANOVA (Zar, 1999) since there was no crab sediment-mound associated with the artificial burrows we did not expect differences in direction.

2.2. The density and distribution of crab burrows

Given that crab burrow openings are not used by feeding shorebirds (see Results), their presence decreases the available area for foraging or resting. Thus, to evaluate the importance of this effect, burrow density, spatial distribution and area covered by burrows was quantified from several crab beds. These crab beds are always well-defined areas dominated by burrowing crabs (see Iribarne et al., 1997; Botto and Iribarne, 2000). Based on the tidal level, crab beds were divided into seven intertidal zones (upper=A to lower=G) parallel to the shore, each zone with a tidal amplitude of 10 cm, which defines zones of similar exposure time. Given that the area of mudflat available for shorebirds depends on the area occupied by crab burrows, their density (in 1 m^2) and diameter (n=20 for each level) were sampled in the different intertidal zones inside crab beds. The available area without burrows was estimated from these samples, using the difference between total area and area occupied by crab burrows. We also made a better approximation to the available area for shorebirds by adding to the burrow size the surrounding areas affected by crab sediment removal, which is also not used by shorebirds (see results from previous sections). One-way ANOVAs (Zar, 1999) were used to evaluate the null hypothesis of no difference in the number of burrows and available area for birds between intertidal zones (A to G) using both area estimates.

2.3. Comparison of areas inhabited by crabs in the Mar Chiquita coastal lagoon and Bahia Blanca estuary

Previous studies have hypothesized that the lower diversity of neotropical migrant shorebirds in the Bahia Blanca estuary compared with Mar Chiquita is due to the larger proportion of the intertidal area occupied by crabs (Botto et al., 1998, 2000). To assess if this difference exists, we measured the amount of intertidal area with crab beds in Mar Chiquita (~4500 ha) coastal lagoon and in the Bahia Blanca (~110,000 ha) estuary. Given difference in size of these two estuaries, we used different approaches.

To assess variation of crab density along the mudflat at the Mar Chiquita coastal lagoon, a transect was sampled through the mid-intertidal area (0.4 m above mean low tidal level, hereafter amltl) and parallel to the shore. Every 20 m alongshore, a 1 m^2 sampling frame was placed haphazardly on the sediment and the number of crab burrows counted. This procedure was done for approximately 20 km of coastal area (60% of the lagoon perimeter). Crab density and location were marked on a map, and the data used to estimate the proportion of mid-intertidal are occupied by crab beds.

The Bahia Blanca estuary has one of the largest intertidal areas on the Argentinean coast mainly due to the 4.6 m of tidal amplitude. In this area, the proportion of the intertidal area occupied by crabs was evaluated using a mixed strategy that included field sampling and analysis of satellite images. Seven LANDSAT 5-TM images were analyzed to evaluate the amount of intertidal available for crabs. The area considered from the images encompasses the NW extreme of the Bahia Blanca estuary (21,168 ha; 38°50′–38°43′S; 62°16′–62°27′W). Images were obtained from January 1998 to February 1999. Each image was obtained with a different tidal level (January 15, 1999=0.19 m; July 7, 1998=0.47 m; January 28, 1998=1.57 m; February 16, 1999=2.55 m; November 28, 1998=3.07 m; April 2, 1998=3.97 m; October 27, 1998=4.4 m; all amltl). Images were processed with ERDAS IMAGINE software. For comparison purposes, images were geometrically corrected and referenced to the Transverse Mercator projection. An unsupervised classification, using an ISODATA algorithm, was performed on the image

with the highest tide (October 27, 1998). The possible maximum number of classes was set at 200, and a value of 98% of unchanged pixels between iterations was set as the threshold value for the convergence of the algorithm. Five principal classes were differentiated by analyzing the spectral signatures of the classes obtained: water, marsh, coastal land, salt deserts and inland. The classification map was recoded unifying the three classes belonging to areas that were never covered by water (coastal land, salt deserts and inland), resulting in a final map with three defined areas: water, intertidal and land. The class "land" was used to mask the surface always occupied by land in the other images, and the classification procedure was performed using the same parameters. The class "water" was defined on each classification map by analyzing the spectral signatures, and the remaining classes were assigned to the "intertidal" class. The area covered by water and the intertidal zone in each map was calculated in hectares. Finally, all maps were superimposed to obtain through the period analyzed two new maps, one corresponding to the area covered by water and the other one to the area covered by intertidal. Then we calculate the surface (in ha) occupied by water and intertidal in each map. Having calculated the intertidal surface area for each tidal height, using a stratified sampling design (Scheaffer et al., 1996), we estimated the number of burrows in the areas estimated by the satellite images using the densities obtained from the field sampling.

To determine the crab density, randomly allocated transects perpendicular to the coast and covering the entire intertidal were performed in 50 sites (see Fig. 5). In each site, we sampled crab density in the strata defined by the analysis of the satellite images. At each level, crab density was obtained by randomly throwing a 1 m^2 sampling frame. Using this data, we calculated the mean (S.D.) crab density for each stratum and the proportion of the intertidal area occupied by crab beds. The null hypothesis of no difference between estuaries in the proportion of the area occupied by crab beds was evaluated by a test for proportions (Zar, 1999).

2.4. Habitat use by shorebirds at the Bahia Blanca estuary

To evaluate the different uses of areas by shorebirds, three sites were selected in the NW part of the

estuary (38°50′44″S, 62°07′32″W), each one had a high crab density and nearby areas with a low crab density (each area approximately 150 m long and 60 m wide). Areas were located at the same tidal level and had a similar slope and orientation (NW–SE). These areas are known to be used by shorebirds. The percentage of birds feeding was noted each time and the number of birds was counted. Yates corrected χ^2 was used to evaluate the null hypothesis of no difference in bird activity between habitats. These censuses were performed, whenever possible, once a week throughout the migratory season from September 28, 2000 to April 23, 2001. The abundance of each shorebird species was compared between sites and months with repeated measures ANOVA (Neter et al., 1990).

To measure food resources available for shorebirds in areas with and without crabs, 10 randomly located cores (10-cm diameter, 10 cm deep) were taken monthly in each area during the period of shorebird observations. Individuals of all benthic species were identified and counted. Differences in the abundance of each benthic species between sites and areas were evaluated with a two-factor ANOVA, and a posteriori Tukey test when significant differences were found (Zar, 1999).

3. Results

3.1. Small-scale observations and experiments

3.1.1. Relationship between shorebird foraging paths and crab burrows

None of the foraging tracks went through a burrow or their area of influence delimited by the sediment removed by the crab. Moreover, an analysis of the distance of tracks from burrows showed that they are avoided by all shorebirds (Fig. 1). The RDI showed that C. falklandicus was less affected by burrows than T. melanoleuca (χ^2=10.5, df=4, p<0.05). However, there were no differences in the other comparisons (T. melanoleuca vs. P. squatarola: χ^2=5.15, df=4, p>0.05; T. melanoleuca vs. C. fuscicollis: χ^2=1.64, df=4, p>0.05; P. squatarola vs. C. fuscicollis: χ^2=1.08, df=4, p>0.05; P. squatarola vs. C. falklandicus: χ^2=1.34, df=4, p>0.05; C. falklandicus vs. C. fuscicollis: χ^2=2.44, df=4, p>0.05; Fig. 1).

3.1.2. Experimental evaluation of the effect of burrow size on the foraging path of shorebirds

The two most common species in the area, C. falklandicus and C. fuscicollis, avoided artificial burrows along their foraging path, and large burrows
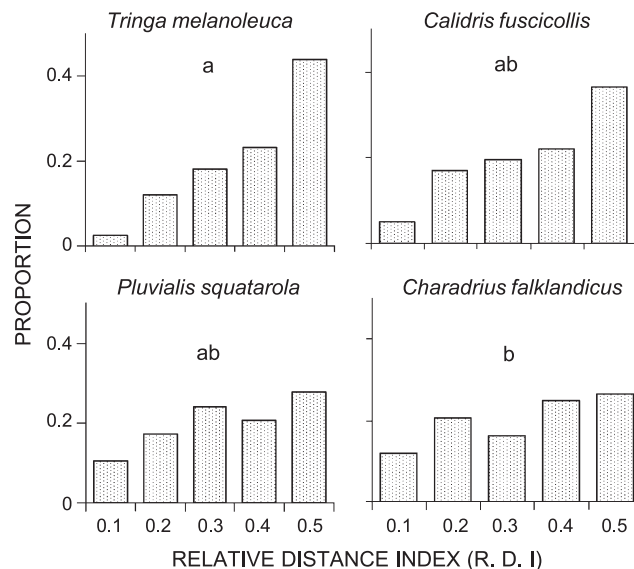

Fig. 1. Results of the relative distance index [RDI] obtained from field sampling using the ratio a/b, where a is the distance between both burrows and b is the distance to the nearest burrow.

more than small (Fig. 2). When both species walked between two large burrows, the distribution of the RDI was symmetrical (*C. falklandicus*: $g_1=-1.21\times10^{-15}$; $n=74$, $p>0.05$; *C. fuscicollis*: $g_1=0.0145$, $n=57$, $p>0.05$), but platikurtic for *C. falklandicus* ($g_2=-0.964$, $n=74$, $p>0.05$) and leptokurtic for *C. fuscicollis* ($g_2=-0.265$, $n=57$, $p<0.05$). A difference in kurtosis indicates that *C. falklandicus* was less affected by burrows and thus used a wider area than *C. fuscicollis*. However, when they went between burrows of different sizes, all birds avoided larger burrows more than the smaller ones, thus generating an asymmetric distribution. The distributions showed the same pattern as the samples previously described, *C. fuscicollis* used paths that went further from the large burrows ($g_1=0.93$, $n=26$, $p<0.05$; Fig. 2), while *C. falklandicus* had a smaller avoidance distance (*C. falklandicus*: $g_1=0.87$, $n=36$, $p<0.05$; Fig. 2).

3.1.3. Relationship between crab burrows and shorebird infaunal preys

The density of polychaete fecal pellets increased away from the whole burrow structure (ANOVA distance: $df=3,444$, $F=23.3$; $p<0.01$; Fig. 3). However, there was no interaction effect (ANOVA interaction: $df=6,444$, $F=1.82$, $p>0.05$), which indicates that

distance has the same effect in any direction (Fig. 3). The number of fecal pellets increased from the edge of the burrow reaching their highest values at 10 cm from the burrow. However, the effect was greater in the direction of the sediment mound (the effect of crab removal; ANOVA direction: $df=2,444$, $F=9.27$; $p<0.01$) since the higher densities were at 20 cm from the burrow (Fig. 3). Comparing the three studied directions, the lowest amount of polychaete fecal pellets was always in the area of the sediment mound.

The analysis of polychaete fecal pellets on artificial burrows showed no distance effect (ANOVA: $F=0.639$, $df=3,132$, $p>0.05$; Fig. 3). Thus, in this experiment, any effect found in the behavior of shorebirds is not due to changes in prey availability.

3.2. Crab burrows density and distribution

Crab beds showed different burrow densities in the Mar Chiquita coastal lagoon varying between 5.5 burrows m^{-2} (S.D.=3.7, $n=21$) up to 32.2 burrows m^{-2} (S.D.=9.1, $n=25$). Mean distance between burrows varied between 11.07 cm (S.D.=8.2, range=2–47 cm, $n=100$) and 53.5 cm (S.D.=41.6, range=2.3–173 cm, $n=101$). Burrow maximum diameter also varied between 4.1 cm
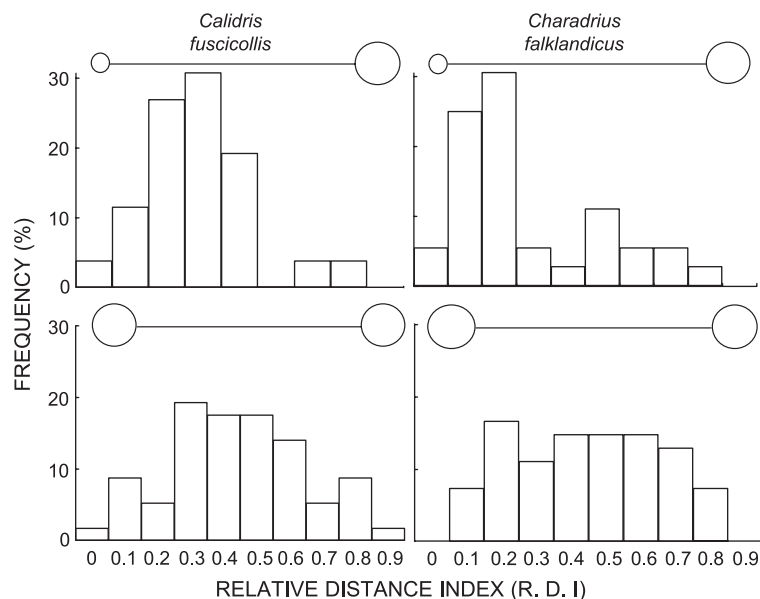

Fig. 2. Results of the relative distance index [RDI] obtained from experiments using the ratio a/b, where a is the distance between both burrows and b is the distance to the nearest burrow.
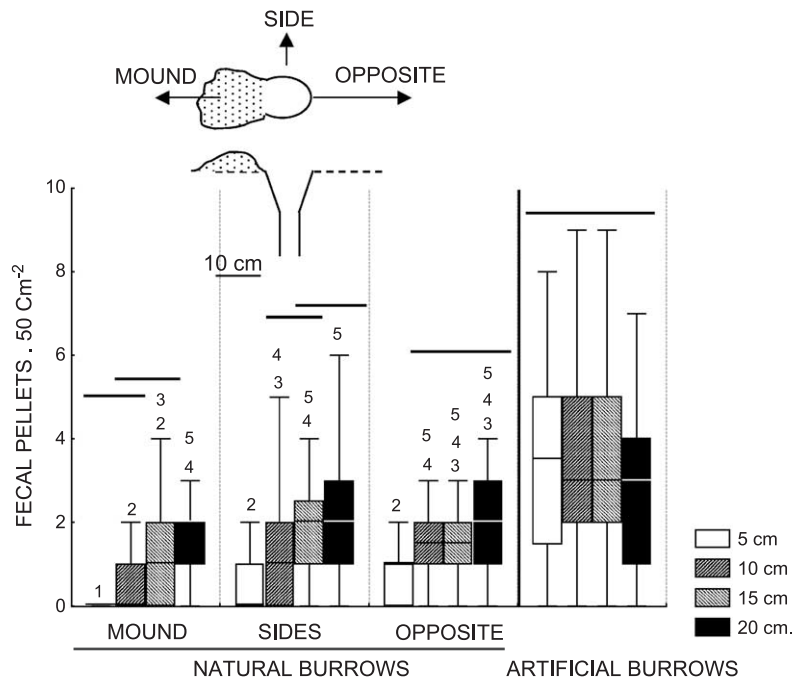
Fig. 3. A comparison of natural and artificial crab burrows and the density of polychaete fecal pellets at different distances (5, 10, 15, 20 cm) from their borders. The diagram above depicts the shape of a natural burrow and the location of samples. Artificial burrows were just straight tubes without sediment mound. Box plots are constructed with the limits of the boxes being the 25th and 75th percentile, lines outside boxes represent 10th and 90th percentiles, lines inside boxes are medians, and circles are outliers. Lines connect means with no significant differences between distances within same orientation. Different numbers represent significant differences between distances from the burrow.
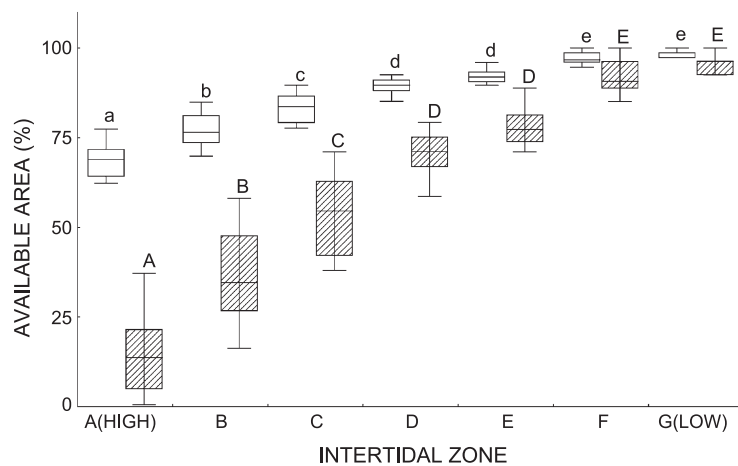

Fig. 4. Crab density across the intertidal area. Available area for shorebirds is expressed as the sum of the percentage of available area across the intertidal zones (A to G) inside the crab beds. Empty boxes show the area calculated by adding the burrow area plus the area affected by the sediment disturbance, and crossed boxes shows only the area occupied by the burrows. Different letters represent significant differences between intertidal zones (LSD test with $\alpha=0.05$).

Table 1
Results from the estimation from the composite of satellite images of the surface area (ha) defined by the tidal altitudes (tidal altitude) and the burrows density (burrows·m^{-2}; mean±S.D.) in each of these intertidal areas

Tidal altitude (m)	Area (ha)	Percentage	Burrow density (mean±S.D.)	Reference in Fig. 5
4.4				
	1036	20.2	40.3±10.9	A
3.97				
	2279	44.4	2.0±0.36	B
3.07				
	569	11.1	5.2±0.8	C
2.55				
	806	15.7	7.1±1.5	D
1.57				
	295	5.7	2.0±0.8	E
0.47				
	140	2.7	0.2±0.1	F
0.19				

(S.D.=2.5, range=0.5–10.5 cm, n=101) in the high-density patch and 6.5 cm (S.D.=2.1, range=1.6–12.7 cm, n=102) in the low-density patch.

The highest burrow density of *C. granulatus* was in the high intertidal zones and it decreased towards the lower zones (ANOVA: df=6,63, F=63.9, p<0.001). The available area for shorebird predation (total area−area occupied by burrows) decreased considerably in the high intertidal zones (ANOVA: df=6,63, F=76.67, p<0.001), reaching a maximum loss of potential feeding area of ~30% (Fig. 4). When the area occupied by burrows was added to the area avoided by shorebirds, the reduction in the available area showed the same pattern (ANOVA: df=6,63; F=104.4; p<0.001), but the loss of habitat reached ~70%.

3.3. Comparison of the areas inhabited by crabs in the Mar Chiquita coastal lagoon and the Bahia Blanca estuary

At the Mar Chiquita coastal lagoon, crabs were restricted to discrete patches in creeks, small embayment and the heads of channels. Transect along the beach showed variations in density between 0 and 60
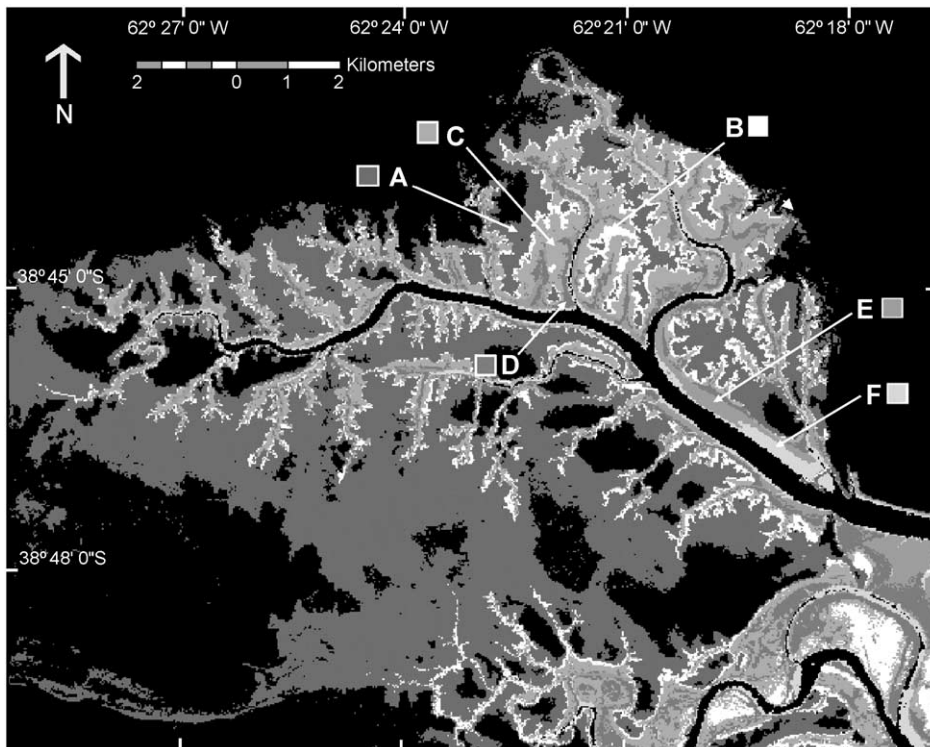

Fig. 5. Satellite image of tidal levels at the Bahia Blanca estuary. Each strata encompass areas with different tidal levels: *A*=4.4–3.97 m above mean low tidal level (amltl), *B*=3.97–3.07 m amltl, *C*=3.07–2.55 m amltl, *D*=2.55–1.57 m amltl, *E*=1.57–0.47 m amltl, *F*=0.47–0.19 m amltl.

crab m^{-2}. Crab beds occupied 39% of the mid-intertidal flats creating discrete burrowing assemblages.

At the Bahia Blanca estuary, we only found areas with different densities of crabs, but crabs were present everywhere. The total area analyzed with the satellite image was 5124 ha, and because the slope of the mudflat varied, the strata at different tidal heights also varied in the percentage of the total intertidal areas that they constituted. The areas at the different levels and the crab density of each strata (Table 1; Fig. 5) shows that the larger part of the intertidal is dominated by relatively high density of crabs. For example, the areas A, the upper part of the intertidal, cover more than 20% of the intertidals and show burrow densities of more than 40 burrows·m^{-2}. Moreover, more than 40% of the area shows densities of 2 burrows·m^{-2}.

3.4. Habitat use by shorebirds at the Bahia Blanca estuary

The shorebirds found during this study were the two-banded plover (*C. falklandicus*), the white-rumped sandpiper (*C. fuscicollis*), the common
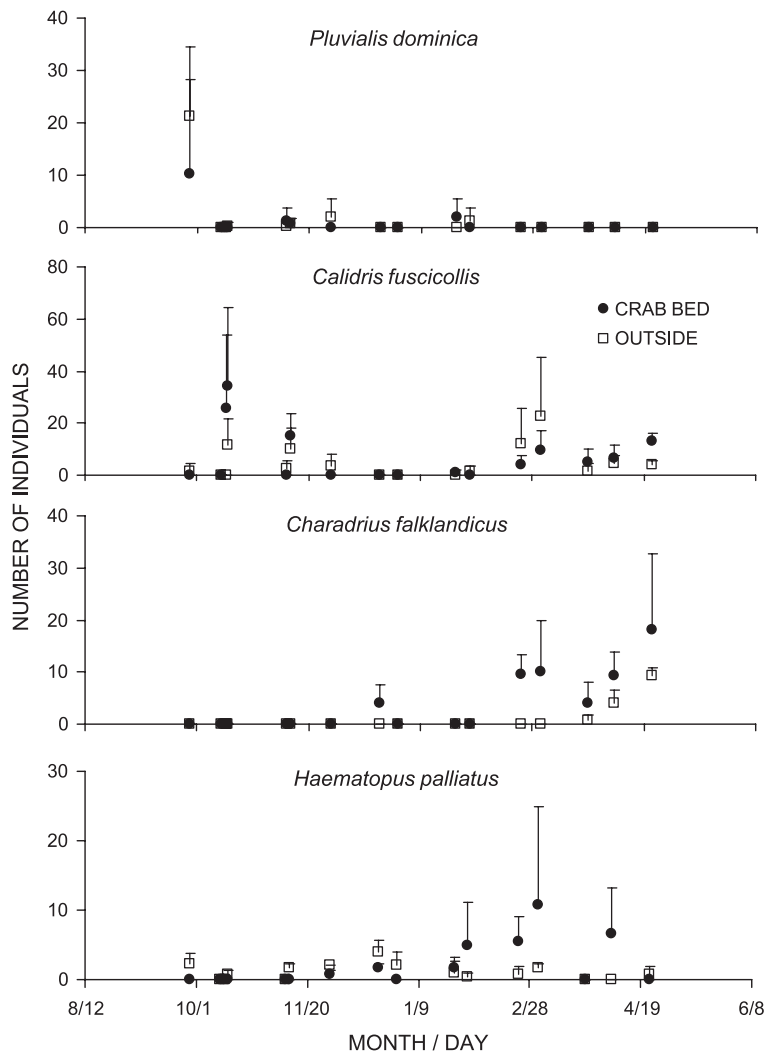

Fig. 6. Mean abundance (+1S.E.) of the different species of shorebirds in CRAB BED and OUTSIDE.

Table 2
Two-way repeated measures ANOVA of the numbers of each shorebird species in two areas, high crab density and low crab density

Source	DF	*Pluvialis dominica*		*Calidris fuscicollis*		*Charadrius falklandicus*		*Haematopus palliatus*	
		MS	F	MS	F	MS	F	MS	F
Between									
Area	1	12.7	0.67	145	1.2	157.6	5.95	15.8	0.58
Error	4	18.7		121.1		26.5		27.2	
Within									
Day	15	91.5	5.54*	292	3.34*	85.85	7.68*	16.51	1.88*
Day×Area	15	12.3	0.74	145	1.66	21.9	1.96*	16.64	1.89*
Error	60	16.5		87.3		11.18		8.76	

Each day of census was considered as the repeated factor.
 * $p < 0.05$.

oystercatcher (*Haematopus palliatus*) and the golden plover (*P. dominica*). In addition, one individual of greater yellowlegs (*T. melanoleuca*) was found once using the crab beds and one lesser yellowlegs (*T. flavipes*) was seen once in areas of low crab density. These two species were not considered in the statistical analysis due to their low abundance.

The repeated measures ANOVA showed an effect of day for all species of shorebirds (Table 2), indicating the variability of shorebird abundance during the summer season (Fig. 6). For two-banded plovers and oystercatchers, there was also an interaction between day and area (Table 2). These two species were more abundant in high-density crab areas in February, March and April (Fig. 6).

Almost all bird species fed most of the time (95–100% of the observed time). The exception was the oystercatcher, which was often resting. A comparison of areas showed that oystercatchers more often rested in crab beds and more frequently fed outside them (Yates corrected $\chi^2 = 21$, $df = 1$; $p < 0.05$; Fig. 6).

Table 3
F-values of the two-way ANOVA comparing abundance of polychaetes between sites (1, 2 and 3) and areas inside and outside the crab bed

Source	October	November	January	February	March
Sites	7.48**	5.81 NS	0.22 NS	0.35 NS	15.8**
Areas	46.34**	18.59**	0.01 NS	4.26*	6.63**
Areas×Sites	14.11**	6.97**	4.02 NS	0.11 NS	19.64**

Degree of freedom for Sites is 2, for Areas is 1 and for the interaction Sites×Areas is 2.
 * $p < 0.05$.
 ** $p < 0.01$.

The most abundant infaunal species was the polychaete *Laeonereis acuta*. The density of this species varied among sites (1, 2 and 3) and between areas (high crab density, low crab density; log transformed two-way ANOVA) for the different months sampled (see Table 3). In October and November, this polychaete was more abundant in the high-density crab areas in site 3 than in sites 1 and 2, where it was more abundant in the low crab density areas. However, there was no difference in worm density inside and outside the crab bed at site 3 (Tukey test, $p > 0.05$, Fig. 7). In January, worm abundance decreased and no effects of area or site were found (Table 3). In February and March, polychaetes were again generally more abundant in areas with high crab density (except for site 3 in March; see Table 3 and Fig. 7).

4. Discussion

Our small-scale observations and experiments showed that most migratory shorebirds observed in our study site avoided areas of high crab burrow density or when using a crab bed they avoided burrows and used paths that maximized the relative distance to the burrows. Moreover, larger burrows had a larger effect on the foraging paths of shorebirds, even when they were artificially made and did not affect the distribution of the bird's prey. However, the Neotropical migrant shorebirds (i.e., *C. fuscicollis*, *P. squatarola* and *T. melanoleuca*) were more affected by the burrows than the southern migratory shorebird *C. falklandicus*. The proportion of the intertidal are dominated by burrowing
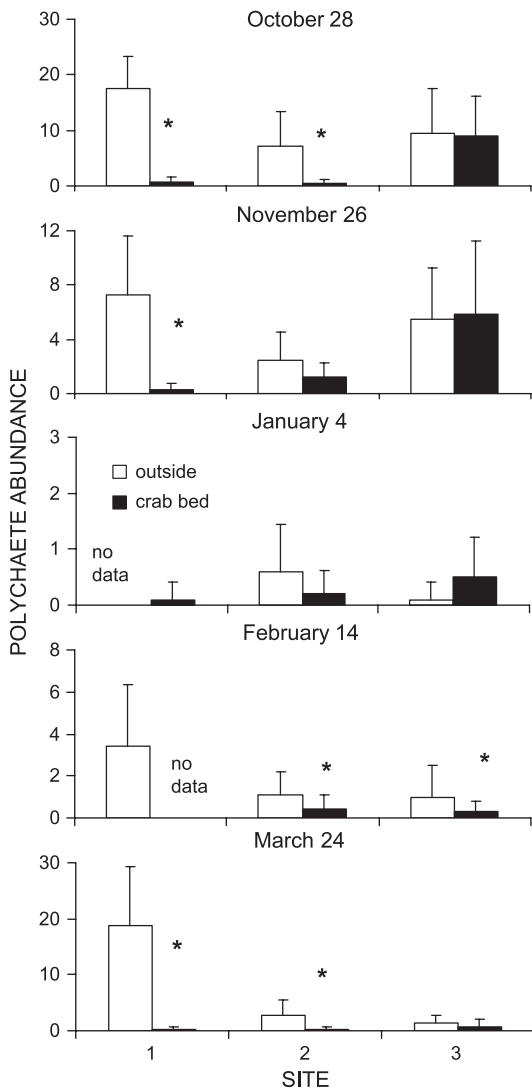
Fig. 7. Abundance of polychaetes (mean+S.D.) in each site (1, 2 and 3) and in each area (crab bed and outside), on five sampling occasions during the period studied.

crabs was much lower at the Mar Chiquita coastal lagoon (40%) than at the Bahia Blanca estuary (100%). Thus, everything suggests that burrowing crabs have a large effect on shorebird habitat use.

Burrowing species, including shrimps and crabs, often dominate the intertidal are due to their bio-turbating activities. Many of the species (e.g., thalassinids shrimps) construct extensive feeding galleries and are good examples of 'keystone species' (Mills et al., 1993) or more properly 'physical ecosystem

engineers' (Jones et al., 1994) in the soft sediment benthos (Aller and Dodge, 1974; Peterson, 1977, 1979; Bird, 1982; Murphy, 1985; Posey, 1986; 1990). Burrowing species, such as *Callianassa* and *Upogebia*, are very common in intertidal mudflats of both coasts of North America (Suchanek, 1985; Posey, 1986; Posey et al., 1991), in South Africa (Suchanek, 1985; Branch and Pringle, 1987), in the North Sea (Rowden and Jones, 1995) and in the western coast of Scotland (Nickell and Atkinson, 1995). They have high sediment turnover rates (e.g., Branch and Pringle, 1987; Swinbanks and Luternauer, 1987; Witbaard and Duineveld, 1989) greatly modifying intertidal mud-flats (e.g., Posey, 1986; Posey et al., 1991). The burrowing crab *C. granulatus* plays a similar role in SW Atlantic estuarine environments (Iribarne et al., 1997; Bortolus and Iribarne, 1999; Botto and Iribarne, 2000; Botto et al., 1998, 2000). There is no doubt that in most cases they structure the community by a strong 'top-down' process mediated by disturbance, but their effect on shorebird habitat use has not received much attention.

Burrowing species may affect shorebirds by altering sediment characteristics and indirectly affecting prey availability. Food resources together with sediment softness are the most common factors in determining shorebird habitat selection (Bryant, 1979; Goss-Custard, 1985; Gerritsen and van Heezik, 1985). In our case, the crab increases sediment softness (Botto and Iribarne, 2000), but still these habitats are not selected by shorebirds. One of the reasons is the disturbance by crabs (up to 5 kg·m^{-2}·day, Iribarne et al., 1997) which homogenizes the sediment down to 30-cm depth (Botto and Iribarne, 2000). The infauna always buries much deeper in these areas, decreasing their availability for surface predators (Escapa et al., 2004). Thus, even when prey density is the same inside and outside crab beds (Botto and Iribarne, 2000; Botto et al., 2000; Palomo et al., 2003, our data), their availability to shorebirds is different. There is no information about this relationship for other burrowing species, but we suspect that their effect may be similar on other infauna; indeed, it may be a general pattern.

However, burrowing species may also affect shorebirds by decreasing the habitat due to the empty space created by the burrow itself. In fact, no one of the shorebird species seen in our study walked through

burrows, even when the funnel-shaped entrances are shallow depressions. Thus, bird habitat decreases in quality because less of it is available for feeding around the burrows. In some sites, the actual surface area available for shorebirds to feed decreased by more than 50%. Finally, an increase in sediment softness due to bioturbation may be another cause of area avoidance. It is generally agreed that birds prefer to walk on firm sediments rather than on soft mud (referee communication). Walking in soft sediments might have an extra energetic cost.

The effect is not restricted to the area occupied by burrows, but shorebirds also tend to use paths that maximize the distance to burrows and show a greater avoidance of larger burrows. However, not all shorebird species are equally affected. The species that use the crab burrow beds least often (*C. fuscicollis*, *P. squatarola* and *T. melanoleuca*; see Botto et al., 2000) showed a greater avoidance of burrows. However, *C. falklandicus*, a shorebird that only migrates regionally (Myers and Myers, 1979; Myers, 1980) and spends most of the year in this region, was the species that showed the least avoidance of burrows. What is also interesting is that most shorebirds tend to avoid the burrows by a wider margin than their prey are affected by the crab. One possible explanation is that effects of food density on shorebirds may be non-linear. Thus, if densities were lowered below a critical point (i.e., the plateau region of a functional response), no effect on foraging success would be expected. However, small changes in density could have a larger effect at lower prey densities. Although this hypothesis needs to be evaluated, our information show that the interaction between crabs and shorebirds is due to more than the space taken by their burrows.

The pattern of differences in diversity of shorebirds between SW Atlantic estuaries (Botto et al., 1998, our data) is also interesting because it indicates that the size of the intertidal habitat per se is not necessarily factor in determining their value for shorebirds. Burrowing species, such as the crab described here, are common worldwide. They inhabit intertidal areas that are important stopover sites for many species of shorebirds, and our evidences suggest that they have a major effect on the habitat selection of these shorebirds. In some cases, the burrowing shrimps are the food source (e.g., *Upogebia africana* as a food source of the gray plover *P. squatarola* and whimbrels

Numenius phaeopus; Turpie and Hockey, 1996). In other cases, they may have a negative effect. For example, the western sandpiper *Calidris mauri* and the Ruddy turnstone *Arenaria interpres* use as stopover site Grays Harbor (Washington, USA; O'Reilly and Wingfield, 1995), an area densely populated by burrowing shrimps (e.g., Posey et al., 1991), which are not used for food.

Summing up all the evidences suggests a direct (decrease of habitat) and indirect (changing prey availability) effect of burrowing crabs on migratory shorebirds in the SW Atlantic estuarine environments. We believe that a similar interaction is likely to occur with other burrowing species that form dense intertidal beds.

Acknowledgements

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