High water roost selection by waders: maximizing feeding opportunities or avoiding predation?

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During the highest spring tides the intertidal sediment flats of estuaries are fully inundated at high water, and waders have no choice but to move to supratidal roosts, e.g. on open farmland, saltpans or beaches. However, in many estuaries during the lowest neap or intermediate tides there are sectors of upper intertidal sediment flats that remain exposed even at the peak of high water, and so waders have the choice of roosting either there or in supratidal sites. In the Tagus Estuary, Portugal, as elsewhere, waders use both types of roosts during high water. Our main objective was to understand what makes waders opt for one of these two types of available roosts. We monitored wader use of saltpans and intertidal roosts from spring to neap tides, and measured foraging and alarm behaviour, prey availability and disturbance by predators. Most of the wader species studied chose intertidal (mudflat) roosts whenever these were available, and only roosted in saltpans during the peak of spring tides. We hypothesized that this preference was explained either by an attempt (i) to continue feeding into the high water period, or (ii) to minimize predation risk. Extending feeding time into the high water period did not seem to be very relevant for roost choice because both prey availability and foraging activity were low in both types of roosts. However, predator disturbance was several times higher in the saltpans than in the intertidal roosts, suggesting that this factor may be the determinant in the choice of roost type.

Through most of the winter, estuaries harbour large concentrations of waders, which forage on the intertidal sediment flats during low tide. However, as the tide advances, birds are forced to move to high water roosts, where they must remain until the receding tide exposes their feeding grounds. During the high water, birds congregate in these areas in very dense flocks and spend most of their time there sleeping, preening and, in some cases, feeding.

During spring tides the intertidal sediment flats of the estuaries are fully inundated at high waters and birds have no other choice than to move to supratidal roosts. However, in many estuaries at neap or intermediate tides there are small sectors of upper intertidal sediment flats that remain exposed and thus available for waders even at the peak of high water. Whenever these intertidal sectors are available at high water, waders have to choose between roosting in them or at other sites, such as saltpans.

Although these roosts are critical for waders, they are frequently under great pressure because they are generally located in areas that are highly modified by human activity such as open farmland and saltpans. Such sites often have to be protected and managed in order to maintain their attractiveness to birds; however, knowledge of the factors that underlie the choice of roosts by waders is very limited (Rogers 2003).

Some wader species may spend a substantial percentage of high water time feeding, in order to complement the low-tide food intake (Masero et al. 2000, Luis et al. 2002). This suggests that in some circumstances waders, unable to fulfil their energetic requirements during low tide, may base their selection of high water roosting sites on their feeding potential. The presence or absence of predators is also an important factor in the choice of roost (Luis et al. 2001). In fact, predator avoidance may also have a strong effect on wader behaviour, even when the risk of predation is low (Rogers 2003).

It is clear that both factors, extended feeding time and predator avoidance, have the potential to
influence the choice of roost. In this study we tested the following predictions in order to determine which of the two factors – feeding potential or predator avoidance – is more important in determining the choice of high water roost. If roost selection is driven by the need to extend the feeding period, we would predict that birds will continue to feed during the high water period. If predator avoidance is the determinant, we would predict that in the preferred sites there would be fewer predator visits and alarm flights, and that the birds will spend less time in vigilance activities.

We compared roosting sites in saltpans with those located in the adjacent upper intertidal sediment flats. In addition, we measured the use made by waders of high water roosts from neap to spring tides, in order to examine how tidal condition influences roost selection by waders.

**METHODS**

**Study area**

This study was carried out in the Tagus Estuary, Portugal (38°45′N, 8°55′W) (Fig. 1), one of the most important estuarine wetlands in Europe. Tidal amplitude ranges between 1 and 3.8 m, from neap to spring tides. In the Portuguese ordnance datum level, the annual minimum and maximum high water heights are 2.6 and 4.2 m, respectively (referred to the hydrographic zero).

When the tides exceed 3.3 m, the high water reaches the saltmarshes and the dykes that separate

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**Figure 1.** Location of the study areas in the Tagus Estuary. The dotted line represents the limit of lowest neap high waters. The area between this line and the saltmarsh is not inundated in every tidal cycle.
the estuary from farmland or built-up areas, leaving no space for waders on the sediment flats. During neap high waters (from 2.6 to 3.2 m), a band of sediment flats (of c. 600 m in the lowest tides) remains exposed even at high water (see Fig. 5). Some of these areas are used by waders during high water. Our study contrasted the most important supra-tidal wader roosts in the estuary (part of a large saltpan complex) with three nearby areas delimited in the upper intertidal mudflats, where birds gather in neap high waters. We will refer to these areas as ‘saltpans’ and ‘mudflat roosts’, respectively.

**Number of waders at roost sites**

The relationship between the height of the high water and the number of waders using the two types of roosts was examined by carrying out bird counts within ± 30 min of peak high water simultaneously in the saltpans (in a 10-ha sector, where most of the waders in the saltpan complex stay) and in three sectors in the mudflats roosts (with a total surface area of 40.1 ha; Fig. 1). Counts were carried out during six or seven consecutive days, to cover the whole tidal gradient (from neap to spring tides). This procedure was repeated three times in February–March 2002. The three selected sectors (Fig. 1) represent only a fraction of the total mudflat roost area. Consequently, the number of birds counted in these sectors is lower than the total numbers in the saltpans. A local regression technique was used to illustrate the relationship between tidal height and wader abundances. We used the technique known as lowess (locally weighted regression scatterplot smoothing), which is a non-parametric regression method, where y-values are calculated from a neighbourhood of x-values, whose weights vary according to the distance to the central x-value (Venables & Ripley 2002).

**Foraging and prey availability at roost sites**

To determine the importance of feeding activity at the roosts, we recorded the percentages of feeding birds for all the species. We also estimated prey availability in May 2002, using a total of 40 cores of sediment, each having an area of 87 cm², taken to a depth of 20 cm. We stratified our sampling by defining five lines parallel to the coast. The first three lines (located at 200, 400 and 600 m from the coast) coincided with the mudflat roosts; the following sampling lines (at 800 and 1000 m) were taken in the adjacent lower area, lying below high water level in neap tides. The superficial 5 cm of the sediment cores were sieved using a 0.5-mm mesh size and the remaining 15 cm with a 1-mm mesh. The invertebrates retained in the sieve were preserved in 70% ethanol, and later identified and counted.

In order to quantify the biomass available for birds we measured the total length of the gastropod *Hydrobia ulvae*, the antero-posterior length of the bivalve *Scrobicularia plana* and the jaw length of the ragworm *Hediste diversicolor*. These parameters were then used to estimate ash-free-dry-weight (AFDW) from regression equations derived from local specimens (Moreira 1996, Santos et al. in press). Siphons of large *S. plana* are also consumed by waders (Moreira 1995a), so we also calculated their AFDW, using the equations from Zwarts et al. (1994) and Moreira (1996). The AFDW of the remaining species, the crustacean *Cyathura carinata*, the polychaete *Streblospio shrubsolii* and individuals of the Class Oligochaeta, were determined by loss-on-ignition at 500 °C for 2 h.

In the saltpans most birds roosted on the compacted dry and coarse substrate dykes, unsuitable for typical prey, so we did not sample prey abundance there. Only the invertebrates in the top 5-cm layer of sediment in our cores were considered to be available to birds (Bryant 1979, Kalejta 1993, Zwarts & Wanink 1993) and only *H. ulvae* smaller than 4 mm and the *S. plana* between 2 and 20 mm were considered (Goss-Custard 1977, Worral 1984, Moreira 1994, 1995b, Pérez-Hurtado et al. 1997, Dierschke et al. 1999a, 1999b, Scheiffarth 2001, Santos et al. in press). We also included *H. diversicolor* and *S. plana* from the full cores; the former because it is highly mobile and makes extensive vertical movements, and the latter because the siphon that extends to the surface is often consumed by birds (Moreira 1995a).

**Risk of predation**

We compared predator pressure on saltpans and mudflat roosts during high water using four parameters: (i) number of raptors flying over the roosts, (ii) number of alarm flights caused by raptors, (iii) total number of alarm flights and (iv) proportion of time spent in vigilance.

We measured the proportion of time spent in vigilance by the commonest species, Dunlin *Calidris alpina* and Grey Plover *Pluvialis squatarola*, using 4-min
focal observations, during which we recorded the number of scans and their durations. We considered that a bird was scanning when its head was raised and its beak was not touching the plumage (Roberts 1995). These observations were carried out during high water, in an area of c. 10 ha in the saltpans in spring and neap tides and in 12 ha of the nearest mudflat roosting area in neap tides, during the winter and spring of 2002 and the spring of 2003.

RESULTS
Roost site characteristics and their use by waders
The great majority of the birds of most species preferred mudflat roosts during tides up to 3.2 m high, i.e. about 3 days before and after the neap tides (Fig. 2). When tides are higher than 3.3 m, the water

Figure 2. Variation in wader abundance in saltpans and mudflat roosts in relation to tide heights. Below 3.2–3.3 m the abundance of most species is higher on mudflat roosts; above 3.2–3.3 m these roosts are submerged and wader abundance increases in saltpans. The shaded area represents the tidal heights when both types of roost are available. Closed dots: number of birds roosting in saltpans; open dots: number of birds roosting in mudflats; lines: overall tendency for saltpans (loess lines).
reaches the margins of the saltmarsh, birds are forced to move to the saltpans and these mudflats become submerged (see Fig. 5). Only Ringed Plover *Charadrius hiaticula* and Kentish Plover *Charadrius alexandrinus* did not show this trend (Fig. 2).

Prey available for waders in the mudflat roosts, which remained exposed during some high waters, was very low (Table 1). In fact, with the exception of *H. diversicolor*, AFDW of prey in these areas was several times lower than that on the adjacent lower mudflats, inundated in all daily tidal cycles. Apart from a few areas that had small numbers of insects, the soil of the dykes separating the tanks of the saltpans had no prey. All the invertebrate species reported (Table 1) are potential prey for the study species.

### Foraging at roost sites

The overall proportion of waders feeding in the roosting areas was very low in both types of roost, but higher at the mudflats (13%) than at the saltpans.
(1%). However, there was a substantial variation among species; although most species fed very rarely, a high proportion of Common Redshank *Tringa totanus* continued to feed at high water, especially when using the mudflat roosts (Fig. 3). When feeding in the dykes that separate the tanks of the saltpans, Common Redshanks were probably eating insects or other terrestrial invertebrates. Ruddy Turnstone *Arenaria interpres* did not feed in the mudflat roosts at high water. Kentish Plover and Ringed Plover did not occur at all in mudflat roosts, despite a reasonable abundance of their preferred prey (*H. diversicolor*).

The water in the tanks of the saltpans was too deep for most species to reach the bottom, although the species with longer legs (Black-tailed Godwit *Limosa limosa* and Pied Avocet *Recurvirostra avosetta*) occasionally fed in the tanks. Pied Avocet would most often feed while swimming.

**Risk of predation**

All the results indicate that predator pressure was substantially higher in the saltpans than in the mudflat roosts (Table 2, Fig. 4). During the 54 h of observation, nine species of raptors flew over saltpans and only five were observed over the mudflat roosts. During high water there were more individual raptors flying over the saltpans than over the mudflats (Mann–Whitney *U*-test: *U* = 196, *P* = 0.01, Table 2). On average, there were three times more raptors flying above saltpans than mudflats.

The higher number of raptors in the saltpans resulted in more frequent flock alarm flights and

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**Table 2.** Number of raptors/h that flew over salt pans and mudflat roosts during high waters (35 h of observation in salt pans and 19 h in mudflat roosts)

<table>
<thead>
<tr>
<th>Species</th>
<th>Saltpans</th>
<th>Mudflat roosts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eurasian Marsh Harrier <em>Circus aeruginosus</em></td>
<td>1.11</td>
<td>0.47</td>
</tr>
<tr>
<td>Booted Eagle <em>Hieraetus pennatus</em></td>
<td>0.54</td>
<td>0</td>
</tr>
<tr>
<td>Peregrine Falcon <em>Falco peregrinus</em></td>
<td>0.17</td>
<td>0.05</td>
</tr>
<tr>
<td>Short-toed Eagle <em>Circaetus gallicus</em></td>
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<td>0.05</td>
</tr>
<tr>
<td>Common Buzzard <em>Buteo buteo</em></td>
<td>0.09</td>
<td>0.05</td>
</tr>
<tr>
<td>Hen Harrier <em>Circus cyaneus</em></td>
<td>0.06</td>
<td>0</td>
</tr>
<tr>
<td>Montagu’s Harrier <em>Circaetus pygargus</em></td>
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<td>0.05</td>
</tr>
<tr>
<td>Common Kestrel <em>Falco tinnunculus</em></td>
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<td>0</td>
</tr>
<tr>
<td>Osprey <em>Pandion haliaetus</em></td>
<td>0.03</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>2.14</td>
<td>0.68</td>
</tr>
</tbody>
</table>

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**Figure 3.** Proportion of waders feeding (mean ± se) in high water in salt pans and mudflat roosts. Most birds did not feed at high water, but mudflats were more important for foraging than salt pans. Turnstone = Ruddy Turnstone, K. Plover = Kentish Plover, R. Plover = Ringed Plover, Bar-t. Godwit = Bar-tailed Godwit, Black-t. Godwit = Black-tailed Godwit, G. Plover = Grey Plover, Avocet = Pied Avocet, Redshank = Common Redshank.

**Figure 4.** Disturbance indexes calculated for salt pans and mudflat roosts. (a) Number of raptors/h above roosts; (b) number of alarm flights/h (for all the birds present in the roosts); and (c) proportion of time spent in vigilance. Note that all disturbance measures were higher in salt pans. Data are expressed as medians ± interquartile range.
higher levels of vigilance. Both the total number of flock alarm flights and the number of alarm flights caused by raptors were several times higher in salt‐pans than in mudflat roosts (Mann–Whitney U-tests: \( U = 69.5, P < 0.001 \), and \( U = 194, P = 0.007 \), respectively). Dunlins spent 3.5 times more time in vigilance in the saltpans than in the mudflat roosts (Mann–Whitney U-test: \( U = 1093.5, P = 0.012 \)), and the difference was even greater for Grey Plovers, which spent eight times more time in vigilance in the saltpans than in the mudflat roosts (Mann–Whitney U-test: \( U = 1471.5, P < 0.001 \)).

**DISCUSSION**

### Waders prefer to roost in upper mudflats than in saltpans

When both types of roost are available, most waders clearly prefer to roost in mudflats than in saltpans. Kentish Plover and Ringed Plover were the only species that did not show this tendency, and simply did not use any of the monitored mudflat roosts. They always roosted in the saltpans, a choice that may be related to their anti‐predator strategy. In fact, they tended to be less reactive to the presence of predators, and often relied on immobility and their high degree of crypsis to escape the predators’ attention. Substrate preferences may also play a role in roost‐site selection. In fact, both species are known to specialize on fairly hard sandy substrates (Moreira 1995a, Granadeiro et al. 2004), and so they may not feel comfortable roosting in the soft and muddy tidal flat roosts. Saltpans are mostly used when mudflat roosts become unavailable, which occurs at tidal heights greater than 3.3 m. Having established the clear preference for roosts in mudflats, it becomes important to understand the reasons for the preference, as this may shed light on the factors that make a potential roosting site attractive to waders, information that is critical for the correct management of high water roosts. This issue is of particular importance given that most species tend to show a high within‐ and between‐year roost‐site fidelity (e.g. Rehfisch et al. 1996).

### Do waders roost on upper mudflats to feed at high water?

We predicted that, if the need to feed during high water drives the choice of roost, we should observe a high proportion of the birds foraging while in their preferred high water roosts, i.e. on the mudflats. However, with the exception of Common Redshank (and, to a lesser extent, Bar‐tailed Godwit Limosa lapponica), the number of birds feeding in mudflat roosts was very low. This suggests that bird choice between roosting sites was not driven by substantial foraging advantages in the mudflats.

These results are consistent with observations of Dunlins in the Yukon–Kuskokwim Delta, Alaska, where most of the birds slept, rather than feeding, in high water roosts (Handel & Gill 2004). In contrast to our observations, Kalejta (1992) and Masero and Pérez‐Hurtado (2001) found large numbers of wintering waders feeding in their high water roosts, and suggest that this may be explained by a need to complement the low tide foraging bout. One possible explanation for the behavioural difference is that the birds that they studied had less profitable low tide feeding grounds, or were subjected to energetically more demanding climatic conditions. An alternative explanation is that they continued foraging during this period because food was widely available in the roosts. In our study area food was quite scarce in both types of roosts so that this option was unavailable.

Prey densities observed in the upper mudflat roosts, which remained exposed during the high water on consecutive tidal cycles, were much lower than in the adjacent mudflats, flooded on all tidal cycles. This difference in the immersion regimes seems to justify the contrast in prey abundance. For example, one of the main prey items of many waders in our study area, S. plana, was rare in the intertidal mudflats used as roosts, probably because it cannot withstand long periods of desiccation (Hughes 1970). In many estuaries, mudflat areas that have the potential to serve as high water roosts for waders, because they remain exposed during high water on consecutive tidal cycles (Fig. 5), are also likely to have prey densities depressed by the same factor.

The joint interpretation of the information now available suggests that food availability was very low and therefore that maintaining feeding activity would be energetically uneconomic; we must therefore seek alternative explanations for roosting preferences.

An alternative explanation for the preference of mudflat over saltpan roosts might be the shorter distance to feeding areas. However, the distance between the mudflat roosts and the saltpans was very small (c. 300 m), compared with the regular movements of the birds to and from the feeding areas, and we often observed waders flying several kilometres to roost at alternative saltpans, located in...
the south of the estuary. Thus, the distance between mudflats and saltpan roosts appears to be irrelevant in relation to movements usually undertaken by waders in estuaries (Piersma et al. 1993, Rehfisch et al. 1996).

Do waders roost in upper mudflats to minimize the risk of predation?

All the predictions made under the hypothesis that predator avoidance is the determinant in the choice of high water roost were corroborated by our results. At the sites preferred by waders for roosting, the frequency both of raptor visits and of alarm flights was lower, and birds spent less time in vigilance than at other roosting sites. Both vigilance and disturbance events can be energetically costly, because they force birds to perform more alarm flights and so suffer a reduction in resting time and incur further energetic costs. Thus, waders prefer to select roosting sites where they are less disturbed, and where they can minimize vigilance behaviour. In fact, it has been demonstrated that disturbance, whether natural or anthropogenic, may result in roost abandonment (Colwell et al. 2003).

Waders may be more vigilant in the saltpans than on mudflats not only because of the frequent presence of predators but also because of lower visibility. With lower visibility birds have less time to react to a predator attack (Whitfield 1985, Cresswell 1994, Lima 1995). The importance of visibility is supported by the fact that on the mudflats studied waders tended to roost near the water line, where visibility is better than near the edge of the saltmarsh, although this behaviour could also be explained by other factors.

All the disturbance indices measured in the study were lower for mudflat roosts than for saltpans. These data seem to support the hypothesis that waders prefer to roost on mudflats because the predation risk there is lower.

Relevance for management

Our results highlight the great importance of upper intertidal sediment flats as high water roosting sites
for waders on the Tagus Estuary. Although in general less obvious to observers than other more easily accessible supratidal roosts (such as saltpans or farmland), these areas sustained the great majority of the roosting birds of the Tagus Estuary during about half of the tidal cycles. Birds roosting on mudflats were under less predation pressure and probably spent less energy during the roosting period. It is likely that this situation is similar to that found at many other estuaries where mudflat roosts are available. Regrettably, upper intertidal flats tend to be very shallow. The disappearance of these preferred roosting areas reduces the number of days in which waders are able to stay in high-quality roosts, and may result in lower winter survival.

The finding that disturbance by predators may determine the choice of roost underlines the importance of minimizing all sources of disturbance at roosts. In our study area, human disturbance was not high at the saltpans because the saltpans had been abandoned and access to them was quite difficult. The mudflat roosts are particularly undisturbed because of the maintenance of a broad edge covered by saltmarsh. However, on other estuaries disturbance by humans, pets, or vehicles is likely to have an effect similar to that of potential predators, and ultimately force birds to change their selection of roosting site (Pfister et al. 1992, Burton et al. 1996).

Several authors have pointed out the importance of saltpans for the maintenance of wader populations in many estuaries (Rufino et al. 1984, Masero et al. 2000). Our finding of a preference by waders for roosting in upper intertidal flats in no way minimizes the importance of roosts in saltpans or other supratidal sites. Our results demonstrate that in the Tagus Estuary, tidal flat roosts become unavailable around spring tides and waders must roost in saltpans. This is likely to occur in many other estuaries, but the availability of this type of supratidal habitat is rapidly declining in many of them. Consequently, it is critical to protect saltpans and other types of supratidal roosts, and to minimize their anthropogenic disturbance.

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