Hydrobiologia (2007) 587:291–302
DOI 10.1007/s10750-007-0692-8

ECSA39

Environmental factors drive habitat partitioning in birds feeding in intertidal flats: implications for conservation

José P. Granadeiro · C. D. Santos · M. P. Dias · J. M. Palmeirim

Abstract We present data on the low-tide distribution of shorebirds in the Tagus estuary, Portugal, and relate the distribution of the bird assemblage with environmental factors. The study was based on an extensive survey of the majority of the intertidal flats, carried out with a high spatial resolution. The environmental factors that mostly affected the distribution of shorebirds were the exposure period, the type of sediment and the extent of the shell banks. The feeding bird assemblage could be divided into four main groups of species, and these occupied distinct areas of the estuary. These findings imply that maintaining the overall value of the estuaries for foraging shorebirds requires relatively extensive intertidal areas, encompassing sediment flats with the large diversity of ecological characteristics required by different species.

Keywords Canonical correspondence analysis · Low-tide counts · Shorebird · Spatial distribution · Tagus estuary

Guest editors: M. J. Costa, H. Cabral & J. L. Costa
Towards an integrated knowledge and management of estuarine systems

J. P. Granadeiro (✉)
Centro de Biologia Ambiental – Departamento de Zoologia e Antropologia (Museu Bocage), Museu Nacional de História Natural, Rua da Escola Politécnica 58, 1269-102 Lisboa, Portugal
e-mail: jpgranadeiro@fc.ul.pt

C. D. Santos · M. P. Dias · J. M. Palmeirim
Centro de Biologia Ambiental – Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal

Introduction

Large numbers of shorebirds depend on the intertidal areas of estuaries for feeding during the non-breeding season. Many estuaries support important wintering bird populations and some of them hold an additional significance by being located in the migratory "flyways" of some species. The wetlands within the flyways constitute a network of potential stopover points, connecting the breeding and wintering grounds of those species, and so they may temporarily harbor huge (yet often unquantified) numbers of birds, searching for food and rest during migration (Rehfisch et al., 2003).

Many species of shorebirds currently face a steady reduction in their global populations (e.g. BirdLife International & European Bird Census Council, 2000; Stroud et al., 2004), and therefore the conservation and correct management of estuarine wetlands is an issue of increasingly relevance. This task requires information about the numbers of birds staging or stopping over in the area and of their distribution in the intertidal feeding areas. In fact, because many species of shorebirds concentrate in a restricted number of feeding sites, relatively local (but persistent) impacts can ultimately decrease the carrying capacity of the estuaries. Hence, a good knowledge of the bird distribution is of major importance for conservation planning of estuarine wetlands, both at local and regional scales. However, while this information is available for a few areas (e.g. Musgrove et al., 2003), it is still missing for the majority of the estuarine areas.

Several studies have examined the distribution of bird feeding in estuaries in relation to environmental factors (e.g. Bryant, 1979; Symonds et al., 1984; Goss-Custard & Yates, 1992; Yates et al., 1993; Moreira, 1993; Scheiffarth et al., 1996; Granadeiro et al., 2004). In fact, understanding the key determinants of the feeding site selection can be important to predict the effects of impacting human activities. Preferably, such studies should not be based on data collected over a small fraction of the wetland but resource and logistic constraints often force researchers to narrow their samplings (e.g. by concentrating the sampling effort mostly near the coast line). Such data may represent a biased subset of the conditions prevailing over the majority of the estuary, and hence may fail to identify important factors influencing the broad-scale patterns of shorebird distribution.

This study aimed at describing the low-tide distribution of shorebirds in the Tagus estuary, and to interpret it in relation to relevant environmental factors. In particular, we (1) examined the spatial distribution of the most abundant species, (2) investigated the most important factors influencing the distribution of the bird and (3) group the species according to the similarity of their distribution at the level of the estuary.

Methods

Study area

This study was carried out in the Tagus estuary, Portugal (38°45′ N, 09°02′ W; Fig. 1). In this estuary the tides are semi-diurnal, with an amplitude ranging from 1 to 3.8 m in neap and spring tides, respectively. The sediments are relatively diverse, but most of the area consists of mudflats and oyster banks (Calvário, 1984). About 97 km^2 of sediment flats are exposed at low water during an ordinary spring tide (0.6 m). In 1988, the Tagus estuary was designated as a Special Protection Area for Birds (covering about 450 km^2 of intertidal areas and surrounding land), under European Union legislation, and part of it is also classified as Nature Reserve since 1976.

Bird counts

Low-tide bird counts were carried out from December to mid-March in both 2002 and 2003. They covered all the intertidal areas from the marsh or coastal edge to the low water mark. In 2002 we were not able to count the southern portions of the intertidal flats of the estuary (Fig. 1). Therefore the data analysed in this study refers only to the large sediment flats located north of Montijo, which comprise about 73% of the total intertidal area (Fig. 1).

In the inner parts of the estuary (away from the coastline, see Fig. 1), we marked the counting sectors using a grid of canes placed with the help of a GPS. The total area counted during a single day consisted of a rectangle of 2.5 km × 1.2 km (300 ha). In this large area, the individual counting sectors had a surface of about 3.75 ha and were generally triangular shaped (Fig. 1). The center of the area was reached by boat during the receding tide and at low water two observers slowly walked in opposite directions along a transect on the edge of the sectors. Each observer walked ca. 3 km during each count and recorded the number of birds feeding in the ca. 40 triangular sectors.

The intertidal areas not included in this grid, mostly located near the coast or close to the main channels, were divided into sectors using landmarks, chosen to define relatively regular counting areas. Birds were counted with binoculars and telescopes from vantage points on the coast. Counts were carried out in spring tides (tidal height < 1 m) within ±2 h from the time of low water, when most of the feeding areas were exposed and the distribution of birds is believed to be most stable (Yates & Goss-Custard, 1991).

The birds were not particularly disturbed by our counts, and in fact they tolerate our presence very reasonably. In addition, we were always aware of any arrival or departure of flocks of birds in the areas to be counted to avoid missing or duplicating records of bird flying to, out or within the area. It proved difficult to ensure that all Lesser Black-backed Gulls (*Larus fuscus* Linnaeus, 1758) were actively feeding during the counts, and so we possibly included some birds that were just resting.

The boundaries of all sectors and the corresponding count data were entered in a Geographical Information System (GIS) and the densities of birds (expressed as number of birds per 10 ha) were computed after calculating the area of each sector in the GIS.

There were some differences between years in the exact boundaries of some of the sectors. In order to combine the data obtained in 2002 and 2003, we started by determining the geographical coordinates of the centroids of all 2002 and 2003 sectors in the GIS. We then defined a fixed regular grid of plots measuring 230 m * 140 m (3.22 ha) over the entire study area against which we projected the (centroids of the) sectors counted both in 2002 and 2003. These regular plots (hereafter called quadrats) were approximately of the same area of our counting sectors, and thus were the best grid approximation of our

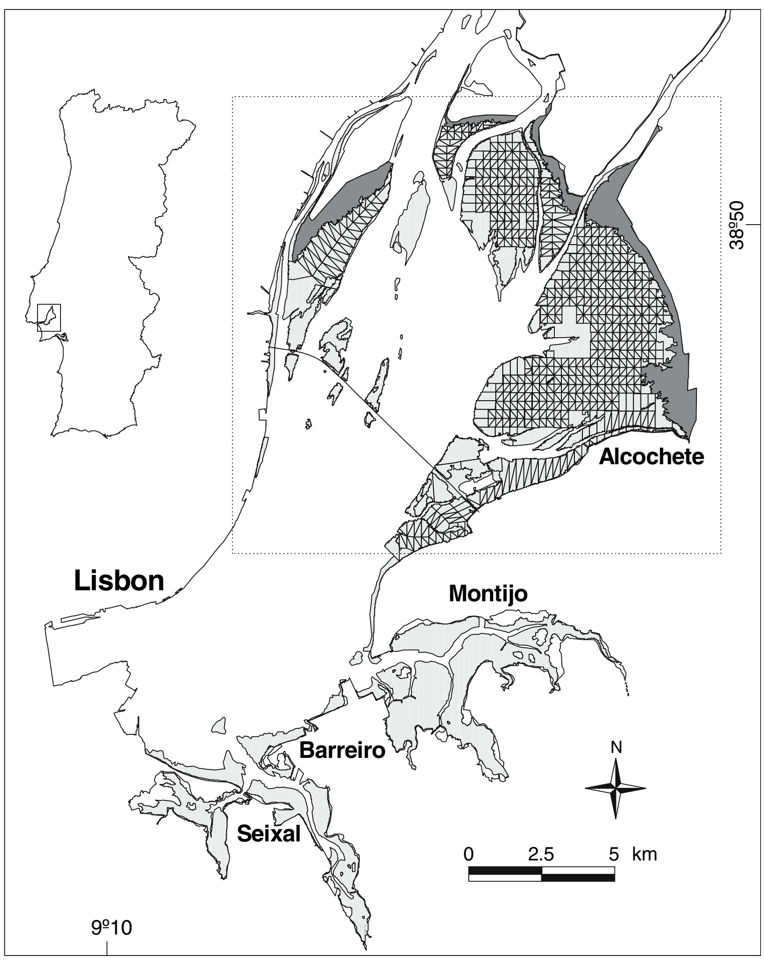

Fig. 1 The Tagus estuary and location of the study area (dotted square). Dark grey areas represent salt marsh, and light grey areas represent intertidal flats

sampling scheme. The density of birds in each quadrat was calculated as the average of the centroids lying within the limits of the quadrats. After applying this procedure to data collected in 2002 (1069 quadrats) and 2003 (1114 quadrats), we overlapped (and averaged where appropriate) the quadrats from the 2 years, resulting in a final dataset consisting of 1239 quadrats.

Environmental and GIS variables

Environmental data were collected during the counts carried out in 2003. Two hundred and sixty nine sampling points were selected in the study area, close to the transect walked for counting the birds. These points were regularly spread throughout the entire study area, and we measured the following variables in each of them:

- *Mud*—Mud (and silt) content of one small core of sediment (about 50 ml), calculated as percentage dry weight of particles < 0.063 mm;
- *Organic content of the sediment*—Difference between the dry mass of a sediment sample (ca. 1 g) before and after ignition at 500°C during 4 h, divided by the initial dry mass;
- *Surface water*—Percentage of the area covered by water (depth < 10 cm);
- *Algae*—Percentage of the area covered by macrophyte algae, regardless of the species;
- *Shell banks*—Percentage area covered by dead shell banks, either oysters *Cassostrea spp.* or the bivalve *Scrobicularia plana* (da Costa, 1778).

The surface water, amount of algae and shell coverage were estimated in 4 plots measuring 4 m × 4 m, evenly spaced along a 30 m transect in the vicinity of the sampling point. The values of the four plots were then averaged, in order to improve the accuracy of the estimates.

Environmental variables were measured on a grid wider than that of bird counts. Therefore, the value assigned to each bird quadrat was calculated as the average of the environmental sampling stations within 500 m of the quadrats (usually between 1 and 3 sampling stations), weighted by the inverse of its distance to the centroid of the quadrat. Quadrats without environmental data (i.e. further than 500 m from a sampling point) were excluded from the analysis (n = 162).

In addition to these variables, we also calculated the distance of each quadrat to the main channels (*Distance to channels*), to the coast (*Distance to coastline*) and to the nearest high water roost sites (*Distance to roost*), using the GIS facilities. Finally, we calculated the approximate exposure period of each quadrat (*Exposure*), by modelling the progress of a tide line in the estuary. The position of the water edge was digitized in five satellite images, obtained in different phases of the rising tide. Each of these digitized lines was associated with a value of tidal height, estimated from the exact time of image collection and from local tide tables. An additional line was digitized along the limits of the salt marsh, which we associated with the high water height known to reach its edge (3.4 m, personal observations). We then calculated height values for the entire estuary, by linearly interpolating between these lines, using the Contour Gridder extension to ArcView. The progress of the tidal line differs between rising and receding tides, which means that the results of our model may not be exactly proportional to the exposure period. Nonetheless, the procedure offers an approximation that we believe is adequate for the purposes of our study. Hereafter GIS and site-measured environmental variables will be jointly referred to as ‘‘environmental variables’’.

Data analysis

In order to test the spatial agreement in the densities of birds counted in 2002 and 2003, we used Spearman rank correlations. This method allowed us to test the concordance between the rank importance of quadrats. Association between the bird assemblage and environmental variables was examined using a canonical correspondence analysis (CCA). CCA is a non-linear ordination technique, and differs from a correspondence analysis (also known as ‘‘reciprocal averaging’’) because during each iteration the site scores are entered as dependent variable in a multiple (least-square) regression with the environmental variables (Braak, 1986; Palmer, 1993). Thus, CCA provides an ordination of a matrix of species by sites, where the axis are constrained to be maximally correlated with a set of environmental predictors. Prior to the analysis, count data were $\log(x + 1)$-transformed and environmental variables were centred and scaled to unit variance (Braak, 1986; Palmer, 1993). Sectors where no birds were counted ($n = 199$) were excluded from this analysis, so the CCA was based on species and environmental matrices with 878 quadrats. The solution of the CCA was displayed in an ordination diagram, where species were represented as points and variables represented as vectors. The directions defined by these vector represent gradients of the corresponding variables, and thus the (perpendicular) projection of the species points in these directions represent their position along the gradient (Braak, 1986).

In order to better visualize the structure of the distribution of species along the gradients generated by the CCA, we carried out a cluster analysis (based on the Unweighted Pair Group Method with Arithmetic Mean algorithm, Gauch (1982)) using the scores in the first three axis of the CCA.

We tested the differences in the distribution of the groups of species (see Results) using the Jaccard coefficient. This index measures the degree of overlap between two datasets and was computed as the ratio between the number of quadrats not shared by two groups and the total number of quadrats where one or both groups occurred (Venables & Ripley, 2002). The value calculated for each pairwise comparison of groups was tested against a distribution of 2000 random permutations of the data sets, which would represent the expectations assuming a fully random distribution of the two groups.

All computations were carried out using the freely available statistical package R (R Development Core Team, 2005), and the CCA was carried out using the *vegan* package (Oksanen et al., 2005), running under R.

Results

Number of birds in the estuary and between-year variability

Overall, in our study area we counted ca. 28,000 birds in sectors covering 59.4 km^2 in 2002, and ca. 20,800 birds in 58.6 km^2 in 2003. The densities of Avocet (*Recurvirostra avosetta* Linnaeus, 1758), Black-tailed Godwit [*Limosa limosa* (Linnaeus, 1758)] and Flamingo (*Phoenicopterus ruber* Linnaeus, 1758) decreased substantially from 2002 to 2003, whereas the number of Dunlins [*Calidris alpina* (Linnaeus, 1758)] followed the inverse trend (Table 1). In both years Dunlin was the most abundant species, with an average count of ca. 8000 birds. The density of Lesser Black-backed Gulls was very similar in both years, and in average this was the second most abundant species. A few species occurred in very low densities (< 0.1 birds per 10 ha), such as the Curlew [*Numenius arquata* (Linnaeus, 1758)], Whimbrel [*Numenius phaeopus* (Linnaeus, 1758)], Curlew Sandpiper [*Calidris ferruginea* (Pontoppidan, 1763)], and these are not listed in Table 1.

The correlation between the densities recorded in quadrats containing data from both 2002 and 2003 varied among species. Lesser Black-backed Gull, Little Egret [*Egretta garzetta* (Linnaeus, 1766)], Redshank [*Tringa totanus* (Linnaeus, 1758)], Kentish Plover (*Charadrius alexandrinus* Linnaeus, 1758), Ringed Plover (*Charadrius hiaticula*), Black-headed Gull (*Larus ridibundus*), Dunlin, Sanderling [*Calidris alba* (Pallas, 1764)] and Grey Plover [*Pluvialis squatarola* (Linnaeus, 1758)] showed significant correlation between the densities in both years (Spearman r: range 0.12–0.40, all $P < 0.05$), whereas the remaining 9 species showed little concordance between years (Spearman r: range 0.01–0.02, all non-significant). Establishing larger sectors (by duplicating the length and width of each quadrat, i.e. multiplying the area of the quadrats by four) and averaging the density estimates from neighbour sectors did not produce a very substantial improvement in these correlations. In fact, only two more species [Turnstone *Arenaria interpres* (Linnaeus, 1758) and Bar-tailed Godwit *Limosa lapponica* (Linnaeus, 1758)] achieved marginal significances between their distribution in 2002 and 2003. The between-year agreement was not related with the density of the species (Spearman $r = -0.2$, $n = 18$, n.s.), but it was positively correlated with their frequency of occurrence (Spearman $r = 0.48$, $n = 18$, $P < 0.05$).

Table 1 Densities (number of birds per 10 ha ± SD), frequency of occurrence (Freq.: expressed as the proportion of sectors where the species was detected), and total number of birds counted in the Tagus estuary during the surveys carried out in 2002 and 2003. Species are sorted by their average density

	Survey in 2002 (n = 1069 quadrats)			Survey in 2003 (n = 1114 quadrats)			Average 2002–2003 (n = 1239 quadrats)		
	Density	Freq	Total	Density	Freq	Total	Density	Freq	Total
Dunlin	11.9 ± 30.3	0.39	7083	15.3 ± 39.1	0.44	8953	13.6 ± 35.0	0.40	8018
L.Black.b.Gull	5.7 ± 21.2	0.22	3383	6.3 ± 21.4	0.21	3698	6.0 ± 21.3	0.21	3540
Avocet	8.8 ± 102.4	0.16	5200	2.8 ± 14.1	0.09	1651	5.8 ± 73.4	0.12	3425
Black-t.Godwit	8.7 ± 151.7	0.09	5145	1.2 ± 11.9	0.04	718	5.0 ± 108.0	0.06	2932
Grey Plover	3.5 ± 9.6	0.37	2100	3.8 ± 18.5	0.37	2248	3.7 ± 14.7	0.36	2174
Black-h.Gull	2.4 ± 11.7	0.09	1438	1.6 ± 14.8	0.06	943	2.0 ± 13.3	0.07	1190
Flamingo	2.4 ± 23.4	0.03	1444	0.4 ± 14.9	0.00	229	1.4 ± 19.6	0.02	836
Redshank	1.2 ± 4.2	0.16	718	1.0 ± 3.6	0.14	593	1.1 ± 3.9	0.15	656
Bar-t.Godwit	0.5 ± 3.7	0.06	304	1.0 ± 5.7	0.08	561	0.7 ± 4.8	0.07	432
Ringed Plov.	0.3 ± 2.0	0.05	183	0.5 ± 4.8	0.06	295	0.4 ± 3.6	0.05	239
Sanderling	0.4 ± 3.2	0.02	217	0.2 ± 1.0	0.03	97	0.3 ± 2.4	0.02	157
Grey Heron	0.2 ± 1.4	0.03	111	0.4 ± 2.3	0.06	221	0.3 ± 1.9	0.05	166
Knot	0.2 ± 3.0	0.01	140	0.3 ± 4.4	0.02	187	0.3 ± 3.8	0.02	164
Kentish Plov.	0.5 ± 2.7	0.05	268	0.2 ± 1.4	0.04	138	0.3 ± 2.1	0.04	203
Turnstone	0.1 ± 0.5	0.02	42	0.1 ± 1.0	0.03	87	0.1 ± 0.8	0.02	65
Little stint	0.2 ± 1.7	0.02	111	0.0 ± 0.3	0.00	13	0.1 ± 1.2	0.01	62
Little Egret	0.1 ± 0.6	0.03	64	0.2 ± 0.8	0.05	97	0.1 ± 0.7	0.04	81
Greenshank	0.1 ± 1.2	0.02	58	0.1 ± 0.5	0.03	44	0.1 ± 0.9	0.02	51

Species association and relationship with environmental factors

Some of the environmental variables were highly correlated, and therefore were excluded from the analysis. The organic content of the sediment was correlated with amount of mud (r = 0.67, n = 269, P < 0.001), so we excluded the former. Both the distance to the coast and the distance to the nearest roost were correlated with the exposition period (r = –0.54 and r = –0.48, respectively, both P < 0.001, n = 269), so we retained the later.

The structure of bird assemblage was examined using a CCA, and the results of the analysis are shown in Table 2 The canonical axis I and II (explaining respectively 52.3% and 18.4% of the variance, Table 2) ordinated the species along two gradients: (1) exposure period, mainly responsible for the separation of Avocet, Black-tailed Godwit and Flamingo and (2) mud content of the sediment, where Dunlins occupy the muddiest sites and Sanderlings the most sandy areas (Fig. 2). Axis III accounted for 11.8% of the variance and mainly separated sites according to the relative amount of algae and oyster beds (Fig. 2, Table 2). The environmental variables were able to explain ca. 12% of the variability of the bird scores.

A cluster analysis revealed four main groups: Group 1, comprising the Flamingo, Black-tailed Godwit and Avocet; Group 2, which includes the Kentish Plover, Greenshank, Knot, Ringed Plover and Turnstone; Group 3, with Lesser Black-backed Gull, Sanderling, Black-headed Gull, Little Egret and Little Stint; and Group 4 comprising Dunlin, Redshank, Grey Plover, Bar-tailed Godwit and Grey Heron (Fig. 3). Although the Flamingo represents a separate group in the dendrogram (Fig. 3), its position in relation to the gradients of the CCA supports the inclusion in the group formed by the Avocet and Black-tailed Godwit (Fig. 2). The environmental characteristics of quadrats where each group occurred are listed in Table 3.

The groups showed distinct distributions in the estuary, with Group 4 being relatively widespread whereas all the other groups showed a much more localised occurrence (Fig. 4). The patterns of distribution of these groups were significantly different, as assessed by the Jaccard similarity coefficient (all pairwise comparisons P < 0.01).

Table 2 Summary statistics of the canonical correspondence analysis (sum of all eigenvalues = 0.574)

	Axis I	Axis II	Axis III
Eigenvalues	0.30	0.11	0.05
Cum. % variance	52.3	70.7	82.5
Species/environment correlations	0.70	0.46	0.45
Interset correlation of environmental variables with axes			
Mud	0.32	0.25	0.23
Surface water	0.27	–0.24	0.10
Algae	–0.25	–0.09	–0.32
Shell banks	–0.36	–0.12	0.15
Distance to channels	0.51	0.08	–0.20
Exposure	0.61	–0.13	–0.13

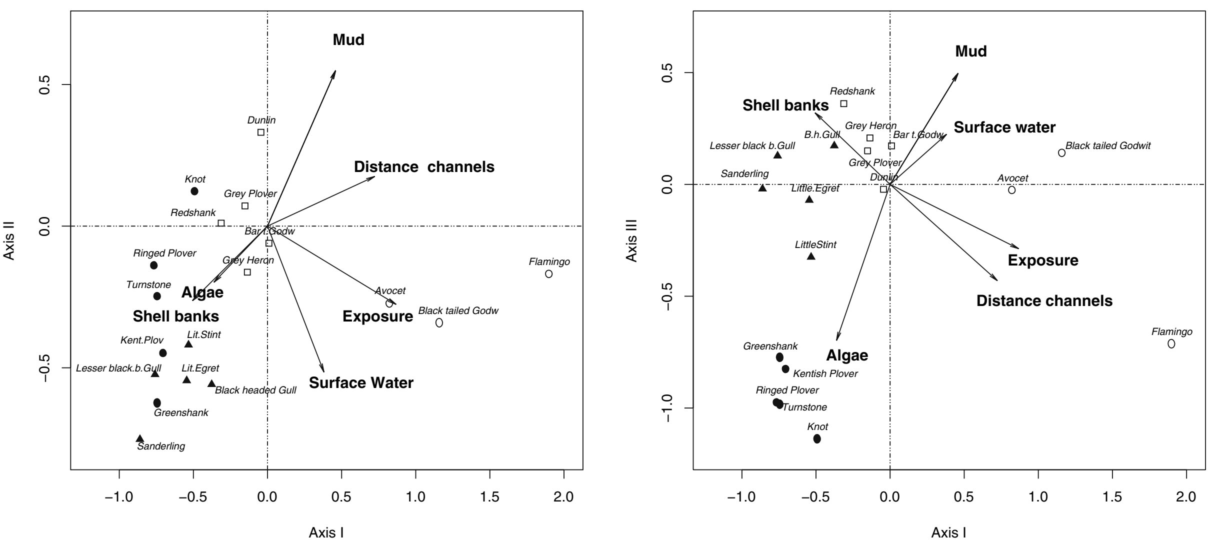

Fig. 2 CCA ordination diagrams based on the (log-transformed) bird density data and (centred and scaled) environmental and GIS variables. Axis I, II and III accounted for 52.3%, 18.4% and 11.8% of the variability that could be explained by the environmental variables, respectively. Symbols represent species clusters, defined according to their relative distance in the CCA space (for explanation, see text)

Discussion

Comparison between years and with previous work

This study presents data on low-tide distribution of shorebirds feeding in the intertidal flats of the Tagus estuary at a high spatial resolution. Our counts covered the vast majority of the intertidal areas, hence our total population estimates will not be affected by bias due to partial sampling of the estuary (Dias et al., 2006). Half of the species counted in the estuary showed a reasonable (and significant) agreement between their patterns of distribution in 2002 and 2003. The lack of between-year concordance in the distribution of the remaining species did not seem to result from the small size of sectors, which could introduce noise due to excessive spatial detail. The agreement was lower in the case of species that occurred in a smaller number of quadrats, either due to a low abundance or to a high concentration of the individuals. In these circumstances the sampling obtained in each year is likely to underestimate the area used by the species, resulting in a smaller agreement between years. However, the combination of the results of the two years should yield a better characterization of the use of space by these birds.

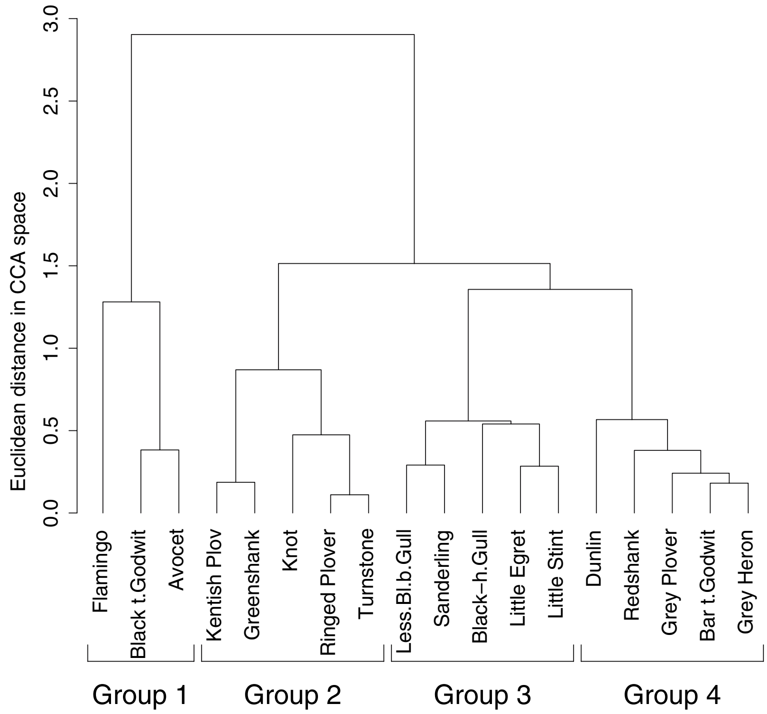

Fig. 3 Dendrogram (based on euclidean distances and UPGMA algorithm, Gauch (1982)) representing the similarities among species in the space defined by the first three axis of the CCA (see Methods)

Table 3 Summary of environmental characteristics (means ± SE) in the areas of occurrence of each group of species (sample sizes are indicated in parenthesis)

	Group 1 (*n* = 252)	Group 2 (*n* = 169)	Group 3 (*n* = 328)	Group 4 (*n* = 776)	Total (*n* = 878)
Mud (%)	91.1 ± 1.11	71.9 ± 2.50	74.8 ± 1.60	85.4 ± 0.79	84.6 ± 0.77
Surface water (%)	59.1 ± 1.89	46.5 ± 1.72	46.5 ± 1.31	48.9 ± 0.89	49.8 ± 0.86
Algae (%)	0.6 ± 0.16	5.7 ± 0.98	4.2 ± 0.54	2.1 ± 0.25	2.1 ± 0.23
Shell banks (%)	5.3 ± 1.03	13.6 ± 1.55	18.8 ± 1.29	12.1 ± 0.66	11.8 ± 0.61
Distance to channels (m)	1192 ± 51.4	608 ± 30.6	603 ± 21.8	874.1 ± 21.4	892 ± 21.0
Exposure (h)	6.9 ± 0.12	5.0 ± 0.11	4.8 ± 0.08	5.6 ± 0.06	5.6 ± 0.06

Group 1: Flamingo, Black-tailed Godwit and Avocet; Group 2: Kentish Plover, Greenshank, Knot, Ringed Plover and Turnstone; Group 3: Lesser Black-backed Gull, Sanderling, Black-headed Gull, Little Egret and Little Stint; and Group 4: Dunlin, Redshank, Grey Plover, Bar-tailed Godwit and Grey Heron

We did not carry out counts in the extensive salt marsh area located in eastern part of the estuary (Fig. 1). Our observations showed that the vast majority of the birds fly directly from the high-tide roosts to the exposing sediment flats, bypassing the vegetated marsh areas, so we believe that any numbers that may have remained in the salt marsh represented a very small fraction of the birds feeding in the estuary.

The only complete low water count of shorebirds feeding in the Tagus estuary was carried out in the winter 1981/1982 (Teixeira, 1985). In spite of the time separation of the two counts and of methodological differences (very large sectors, some of which counted by airplane), our results for most species are quite similar to those of Teixeira (1985). The most pronounced differences between the two sets of data relates to the numbers of *Larus* gulls and Avocet. Teixeira

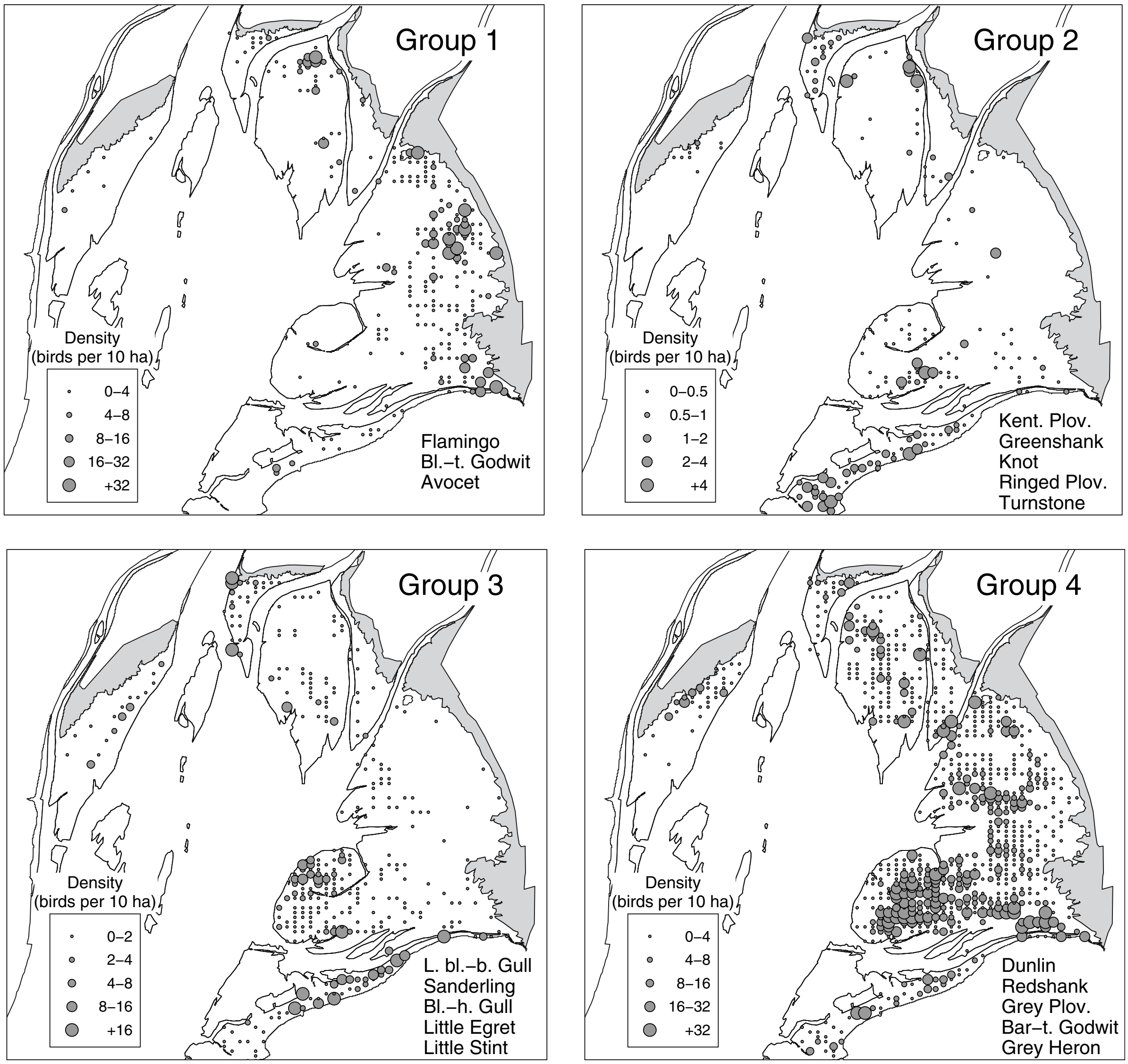

Fig. 4 Joint distribution of the four groups of species identified in the CCA. Densities (in birds per 10 ha) are represented on a logarithmic scale

(1985) counted 19570 Black-headed Gulls in the winter 1981/1982, a total many times higher than what we observed. The same is true for Lesser Black-backed Gull and Avocet, with 12,900 and 10,280 birds counted by Teixeira (1985) and ca. 3500 and 3400 recorded in this study, respectively (Table 1). We can not exclude the possibility that the differences are due to a real reduction of the numbers of birds of these species wintering in the estuary. However, there is evidence that at least part of the differences are due to changes in the preferred foraging areas, which may have shifted to sediment flats located in the southern end of the estuary, not included in the counts reported in this study (Fig. 1). Counts that we made in 2003 in this area resulted in 10,250 Lesser Black-backed Gulls, 3800 Black-headed Gulls and 1479 Avocets, and Moreira (1999) also reported a high abundance of the three species there. Nonetheless, the level of discrepancy found in our study is not unexpected, given the high interannual variability in bird numbers, their high mobility and the likely variation in the abundance of their prey, a factor well known to affect the birds distribution

(Wolff, 1969; Goss-Custard & Yates, 1992; Zwarts et al., 1992; Yates et al., 1993).

Factors affecting the distribution of the bird assemblage

The combination of the first two axis of the CCA showed that the most influential factors for the distribution of the shorebird species were the exposure period, the mud content of the sediment and the presence of shell banks. The third CCA axis was mainly responsible for the separation of species occurring in areas with relatively higher macrophyte coverage. These three axis represented 82.5% of the variance of the species data. Species were clearly ordinated along these gradients, and hence the different groups occupied well defined and distinct areas in the intertidal flats.

A substantial proportion of the variance of our data derived from the high preference of the Flamingo, Black-tailed Godwit and Avocet (Group 1) for areas with high exposure period (Fig. 2, Table 3). This is consistent with previous observations of the influence of the exposure period in the distribution of several species, both in the Tagus estuary (Moreira, 1993; Rosa et al., 2003; Granadeiro et al., 2004) and elsewhere (e.g. Yates et al., 1993; Scheiffarth et al., 1996). However, we can not rule out the possibility of a strong influence of the location of the high-tide roosts in the bird densities (rather than the exposure period alone), because these two variables were (inversely) correlated in the estuary.

Most sectors occupied by species of Group 1 were located in the higher reaches of the estuary, close to the salt marsh and hence generally away from the main channels (Figs. 2, 4, Group 1). These sectors consisted primarily of muddy sediments most of which retaining a thin layer of water (Table 3). A permanent water coverage is important to maintain the feeding efficiency of species like the Flamingo and Avocet (Moreira, 1995; Zweers et al., 1995).

The remaining species were aligned along a gradient of mud content, which is very clear in the joint plots of axis I and II (Fig. 2). Dunlins (Group 4) preferred the muddiest sediments while Gulls, Greenshank and Sanderling (Group 3) occurred in the sectors with coarser sediments, many of which were associated with shell banks. These data are consistent with previous observations in the Tagus estuary (Moreira, 1993; Granadeiro et al., 2004; Santos et al., 2005). In fact, sediment composition is a well-known factor affecting distribution of shorebirds. It influences both the type and abundance of invertebrate prey (Wolff, 1969; Evans, 1979; Yates et al., 1993), and the access of birds to this prey for example, through penetrability and sediment wetness (Goss-Custard & Yates, 1992; Mouritsen & Jensen, 1992).

Two groups of species could be defined in the sectors with coarser sediments, which were mainly separated by the relative amount of macrophyte coverage and of shell banks (Table 3). Greenshank, Kentish Plover, Ringed Plover, Knot and Turnstone (Group 2 in Fig. 3) were more abundant in areas with higher density of macrophytes (generally with less dense shell banks), whereas *Larus* Gulls, Sanderling, Little Egret and Little Stint (Group 3) preferred areas with less macrophytes but a comparatively higher shell bank coverage (Table 3).

Species in Group 4 (Dunlin, Grey Plover, Redshank, Bar-tailed Godwit and Grey Heron) were located close to the centre of CCA plot, which indicates that they occur in a large variety of conditions, and thus show no marked preference along the gradients previously described. In fact, this is the group of species most widely distributed, occurring both in coastal and inner areas of the estuary (Fig. 4) and in the average conditions of the entire estuary (Table 3).

Our study provided the first description of the patterns of distribution of several species of shorebirds at a high spatial detail in the Tagus estuary. The analysis of these data can further be refined and enhanced by incorporating additional key drivers of bird distribution, such as the abundance of invertebrate prey and the intensity of third party disturbance. Such combination of environmental and anthropogenic effects constitute the ideal dataset for fine-scale modelling of the distribution of foraging birds. While part of these data has been collected concurrently with our bird counts, they are currently being processed and hence still unavailable for analysis. Anyway, the data we presented here are useful baseline information against which future monitoring work can be compared. Thus, they can aid in the prediction of impacts and planning of management actions. It is clear from our analysis that different groups showed a high spatial segregation and occupied a variety of ecological conditions while foraging. This observation implies that maintaining high-quality feeding habitats for shorebirds requires preserving and managing large areas, as to encompass the diverse requirements of different species.

Ackowledgements We thank the many volunteers who provided assistance during fieldwork. We are particularly grateful to Ana Tavares, Ricardo C. Martins and Susana L. Rosa for their continuing support. Two anonymous referees offered useful and constructive comments. This work was funded by Fundação para a Ciência e a Tecnologia, through research projects Sat-Tagis (Contract POCTI/C/MAR/15256/1999) and Pred-Tagis (POCTI/POCTI/BSE/47569/2002), both co-financed by the ERDF and grant SFRH/BPD/11544/2002 to JPG.

References

ArcView. http://users.skynet.be/contourgridder/.

BirdLife International, European Bird Census Council, 2000. European Bird populations: estimates and trends. Cambridge, UK.

Braak, C. J. F. T., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 675: 1–1826.

Bryant, D. M., 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). Estuarine and Coastal Marine Science 9: 369–384.

Calvário, J., 1984. Étude preliminaire des peuplements intertidaux (substrats meubles) de l'estuaire du Tage (Portugal) et sa cartographie. Arquivos do Museu Bocage 2: 187–206.

Dias, M. P., J. P. Granadeiro, R. C. Martins & J. M. Palmeirim, 2006. Estimating the use of tidal flats by waders: inaccuracies due to the response of birds to the tidal cycle. Bird Study 53: 32–38.

Evans, P. R., 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal prey. In Naylor, E. & R. G. Hartnoll (eds), Cyclic Phenomena in Marine Plants and Animals. Pergamon Press, New York, 357–366.

Gauch, H. G., 1982. Multivariate analysis in Community Ecology. Cambridge University Press, Cambridge, UK.

Goss-Custard, J. D. & M. G. Yates, 1992. Towards predicting the effect of salt-marsh reclamation on feeding bird numbers on the Wash. Journal of Applied Ecology 29: 330–340.

Granadeiro, J. P., J. Andrade & J. M. Palmeirim, 2004. Modelling the distribution of shorebirds in estuarine areas using generalized additive models. Journal of Sea Research 52: 227–240.

Moreira, F., 1993. Patterns of use of intertidal estuarine areas by feeding bird assemblages: a study in the Tagus estuary (Portugal). Ardeola 40: 39–53.

Moreira, F., 1995. The winter feeding ecology of avocets *Recurvirostra avosetta* on intertidal areas. II. Diet and feeding mechanisms. Ibis 137: 99–108.

Moreira, F., 1999. On the use by birds of intertidal areas of the Tagus estuary: implications for management. Aquatic Ecology 33: 301–309.

Mouritsen, K. N. & K. T. Jensen, 1992. Choice of microhabitat in tactile foraging dunlins *Calidris alpina*: the importance of sediment penetrability. Marine Ecology Progress Series 85: 1–8.

Musgrove, A. J., R. Langton, H. Baker & R. M. Ward, 2003. Estuarine Waterbirds at low tide. The WeBS Low Tide Counts 1992–93 to 1998–99. Thetford, Wader Study Group/ British Trust for Ornithology, The Wildfowl and Wetlands Trust, Royal Society for the Protection of Birds and the Joint Nature Conservation Committee.

Oksanen, J., R. Kindt & R. B. O'Hara, 2005. vegan: Community Ecology Package version 1.6–10. http://cc.oulu.fi/~jarioksa/.

Palmer, M. W., 1993. Putting things in even better order: the advantages of canonical correlation analysis. Ecology 74: 2215–2230.

R Development Core Team, 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org.

Rehfisch, M. M., G. E. Austin, M. J. S. Armitage, P. W. Atkinson, S.J. Holloway, A. J. Musgrove & M. S. Pollitt, 2003. Numbers of wintering waterbirds in Great Britain and the Isle of Man (1994/1995–1998/1999): II. coastal waders (Charadrii). Biological Conservation 112: 329–341.

Rosa, S., J. M. Palmeirim & F. Moreira, 2003. Factors affecting waterbird abundance and species richness in an increasingly urbanized area of the Tagus Estuary in Portugal. Waterbirds 26: 226–232.

Santos, C. D., J. P. Granadeiro & J. M. Palmeirim, 2005. Feeding ecology of Dunlin *Calidris alpina* in a southern european estuary. Ardeola 52: 235–252.

Scheiffarth, G., G. Nehls & I. Austen, 1996. Modelling distribution of shorebirds on tidal flats on Wadden Sea and visualisation of results with the GIS IDRISI. In Lorup, E. & J. Strobl (eds), IDRISI GIS 96: Salzburger Geographische Materialien, Vol 25. Selbsiverlag des Instituts für Geographie der Universitat Salzburg. http://www.clarklabs.org/10applic/idr96cd/scheiff/idrisicd.html.

Stroud, D. A., N. C. Davidson, R. West, D. A. Scott, L. Haanstra, O. Thorup, B. Ganter & S. Delany, 2004. Status of migratory wader populations in Africa and Western Eurasia in the 1990s. International Wader Studies 15.

Symonds, F. L., D. R. Langslow & M. W. Pienkowski, 1984. Movements of wintering shorebirds within the Firth of

Forth: species differences in usage of an intertidal complex. Biological Conservation 28: 187–215.

Teixeira, A. M., 1985. Dispersão intertidal da avifauna aquática invernante no estuário do Tejo. Serviço Nacional de Parques, Reservas e Conservação da Natureza (unpublished report) 71 pp.

Venables, W. N. & B. D. Ripley, 2002. Modern applied statistics with S. 4th Edition. Springer-Verlag, New York, 495 pp.

Wolff, W. J., 1969. Distribution of non-breeding waders in an estuarine area in relation to the distribution of their food organisms. Ardea 57: 1–28.

Yates, M. G. & J. D. Goss-Custard, 1991. A comparison between high-water and low-water counts of shorebirds on the Wash, east England. Bird Study 38: 179–187.

Yates, M. G., J. D. Goss-Custard, S. McGrorty, K. H. Lakhani, S. E. A. Durell, R. T. Clarke, W. E. Rispin, I. Moy, T. Yates, R. A. Plant & A. J. Frost, 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. Journal of Applied Ecology 30: 599–614.

Zwarts, L., A. M. Blomert & J. H. Wanink, 1992. Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. Marine Ecology Progress Series 83: 129–139.

Zweers, G., F. Jong, H. Berkhoudt & J. C. V. Berge, 1995. Filter feeding in flamingos (*Phoenicopterus ruber*). Condor 97: 297–324.