Variation in numbers and behaviour of waders during the tidal cycle: implications for the use of estuarine sediment flats

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ABSTRACT

Estuarine sediment flats are essential feeding areas for waders, but their exploitation is constrained by the movements of tides. In this cyclic environment the exposure period of sediment flats decreases several fold from upper to lower flats, and the moving tidal waterline briefly creates particular conditions for waders and their prey. This study attempts to determine how the exposure period and the movement of the tide line influence the use of space and food resources by waders across the sediment flats. Wader counts and observations of feeding behaviour were carried out in all phases of the tidal cycle, in plots forming a transect from upper to lower flats, thus representing a gradient of exposure periods. Pecking, prey intake, and success rates varied little along the gradient. Some species actively followed the tide line while foraging, whereas others are evenly spread over the exposed flats. Black-tailed Godwit, Dunlin and Avocet were 'tide followers', whereas Grey Plover, Redshank and Bar-tailed Godwit were 'non-followers'. Densities of 'followers' near the tide line were up to five times higher than elsewhere. Species differed markedly in the way they used space on the flats, but in general the rate of biomass acquisition (in grams of ash-free dry weight per time exposed) was much higher in lower flats. However, this preference was insufficient to counter the much longer exposure of the upper flats, so the total amount of biomass consumed on the latter was greater. Therefore, it was in these upper flats that waders fulfilled most of their energetic needs. Consequently, upper flats are of particular importance for the conservation of wader assemblages, but because they are usually closer to shore they tend to suffer the highest pressure from disturbance and land reclamation.

1. Introduction

Many species of waders depend on the abundant invertebrate prey of estuarine areas to survive during the non-breeding season. In these wetlands, the feeding rhythms of birds are partly determined by the tidal cycles, which cause predictable temporal and spatial changes in their foraging environment (Burger et al., 1977; Fleischer, 1983). In general, twice a day their feeding grounds progressively expand to the lower reaches of intertidal flats during ebbing tide, and contract to upper areas and force the birds to move to their roosting sites as the tide rises.

During these cycles some species concentrate their foraging efforts in exposing or covering areas during ebbing and rising water, respectively, whereas others avoid the tidal line and tend to arrive at the intertidal flats well after the tidal passage (Burger et al., 1977; Connors et al., 1981; Nehls and Tiedemann, 1993; Evans and Harris, 1994; Scheiffarth et al.,...
These differences in the response of birds to the tidal cycle and particularly to the progress of the tide line have implications in the way they use the space in the sediment flats (Nehls and Tiedemann, 1993; Dias et al., 2005, in press).

Within an estuary, the period of exposure of tidal flats can vary by several fold. The intensity of use of space by waders is not only a function of the time during which the areas are available, but also of the bird’s behaviour in relation to the advancing and receding tides. Species that show a strong preference to feed close to the tide line will tend to use areas with similar intensity, irrespective of their exposure period. Conversely, species showing a weak bound to the tide edge, will tend to use them in approximately direct proportion of its exposure period (Bryant, 1979; Nehls and Tiedemann, 1993). Therefore, it is useful to combine the knowledge of how waders use the space along gradients from high to low-lying flats, with data on their feeding behaviour in different phases of the tidal cycle, in order to obtain a more realistic portrait of the importance of different areas in providing food resources for waders.

The overall objective of this study was to examine how the constraints imposed by the tidal movements influence the use of space and food resources by waders in estuarine sediment flats. We selected a range of areas from high to low tidal flats to represent a gradient of exposure periods and determined (i) the response of the birds to the moving tidal water line, and (ii) the influence of the exposure period of sediment on its use by waders. In addition, we (iii) characterised the foraging behaviour of the waders in areas with different exposure periods. Combining the information obtained on the use of space and on the foraging behaviour we (iv) determined the relative importance of high, medium, and low sediment flats in provisioning food resources for waders.

2. Methods

2.1. Study area

This study was carried out in the Tagus estuary, Portugal (38°45’N, 09°50’W). The Tagus estuary is among the largest wetlands in Western Europe, holding over 50,000 shorebirds during the winter (e.g. Moreira, 1997). It is also a key stopover during migration periods. The intertidal areas of the Tagus estuary cover about 130 km² and are dominated by mudflats, and to a lesser extent by dead oyster beds and sandy flats (Granadeiro et al., 2005, in press). The tides are semi-diurnal, and the amplitude ranges from 1–3.8 m in neap and spring tides, respectively.

The study site was located in the southern margin of the estuary. We marked 18 plots (100 m × 200 m) with a GPS (accuracy ca. 5 m), forming a transect extending from near the saltmarsh (plot 18) down to the low-water mark (plot 1, Fig. 1) of an average tide (high-water ca. 3.5 m, low-water about 1.0 m). The average exposure period of each plot was estimated from repeated records of the time when the tide line was crossing the plots. In this study, the exposure periods are reported to an average tide with amplitude 2.5 m, and ranged from 0.58 h to 6.45 h in the lowest and highest plots, respectively.

The site was homogeneous in terms of sediment, representing a typical intertidal mudflat of the Tagus estuary (particles < 63 μm representing more than 95% weight in all plots).

2.2. Bird counts

Bird counts were carried out regularly between January and March 2002, during daytime and only under favourable weather conditions. We recorded the number of feeding birds in each exposed plot, during 22 half-tidal cycles (11 high-water to low-water counts and 11 low-water to high-water counts), under conditions varying from neap to spring tides. Birds were counted at 15 min intervals while the tide line was crossing the study area, and at 30 min intervals when it was fully exposed. Birds resting or sleeping represented less than 5% of all observations and were excluded from the analyses.

We stratified our observation by considering two distinct phases: (1) tidal passage, corresponding to the periods when the water was leaving or reaching the study plots (during ebbing and rising tides, respectively), and (2) full exposure when plots were fully exposed, around low tide. A given plot...
was considered to be inundating when the advancing water crossed it from its lower to its upper limits, but classified as exposing when the retreating tide line was within 100 m from its lower limits. This decision was due to the difficulty in determining the exact position of the tide edge during the ebbing tides and also because the sediment of a plot remained wet well after the passage of the tide edge. On all other occasions, plots were considered as fully exposed.

In order to represent graphically the variation in the number of birds in all study plots during the entire tidal cycle, we smoothed our count data, using two-dimensional thin plate regression splines (Hastie and Tibshirani, 1990; Wood, 2003) and assuming a Poisson error structure. The complexity of the regression surfaces is determined by the degree of freedom (Hastie and Tibshirani, 1990), which we fixed at 20 df, to obtain comparable levels of smoothness among species. This level of flexibility adequately captured the trends in the data, without overfitting them. We did not use these models for statistical inference, and thus we do not present the details concerning model fitting and assessment. The computations were carried out using the mgcv routine (Wood, 2000, 2003, 2005) running under the R statistical software (R Development Core Team, 2005, freely available at http://www.R-project.org).

### 2.3. Feeding behaviour

We used focal observations to quantify the feeding behaviour of the most abundant species: Avocet (Recurvirostra avosetta), Grey Plover (Pluvialis squatarola), Dunlin (Calidris alpina), Black-tailed Godwit (Limosa limosa), Bar-tailed Godwit (Limosa lapponica), and Redshank (Tringa totanus). During the observations of feeding behaviour, birds were selected at random and their activity recorded during 1 min. We noted the number of pecks, probes or scyths (hereafter jointly referred to as pecks), and whenever possible whether any prey was taken. While for some species the intake of prey could generally be detected from the typical swallowing movements of the head, it proved impossible to obtain accurate information about the type and size of the prey taken, given our distance to the plots. Also, we could not estimate the prey intake rate (and hence success rates) of Dunlin and Avocet due to the very small size of their prey. We did not record the number of swallowing movements of avocets, because in each movement they ingest large lumps of mud and so they may be poorly correlated with the number of prey taken (Moreira, 1996c). Also, our distance from the plots did not enable an accurate measure for this parameter in Dunlin. We also calculated the success rate (prey per peck) to check for changes in prey accessibility in different parts of the exposure gradient.

### 2.4. Estimating the intensity of use and biomass consumption at the plots

We estimated the intensity of use of the plots during a daily tidal cycle by integrating the successive counts of each plot through the duration of each tidal phase (tidal passage and full exposure), and expressed it as number of birds per hour. For this purpose, we pooled our count and behavioural data from six adjacent plots, to ensure larger sample sizes and help stabilising the means. Thus, we defined three areas, hereafter referred to as upper, middle and lower plots.

We calculated the total number of prey consumed during a tidal cycle in upper, middle and lower plots by multiplying the average intensity of use (in bird.hours) by the prey intake rate (number of prey taken per hour). The biomass consumed in each area by each wader species was by multiplying the total number of prey consumed by the average biomass of each prey. The latter parameter was derived from the proportion of each prey type in their diet, and the average biomass of each prey type (in grams of ash-free dry weight per prey—AFDW). Data on the diets of different species was mostly obtained from Moreira (1997, Appendix B). There are no published data on the diet of Bar-tailed Godwits in the Tagus estuary, so we combined information collected in Spain (Pérez-Hurtado et al., 1997) and in Germany (Scheiffarth, 2001). The average size of each prey and the corresponding biomass (both varying among bird species) were derived from studies carried out in the Tagus estuary (Moreira, 1994, 1995a–c, 1996, 1997; Santos et al., 2005, in press).

### 3. Results

#### 3.1. Changes in numbers in relation to the moving tide line

Species differed in their preferred foraging period in the study area. Black-tailed Godwit, Dunlin and Avocet were far more abundant in plots when the water line was inside them, during ebbing or rising tide, than when it was fully exposed (Fig. 2). They closely followed the moving tide edge, so we refer to these species as “tide followers”. In contrast, Grey Plovers and Redshanks were scarce in recently exposed or covering areas, and their highest abundance occurred when the flats were fully exposed (Fig. 2). The densities of Bar-tailed Godwit did not differ between these two tidal phases (Fig. 2). Because the three latter species did not show any attraction to the tide line, they will be referred to as “non-followers”. Fig. 3 illustrates the variation in the numbers of birds along the transect of plots during a complete tidal cycle in a typical “follower” (Dunlin) and in a “non-follower” (Grey Plover).

#### 3.2. Intensity of use and foraging behaviour in relation to exposure period

“Non-followers” used the area much more intensively during the period of full exposure than during the tidal passage (two-way ANOVA: effect of the tidal phase, $F_{1, 108} = 26.5, 30.4$ and $71.7$, respectively for Bar-tailed Godwit, Redshank and Grey Plover, all $P < 0.001$; Fig. 4). In contrast, “followers” used all plots almost equally during these two phases. In fact, we found no differences between the intensity of use during the two tidal phases in Black-tailed Godwit (two-way ANOVA: effect of tidal phase, $F_{1, 104} = 1.7$, not significant) and there were only marginal differences in Dunlin ($F_{1, 104} = 4.1, P = 0.045$) and Avocet ($F_{1, 104} = 3.9, P = 0.05$). Avocet and Grey Plover preferred the upper plots (two-way ANOVA: effect of plot, $F_{2,104}$...
= 13.7, and $F_{1, 120}$ respectively), whereas the other species did not show a clear preference within the exposure gradient.

The foraging behaviour of the study species did not show major trends along the gradient of exposure periods. Avocet and Grey Plover pecked a little more frequently in upper plots than in middle and low plots (Table 1), while the remaining species did not show any significant differences. With the exception of Bar-tailed Godwit, there was slightly lower success rate (number of prey per peck) in the upper plots.

3.3. Variation in biomass consumption along the exposure gradient

The amount of biomass obtained by the bird assemblage in upper, middle and low plots was related to their exposure period (bars in Fig. 5). The upper plots provided most of the biomass required by the birds, because they were exposed for a longer period. However, the maximum rate of biomass acquisition (calculated as the amount of biomass obtained in the plots divided by the time during which they were available for foraging) was observed in lower plots (lines in Fig. 5).

4. Discussion

4.1. Species differed in their attraction to the moving tide line

Our study area spanned from the uppermost reaches of the estuary, down to the low-water mark, and thus included plots along the full course of the water during an average ti-
dal cycle. Also, the study area was very homogeneous in terms of sediment type. Therefore, the patterns of distribution and use of the areas were not influenced by the sequential availability of different types of habitat.

All species showed very substantial variation in their distribution in the intertidal flats during the tidal cycle. This is in line with previous findings in a number of estuarine areas elsewhere (e.g. Burger et al., 1977; Bryant, 1979; Nehls and Tiedemann, 1993; Hötker, 1999). Clearly, species differed in their behaviour in relation to the movement of the tide line. All “followers” were tactile predators, and they showed a strong attraction to exposing or recently exposed plots as the tide ebbed, when sediments were wet or still covered by a thin layer of water. Although a few birds started to disperse in the area as the tide progressed, the bulk of the birds kept following the tide down to the lower plots. They kept foraging in these low areas until the beginning of the rising tide, when they started to be pushed towards upper areas. Therefore, “followers” occurred in the plots mostly during the brief tidal passage, when their densities were 3–5 times higher than those recorded at other tidal phases.

“Non-followers” showed the reversed pattern, with similar or higher densities in sediments that were already exposed for a period of time. They were generally present in the plots after their full exposure, and gained access to the lowest areas around the low-tide period. Therefore, the shifts in the densities recorded in the different phases of the tidal cycle are clearly linked to the response of birds to the moving tide line.

These results corroborate the idea that low tide counts alone will often fail to provide an accurate portrait of the average density of birds in intertidal areas (Bryant, 1979; Nehls and Tiedemann, 1993; Dias et al., 2005, in press). In fact, low tide counts will generally tend to overestimate the number of birds in lower areas and underestimate those of upper areas, because most birds (mainly “followers”) will be concentrated in the former areas (Nehls and Tiedemann, 1993; Dias et al., 2005, in press). Hence, density comparison among sites with different exposure period (either in the same or among different estuaries) should be made with great caution (Dias et al., 2005, in press).

4.2. The bird’s response to the tide line influences overall use of sediment flats

“Followers” and “non-followers” differed in the way they used the plots. The former group used the area intensively during the relatively brief phase of tidal passage, which in
our study area corresponded only to ca. 28% of the duration of a complete tidal cycle. Despite the large difference between the duration of these two phases, they were almost equally important to “followers” (as indicated by the proximity of the solid and dashed lines in Fig. 4). In contrast, “non-followers” were mostly present in the plots when they were fully exposed, and so in these species the brief period of tidal passage was only marginally important.

In addition, because “followers” showed a strong attraction to the moving water edge, they tended to use the plots equally, irrespective of their exposure period. This pattern was very clear in Black-tailed Godwit and Dunlin, which showed the strongest attraction to the water, but it was less obvious in Avocet. This species actively followed the tide line, as indicated by the considerable use made during the ebbing and rising water (dashed line in Fig. 4). However, on several occasions some individuals started to move into upper areas before the start of the rising tide, ahead of the remaining individuals. We could not find any satisfactory explanation for this behaviour, but it resulted in an increased importance of the upper plots, a situation typically found in “non-followers”. To some extent, the pattern of use of space by Grey Plover was also unexpected. This species was generally absent from the middle plots, but still used the lowest areas to some extent. In fact, most birds remained in the upper plots while the tide was ebbing, where they tried to establish feeding territories (Moreira, 1996). Afterwards, a few birds (perhaps those with lower quality or smaller territories) moved to low plots, lying close to the low-water mark, and skipped the intermediate plots, perhaps in search of more profitable feeding grounds, in the lower reaches of the estuary.

Species did not show much variation in feeding behaviour along the gradient of exposure. In fact, the foraging parameters varied little between lower, middle and upper plots. The most consistent result suggests a trend towards a lower success rate (prey per peck) in upper plots, but the effect was

Table 1 – Pecking (peck min$^{-1}$), prey intake (prey min$^{-1}$) and success (prey peck$^{-1}$) rates in different parts of the study area. Significantly different mean values (as assessed by Kruskall–Wallis tests, followed by non-parametric post-hoc comparisons) are indicated in bold. Means are presented ± S.D., sample sizes in parentheses

<table>
<thead>
<tr>
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<th>Lower plots</th>
<th>Middle plots</th>
<th>Upper plots</th>
<th>Total</th>
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<td>Peck rate</td>
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<td>Grey Plover</td>
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<td>Redshank</td>
<td>13.8 ± 7.93</td>
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<td>12.4 ± 4.94</td>
<td>12.8 ± 5.3</td>
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<td>Bar-t. Godwit</td>
<td>18 ± 7.33</td>
<td>19.9 ± 12.12</td>
<td>20.5 ± 9.66</td>
<td>19.5 ± 8.2</td>
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<td>Black-t. Godwit</td>
<td>21.2 ± 6.41</td>
<td>26 ± 7.96</td>
<td>24.3 ± 7.38</td>
<td>34.3 ± 7.6</td>
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<td>Avocet</td>
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<td>42 ± 10.91</td>
<td>51.9 ± 11.18</td>
<td>46.7 ± 12.4</td>
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<td>Dunlin</td>
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<td>54.4 ± 10.94</td>
<td>56 ± 15.85</td>
<td>53.6 ± 15.7</td>
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<td>Prey intake rate</td>
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<tr>
<td>Grey Plover</td>
<td>1.7 ± 1.2</td>
<td>1.7 ± 1.4</td>
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<td>Redshank</td>
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<td>6.8 ± 3.0</td>
<td>4.7 ± 3.0</td>
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<td>9.2 ± 3.2</td>
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<td>Success rate</td>
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<td>38 ± 17.1</td>
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</table>

Fig. 5 – Biomass consumed by the feeding assemblage during a complete tidal cycle (bars: gram of ash-free dry weight, AFDW), and rate of biomass consumption (lines and symbols: in grams AFDW per time exposed).
relatively weak and did not result in actual differences in prey intake rates. We conclude that, despite a few significant differences amongst plots, the species did not alter their behaviour substantially under different exposure regimes.

We calculated the overall biomass consumption of prey by waders in upper, middle and lower sediment flats by combining the intensity of use of space (in bird-hours) with the prey intake rates (converted to grams of AFDM) recorded in plots. The lower plots offered the highest rate of biomass acquisition (expressed as grams of AFDM per time available) for the bird assemblage. Thus, during their brief exposure, lower areas make a relative contribution of biomass well above that expected from their relatively short exposure period. However, this preference did not compensate for the much longer exposure period of the upper areas, which ended up providing the largest fraction of the biomass required by the birds, that is, where the heaviest predation occurs. Consequently, either these areas have a higher invertebrate production, or it will be here where any depletion effect of shorebirds over their prey is more likely to be observed.

The fact that upper areas are often voided of birds around low-tide generally leads to the wrong idea that they are less important feeding grounds for waders. To a large extent, this idea is due to the greater attention traditionally given to low-tide distribution of birds in relation to movements and numbers during the progress of the tides (e.g. Musgrove et al., 2003; see also Burton et al., 2004; Dias et al., 2005, in press). However, this is clearly not the case, as we showed in this study. In fact, a high correlation between the biomass consumed by birds in the intertidal flats and their exposure period is likely to be the norm in many estuarine areas worldwide.

Unfortunately, upper sediment flats are currently under considerable threat, because they are usually located close to the shore, where human impacts are often more intense. Large areas of salt-marsh and high sediment flats have been lost mainly due to land reclamation in the last decades (e.g. Goss-Custard and Yates, 1992; Yates et al., 1996; Healy and Hickey, 2002), while others continue to suffer considerable impacts from various sources of disturbance and pollution (Fitzpatrick and Bouchez, 1998; Gill et al., 2001). It is therefore urgent to increase the awareness of conservation managers and decision-makers of the importance of upper estuarine flats for the survival of wintering waders.

Acknowledgements

Thanks are due to the Director of Reserva Natural do Estuário do Tejo, for facilities made available during this study. Many persons helped with fieldwork and their effort is well acknowledged. Draft versions of this manuscript benefited from comments of A. Leal, P. Lourenço, C.D. Santos and S.L. Rosa and two anonymous referees. This research was funded by Fundação para a Ciência e a Tecnologia with EU-ERDF support, through research project Sat-Tagis (Contract PDCTM/C/MAR/15256/1999) and grant to J.P.G. (grant SFRH/BPD/11544/2002).

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