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FACTORS AFFECTING THE USE OF ESTUARINE AREAS BY

WADERS: IMPLICATIONS FOR THEIR CONSERVATION

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Nota Prévia

A presente tese apresenta resultados de trabalhos já publicados ou submetidos para publicação (capítulos 2 a 6), de acordo com o previsto no nº 1 do artigo 41º do Regulamento de Estudos Pós-Graduados da Universidade de Lisboa, publicado no Diário da República II série nº 209 de 30 de Outubro de 2006. Tendo os trabalhos sido realizados em colaboração, a candidata esclarece que participou integralmente na concepção dos trabalhos, obtenção dos dados, análise e discussão dos resultados e redacção dos manuscritos dos artigos referentes aos capítulos 2,3,5 e 6. No artigo referente ao capítulo 4 a candidata participou integralmente na concepção do trabalho e na obtenção dos dados, e colaborou activamente na análise e discussão dos resultados e na redacção do manuscrito.

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Maria Ana Figueiredo Peixe Dias

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Abstract

Estuarine intertidal flats are amongst the most important habitats for waders during the non-breeding season. These environments face increasing pressures from human activities, which are contributing to a general decline in wader populations. It is therefore essential to know the factors driving the use of intertidal flats by wintering waders, particularly their implications to the conservation of these species. The analysis of such factors was the main focus of this thesis, what was attained by answering several specific questions related with the use of sediment flats at different spatial scales, using the waders wintering in Tagus estuary as model. It was demonstrated that dunlins *Calidris alpina* avoid performing long flights between roost sites and foraging grounds, what highlights the importance of the maintenance of a network of good-quality roosts for waders in estuarine areas. It was also shown that species vary in their response to the tidal movement, what has large implications in the estimates of use of tidal areas. Upper tidal flats (which are under considerable threat due to their proximity to shoreline) proved to be particularly important in providing food resources for waders. The fine scale use of tidal areas was studied by testing several predictions related with the searching behaviour of waders. It was shown that only tactile species, as black-tailed godwits *Limosa limosa*, are expected to present an area-restricted search, a type of movement usually adopted by foragers in clumpy environments. Finally, it was evaluated the impacts of traditional shellfishing on waders. Current levels of shellfishing seem to be compatible with the preservation of the Tagus estuary as a key site for waders, but the predictable increase in disturbance due to urban expansion in the vicinity of the Tagus estuary can result in serious impacts on some wader species.

key-words: estuaries; foraging behaviour; high tide roosts; intertidal flats; shorebirds; waders.

Resumo

Os estuários constituem importantes habitats para as aves limícolas durante o inverno e nas passagens migratórias. A maioria das espécies que aí ocorrem alimenta-se de invertebrados bentónicos nas zonas entre-marés durante a baixa-mar, concentrando-se em refúgios supra-tidais durante a preia-mar. Estes habitats encontram-se actualmente bastante ameaçados pelas actividades humanas, sendo o seu desaparecimento e/ou deterioração apontados como das principais causas do declínio de muitas das populações de limícolas em todo o mundo. Desta forma, torna-se fundamental a análise dos factores que influenciam a utilização das áreas estuarinas pelas aves limícolas, e da relevância dos mesmos numa perspectiva da sua conservação. Esta análise constituiu o principal objectivo geral do presente estudo, o qual utilizou como modelo as limícolas invernantes no estuário do Tejo.

O estuário do Tejo é uma das mais importantes zonas húmidas para as aves limícolas que utilizam a rota de migração do Atlântico Este. Aqui inverna uma importante fracção das populações de algumas espécies, destacando-se o alfaiate *Recurvirostra avosetta*, o maçarico-de-bico-direito *Limosa limosa*, a tarambola-cinzenta *Pluvialis squatarola* e o pilrito-de-peito-preto *Calidris alpina*. No conjunto, estas quatro espécies representam mais de 90% do total de aves limícolas que utiliza o estuário durante o Inverno. Uma análise da variação da abundância de limícolas no estuário do Tejo nos últimos 30 anos indica um decréscimo nas populações de tarambola-cinzenta e de pilrito-de-peito-preto. As causas precisas de tais declínios não são conhecidas, mas podem estar também relacionadas com a deterioração de alguns habitats de grande importância para as aves neste estuário. De realçar a acentuada perda de habitat de refúgio de preia-mar nas últimas décadas, sobretudo devida ao abandono das salinas ou da sua conversão em aquaculturas.

As implicações do desaparecimento dos refúgios de preia-mar na utilização dos estuários são abordadas no capítulo 2 desta tese. Foi estudada a influência da proximidade aos refúgios de preia-mar no uso das zonas de alimentação entre-marés pelo pilrito-de-peito-preto. Para tal foram marcadas mais de 500 aves em dois dos principais refúgios do estuário do Tejo, e a sua distribuição nas zonas de alimentação foi subsequentemente caracterizada. Os resultados mostram claramente que os indivíduos tendem a evitar as áreas de alimentação demasiado afastadas dos refúgios, mesmo que estas apresentem uma boa qualidade em termos de disponibilidade de alimento. Desta forma, é fundamental garantir a existência de uma rede de refúgios de preia-mar localizados nas imediações das zonas entre-marés. Através do desenvolvimento e da aplicação de uma metodologia baseada em Sistemas de Informação Geográfica, foi possível avaliar as consequências da perda e criação de refúgios no estuário do Tejo. Esta metodologia pode ser também aplicada em muitos outros estuários onde a disponibilidade de refúgios possa ser um factor limitante para o uso das zonas entre marés.

Para além da proximidade aos refúgios de preia-mar, outro dos factores que potencialmente afecta o uso das áreas de alimentação é o movimento periódico da linha de maré. Nos capítulos 3 e 4 é estudada a resposta de seis espécies de limícolas ao movimento da maré, e a sua implicação no uso de áreas com diferentes tempos de exposição. Para tal, foram efectuadas contagens de aves em 18 sectores, cujo tempo de exposição variava entre uma hora (sector 1) e sete horas (sector 18) por ciclo de maré. As contagens foram efectuadas ao longo de todo o ciclo de maré, desde o início da exposição dos sectores, até à sua total submersão. Espécies como o maçarico-de-bico-direito, o pilrito-de-peito-preto e o alfaiate tendem a seguir a linha de água, dirigindo-se para zonas de cota mais baixa (i.e., com menor tempo de exposição) à medida que a maré baixa se aproxima, e regressando para zonas de cota mais alta (com maior tempo de exposição) com a subida da maré. Como consequência, o

padrão de utilização de áreas com diferentes tempos de exposição é muito variável ao longo do ciclo de maré, e pode não ser correctamente avaliado ao considerar apenas o uso durante o pico de baixa-mar (Capítulo 3). Por outro lado, espécies, como a tarambola-cinzenta, o fuselo *Limosa lapponica* e o perna-vermelha *Tringa totanus*, não apresentam uma associação clara com a linha de água, sendo o seu uso das zonas entre-marés menos variável ao longo do ciclo.

A comparação do comportamento alimentar das limícolas (nomeadamente da taxa de ingestão de presas) foi também estudada nos referidos sectores (capítulo 4). A taxa de aquisição de biomassa é muito superior nas zonas de cota mais baixa, reflectindo a sua elevada utilização durante o pico de baixa-mar. No entanto, por estarem expostas por muito mais tempo, são as áreas de cota mais alta que fornecem a maior parte do alimento para suprir as necessidades energéticas diárias da globalidade das espécies. Estas áreas são também particularmente vulneráveis à pressão humana, dada a sua proximidade à costa.

O estudo do comportamento de procura de alimento foi também analisado a uma escala mais fina (capítulo 5). Estudos anteriores mostraram que, quando as presas se distribuem em agregados, os seus predadores tendem a intensificar a procura de alimento após ingerirem uma presa. No presente trabalho foi analisado se este tipo de comportamento, designado por "area-restricted search" (ARS), se verifica em espécies de limícolas com diferentes estratégias de procura de alimento. Foram estudadas três espécies modelo: o maçarico-de-bico-direito (cuja procura de alimento é baseada sobretudo em pistas tácteis), o perna-vermelha (que recorre sobretudo a pistas visuais para encontrar as presas) e o alfaiate (que se alimenta através de "varrimentos" na superfície do sedimento, nos quais ingere pequenas presas juntamente com alguma vasa). O tipo de percurso efectuado por estas espécies foi analisado em detalhe através da filmagem de 190 indivíduos e posterior análise dos seus movimentos. Os resultados indicam que apenas as espécies tácteis apresentam

um comportamento que se pode caracterizar como ARS, intensificando a procura de alimento (diminuindo a velocidade e aumentando a tortuosidade do seu percurso) logo após ingerirem uma presa. Os resultados mostram também que o movimento destes indivíduos é condicionado por um conhecimento prévio da distribuição das presas, o que nunca tinha sido documentado em espécies de limícolas.

Por último, foi avaliado o impacto da apanha manual de moluscos bivalves no uso das áreas entre-marés pelas aves limícolas (capítulo 6). A apanha de bivalves, em particular de lambujinhas *Scrobicularia plana*, é muito frequente no estuário do Tejo, e pode potencialmente ter influência na comunidade de aves que se alimenta na zona entre-marés, à semelhança do que sucede noutros estuários. Foram analisados três impactos potenciais desta actividade nas aves: a remoção de presas de aves limícolas (uma vez que a lambujinha é também uma das principais presas de limícolas no estuário do Tejo), a perturbação directa resultante da presença humana nas áreas de alimentação das aves, e a alteração da estrutura do micro-habitat de alimentação das aves devido ao remexer do sedimento. A intensidade da apanha foi quantificada ao longo do ciclo anual, pela contagem directa do número de mariscadores presentes em todo o estuário, e por estimativas da taxa de remoção de lambujinhas pelos mesmos. Os níveis actuais de apanha de bivalves parecem ser compatíveis com a manutenção da qualidade global do estuário para as aves limícolas. No entanto, através da simulação do aumento da intensidade da apanha de bivalves, concluiu-se que a perturbação causada pela presença de mariscadores nas zonas entre-marés pode ter impactos graves na sua utilização pelas espécies menos tolerantes à aproximação de pessoas.

Palavras-chave: áreas entre-marés; comportamento alimentar; estuários; limícolas; refúgios de preia-mar

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Chapter 1

General Introduction

1. General Introduction

1.1. Waders: general overview

Waders are a widespread group of birds that comprises more than 200 species belonging to 12 families within the Order Charadriiformes (Hayman et al. 1986). Most of these species are typically associated with wetland or coastal environments, so they are also frequently referred to as "shorebirds". Waders are often remarkably gregarious during the non-breeding season. They can be found feeding and roosting in large flocks, sometimes with hundreds of thousand individuals, and are thus a very conspicuous group of birds.

Many wader species are long-distance migrants, undertaking some of the most prodigious journeys of any bird species (Message & Taylor 2005). Some of them undertake annual migrations from their breeding grounds, usually located in high Arctic tundra, to the wintering quarters located in the southern limits of Australasia, Africa and South America. Others, like the bar-tailed godwits *Limosa lapponica baueri*, are able to perform a nonstop flight of more than 11 000 km, by far the longest ever registered in birds (Gill et al. 2005). In these journeys between breeding and wintering areas waders usually follow species-specific migration routes, called flyways (IWSG 1992). There are ten major flyways currently recognized: East Atlantic, Mediterranean, East African, Indian, East Asia/Australian, Central Pacific, East Pacific, Patagonian, Interior American and West Atlantic (Van de Kam et al. 2004). The East Atlantic Flyway (EAF; Fig. 1.1) comprises the breeding areas located in Siberia, northern Europe and Russia, Iceland, Greenland and NE Canada, and wintering areas located in the Atlantic and West Mediterranean coasts of Europe and West Africa (e.g. Smit & Piersma 1989).
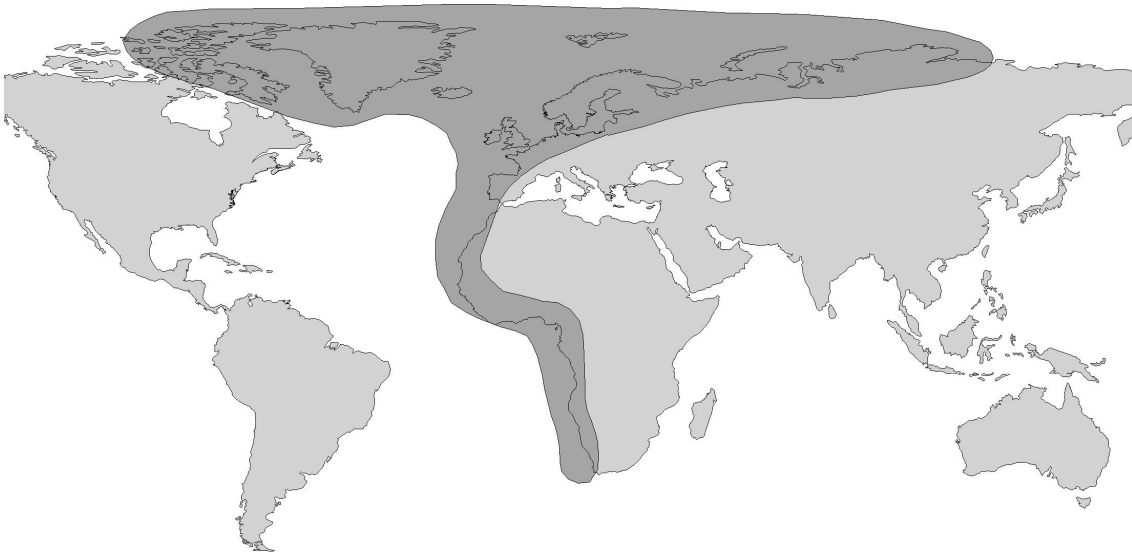
Figure 1.1. The East-Atlantic Flyway (adapted from IWSG 1992)

During the non-breeding season (that includes the wintering and migratory phases of the life-cycle) most wader species concentrate in estuaries and other coastal wetlands. In the estuarine areas their daily cycle is totally constrained by the movement of the tides (e.g. Burger et al. 1977). Birds usually feed on intertidal flats exposed during the low-tide period, and are forced to move to supra-tidal areas when the tide rises. Most estuarine areas worldwide have two low-tides a day (i.e., tides are semi-diurnal), which means that birds have to move between high-tide roosts and low-tide feeding areas twice a day. The ecological implications associated with these movements are still poorly known, and are the focus of the chapter 2 of this thesis.

1.2. Tidal flats as major foraging areas for waders during the non-breeding season

Most waders that forage in intertidal flats prey upon invertebrate species that live buried in the sediment. The most common prey items for waders in temperate estuaries are the bivalves (Mollusca: Bivalvia), mudsnails (Mollusca: Gastropoda), polychaete worms (Annelida: Polychaeta) and crustaceans (Arthropoda: Crustacea) (Van de Kam et al. 2004). Waders present numerous adaptations to forage in these soft-bottom environments. For example, Scolopacidae species (particularly genus *Limosa* and *Numenius*) have long bills that allow them to catch prey that lives deeper in the sediment column; the large eyes of plovers (Charadriidae) enable them to search for food during nocturnal low-tides (McNeil et al. 1992); heavily muscled stomachs allow the mollusc-eaters (as knots *Calidris canutus* and purple sandpipers *Calidris maritima*) to crush shells (Piersma et al. 1993a); knots possess large numbers of sensors on the bill tips (Herbst corpuscles) that allow the remote detection of their prey (Piersma et al. 1998). Nonetheless, wader species present a large amount of variation in these features, particularly in bill morphology (Durell 2000), which allows them to exploit several different niches (Fig. 1.2).

Waders also vary in the strategy used to search for food. Plovers usually detect their prey by sight (e.g. Turpie 1994), whilst most Scolopacidae species use mostly tactile cues (e.g. Gerritsen & Meiboom 1986; Piersma et al. 1998). Avocets (genus *Recurvirostra*) use a unique strategy, that consist in sweeping their bill in the sediment surface to ingest small prey items (Moreira 1995a,b). Although each species tends to adopt a particular type of searching strategy, they can switch from one to another in response to environmental conditions (e.g. Robert & McNeil 1989; Moreira 1995a; Lourenço et al. 2008).
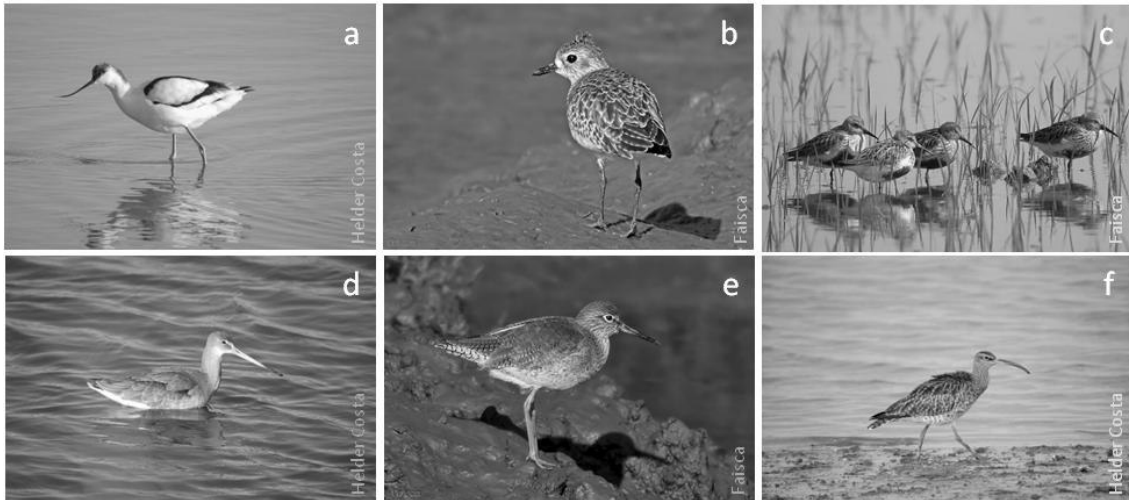
Figure 1.2. Some of the most common wader species of the EAF. a: avocet *Recurvirostra avosetta*; b: grey plover *Pluvialis squatarola*; c: dunlin *Calidris alpina*; d: black-tailed godwit *Limosa limosa*; e: redshank *Tringa totanus*; f: whimbrel *Numenius phaeopus*.

Estuarine sediment flats are highly dynamic environments, where accessibility to foraging grounds is continuously changing due to the movement of the tides. This has obvious impacts on the distribution and behaviour of waders that forage there, since they are limited to the exposure period of the flats to gather food (Burger et al. 1977; Connors et al. 1981; Nehls & Tiedemann 1993). Within an estuary, the exposure period of the flats can vary by several folds, so waders can move from one area to another in order to maximize feeding opportunities and the time available to find food. Species differ in their response to this periodical change in flats' availability: some concentrate their feeding effort near the tidal line, whereas others tend to arrive to their foraging grounds well after the tidal passage (Burger et al. 1977; Connors et al. 1981; Nehls & Tiedemann 1993; Evans & Harris 1994; Scheiffarth et al. 1996). The consequences of these different behaviours on the overall use of estuarine flats by waders, as well in the validity of the methods used to study it, are analysed in detail in chapters 3 and 4.

The tidal cycle may also affect the foraging decisions of waders by constraining the time available for feeding to a limited part of the day. Some species are able to complement their energetic requirements by feeding in alternative habitats during high tide (Velasquez & Hockey 1992; Masero & Pérez-Hurtado 2001), but these are often of poorer quality (Smart & Gill 2003a). Thus, waders that forage in intertidal habitats need to maintain their intake rates at high levels in order to fulfil their daily energetic demands that are amongst the highest found in birds (Piersma 2002; Rogers et al. 2006a). For these reasons, and also because they are easily surveyed while foraging, wintering waders have often been used as models to test predictions derived from the Optimal Foraging Theory (Emlen 1966; MacArthur & Pianka 1966). Strikingly, such studies have been mostly restricted to optimal diet and patch choice (Goss-Custard 1977a; Piersma et al. 1995; Meire 1996; Stillman 2003; Van Gils et al. 2005a, b), while studies related with their immediate foraging decisions, and particularly with their fine-scale movements in tidal flats, are still scarce (but see Goss-Custard 1970, 1977b; Speakman & Bryant 1993; Wilson & Vogel 1997). This question is addressed in chapter 5.

1.3. Major threats to the wader conservation in wintering areas

Almost half of the waders with known population trends are declining all around the world (IWSG 2003). The causes of this decline are diverse, the most relevant being probably related with habitat loss and deterioration (e.g. Goss-Custard & Yates 1992; Yates et al. 1996; Rehfisch et al. 2003) and human disturbance (e.g. Cayford 1993). Changes related with global warming are also of major concern for the wader conservation (e.g. Norris et al. 2004). Among the most serious issues related with climate change are the reduction of the available breeding habitat in high Arctic tundra

(Rehfisch & Crick 2003; Smart & Gill 2003b) and the loss of intertidal areas due to the sea-level rise (Austin & Rehfisch 2003; Crooks 2004).

The loss of estuarine habitats has been pointed as one of the major threats for migratory waders. The overall available area of tidal flats was dramatically reduced over the last decades (Van de Kam et al. 2004). Intertidal area losses within an estuary can affect its carrying capacity, by reducing the total amount of food available for waders (e.g. Goss-Custard et al. 2002). Furthermore, the expected increases in densities in the remaining areas may promote the interference among feeding birds (Stillman et al. 2003; Goss-Custard et al. 2004), and the consequent reduction in their intake rates, which may compromise their survival (e.g. Triplet et al. 1999; Yates et al. 2000). Ultimately, the loss or degradation of sediment flats may increase the wader mortality during winter and/or migration periods (e.g. Durell et al. 2006; West et al. 2007), when their energy requirements are very high. The magnitude of the impact of these factors on the overall population size depends on the strength of any compensatory reproduction on the breeding grounds, and on the availability of alternative wintering and stopover sites (Stillman & Goss-Custard 2006). Nonetheless, recent studies confirms that the situations faced by migratory birds in their wintering grounds can carry-over negative effects in the breeding success in the following season (Marra et al. 1998; Norris 2005). This exacerbates the potential negative effect of intertidal loss during the non breeding season, and highlights its important implications for the dynamics of migratory populations (Norris 2005).

Human disturbance is also pointed as one of the major threats for waders during winter. Disturbance can imply a temporary loss of habitat, because birds are prevented to feed where disturbance occurs (Stillman et al. 2000). As in the case of a permanent loss of habitat, disturbance may cause the densities of waders to rise in adjacent undisturbed areas, increasing the potential for interference among birds. Moreover, disturbance will also force birds to spend time and incur energetic costs

while commuting between areas, which may also have a negative impact on birds fitness and, ultimately, on their chance to survive during the winter (West et al. 2002; Goss-Custard et al. 2006a). On the other hand, some waders can adapt their tolerance to human disturbance (Goss-Custard & Verboven 1993), which ultimately will depend on the body condition of the birds (Beale & Monaghan 2004) and on the availability of alternative habitats (Gill et al. 2001a). However, the combined effects of disturbance with other causes of habitat loss may have severe impacts on the survival of birds (Durell et al. 2006), as when associated with severe winters (Goss-Custard et al. 2006a).

One type of potential human disturbance, with worldwide occurrence, is the exploitation of estuaries as source of food, particularly shellfish. Shellfish exploitation has raised some important conservation questions, because the main target species of the shellfisheries are also important food resources for waders (e.g. Piersma & Koolhaas 1997; Stillman et al. 2003). The potential conflict between shellfishers and waders has been the focus of several studies (e.g., Piersma & Koolhaas 1997; Norris et al. 1998; Atkinson et al. 2003; Goss-Custard et al. 2004). Most of these studies have been conducted in northern estuaries, which are intensively exploited by mechanical shellfishing (e.g. Piersma et al. 2001; Camphuysen et al. 2002; Atkinson et al. 2003). This type of shellfishing is usually carried out during the high tide, and can substantially reduce bivalves and other non-target populations (e.g. Ferns et al. 2000), hence affecting the availability of food for waders. Mechanical methods will also cause sever reworking of tidal sediments, affecting both its composition (sediments become more sandy) and affecting the settlement and recovery of invertebrate populations (e.g. Piersma & Koolhaas 1997; Collie et al. 2000). The consequences of this can be dramatic, particularly if associated with other events as severe winters. For example, the intense exploitation of mussels *Mytilus edulis* and cockles *Cerastoderma edule* in the Wadden Sea during the 1990s have contributed to a mass mortality of 21 000

common eiders *Somateria mollissima* (Camphuysen et al. 2002), and to the decline in numbers of wintering oystercatchers *Haematopus ostralegus* from 260 000 to 170 000 (Ens 2006). The traditional shellfishing, usually performed by hand during the low-tide period, tends to cause much less damage on the bivalve population. However, the presence of shellfishers and bait-diggers on the feeding areas of birds can be a source of disturbance, with the already referred associated consequences. In chapter 6 the main potential effects of the traditional shellfishing on waders are addressed, using as case study the Tagus estuary.

1.4. Tagus estuary: characterization and importance for non-breeding waders

Overall characterization of the Tagus estuary

The Tagus estuary is the most important wetland in Portugal for aquatic birds (Costa et al. 2003), and one of the most important estuarine systems for waders along the EAF (Stroud et al. 2004; Van de Kam et al. 2004). It covers an area of 320 km^2 and a linear extension of 80 km of tidal influence (Costa 1999). Tides in the Tagus estuary are semi-diurnal, with an amplitude that ranges from 1 to 3.8 m in neap and spring tides, respectively. This difference in amplitude strongly affects the total area exposed during the low-tide: it varies from about 56 km^2 in median neap tides (1.3 m) to ca. 100 km^2 in median spring tides (0.5 m; Fig. 1.3). Intertidal areas of Tagus are predominantly composed by mud (particles smaller than 63 μm), with some dead oyster banks near the main channels (Rodrigues et al. 2006; Figs. 1.3 and 1.4).
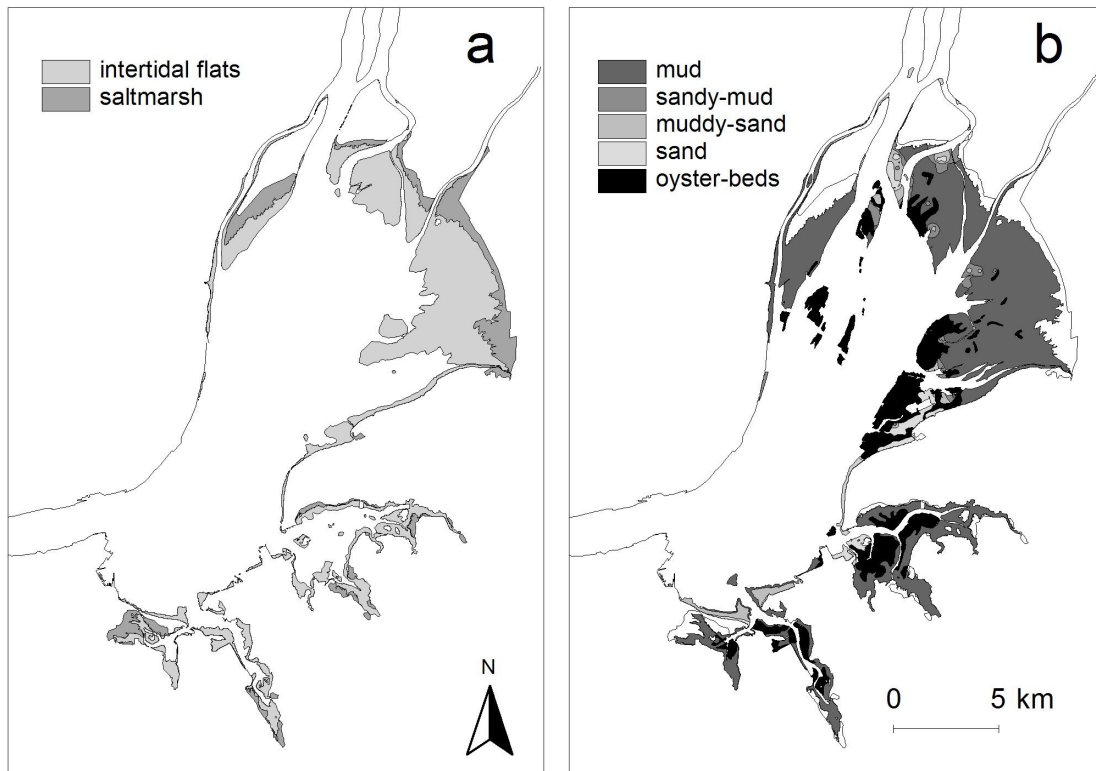
Figure 1.3. Available intertidal area during a) median neap low-tide (1.3 m) and b) median spring low-tide (0.5 m). Main sediment types are also indicated in b).

The most abundant and widespread invertebrate species on Tagus intertidal flats are the polychaetes *Streblospio shrubsolii* and *Tharyx* sp., and the crustacean *Cyathura carinata* (Rodrigues et al. 2006). The biomass is dominated by the bivalve *Scrobicularia plana* and the polychaete *Hediste diversicolor*. All these species, particular the later ones, are potential prey for the waders that winter in Tagus estuary (Moreira 1995c, 1997). They are also important food items for fishes that feed in intertidal flats during the high-tide, such as the Gobies *Pomatoschistus* spp. and the Soles *Solea* spp. (Cabral 2000; Salgado et al. 2004).

Figure 1.4. Two main typical habitats in Tagus estuary: muddy tidal flat near Gaio (left image) and dead oyster bank near Alcochete (right image).

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. The Tagus estuary is an internationally important wintering area as (i.e., its hold more than 1% of the EAF population; Stroud et al. 2004) for avocet *Recurvirostra avosetta*, grey plover *Pluvialis squatarola*, black-tailed godwit *Limosa limosa* and dunlin *Calidris alpina* (based in counts carried out during the 1990s; Rufino 1990, 1992, 1993, Rufino & Costa 1993, 1994, 1996a, 1996b, 1997 and ICNB unpublished data; Fig. 1.2. a-d). These are by far the most numerous wader species of the Tagus estuary and, together, comprise about 90% of all the waders present in this wetland during the winter (estimated in about 50 000 individuals during the 1990s). The importance of the Tagus estuary for waders during the migration period is almost unknown, despite its strategic location between some of the most important wintering areas of the EAF (as the Banc d'Arguin, Mauritania; Zwarts et al. 1997) and the breeding areas located in Northern Europe and Russia (Fig. 1.1). First evidences of this importance were given by Lourenço and Piersma (2006), referring that ca. 50% of black-tailed godwit

subspecies *L. l. limosa* stage in Tagus and Sado estuaries during their northern migration.

The first major ecological study of the waders that winter in Tagus was carried out by Teixeira (1985), who analysed the distribution of the species among the intertidal flats. The major patterns of use of intertidal areas at the estuarine levels were also addressed by Moreira (1993a) and Granadeiro et al. (2007), with both studies pointing to the importance of the sediment type on the distribution of the species. Finer scale studies, also related with the habitat selection in the intertidal feeding areas, were conducted by Rosa et al. (2003) and Granadeiro et al. (2004). Moreira (1994, 1995b, 1996) had provided the first studies on the diet and foraging behaviour of several wader species in Tagus estuary, and on the role of the community of aquatic birds in the overall estuarine food web (Moreira 1997). Since then, Tagus estuary has been the target of some important ecological studies regarding the foraging ecology of waders, as the influence of prey availability and activity on their feeding behaviour (Rosa 2007), the relevance of night foraging (Lourenço et al. 2008) or the consequences of public illumination on birds (Santos et al. in prep).

Evolution of Wintering Populations in Tagus estuary in the last decades

Since the middle 1970s the number of waders wintering on Tagus estuary has been regularly monitored by Portuguese authorities (now Instituto da Conservação da Natureza e da Biodiversidade, ICNB). Counts have been performed during mid-January spring tides, in the most important roosts of Tagus estuary (and also in other major wetlands in Portugal). However, there are some gaps in the temporal coverage, and in some years there was not a complete coverage of the Tagus main roosts. Nonetheless, the data obtained in the last three decades allow a broad analysis of

some wintering population trends during this period. Figure 1.5 shows the trends of the species for which the Tagus is internationally important.

Numbers of waders were highly variable among years, what is probably due to differences in the coverage, but also to natural inter-annual variation in the populations (Atkinson et al. 2006). In the case of black-tailed godwit, the large variations can also be due to the fact that in January several birds have already started their northward migration (Gill et al. 2007; Lourenço & Piersma 2008). Flocks of more than 20 000 individuals were observed in some years and might correspond to migrating birds. Although also presenting some variation between years, the trends of grey plovers and dunlins seem to correspond more clearly to a decrease in their numbers. In grey plovers, counts of more than 4000 birds were frequent during the 1970s and 1980s, but since 1995 counts of more than 2500 birds were rather uncommon. In dunlins the decrease seems to be even sharper: from an average of 20 000 – 30 000 individuals during the 1970s and 1980s, for less than 12 000 since 2001.

The main causes for the observed trends are unknown. Being migratory birds, changes in wintering numbers can be related with external factors, such as the loss of breeding habitat. One might think that this is probably the case of dunlins, given that one of subspecies that winter in the Tagus – *C. a. schinzii* – is globally declining (Stroud et al. 2004). However, the majority of the wintering dunlins seems to belong to the subspecies *C. a. alpina* (Lopes & Wennerberg 2006), so that is probably only part of the explanation. A decrease in mid-winter numbers of grey plovers was also noted in some of the main African wintering grounds of the species (Stroud et al. 2004). However, populations wintering in Western Europe (Britain, Germany and France) are increasing, suggesting a northward shift in the distribution of wintering grey plovers (Stroud et al. 2004).

Avocet

Grey Plover

Black-tailed Godwit

Dunlin
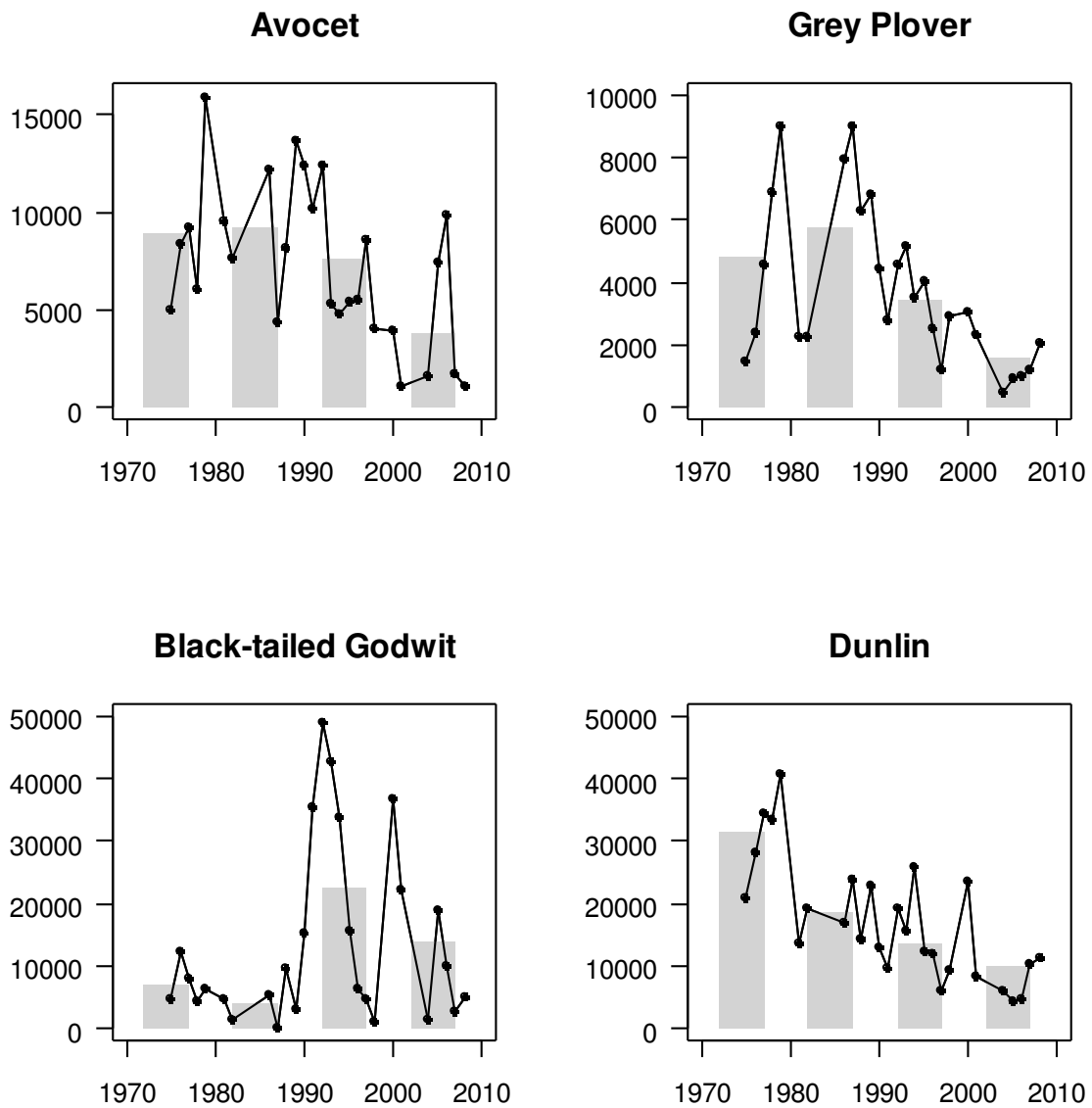
Figure 1.5. Population trends of the four most abundant wader species in Tagus Estuary. Data until 1997 were obtained from Rufino (1978, 1982, 1988, 1990, 1992, 1993) and Rufino & Costa (1993, 1994, 1996a, 1996b, 1997). More recent data was provided by ICNB. Grey bars represent the mean value per decade.

It is also possible that dunlins and grey plovers that winter in Tagus may be affected by changes in the conditions within the estuary. However, the lack of long term studies of the habitat quality for waders (for example, of total amount of food available) precludes any conclusion about potential internal factors that may lead to the

decreases observed. Nevertheless, some important changes have occurred in Tagus estuary during the last few decades, and probably the most relevant are related with loss of high-tide refuges.

In Tagus estuary, waders roost mainly in saltpans (Fig. 1.6). Historically, the most important roost areas were the Vasa-Sacos, Vale de Frades and Samouco saltpans, and the saltmarsh area located near Pancas (Fig. 1.6). During the last few decades some of this and other important refuges were lost. Alverca saltpans, one of the few roosts located in the northern area of the estuary, lost its quality as roosting site mainly due to habitat degradation. The conversion of saltpans to aquaculture was another cause of habitat loss, and the same recently occurred in Vasa-Sacos. This later roost used to be the most important refuge area in Tagus estuary, holding usually more than 40 000 waders during the winter and migration periods. Despite being located inside the Nature Reserve and the Special Protected Area (Fig. 1.6), it is currently managed for the production of grass shrimp *Palaemonetes varians*. The high water level in the ponds restrains its use by almost all the wader species. Currently, no more than few dozens of waders and other waterbirds can be found there. The Samouco saltpans are under the threat of abandonment, due to lack of financial support. This site is also one of the most important roosts in Tagus estuary, and the lack of a proper management can seriously jeopardize its importance for waders (e.g. Paracuellos et al. 2002). Finally, none of the major roosts in the southern part of the estuary have any type of protection status (Fig. 1.6). Therefore, and considering the increasing human pressure in the coastal areas in the last few decades (Correia 2003), the maintenance of the quality of these sites as roosting areas for waders is uncertain.
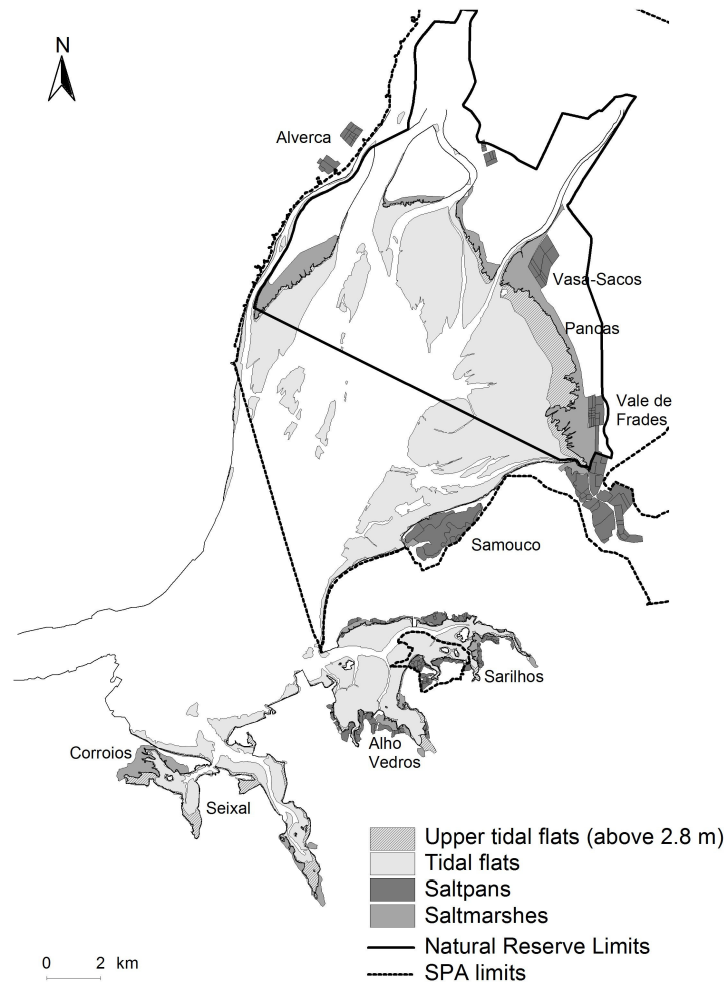
Figure 1.6. Main roost areas in Tagus estuary. Nature Reserve and Special Protected Area (SPA) limits are also indicated.

1.5. Thesis main aims and outline

This thesis aimed to analyse some of the major factors driving the use of tidal flats by non-breeding waders, using the waders wintering in Tagus estuary as model. Several spatial and temporal scales were addressed: a broad scale, by analysing the relationship between the use of low-tide feeding areas and high-tide roosts, at an intermediate scale, by evaluating the influence of the tidal cycle on feeding behaviour of waders, and at a fine scale, by describing their immediate decisions while foraging.

The conservation implications of the findings are also described in each chapter. Finally, the impact of one of the major human activities carried out in tidal flats of the Tagus estuary – the shellfishing – is addressed in chapter 6. The specific aims of each chapter are described below, along with the main methodological approaches.

Chapter 2: Distance to high-tide roosts constrains the use of foraging areas by dunlins: Implications for the management of estuarine wetlands

The major aim of this study was to quantify the effect of the location of high-tide refuges on the use of tidal flats by waders. This was achieved by dye-marking more than 500 dunlins (the most abundant wader in the west Palaearctic Region) in two of the most important roosts of the Tagus estuary, and by subsequently analyse their low-tide distribution.

A Geographic Information System (GIS) methodology was developed to evaluate the potential impact of refuges loss on the use of the space by foraging waders. A simple method to identify the best roost location in estuary, based on distances to adjacent foraging areas, is proposed. Based on this methodology, it was also derived the best location for additional roosts in Tagus estuary.

Chapter 3: Estimating the use of tidal flats by waders: inaccuracies due to the response of birds to the tidal cycle

This study set out to elucidate some of the complexities of estimating habitat use by waders in the highly dynamic estuarine tidal flats. In particular, it was evaluated whether low tide counts provide good estimates of use of intertidal areas by waders,

and analysed how the response of birds and the exposure period of the flats influence the accuracy of these estimates.

The total use of several intertidal plots (that differed in their exposure period) by six wader species was estimated through regular counts during entire tidal cycles. These "full-cycle" estimates were then compared to estimates based only on low-tide counts, and also with a new proposed approach that combined low and mid-tide counts.

Chapter 4: Variation in numbers and behaviour of waders during the tidal cycle: implications for the use of estuarine sediment flats

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 intertidal flats. Several wader counts were performed in a range of tidal flats with different exposure periods. These counts were carried out during several phases of the tidal cycle, allowing the analysis of the response of waders to the moving tidal line, and the influence of the exposure period of sediment on its use (in terms of abundance and foraging behaviour). It was also determined the relative importance of high, medium and low sediment flats in provisioning food resources for waders.

Chapter 5: Searching behaviour of foraging waders: does feeding success influence their walk?

This study provides the first detailed description of several parameters of the fine-scale movement of three wader species that differ in their searching strategies:

avocet (a "sweeper"), black-tailed godwit (a "tactile predator") and redshank *Tringa totanus* (a "visual predator").

The feeding behaviour of 190 individuals was filmed and, using GIS facilities, more than 12 000 foraging spatial positions were obtained, along with detailed record of feeding activity. This allowed testing predictions related with the searching behaviour of waders, in particular if it can be characterized as an "area-restricted" type of movement.

Chapter 6: Does traditional shellfishing affect foraging by waders? The case of the Tagus estuary (Portugal)

In this study the impact of traditional shellfishing on several wader species that use the Tagus estuary was analysed. A particular focus was given to hand raking of clams *Scrobicularia plana*, which constitutes the most consumed food by waders in the estuary. Three potential effects of this activity were addressed: the decrease of clam availability for waders, the disturbance caused by the presence of shellfishers in the intertidal feeding areas, and the impact of sediment reworking on non-target invertebrates and on the foraging efficiency of birds.

The shellfishing activity was characterized through regular visits to the tidal flats of the Tagus estuary (covering a year cycle), in which the number of shellfishers and bait-diggers was assessed. The prey availability and foraging activity of waders was compared in raked and in adjacent control areas. Finally, using a simulation approach ran in a GIS, it was predicted the potential consequences for waders of the increase of the number of shellfishers.

Chapter 2

Distance to high-tide roosts constrains the use of

foraging areas by dunlins: implications for the

management of estuarine wetlands

2. Distance to high-tide roosts constrains the use of foraging areas by dunlins: implications for the management of estuarine wetlands

2.1. Abstract

Shorebirds are declining all around the world, mostly due to deterioration of the estuarine habitats used in winter and migration. Estuaries cover small areas, so it is essential to guarantee that shorebirds can access all the tidal flats where they usually feed at low-tide.

Studying use of space by dunlins (*Calidris alpina*) in the Tagus estuary (Portugal), we noted that lack of suitably located high-tide roosts can limit the access of shorebirds to feeding habitats. Density of dunlins on foraging areas declined significantly with distance to the nearest roost, and fewer than 20% individuals foraged more than 5 km from two roosts where they were dye-marked.

So to permit full access to feeding areas it is important to maintain a network of suitably located high-tide roosts. We developed a GIS modelling methodology to evaluate the adequacy of existing roost networks, and to estimate the consequences of losing or creating new roosts. The methodology requires maps with the location of roosts and foraging habitats, and knowledge of the distances that birds are willing to fly to reach foraging areas. It quantifies the proportion of foraging areas close to the existing roosts and the average distance that birds have to fly to reach potential feeding sites.

Applying this methodology to the Tagus estuary we concluded that lack of roosts probably explains why the intertidal flats in the north-west of the estuary are

underused by shorebirds. A modelling exercise suggested that this gap could be eliminated by creating a roost in an old drained wetland area. We also modelled the impact of the loss of two roosts that are currently threatened. Without them almost half of the available feeding areas will be too far from roosts to be efficiently used by dunlins, and possibly by other shorebirds.

2.2. Introduction

The majority of populations of shorebirds with known trends are declining all around the world (review in IWSG 2003). Most species spend their non-breeding season concentrated in estuaries or other coastal wetlands, and depend for food on their highly productive intertidal flats. However, in many estuaries the area of this critical foraging habitat has been substantially reduced, especially by land reclamation projects (Goss-Custard & Yates 1992), and further reductions are expected due to the ongoing sea-level rise caused by climate change (Crooks 2004).

With the area of intertidal flats declining worldwide, it is essential to minimize any factors that may limit the access of shorebirds to the extant areas of this foraging habitat. Failing to do so may result in a decline of the carrying capacity of estuaries for shorebirds (Goss-Custard et al. 2002; West et al. 2005). Consequently, it is important to identify such limiting factors, particularly if human-related, and find ways to minimize their impact.

Shorebirds feed on the intertidal flats when these are exposed, but as the tide rises they are forced to leave their foraging grounds and concentrate at high water roosting sites, usually located in salt marshes, saltpans, fields, or beaches (Britton & Johnson 1987; Rehfisch et al. 1996). During neap tides some upper intertidal areas

may remain exposed at high-tide, and the birds can also choose to roost there (Rosa et al. 2006).

Most shorebirds are forced to make frequent flights between their foraging grounds in intertidal flats and high-tide roosts, and in medium and large estuaries such flights can be quite long (Symonds et al. 1984; Piersma et al. 1993b; Drake et al. 2001; Gabbard et al. 2001). Several authors have tentatively suggested a link between the usage of foraging areas and the availability of high-tide roosts in their vicinity (Handel & Gill 1992; Scheiffarth et al. 1996; Fox & Madsen 1997), but so far no study has tested if the use of intertidal flats declines with increasing distances to high-tide roosts. This is likely to occur if flights to and from the roosts involve an energetic expenditure that is relevant for the birds (Warnock & Takekawa 1996; Luís et al. 2001; Rogers 2003). A study in the Dutch Wadden Sea estimated this expenditure in knot (*Calidris canutus*), and concluded that it corresponds to about 10% of the daily energy spent by the species (Piersma et al. 1993b), suggesting that flights between roosts and foraging areas can be energetically important.

If distance to high-tide roosts influences the access to foraging areas by shorebirds, then the loss of roosts may affect the carrying capacity of estuaries for birds, with negative consequences for shorebird populations (Tubbs et al. 1992; Burton et al. 1996). Regrettably, many high-tide roosts located around estuaries have been lost or are under pressure from development (Rogers 2003). The Tagus estuary, where this study was done, is no exception, and many of its roosts have disappeared in the last decades or are presently under threat. This factor is likely to aggravate the consequences of the loss of potential feeding areas on tidal flats.

Since it is critical to minimize factors that may limit access of shorebirds to intertidal flats, it is important to understand if distance to high-tide roosts is indeed a limiting factor. If so then this factor should be incorporated in the planning strategies for estuarine wetlands. To this end it is desirable to develop methodologies to evaluate

how well the potential foraging areas are covered by existing roosts, and to model the consequences of losing or creating high-tide roosts.

In this study (1) we tested and quantified the effect of distance to high-tide refuges in the use of tidal flats by the dunlins (*Calidris alpina*), the most abundant shorebird in the western Palaearctic region (Stroud et al. 2004). In addition, (2) we developed a Geographic Information System (GIS) methodology to evaluate the potential impact of losing or creating new refuges on the use of space by foraging shorebirds. Finally (3) we applied this methodology to the Tagus estuary, both to quantify the impact of the loss of presently threatened roosts, and to evaluate alternative locations for new roosts near intertidal flats that at present are apparently underused by birds.

2.3. Methods

Study area

The study was done in the Tagus estuary, Portugal, one of the largest and most important wetlands in the Iberian Peninsula. It holds about 50 000 shorebirds during winter (Moreira 1997), of which about 14 000 are dunlins (Santos et al. 2005), and much of it is classified as a Nature Reserve and as a Special Protection Area under the European Birds Directive. Intertidal flats occupy about 97 km^2 (Granadeiro et al. 2007), but in this study the southern portion of the estuary was not included because not all roost sites could be adequately identified and monitored.

Birds roost mostly in saltpans during spring high-tides, but during neap tides they tend to use a narrow mudflat area adjacent to the salt marsh, which remains exposed at high-tide (Rosa et al. 2006). In the Tagus estuary, birds rarely used the

saltmarsh to roost. Our study focused on roosts that are currently used by large numbers of shorebirds. These are Vasa-Sacos saltpans (roost 1), Vale de Frades saltpans (including Tarouca and Belavista; roost 2), Samouco saltpans (roost 3) and Alverca saltpans (roost 4) (Fig. 2.1).

Bird trapping and counts

During two consecutive winters we mist-netted and dye-marked (with picric acid) 570 dunlins at two of the most important roosts: Vasa-Sacos (370 birds, in 2001/2002) and Vale de Frades (200 birds, in 2002/2003) (Fig. 2.1). More than 90% of the marked birds were adult.

After the marking sessions most of the tidal flats of the study area were systematically searched for dunlins. We carried out two types of counts: (1) during spring low-tides, when all the intertidal area was available and birds were feeding; and (2) during neap high-tides, when only the upper parts of the tidal flats were exposed and birds were mostly resting (in neap tide roosts).

Low-tide (± 2 hours) counts were carried out on 59 km^2 of tidal flats in January-March 2002 and on 57 km^2 during the same period of 2003. These areas were divided into 1063 and 1109 sectors respectively, and counted once each year. In each count we recorded the number of marked and non-marked dunlins present in the sectors (see Granadeiro et al. 2007, for detailed procedures).
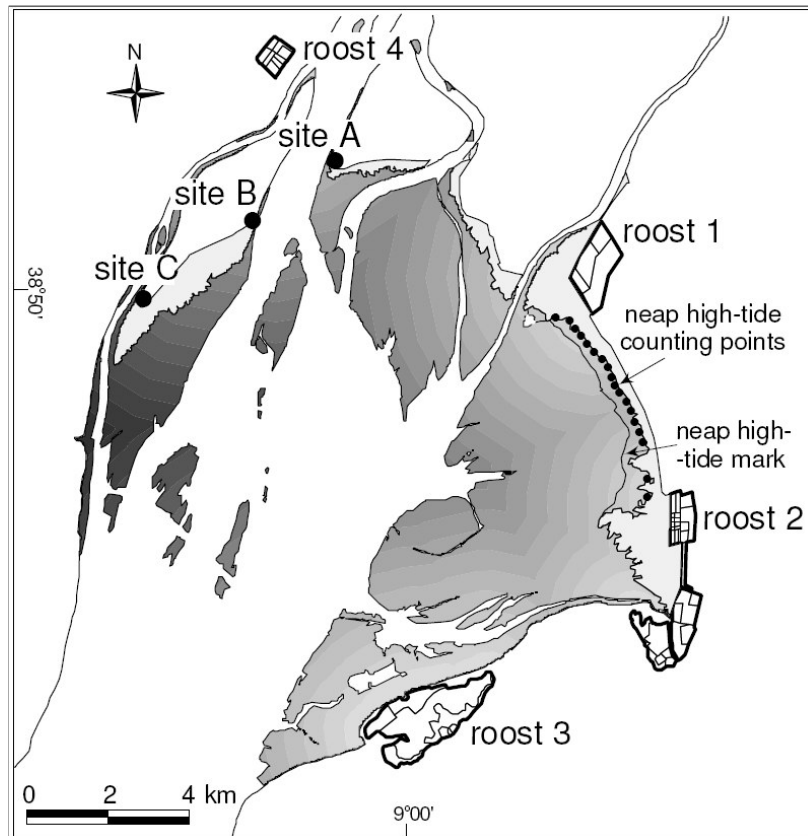
Figure 2.1. Study area, indicating the main roosting sites (roosts 1 to 4) and the potential locations for new roosts (sites A, B and C). Lighter grey corresponds to saltmarsh and the grey gradient represents increasing distance between mudflat areas and existing spring high-tide roosts, in 500 m steps.

The neap high-tide counts were carried out from 18 points located between roosts 1 and 2. In each count we recorded the number of marked and non-marked dunlins present in the area delimited by the salt marsh and the high-tide mark (Fig. 2.1). These counts were repeated five to eight times in 2002 and seven times in 2003.

All the main roosts in the study area were regularly visited at spring high-tides during the two winters in order to monitor inter-roost dispersal of marked birds.

We calculated the proportion of marked birds from low-tide counts, which we pooled in 1 km distance classes around each of the two marking roosts. Distance classes with less than 20 dunlins were excluded from the analysis because they were considered unsuitable to estimate the proportion of marked birds. Therefore we

excluded the first two classes (0-1 km and 1-2 km) in both years. Standard errors for the percentages of marked dunlins in these classes were calculated by bootstrap.

We also analyzed the relationship between the distance to the nearest high-tide roost and the overall low-tide density of dunlins, calculated for the 1-km distance classes. In this analysis we only included the areas of suitable feeding habitat for dunlins in the Tagus estuary. The classification of the areas as "suitable" or "unsuitable" was based on maps of sediment characteristics (see Granadeiro et al. 2007 for methods used for habitat mapping), and on data on habitat preferences of dunlin obtained in the Tagus estuary (Granadeiro et al. 2004). Statistical computations were carried out using the R package (R Development Core Team 2005).

Modelling the impact of the removal or addition of refuges

To evaluate the likely impact of losing or creating roosts in the use of intertidal flats, we developed a GIS-based modelling method to calculate two parameters: (1) the average distance that birds have to fly between potential foraging sites and available high-tide roosts, and (2) the percentage of the total intertidal flats that lies within a threshold distance from a high-tide roost. By removing existing (or adding new) roosts in the GIS model these parameters were recalculated, allowing the evaluation of different roost availability scenarios. The models use as input (1) a map with the distribution of intertidal flats suitable for foraging, (2) a map with the distribution of existing and potential roosting sites, and (3) knowledge about how far a shorebird species is willing to fly to reach a foraging area. We applied this method to the dunlins in the Tagus estuary.

Application of the model to the Tagus estuary

Some important roosts in the estuary are currently under threat and we modelled the potential impact of their disappearance. We also modelled the consequences of creating new high-tide roosts. A total of nine scenarios were studied: including all the existing main roosts (scenario 1), removing these roosts one at a time (scenarios 2 to 5), removing simultaneously the two most threatened roosts (scenario 6), and creating new roosts at three alternative locations (scenarios 7 to 9) (Fig. 2.1). The choice for the location of these sites for the new roost was justified by the scarcity of roosting alternatives along the western banks of the estuary (Fig. 2.1).

For each scenario we calculated the two GIS parameters (see 2.3). The mean distance between suitable foraging areas and roosts was estimated by creating 100 m wide distance bands from the roosts included in each scenario, calculating the area of each band, and averaging the mean values of the bands (150 m, 250 m, etc.) weighted by their area. The total area within the threshold distance was calculated by summing the areas of the correspondent bands. These computations were done using Arcview 3.2.

2.4. Results

Influence of the distance to roosts in the distribution of dunlins in the tidal flats

Virtually all birds remained associated with the marking roosts during both years. In fact, more than 99 % of the sightings of marked birds during spring high-tides (N = 710) were made at the roosts where they were caught.

Marked dunlins tended to forage close to their high-tide roosts (Fig. 2.2). We found a significantly negative correlation between the percentage of marked dunlins in the feeding grounds and the distance to the corresponding marking roost (roost 1: Spearman r = -0.92, P< 0.01, N = 9; roost 2: Spearman r = -0.73, P < 0.05, N = 9) (Fig. 2.3a). More than 80% of the marked birds were observed within 5 km from their roost.

The overall density of dunlins (marked and non-marked) was also lower in feeding grounds further away from the main roosts (Fig. 2.3b). In fact, there was an inverse relationship between the density of dunlins and the distance to the nearest roost (Spearman r = -0.82, P < 0.05, N = 9).
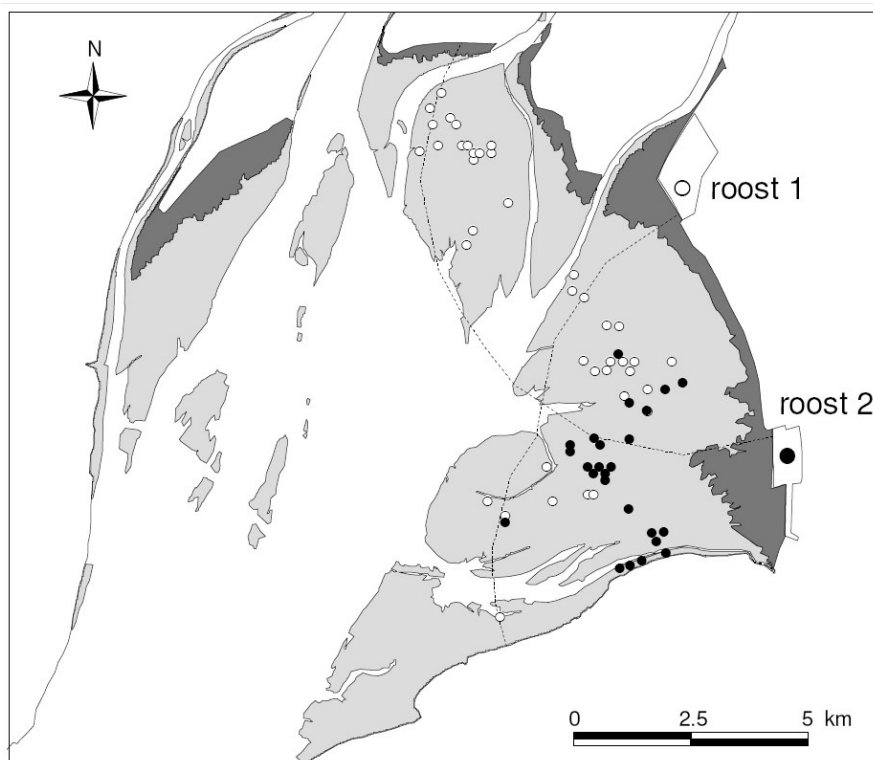
Figure 2.2. Location of marked dunlins in the feeding areas. Open circles represent locations of dunlins marked in roost 1, and filled circles indicate the locations of dunlins marked in roost 2. Light and dark grey shading represents intertidal flats and salt marsh vegetation, respectively. Dashed lines indicate 5 km distance from marking roosts. Notice that more than 80% of the locations were closer than 5 km from the marking roost.

Both the percentage of marked birds and the density of dunlins on the intertidal flats became very low at more than 5 km from the roosts (Fig. 2.3). Consequently, we assumed that areas beyond that distance threshold are poorly covered by roosts.

During neap high-tides dunlins stayed in the upper intertidal flats closer to marking roosts (Fig. 2.4). There was a significantly negative correlation between the percentage of marked birds and the distance between neap and spring tide roosts, in both studied roosts (roost 1: Spearman r = -0.83, P < 0.001, N = 18; roost 2: Spearman r = -0.86, P< 0.001, N = 18).
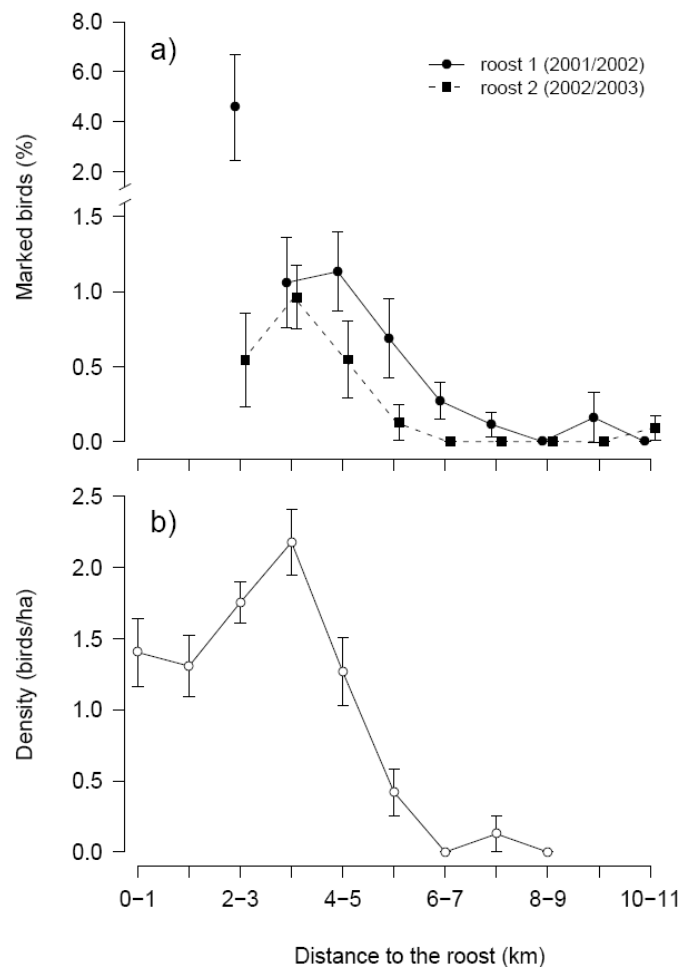
Figure 2.3. a) Relationship between the distance to the marking roosts (in both years) and the percentage of marked dunlins in their feeding areas (means ± SE); b) relationship between the distance to the nearest roost and the overall density of dunlins (marked and non-marked) in their feeding areas (means ± SE). Both graphs show that overall use of feeding areas declines with distance to high-tide roosts.
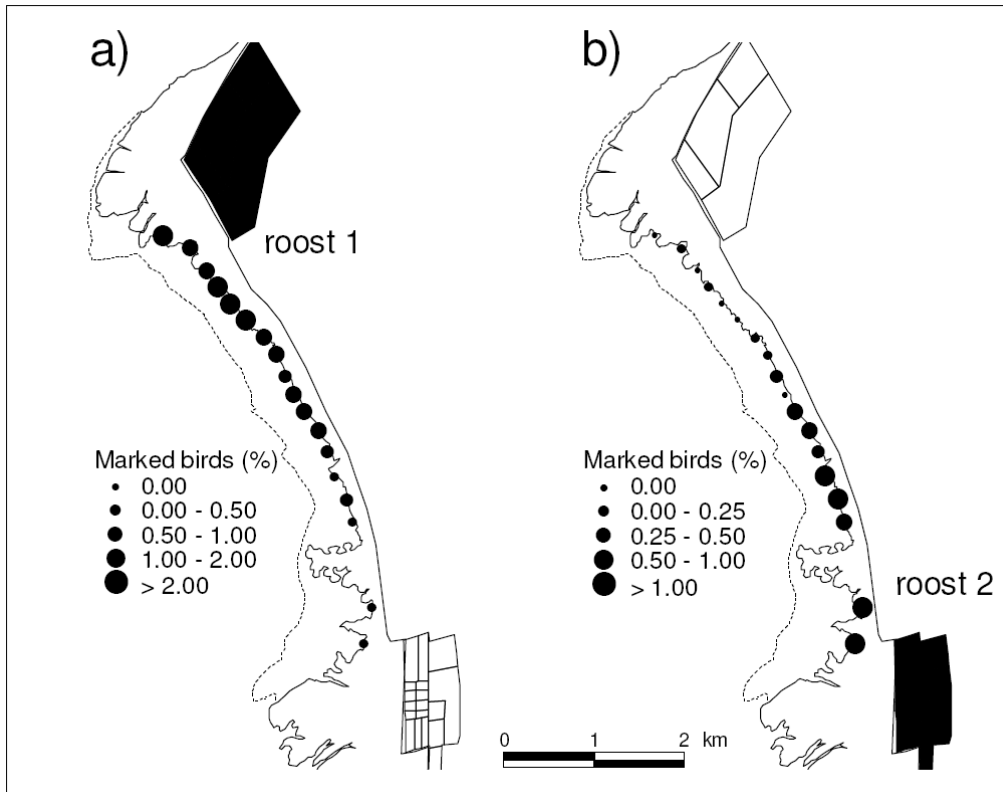
Figure 2.4. Percentage of marked dunlins in their neap high-tide roosts: a) dunlins marked at roost 1; b) dunlins marked at roost 2. There was a clear preference to stay at the neap tide roosts closer to the spring tide roost where the birds were marked.

Evaluation of the impact of losing and creating roosts in the Tagus estuary

The consequences of losing existing roosts varied considerably depending on the roosts involved (Table 2.1). The loss of roost 1 (scenario 2) would have the single greatest negative impact.

Site C would be the most appropriate to create a new high-tide roost in the northern sector of the estuary (scenario 9; Table 2.1). Such a location would result in a decline of 25% in the average distance that birds have to fly to reach potential foraging grounds, and the area of mudflat suitably covered by roosts would increase from 80% to 97%.

Table 2.1. Implications of different roost availability scenarios in the Tagus estuary. Mean distance (in km) between potential feeding grounds and the nearest high-tide roost; mudflat area (in ha) within 5 km from any roost (% represents change in relation to current situation); percentage of suitable tidal flats in study area within 5 km from any roost. The location of roosts is shown in Fig. 2.1.

Scenarios	Distance (km) between feeding grounds and roosts	Area within 5 km from a roost (ha)	Percentage of tidal area within 5 km from a roost
1: all the roosts (current situation)	3.56	4870	80%
2: without roost 1 (Vasa-Sacos)	4.34 (+22%)	3643 (-25%)	60%
3: without roost 2 (V. de Frades)	3.88 (+9%)	4862 (-1%)	79%
4: without roost 3 (Samouco)	4.23 (+19%)	4416 (-9%)	72%
5: without roost 4 (Alverca)	3.98 (+12%)	4613 (-5%)	75%
6: without roosts 1 and 4	5.39 (+51%)	3256 (-33%)	53%
7: potential new site A	3.22 (-10%)	5184 (+6%)	85%
8: potential new site B	2.90 (-19%)	5587 (+15%)	91%
9: potential new site C	2.66 (-25%)	5918 (+22%)	97%

2.5. Discussion

Location of high-tide roosts influences how dunlins use tidal flats

The overall density of dunlins on suitable mudflat foraging grounds declined with the distance to the nearest roost (Fig. 2.3b). This is not likely to be due to a decline in habitat quality because in the studied area the characteristics of the sediment do not change with the distance. In addition, individual dunlins avoided foraging in areas of

intertidal flats far from their spring high-tide roost (Figs. 2.2, 2.3a). Both patterns were clear in 2002 and 2003, and were observed in both studied roosts.

The strong attachment of dunlins to the areas close to their spring tide roosts was obvious even at neap tides, when they are not forced to fly all the way back to the saltpans (Rosa et al. 2006). In these cases, they roosted on the upper intertidal flats that remained exposed, but clearly preferred those near their spring tide roosts (Fig. 2.4).

This association between roosts and feeding grounds is probably a response to the need to minimize the energy costs of flying between them (Luís et al. 2001; Rogers 2003). In fact, an extra energy expenditure on such flights may represent a heavy burden in the tight energy budget of shorebirds during the winter (Rehfisch et al. 1996) and may even affect their survival (Rehfisch et al. 1996; Drake et al. 2001; Durell et al. 2005), particularly in the case of small species, such as the dunlin (Piersma et al. 1993b). Previous works with dunlins (Have et al. 1984) and oystercatchers (*Haematopus ostralegus*) (Swennen 1984) in the Wadden Sea showed that higher status birds tend to roost closer to the best feeding areas than lower status birds, which also suggests a preference for minimizing the distance between roosting and feeding areas.

The distribution of foraging dunlins on the tidal flats clearly indicated that they avoided foraging far from their roosts, but they also made little use of the areas closest to the roosts, located in the upper intertidal flats (Fig. 2.2). However, this may be due to the fact that counts on feeding areas were carried out during low-tide. Dunlins tend to feed close to the tide edge, at least during the earlier stages of falling tides (Nehls & Tiedemann 1993; Dierschke et al. 1999; pers. obs.), so few remain in the upper intertidal flats at low-tide (Dias et al. 2006). However, it is also possible that these birds were avoiding areas near the shore to minimize predation risk (Page & Whitacre 1975). In any case, the patterns of use of intertidal areas should be the result of a trade off

between the need to minimize the energy expenditure in the movements between areas and the choice of good quality and safe feeding grounds (Gabbard et al. 2001). Consequently, such patterns should be highly dependent on the availability of roosting sites in the vicinity of suitable feeding areas.

Modelling the influence of roost location in the use of tidal flats

In many wetlands around the world, large areas of salt marsh were converted to saltpans (Paracuellos et al. 2002), which are currently used as high-tide roosts by large numbers of shorebirds (Britton & Johnson 1987; Pérez-Hurtado & Hortas 1992). However, due to the declining profitability of salt production, many saltpans in Southern Europe and elsewhere are seriously threatened by abandonment or conversion to aquaculture tanks (Paracuellos et al. 2002). High-tide roosts located in habitats other than saltpans have also been lost, mostly due to the expansion of urban areas (Rogers 2003).

The GIS based methodology that we describe here is a simple approach to evaluate *a priori* the likely effects of losing or creating roosts at specific sites. The data required to apply the methodology include a map of the potential feeding areas, the location of existing spring high-tide roosts, and information on the magnitude of bird movements between high-tide roosts and the feeding areas. Although these parameters will vary among sites and species, one can make usable inferences from data already obtained at several wetlands with a variety of shorebirds species.

The application of our technique in the Tagus estuary showed the particular importance of roosts 1 (Vasa-Sacos saltpans) and 3 (Samouco saltpans). According to the model the loss of either of these roosts would result in an underuse of 28-40% of the total intertidal area available for dunlins. In addition, the potential feeding sites of

the whole study area would be on the average more than 4 km from the nearest roosting site. These are in fact the two main roosts, holding in some winters more than half of the birds that occur in the Tagus estuary (pers. obs.), which is probably a consequence of their strategic location.

The results of the model also indicate that the western intertidal flats of the Tagus estuary are too far from any roost (Fig. 2.1). In fact, this may be the reason why densities of shorebirds feeding in them tend to be lower than in similar areas located elsewhere in the estuary (Rosa et al. 2003; Granadeiro et al. 2007). We concluded that this situation may be substantially improved by creating a new roost at site C (Table 2.1).

Implications for management

In the Tagus estuary an important proportion of the tidal flats is currently too far from any good quality spring high-tide roost (Fig. 2.1 and Table 2.1). The situation could worsen in the future because two main roosts are presently highly threatened. Roost 4 (Alverca saltpans) in spite of its classification by BirdLife as an Important Bird Area is under immediate pressure by urban growth, and part of it is now being converted into a sewage treatment station. The largest roost site, roost 1 (Vasa-Sacos saltpans) is included in the Tagus Estuary Natural Reserve and is classified as a Special Protection Area, but is under pressure by aquaculture interests. Our modelling demonstrates that the loss of these two high-tide roosts (roosts 1 and 4) would have serious consequences for the access of dunlins and possibly other shorebirds to the existing foraging areas (Table 2.1).

It follows that it is very important to take measures to avoid the destruction of these roosts and to maintain them. Both are in abandoned saltpans, and the dykes and

gates that allow the control of the water levels in the tanks are deteriorating quickly. Shorebirds can only roost in tanks with water levels within specific limits (Warnock et al. 2002), and unless restoration work is carried out in the near future it will not be possible to maintain water at these levels. In the absence of proper management, invasive vegetation can also become a problem.

Many saltpans once existed along the western shore of the estuary, but they were destroyed by urban development or abandoned and are now overgrown by vegetation. Our modelling application showed that a new roost at site C, located in reclaimed wetland, would be optimal to compensate for these past losses. In order to improve the carrying capacity of the estuary we recommend the creation of this roost, although the decision on its precise location may have to consider factors other than its proximity to the foraging areas.

Although this study focused on a specific case study, the dunlins in the Tagus estuary, the results are likely to apply to other shorebird species in many medium and large estuaries. In fact, there is information suggesting that other species, such as the western sandpiper (*Calidris mauri*), piping plover (*Charadrius melodus*), redshank (*Tringa totanus*), turnstone (*Arenaria interpres*), grey plover (*Pluvialis squatarola*) and oystercatcher avoid making long flights between roosts and feeding areas (Swennen 1984; Symonds et al. 1984; Warnock & Takekawa 1996; Drake et al. 2001). As in the case of dunlins, it is likely that their use of some foraging areas is constrained by the availability of nearby high-tide roosts, thus limiting the suitability and carrying capacity of estuaries.

Most shorebirds found in the Tagus estuary, and many other similar estuarine areas, are migrants using them as wintering or staging areas. What happens to these key areas will therefore determine much of the rest of the annual cycle – and affect survival rates – of these shorebirds (IWSG 2003). Our results underline the importance of maintaining a network of strategically located high-tide roosts in estuaries, to

guarantee easy access to all potential foraging areas. In addition, the methodology described in this paper can be an important tool to help optimize such networks of roosts, because it constitutes an objective framework to identify gaps and to optimize conservation strategies to minimize them.

Chapter 3

Estimating the use of tidal flats by waders:

inaccuracies due to the response of birds to the tidal

cycle

Dias, M.P., Granadeiro, J.P, Martins, R. C. & Palmeirim, J.M. 2006. *Bird Study*,

53, 32-38.

3. Estimating the use of tidal flats by waders: inaccuracies due to the response of birds to the tidal

3.1. Abstract

Capsule Low tide counts can result in inaccurate estimates of habitat use; a combination of low and mid tide counts yields better estimates.

Aims To evaluate whether low tide bird counts provide a good estimate of habitat use of intertidal areas with different exposure periods, to analyse how differences in the response of the birds to the tidal movement influences these estimates, and to evaluate an alternative to the traditional counting scheme.

Methods The total use of intertidal plots by six wader species was estimated through regular bird counts during entire tidal cycles. These estimates were then compared to estimates of use based on both (i) replicate low tide counts, and (ii) a combination of low and mid tide counts.

Results For most species, estimates based on low tide counts alone differed substantially from estimates based on counts repeated over the full tidal cycle. This difference tended to be greater in the upper parts of the sediment flats, and in species that followed the tidal water line while foraging. Using the same number of count replicates, but extending the counting period to the mid tides, we tended to obtain far more accurate estimates of use of space.

Conclusion In studies that compare the use of areas under different tidal conditions, or that evaluate the use of restricted sectors of an estuary, a combination of low and mid tide counts is preferable to the conventional low tide counts, especially in the case of species that tend to follow the tidal line.

3.2. Introduction

Estuarine areas face increasing pressures from human activities, requiring those responsible for planning and management of conservation measures to identify the most important feeding and resting areas for waders within estuaries. This information is important for decision-making as these activities may disturb birds or result in land-claim (Goss-Custard & Yates 1992). Mapping the intensity of use of sediment flats by feeding waders is also important to understand spatial variations in their role in the estuarine food chain.

While the high tide refuge areas of waders are relatively easy to identify and characterize, mapping the intensity of use of large intertidal flats by feeding waders is quite complex due to temporal changes induced by tides. The importance of a given area for feeding waders is traditionally inferred from the number of birds counted during a relatively short time-window from low tide (Moreira 1993a,b; Rosa et al. 2003), when their distribution is believed to be more stable (e.g. Musgrove et al. 2003). While there is evidence that such low tide counts are generally adequate for comparisons of total densities among estuaries (Burton et al. 2004), it has not been tested if they accurately reflect the importance of areas with different exposure regimes, both within the same estuary and in different estuaries.

It is well known that tidal movement has a strong influence on the distribution of the waders, because it constantly changes the area available for foraging and influences the feeding behaviour of several species (Burger et al. 1977; Connors et al. 1981; Nehls & Tiedemann 1993). In several estuaries some wader species are known to forage close to the tidal line, thus following its movements (Wilson 1990; Evans & Harris 1994; Tiedemann & Nehls 1997). As a consequence, the distribution of birds along the tidal cycle can be highly variable, and densities during the low tide period may differ from densities during other tidal phases. In such circumstances, low tide

counts alone are unlikely to provide accurate estimates of the use of different areas (Nehls & Tiedemann 1993), taken as the mean density in the areas during which sediment is available to birds (Petersen & Exo 1999).

This study set out to elucidate some of the complexities of estimating habitat use by birds in the highly dynamic estuarine sediment flats, thus contributing to the improvement of methods to study them. In particular, we (1) evaluated whether low tide counts provide good estimates of use of intertidal areas with different exposure periods, (2) analyzed how the response of the birds to the tidal movement influences the accuracy of these estimates, and (3) evaluated an alternative counting strategy that results in better estimates than low tide counts, with equivalent sampling effort.

3.3. Methods

This study was undertaken in the Tagus estuary (Portugal), the largest estuary in the Iberian Peninsula and among the most important wetlands for birds in Europe (Heath & Evans 2000). Tides in the Tagus estuary are semi-diurnal, with an amplitude range of 1-3.8 m in neap and spring tides, respectively.

We worked on a 1200 m long by 200 m wide strip of homogeneous mudflat (more than 95% of particles < 63 μm), located in an area where the estuary is bordered by a wide saltmarsh (Fig. 3.1). The strip was roughly perpendicular to the shoreline and was divided in six 200 x 200 m plots, whose edges were marked with sticks partly buried in the mud at 20 m intervals. The water tidal line advanced and retreated perpendicularly to the strip, so the six plots represented a gradient of exposures regimes. During each tidal cycle the lowest plot (plot 1) was on average exposed for six hours and the highest (plot 6) for about eight hours.
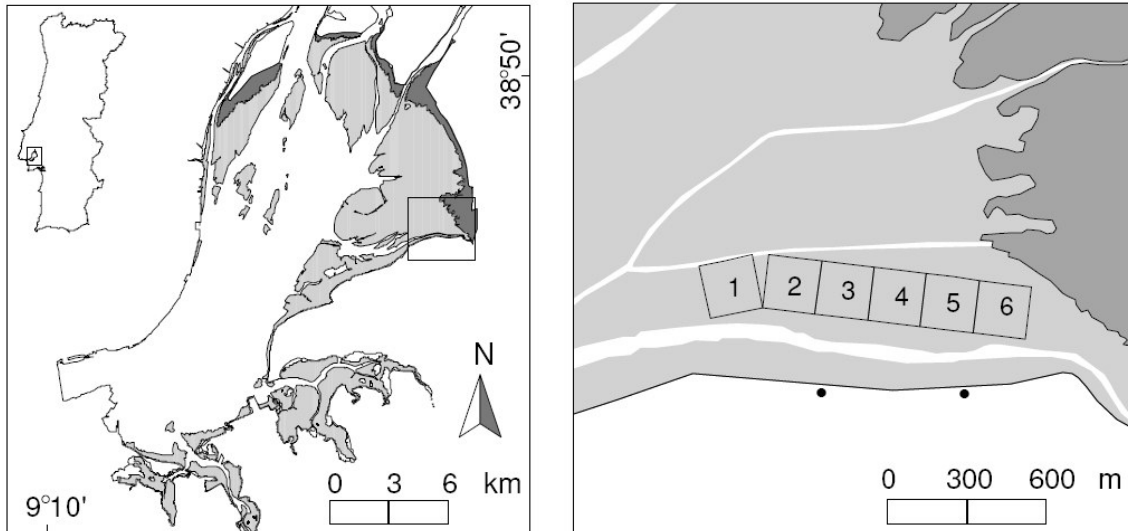
Figure 3.1. Location of the study area in the Tagus estuary. Plots are numbered according to increasing exposure period. Light grey, intertidal flats; dark grey, saltmarsh areas.

We counted the birds in the entire study area during complete half tidal cycles (10 raising tides and 10 ebbing tides) between 8 January and 16 March 2002. Counts were carried out during daylight period by two observers in permanent radio contact, from two vantage points on the coast (Fig. 3.1). Birds present in each of the six plots were counted every 30 minutes. A total of 920 counts were carried out. During each count we recorded time, the submerged proportion of each plot, the number of birds of each species, and their activity. We only included feeding birds in our analysis, which represented more than 95 % of birds in the areas.

For each day and plot we estimated the abundance of bird species, by averaging all the counts carried out during the entire rising or ebbing tide in that day. The estimates obtained during the 20 days are the "full cycle" estimates (composed by the same number of days counted during the ebbing and the rising tides). To evaluate the performance of the traditional "low tide" counts and of an alternative counting strategy that combined low and mid tide counts ("low-mid tide" counts henceforth), we compared both to full cycle counts. The latter were used as a reference in the comparison because they reflect the total average use of a site by the waders, and

were based on a large number of counts, evenly spaced during the tidal cycle, hence incorporating the major source of temporal variability in bird numbers. Low tide estimates were calculated by averaging two counts from each sampling day, randomly chosen among those obtained two hours from the low tide. Low-mid tide estimates also used the average of two randomly chosen counts from each sampling day, but one of those was a low tide count (two hours from low tide) and the other a mid tide count (i.e, outside low tide period).

All the computations were carried out using the R package (Ihaka & Gentleman 1996). Throughout the paper, means are represented with one standard error and statistical procedures follow Zar (1996).

3.4. Results

The most abundant species in the study area were dunlin *Calidris alpina*, avocet *Recurvirostra avosetta*, black-tailed godwit *Limosa limosa*, redshank *Tringa totanus*, grey plover *Pluvialis squatarola* and bar-tailed godwit *Limosa lapponica*. We restricted our analysis to these species.

Conventional low tide versus full cycle estimates

Pooled results of counts carried out in the six plots showed that low tide densities were significantly lower than full cycle densities for all the species, with the exception of bar-tailed godwit (Fig. 3.2). Discrepancies were particularly serious in the case of dunlin and black-tailed godwit, for which low tide density estimates were several times lower than full cycle estimates (c. 10x for dunlin).
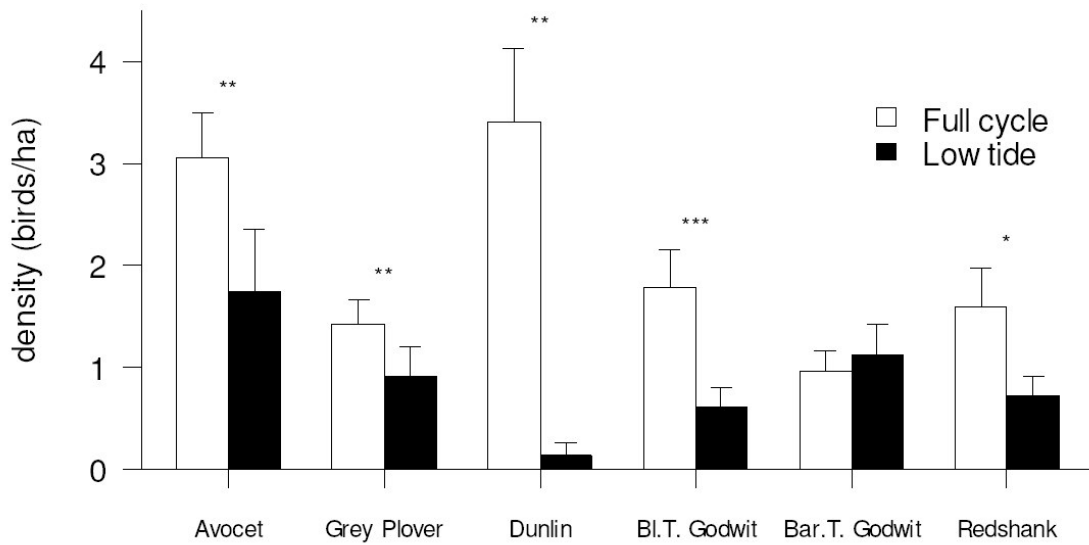
Figure 3.2. Full cycle and low tide densities of the different species in the entire study area (ignoring the subdivision in plots). Significant differences are indicated by asterisks (paired t-test; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; d.f.=5). Conventional low tide counts were not representative of the full use of the area, but the magnitude of this error varied among species.

Effect of exposure period on accuracy of low tide estimates

The difference between density estimates based on low tide and full cycle counts was in general very high, although it varied with the species and the location of the plot along the exposure gradient (Fig. 3.3). There was an inverse relationship between this difference and the exposure period, which was particularly strong and statistically significant in the case of avocet, grey plover and redshank (Pearson $r < -0.93$, $P < 0.01$, d.f. = 4). Habitat use was strongly underestimated in the higher plots, but this error gradually declined towards the lower plots. However, in the case of dunlin and black-tailed godwit low tide estimates were always far below full cycle estimates, because most individuals of these two species did not simply move within the study area, but abandoned it at low tide.
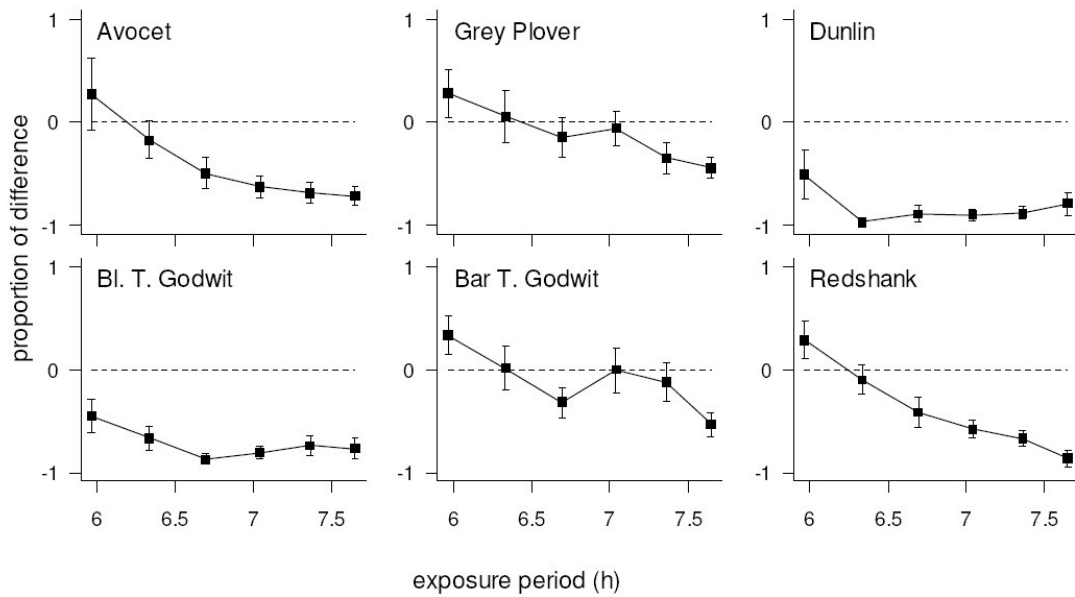
Figure 3.3. Relationship between true use (estimated with counts made during the entire tidal cycle) and estimates based on low tide counts alone (squares). Proportion of difference: (low tide estimate – full cycle estimate)/full cycle estimate. Horizontal dashed lines represent the full cycle estimates. The quality of low tide estimates decrease towards the upper parts of the tidal flats, where estimates were usually several time lower than real use.

Low-mid tide versus conventional low tide counts

Both absolute difference between real use and estimated use and the correlation between the two parameters are relevant to evaluate the relative quality of the sampling schemes. In all species the absolute difference was much lower for estimates based on low-mid tide counts than for those based on the conventional low tide counts (Fig. 3.4 and Table 3.1). Low tide and full cycle estimates were statistically different for three species: avocet, black-tailed godwit and dunlin (paired t-tests, t=10.7, t=5.1 and t=4.7, respectively; all P<0.05; d.f.=5; Fig. 3.4). Likewise, real use was always far better correlated to estimates based on low-mid tide than with those based on low tide counts alone (Fig. 3.4 and Table 3.1).
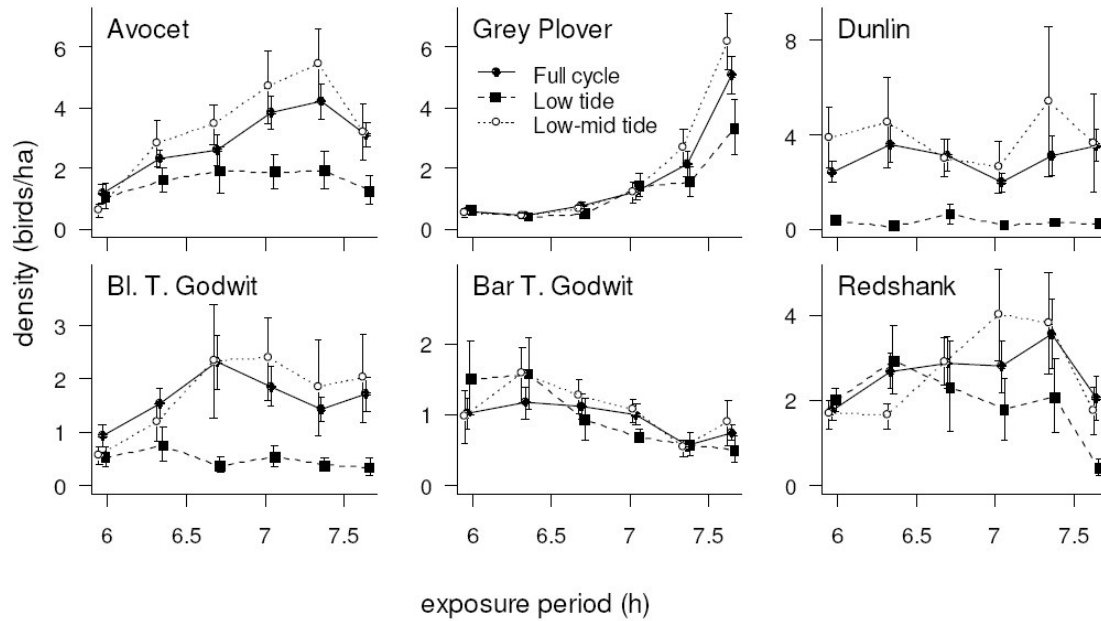
Figure 3.4. Comparison of full cycle estimates, conventional low tide estimates and the proposed low-mid tide estimates of density. For all species, low-mid tide estimates are closer to (hence better correlated with) full cycle estimates, across the six plots.

3.5. Discussion

Low tide counts can result in inaccurate estimates

Low tide counts have long been adopted as a standard approach to collect data for the evaluation of the importance of the mudflats for feeding waders, and are particularly useful as a method to compare densities among estuaries (Musgrove et al. 2003; Burton et al. 2004). In fact, if the majority of the intertidal area of the estuary is included in the count, low tide counts will accurately portray the overall density of the birds in the estuary. In contrast, our results demonstrated that, due to tidal dynamics and the high mobility of waders, estimates of use in partial sectors of sediment flats based on conventional low tide counts can be very inaccurate (Fig. 3.2).

Table 3.1. Pearson's correlation and mean absolute difference (%) between conventional low tide (LT) and full cycle estimates (FC) and between the low-mid tide (L-MT) and full cycle estimates.

Species	Correlation		Mean difference (%)	
	LT *versus* FC estim	L-MT *versus* FC estim.	LT *versus* FC estim.	L-MT *versus* FC estim.
Avocet	0.71	0.98	39.1	26.5
Grey plover	0.98	0.99	20.5	12.1
Dunlin	0.05	0.49	90.1	34.0
Black-tailed godwit	-0.31	0.87	68.8	23.5
Bar-tailed godwit	0.72	0.91	28.2	14.6
Redshank	0.41	0.76	33.7	18.0

In our study, assessing use with the results of low tide counts alone resulted mostly in underestimates of use. This lack of accuracy is by itself a serious problem but it is made worse by the fact that not all species respond in the same manner to tidal dynamics, causing problems to the interpretation of the composition of bird assemblages. For example, based on low tide counts, we would conclude that dunlin was the least abundant species in our study area, whereas it was in fact the most abundant species (Fig. 3.2).

Influences on level of accuracy

Our results show that the accuracy of low tide counts varied, in some cases dramatically, along the gradient of exposure periods (Fig. 3.3). In general, the accuracy declined from the low to the high plots, where densities were consistently underestimated, but the intensity of the observed patterns varied among species. We believe that a combination of two factors explains the observed general pattern and the differences among species: the changes in availability of exposed sediment flats with the tidal movements, and the degree to which species follow the receding and advancing tidal waterline.

The changes in availability of sediment surface justify that, for all the species, low tide counts tended to underestimate more markedly the higher plots. In fact low tide counts do not sample the peaks of abundance of birds in the mid and upper parts of the sediment flats, i.e. when the total surface of sediment available is limited because the lower flats are still inundated. This factor should affect the results for all the species.

Low tide counts should accurately sample the lowest areas, so it is somewhat surprising that in most cases they actually slightly overestimated bird abundance there (Fig. 3.3). This is probably explained by a delay in the occupation of the lowest areas by the birds during the receding tide. Full cycle estimates included counts done as soon as a plot was uncovered, whereas some birds may only arrive to the area later. In such circumstances one would expect full cycle estimates to be somewhat lower then low tide estimates, as observed in our data.

Although all the species tend to be underestimated by low tide counts, this bias is particularly obvious in the case of dunlin, black-tailed godwit and avocet (Table 3.1). This may be explained by the observed tendency for these birds to follow the tidal water line while foraging (Nehls & Tiedemann 1993; Dierschke et al. 1999; Hötker

1999; *pers. obs.*). With most of them concentrated in a moving flock following the tidal line, any sampling scheme that does not include the period during which the flock crosses an area is bound to seriously underestimate its use. In general low tide counts will only include the passage of the birds in the lower parts of the sediment flats. Grey plover and bar-tailed godwit did not follow the tidal line (Turpie 1995; Tiedemann & Nehls 1997; *pers. obs.*), so low tide counts resulted in less biased estimates of use (Table 3.1). The bias for redshank was intermediate between the two groups of species (Table 3.1), probably because it tended to follow the tidal line only during the outgoing tide and even then less closely than the group of "true tide followers" (*pers. obs.*).

It is important to point out that the differences between real use and low tide estimates shown on Fig. 3.2 are for the entire study area, which was selected to include a broad range of exposure times. In an area of similar size, but with a lower range of exposure times, the overall errors would be even greater. In the worse cases, areas located in the upper part of the sediment flat and species that tended to follow the tidal line, the estimates based on low tide counts would be several times lower than the real use. As predicted by Nehls & Tiedemann (1993) larger biases were observed in areas with higher exposure periods and in species that follow the tide line more closely.

Low-mid tide counts: an alternative to low tide counts

Full cycle counts provide the best estimates of the use of tidal flats by waders because they integrate numbers across the entire cycle, but they are very time-consuming, and may not be practical if several areas or estuaries are to be counted.

The conventional low tide counts are less time consuming than full cycle counts but the observed influence of exposure time on the bias of estimates makes them prone to substantial errors when comparing bird use among areas located at different

levels of the sediment flats. Likewise, the influence of the birds' tidal-following behaviour on the bias makes this counting technique unsuitable for comparing how different species use the same area, if located in the mid and upper parts of the sediment flats.

There is a clear need for a sampling strategy that is less time consuming than full cycle counts, but does not suffer from the inaccuracies of the counts restricted to the low tide period. We experimented an alternative survey scheme that involved expanding the counting period well into intermediate phases of tidal cycle (i.e. expanding the counting period beyond the traditional $\pm$ 2 hours from low tide), and calculating the use of each area with an equal number of replicates obtained at low and mid tides (low-mid tide counts). For a similar number of replicates this alternative sampling strategy yielded far more accurate estimates of use than the conventional low tide counts. For all the species and all the plots estimates of use were closer to real use (Table 3.1 and Fig. 3.4). In addition, real use in the six plots was always better correlated with estimates based on low-mid tide counts than on low tide counts (Table 3.1 and Fig. 3.4). This suggests that the former method is superior for the evaluation of the relative importance of plots. However, we cannot be certain that this conclusion also applies to night use of space, because night counts were not included in this study, and day and night behaviour of foraging waders can differ (e.g. Mouritsen 1993, 1994; Dodd & Colwell 1996).

In addition to yielding more accurate and comparable estimates of use, low-mid tide counts have the advantage of broadening the period during which researchers can carry out field work. However, they are applicable only if each area is counted more than once, which in any case is required for good estimates even of low tide use (Moreira 1993b).

In conclusion, conventional low tide counts yield acceptable estimates of use in the low parts of tidal flats, or when the objective is to estimate the overall use of very

large sectors that include the full range of exposure times (Burton et al. 2004). However, when the aim of the study is either to compare wader use of areas under different tidal conditions, or to evaluate the total use of a restricted sector of an estuary, low-mid tide counts are preferable to low tide counts.

Chapter 4

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

Granadeiro, J.P., Dias, M.P., Martins, R. C. & Palmeirim, J.M. 2006. *Acta Oecologica*, 29, 293-300.

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

4.1. 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.

4.2. Introduction

Many species of waders depend on the abundant invertebrate prey of estuarine areas to survive during the nonbreeding 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 & Tiedemann 1993; Evans & Harris 1994; Scheiffarth et al. 1996). 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 & Tiedemann 1993; Dias et al. 2006).

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 & 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.

4.3. Methods

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 100 km^2 and are dominated by mudflats, and to a lesser extent by dead oyster beds and sandy flats

(Granadeiro et al. 2007). 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. 4.1) 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).

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 & Tibshirani 1990; Wood 2003) and assuming a Poisson error structure. The complexity of the regression surfaces is determined by the number of degrees of freedom (Hastie & 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).

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 1996). 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.
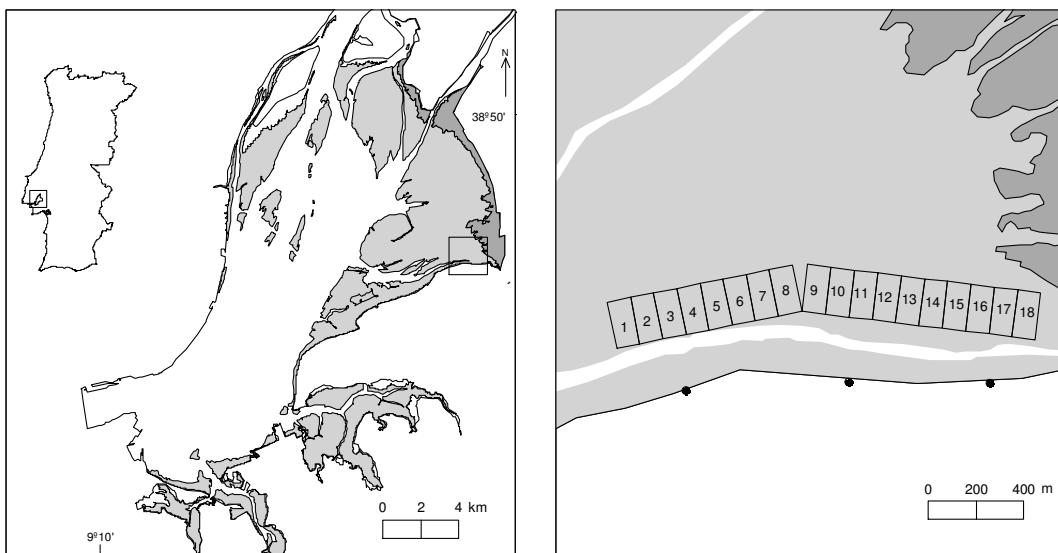
Figure 4.1. Study area, and location of study plot 1 to plot 18. Dark areas represent saltmarsh, light grey areas sediment flats and dots represent the counting points.

Estimating the intensity of use and biomass consumption at the plots

We estimated the intensity of use of the plots during a diurnal 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·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 later 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). 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,b,c, 1996, 1997; Santos et al. 2005).

4.4. Results

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. 4.2). 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. 4.2). The densities of bar-tailed godwit did not differ between these two tidal phases (Fig. 4.2). Because the three latter species did not show any attraction to the tide line, they will be referred to as "non-followers". Fig. 4.3 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).

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. 4.4). 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, $F_{1, 108}$ = 1.7, not significant) and there were only marginal differences in dunlin ($F_{1, 108}$ = 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 $F_{1,\ 110}$, 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 4.1), 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.
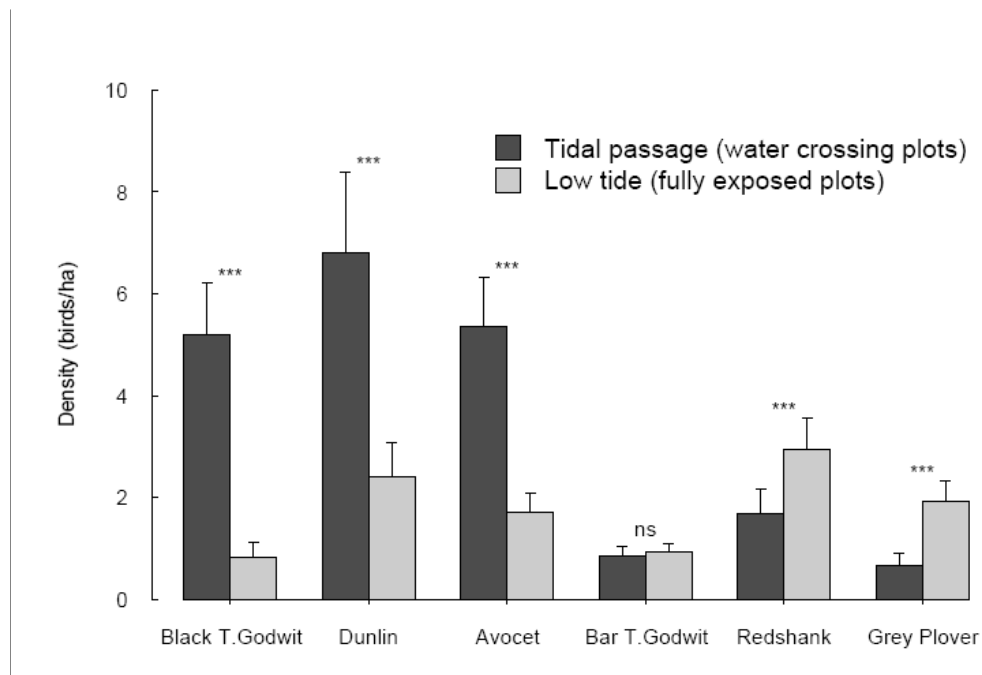
Figure 4.2. Average densities (birds ha^{-1} ± S.D.) of wader species in the entire study area during the tidal passage (ebbing and rising tide) and full exposure (around low tide). Comparisons between tidal passage and full exposure were carried out with paired t-tests (N = 18 plots; ***P < 0.001; ns, not significant).
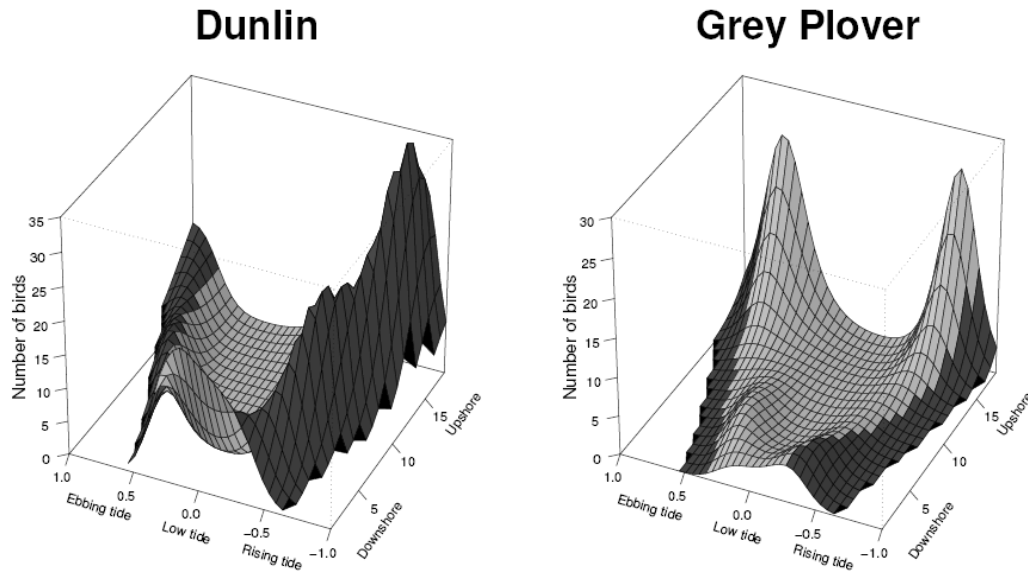
Dunlin

Grey Plover

Figure 4.3. Variation in the number of birds in the study area during a complete tidal cycle in a typical "follower" (dunlin) and a "non-follower" (grey plover). Dark grey areas represent counts carried out during the tidal passage (exposing or inundating plots), and light grey areas represent counts made when plots were fully exposed. The tidal cycle is represented as an interval [−1,1], corresponding to average tide of amplitude 2.5 m (see Methods 4.3.).

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. 4.5). 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. 4.5).

Table 4.1. 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.

		Lower plots	Middle plots	Upper plots	Total
Peck rate	Grey plover	3.6±2.89	3.4±3.35	**4.2±3.22**	3.8±3.2
		(177)	(264)	(565)	(1006)
(peck.min-1)	Redshank	13.8±7.93	12.8±4.45	12.4±4.94	12.8±5.3
		(33)	(166)	(111)	(330)
	Bar-t. godwit	18±7.33	19.9±12.12	20.5±9.66	19.5±8.2
		(39)	(37)	(36)	(112)
	Black-t. godwit	21.2±6.41	26±7.96	24.3±7.38	34.3±7.6
		(56)	(97)	(113)	(266)
	Avocet	42±13.04	42±10.91	**51.5±11.18**	46.7±12.4
		(107)	(197)	(305)	(609)
	Dunlin	50.6±17.53	54.4±10.94	56±15.85	53.6±15.7
		(70)	(41)	(75)	(186)
Feeding rate	Grey plover	1.7±1.2	1.7±1.4	1.7±1.5	1.7±1.4
		(170)	(246)	(545)	(961)
(prey.min-1)	Redshank	6.5±2.5	6.8±3.0	**4.7±3.0**	6.0±3.1
		(44)	(133)	(90)	(267)
	Bar-t. godwit	2.8±3	2.6±1.9	3.5±2.9	3.0±2.6
		(21)	(34)	(34)	(89)
	Black-t. godwit	7.7±3.6	**9.2±3.2**	7.5±3.6	8.2±3.5
		(50)	(90)	(108)	(248)
Success rate	Grey plover	57.6±34.1	64.7±35.4	**50.8±34.6**	55.5±35.1
		(166)	(236)	(529)	(931)
(prey.peck in %)	Redshank	53.6±21.9	55.9±20.2	**39.3±23.7**	50.0±22.9
		(44)	(133)	(90)	(367)
	Bar-t. godwit	16.7±14.4	17.2±17.1	18.4±12	17.5±14.5
		(21)	(34)	(34)	(89)
	Black-t. godwit	39.8±21.3	38±17.1	**32.4±15**	35.9±17.4
		(50)	(90)	(108)	(248)
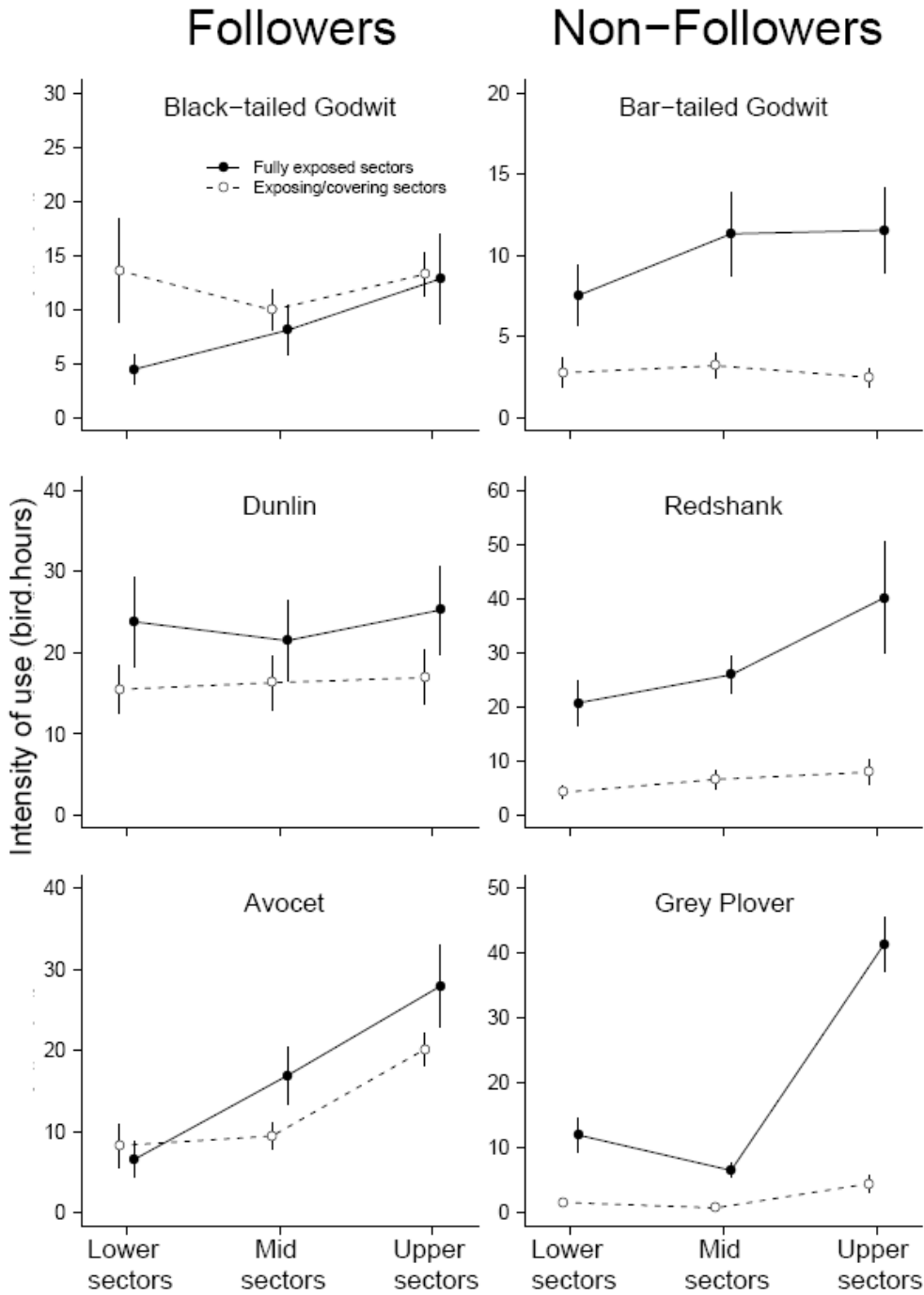
Figure 4.4. Intensity of use during a tidal cycle (bird·hours ± S.E.) of "followers" and "non-followers" in lower, middle and upper plots (plots 1–6, 7–12 and 13–18, respectively).
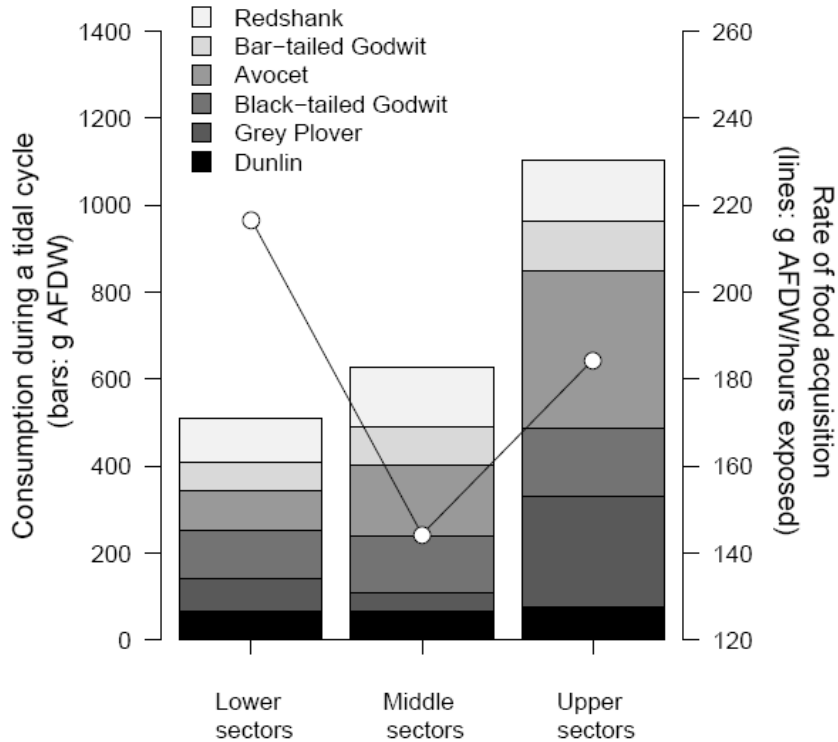
Figure 4.5. Biomass consumed by the feeding assemblage during a complete tidal cycle (bars: gram of ash-free dry weight, AFDW), and rate of biomass consumption (lines and symbols: in grams AFDW per time exposed).

4.5. Discussion

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 tidal 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 & 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 & Tiedemann 1993; Dias et al. 2006). 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 & Tiedemann 1993; Dias et al. 2006). 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. 2006).

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. 4.4). 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. 4.4). 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 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 AFDW) recorded in plots. The lower plots offered the highest rate of biomass acquisition (expressed as grams of AFDW 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. 2006). 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 & Yates 1992; Yates et al. 1996; Healy & Hickey 2002), while others continue to suffer considerable impacts from various sources of disturbance and pollution (Fitzpatrick & Bouchez 1998; Gill et al. 2001b). 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.

Chapter 5

Searching behaviour of foraging waders: does feeding success influence their walk?

5. Searching behaviour of foraging waders: does feeding success influence their walk?

5.1. Abstract

Predators that feed on clustered prey tend to have an "area-restricted search" (ARS), characterized by a combination of a slow and tortuous movement in prey-rich areas, and a fast and straight movement in poorer areas. Waders that forage in intertidal areas usually prey upon buried macro-invertebrates, whose distribution is often clustered. However, species differ in the strategy used to find their prey: some rely mainly on visual cues, a second group on tactile cues, and a third follows a more generalist strategy, simply sweeping the sediment surface with the bill. We hypothesized that these strategies influence the adoption of an ARS by waders. We analysed this hypothesis by comparing the fine-scale movement of a "tactile" predator (black-tailed godwit *Limosa limosa*), with that of a "visual" predator (redshank *Tringa totanus*) and of a "sweeper" (avocet *Recurvirostra avosetta*). We filmed 190 individuals of the three species and, using GIS facilities, obtained more than 12 000 foraging spatial positions, along with detailed records of feeding activity. We analysed several parameters of fine-scale movement of waders, such as their foraging and searching speeds, the tortuosity of their paths, and the relationship between these parameters and foraging success. Only the tactile predator, the black-tailed godwit, followed an ARS, reducing searching speed and increasing spatial turning rate whenever the prey intake was higher. Furthermore, their foraging strategy involves short-term adjustments of movement in order to maximize the likelihood of finding subsequent prey, suggesting a prior knowledge or an ability to rapidly perceive the distribution pattern of their prey.

5.2. Introduction

Several studies have shown that species preying upon clustered-distributed items tend to have an "area-restricted" (or "area-concentrated") search (ARS; e.g. Thomas 1974; Hill et al. 2000; Nolet & Moij 2002; Fortin 2003). This type of strategy involves an increase in the searching effort after finding a prey, because of the high probability of finding another prey in the vicinity (Benhamou 1992). Two major mechanisms to increase the searching effort are reducing the searching speed and increasing the turning rate of the path (Knoppien & Reddingius 1985; Kareiva & Odell 1987), thus increasing the time spent in that area and consequently the likelihood of find prey. Benhamou (1992) showed that the ARS also maximizes the intake rate when prey items are clustered in continuous patchy environments (i.e., when the patches of prey do not have obvious boundaries, resulting in areas where local density is higher than the average).

Most waders that winter in estuarine areas depend on intertidal flats that are only available during low-tide periods. In these areas they mostly prey upon benthic invertebrates, whose spatial distribution can be considered as continuously patchy (Van de Kam et al. 2004). Wader species differ in the strategy used to search for food. Some species detect their prey by sight (for example, plovers – genus *Pluvialis* and *Charadrius* – and redshanks *Tringa totanus*); others use mostly tactile cues (e.g. genus *Limosa*), whereas avocets (genus *Recurvirostra*) sweep their bill and ingest small prey items along with portions of mud (Moreira 1995a, b). Although each species tends to prefer a particular type of searching strategy they can, to some extent, switch from one to another in response to environmental conditions (e.g. Robert & McNeil 1989; Moreira 1995a; Lourenço et al. 2008).

Wintering waders are good models for the study of animal movement, because 1) their feeding behaviour is easy to monitor; 2) they search for food while walking (and

not in the air), allowing their movement to be fully described in two dimensions; 3) species with different searching strategies coexist in the same areas, allowing the comparison between them, and 4) their time budgets are highly constrained by the tidal cycle (Granadeiro et al. 2006), and thus waders have a high pressure for maximizing their immediate intake rate to fulfil their energetic demands (that are amongst the highest found in birds; Piersma 2002; Rogers et al. 2006a). In fact, waders have often been used as models for testing predictions derived from the optimal foraging theory (e.g. Goss-Custard 1977a; Piersma et al. 1995; Meire 1996; Stillman 2003; Van Gils et al. 2005a, b). However, these studies mostly focused on optimal diet and patch choice, whereas the analysis of fine scale movements of waders is still a poorly explored subject (but see Goss-Custard 1970, 1977b; Speakman & Bryant 1993; Wilson & Vogel 1997; Van Gils 2004).

The ARS hypothesis predicts that, in patchy environments, waders should increase their searching effort after ingesting a prey, due to the higher likelihood of finding another prey nearby. This strategy has been recorded in knots *Calidris canutus* and great knots *Calidris tenuirostris* feeding in intertidal areas (Van Gils 2004). However, other waders do not use this type of searching behaviour (e.g. the semipalmated sandpiper *Calidris pusilla*; Wilson & Vogel 1997), presumably because they use a "visual" searching strategy. In fact, for a mostly-visual predator, prey detectability is highly dependent on the activity of prey, which is often depressed by the presence of predators. Most benthonic invertebrates tend to retract to their burrows or cease their activity when predators are foraging nearby (Van de Kam et al. 2004). Consequently, visual predators may not benefit from long residence periods in the same spot, because disturbed invertebrates will remain retracted deep in the sediment or inactive until they leave. On the other hand, an increase in the searching effort after prey ingestion is only to be expected when there is a clear relationship between prey intake rate and prey density. This relationship is probably the norm in most predators,

but does not seem to be the case of some waders, such as avocets, which "sweeps" the sediment and ingests indiscriminately small items along with some mud (Moreira 1995b). Therefore, we predict that waders that rely mostly on tactile cues to find their prey are the most likely to adopt an ARS. We tested this prediction using model species with different searching methods: a "tactile predator" (black-tailed godwit *Limosa limosa*), a "visual predator" (redshank) and a "sweeper" (avocet *Recurvirostra avosetta*). We also provide a detailed characterization of several parameters of the fine scale movement of foraging waders.

5.3. Methods

Study Area

The study was conducted in an intertidal flat located in the southern margin of the Tagus estuary, Portugal (38°45'N, 09°50'W), one of the largest and most important wetlands in the Iberian Peninsula. The study area constitutes a regular feeding ground for several wader species (Lourenço et al. 2005; Dias et al. 2008), including those focused in this study: avocet, black-tailed godwit and redshank. Flocks in excess of one hundred individuals of each species are regularly observed here. Previous surveys of benthic fauna (unpublished data) have shown that prey density is unevenly distributed, but richer patches have gradual boundaries, thus forming a "continuous patchy environment" ("sensu" Benhamou 1992). Two areas (100 x 50 m^2 and 60 x 50 m^2) were defined in the study site, each consisting of a 5 x 10 m grid plots, marked with canes in their corners (Fig. 5.1). The canes were buried in the sediment one month before the beginning of the study, in order to allow the sediment to be flattened by the tides, eliminating our footprints. The exact position of one of the canes was recorded with a

GPS (horizontal accuracy=4 m), and all the other canes were placed using a tape measure and subsequently positioned in a Geographic Information System (GIS) using Arcview 3.2 (ESRI 1999).

Bird Movements

Data on bird foraging movement and behaviour were collected during the winter (December to March 2006 and February 2007), at low-tide period (when the entire tidal flat was exposed). The movements of 190 individuals (52 avocets, 69 black-tailed godwits and 69 redshanks, all randomly selected) were videotaped with a digital camcorder (Panasonic NV-15, 20x optical zoom), from two fixed vantage points on the adjacent coast (Fig. 5.1). Birds usually entered and left the study area walking, and were continuously followed while inside the plots. All filmed individuals were foraging using their more usual searching techniques (i.e., avocets were feeding using "normal strategy" [Moreira 1995a], redshanks were detecting their prey by sight [Goss-Custard 1977b] and black-tailed godwits were probing the sediment [Moreira 1994]). Birds were not individually marked, son we cannot discard the possibility of having filmed the same bird more than once. However, flocks were generally rather large (see above), and we often followed simultaneously the movement of several individuals. Therefore, repeated sampling of the same individuals must have been rare and unlikely to affect our conclusions.

Video sequences (corresponding to each individual recorded) were digitized to be analysed in the computer. The relative positions of the birds were marked at each three seconds on a transparent sheet fixed to the computer monitor, together with the relative positions of each visible cane. These relative positions were then digitized in a GIS, and then geo-corrected using the Arcview extensions *ShapeWarp* and

ImageWarp, based on the known positions of the canes (root mean square error always lower than 1 m). This method allowed us to obtain more than 12 000 positions of foraging birds. The recorded movements lasted between 57 s and 783 s (mean=188 s, corresponding to 63 positions). Hereafter, we use the term "movement" to refer to the entire record observation of each individual, and "path" to discriminate the spatial component of each movement.

During the analysis of the video sequences we also registered every second whether the bird ingested a prey (or sweeped, for avocets), the corresponding handling time (whenever this took longer than 1 second) and the total number of paces along the path. Most of the videotaped redshanks were preying upon small items, most probably mudsnails *Hydrobia ulvae*, ragworms *Hediste diversicolor* and clam's siphons *Scrobicularia plana* (Moreira 1995b). The handling time of most of these prey were less than one second, thus not measurable when analysing the videos at real-time speed. Similarly, the handling time associated to the sweeps of the avocets was almost always shorter than one second. In order to estimate handling times of these two species, a set of the best quality sequences of redshanks and avocets was selected and a sample of 53 pecks (of redshanks) and 70 sweeps (of avocets) were analysed at 1/4 of the normal speed. Based on these analysis, we estimated that all small pecks of redshanks had a mean handling time of 0.31 s (± 0.03 SE), and of avocet sweeps 0.38 s (± 0.03 SE).

Data Analysis

Our digitized paths consisted of sequences of fixed positions, recorded at three seconds intervals. These discrete timed positions provides a mathematically tractable way for analysing the paths (Benhamou 2004), which allowed us to estimate the

following parameters: move length (distance walked during the 3 s interval), turning angle (change in direction between successive moves) and path length (sum of all move lengths of the path). The duration of the movement corresponded to the "foraging time", and was estimated as the sum of the "searching time" (time devoted to search for prey) plus the "handling time" (time devoted to catch and ingest a prey) (Van de Kam et al. 2004). Consequently, the "foraging speed" was calculated by dividing the path length (m) by the foraging time (s), and the "searching speed" by dividing the path length by the searching time (s).

Figure 5.1. Study area. Small dots represent the location of the canes placed on the sediment, delimiting the plots (rectangles); open circles represent the location of video-cameras.

Some usual measures of the tortuosity/directionality of the path include the straightness index (Batschelet 1981), the sinuosity index (Bovet & Benhamou 1988; Benhamou 2004) and the fractal dimension (e.g. Nams & Bourgeois 2004; Biesinger & Haefner 2005), but their usefulness depends on the characteristics of the movement (random or oriented; Benhamou 2004). We therefore checked if the recorded movements followed the assumptions of the random walk model (lack of autocorrelation in move lengths and turning angles), using the method proposed by Turchin (1998). First- and higher-order autocorrelations in move lengths were investigated between all pairs of move lengths. Autocorrelations for turning angles were tested using contingency tables and χ^2 tests for the relative frequency of subsequent right and left turns. Twenty nine percent of the paths of avocets, 54% of black-tailed godwits, and 27% of the redshanks were autocorrelated, which prevented us from using any of the measures referred above. The turning rate, calculated as the number of steep angles (usually larger than 45°) per minute, is also often used as a surrogate for tortuosity (Wilson & Vogel 1997; Lourenço et al. 2005). However, this spatio-temporal parameter also depends on the speed of the movement, so it does not reflect the spatial path structure alone (which is also hypothesised to change in an ARS movement). Therefore, we calculated the turning rate based on the distance travelled, by considering the number of turns (turning angles) larger than 45° per meter (hereafter called "spatial turning rate").

We analysed the relationship between the movement and the feeding success at two different scales. First, we analysed at the "movement scale", checking if higher intake rates occurred in slower and more tortuous movements, as predicted by the ARS hypothesis. Secondly, we studied the immediate response of individuals at a finer scale, by analysing the speed and spatial turning rate variations immediately after the ingestion of a prey (or after a sweep). We averaged all the speeds and spatial turning rates in the different periods following prey ingestion. Averages were first calculated

within each individual, and then among individuals of the same species. As the interval after prey ingestion increases, fewer data became available for the calculations, because longer intervals between prey captures were scarce. We only considered the intervals for which we had data from at least 18 individuals.

All the statistical computations were carried out using the R software (R Development Core Team 2007); means and variances of the angles were calculated with the package "circular" (Lund & Agostinelli 2007). For comparisons among species we used Kruskal-Wallis tests. The relationship between prey intake rate and movement parameters (foraging speed, searching speed and spatial turning rate) was analysed with Pearson correlation coefficients.

5.4. Results

Movement Characteristics

When foraging in intertidal areas, black-tailed godwits were slower (about half of the speed) than avocets and redshanks (Kruskal-Wallis test: $H_2 = 113.04$; $P < 0.01$; Table 5.1). The largest differences between searching and foraging speeds were found in black-tailed godwits, which was due to the larger handling times of these species (mean and SE = 1.67 ± 0.06 s, range = 0.75s - 3s, N = 69).

The paths of black-tailed godwits were significantly more tortuous than those of avocets and redshanks (Kruskal-Wallis $H_2 = 92.07$, $P < 0.01$; Table 5.1). An example of each species "typical" movement (with average foraging speed and spatial turning rate) is presented in Fig. 5.2.

Table 5.1. Main parameters of the movement of the study species (means ± SE)

	Avocet	Black-tailed godwit	Redshank
	N=52	N=69	N=69
Pace length (m)	0.18±0.003	0.14±0.002	0.12±0.002
Pace rates (paces/min)	93±1.8	59±1.6	114±2.5
Foraging speed (m/s)	0.28±0.009	0.14±0.005	0.24±0.008
Searching speed (m/s)	0.29±0.010	0.20±0.006	0.25±0.008
Spatial turning rate (turns/m)	0.51±0.03	1.03±0.04	0.53±0.03
Prey intake rate (prey/min)	24.07±0.95*	9.74±0.32	13.42±0.64

* Sweeps/min

Effects of Feeding Success on Movement Characteristics

Black-tailed godwits with higher prey intake rates showed lower foraging and searching speeds and higher spatial turning rates (Table 5.2). Redshanks with higher intake rates also presented slower foraging speed, but not slower searching speed, or higher spatial turning rate. We did not find any relationship between sweep rates and movement parameters in avocets (Table 5.2).
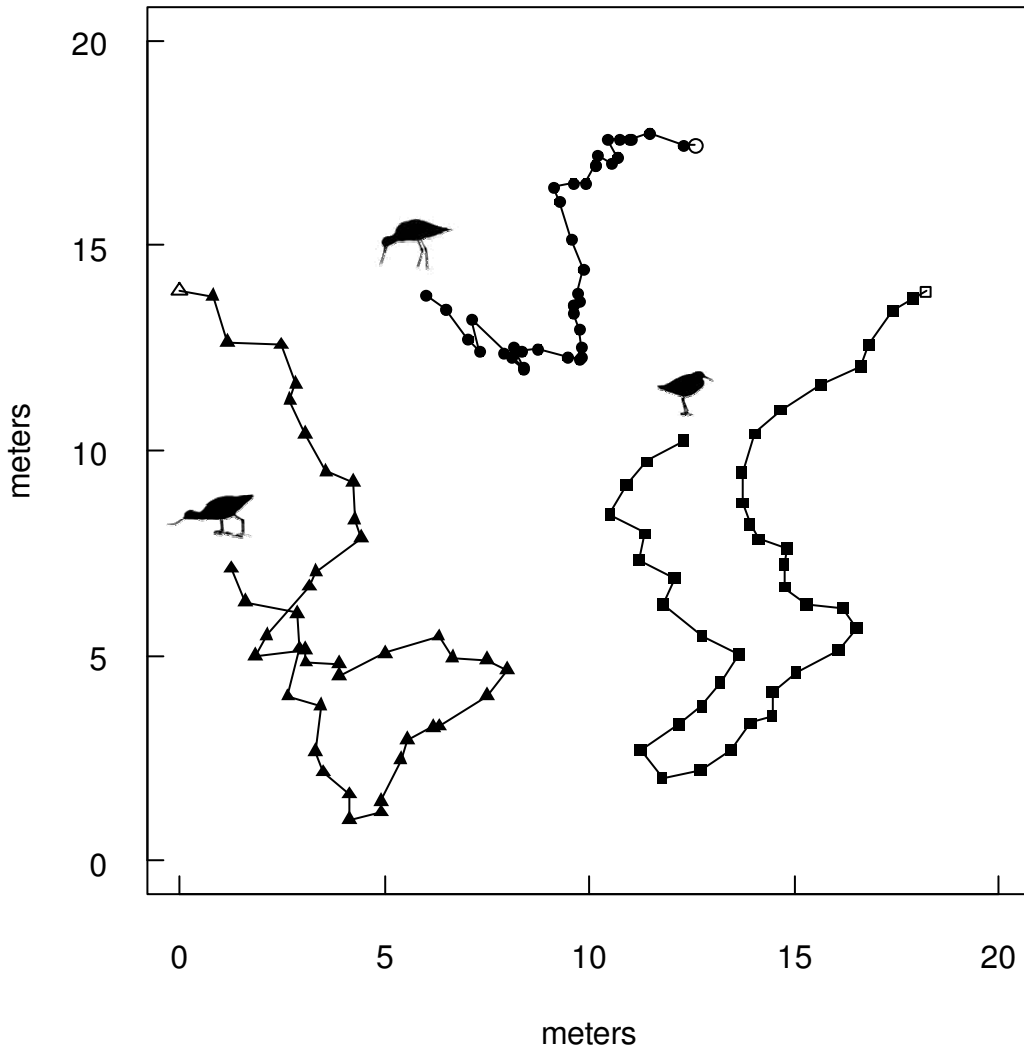
Figure 5.2. Example of a "mean" path (close-to-average speeds and spatial turning rates) of each species. Points represent relative positions of the bird each three seconds. All the examples have the same duration (120 s). Triangles: avocet; dots: black-tailed godwit; squares: redshank. Open symbols represent the beginning of the path.

Black-tailed godwits showed a clear trend in their searching speed and spatial turning rate after prey ingestion. The speed increased up to the 7-9th second after prey ingestion, then stabilizing until the 13-15th second, and after that it increased again. The spatial turning rate continuously decreased after prey ingestion, with a steeper decline after the 15th second (Fig. 5.3).

The searching speed and spatial turning rate of the remaining species did not show any clear pattern and were highly variable (Fig. 5.3).

Table 5.2. Relationship between prey intake rate and foraging speed, searching speed and spatial turning rate. Significant results are indicated in bold.

	Avocet	Black-tailed godwit	Redshank
	N=52	N=69	N=69
Foraging speed and prey intake rate	r=0.05	**r=-0.32**	**r=-0.27**
	P=0.71	**P=0.01**	**P=0.02**
Searching speed and prey intake rate	r=-0.07	**r=-0.24**	r=-0.16
	P=0.61	**P=0.04**	P=0.18
Spatial turning rate and prey intake rate	r=-0.06	**r=0.32**	r=0.19
	P=0.68	**P=0.01**	P=0.12
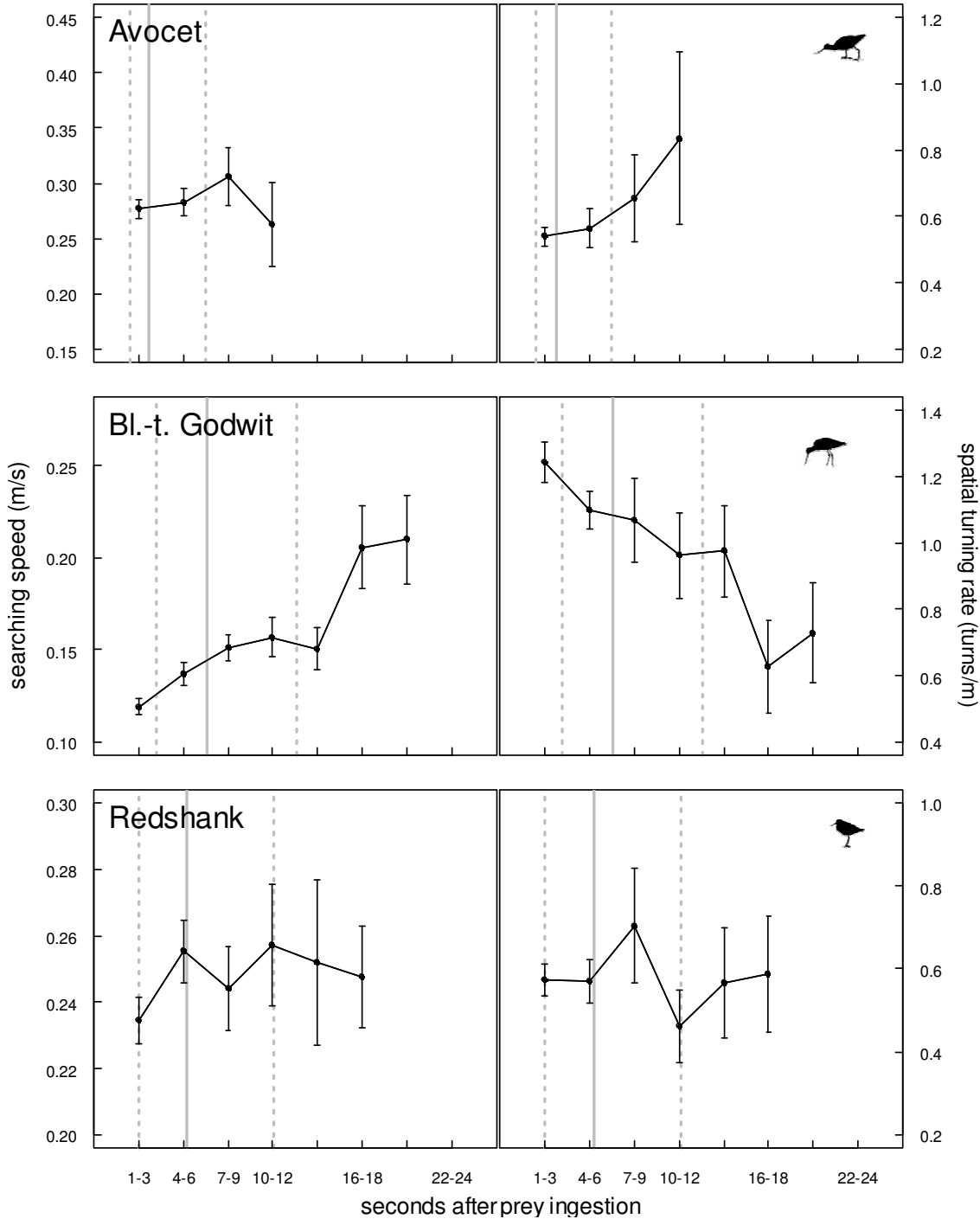
Figure 5.3. Variation of searching speed (m/s, graphs on the left) and spatial turning rate (turns larger than 45°/m) following the ingestion of a prey. Solid grey lines represent mean period between consecutive ingestions, and dashed lines the minimum and maximum.

5.5. Discussion

Basic Movement Parameters: who's the Fastest and who's the Straightest?

The three studied species showed marked differences in their movement parameters. Black-tailed godwit, the tactile predator, exhibited the slowest and the more tortuous movement, whilst the avocet (a "sweeper") was the fastest and the straighter (Table 5.1; Fig. 5.2). These results are coherent with the searching strategies used by each species. Black-tailed godwits spend a considerable amount of time probing the sediment to find their buried prey, which obviously slows down their movements. They were preying upon clams and ragworms, which take time to remove and ingest. Consequently, their handling time was high, leading to a large difference between foraging and searching speeds (Table 5.1). In contrast, avocets fed non-selectively in the top 20 mm of sediment, sweeping the sediment surface with their long bill while walking, which allowed more rapid movements. The redshank, a visual predator, was somewhat in an intermediate position. Its foraging speed is probably a compromise between walking fast in order to avoid the depression of prey activity caused by its own presence, but sufficiently slow to allow the detection of less conspicuous prey items (Goss-Custard 1977b; Gendrom & Staddon 1983, 1984).

Is the ARS the Optimal Solution for Waders?

As predicted, the tactile predator (black-tailed godwit) was the only species to clearly use an ARS. Our results showed that its speed and spatial turning rate were influenced by the feeding success: slowest and more tortuous paths corresponded to higher prey intake rates. This was corroborated by the results of the fine-scale analysis,

which showed a continuous increase in the searching speed and a decrease in spatial turning rate immediately after prey ingestion (Fig. 5.3), exactly as expected in an ARS.

We also found a short-term adjustment of the searching speed in order to maximize the likelihood of finding another prey. After ingesting a prey, black-tailed godwits accelerated, but their speed stabilized between the 7th and 15th seconds, after which they resumed the acceleration. These changes in searching speed closely matched the mean period between two consecutive prey ingestions. A similar pattern was found in spatial turning rate: a steeper decrease in this parameter occurred precisely after the phase of higher probability of finding another prey (Fig. 5.3). These results strongly suggest that the movement decisions of black-tailed godwits are based on a perception of prey distribution pattern, as observed in other animals that prey upon hidden and/or clustered items (Fortin 2003; Klaassen et al. 2007). This is the first evidence, from a non-manipulative in-situ study, that waders make their movement decisions in response to the immediate feeding success, but also based on prior knowledge of their prey distribution pattern.

The other two species did not follow an ARS, which was particularly clear from the analysis of the fine scale variation in movement parameters (Fig. 5.3). In redshanks, however, we found a negative relationship between prey intake rate and foraging speed, when considering the whole movement (Table 5.2). Such a relationship was not found when considering only the searching speed, which indicates that the time spent handling prey was responsible for slowing down the speed when prey intake was higher. In other words, any animal that takes a substantial time handling the prey, would present lower foraging speeds when the prey intake increases. This does not imply that the animal is adapting its movement in response to prey capture, but only that it is spending more time handling its prey. The mean handling time per prey registered for redshanks in this study was very short (0.31 s), but still enough to slow down the movement when they caught more items. This observation highlights the

relevance of consider the searching speed, instead of foraging speed, when analysing the potential use of ARS.

We did not find any relationship between sweep rates and movement parameters of avocets (Table 5.2, Fig. 5.3). The most common feeding mode of this species in the Tagus estuary is the "normal" strategy (Moreira 1995a). This is a non-selective strategy, in which avocets ingest indiscriminately all the items larger than about 1.5 mm in each sweep, along with some mud (Moreira 1995b). In this feeding method there is no clear relationship between the number of sweeps and intake rates (Moreira 1995a), which means that sweeps are probably not good surrogates of the feeding success. Previous studies carried out on the Tagus estuary (Moreira 1995a) showed that avocets can present several types of "foraging strategies" ("normal", "worms feeding" or "siphons feeding" strategies), each with its own set of stereotyped characteristics. The same study showed that they can alter the strategy in response to changes in prey type availability. Therefore, it is more likely that avocets react to changes in prey availability by changing the overall strategy used, rather than by subtle changes in speed and/or tortuosity of the "normal strategy".

Conclusions

In this study we proposed a method for the collection of movement data, and a set of parameters to be derived from such data, which are particularly useful in the study of species that are easily observed at a distance. This approach allows the development of in-situ studies, avoiding the need to capture and maintain birds in captivity and of recreating the natural conditions. Furthermore, large amounts of data and parameters can be obtained by this method. In fact, the great majority of the similar studies conducted so far in the wild used very small sample sizes, which may

limit the reach of the conclusions. The utility of this information goes far beyond the study of movement: it can be used in studies of foraging optimization and decision, or even incorporated in more complex analysis, such as the behaviour-based models, now widely used to predict the impacts of environmental changes (e.g. West & Caldow 2006).

Our results show that the ARS is not always the solution adopted by predators looking for patchy prey. The movement response of predators to feeding success is conditional on the type of searching strategy. Among waders, tactile predators, such as the black-tailed godwits, are those most likely to present an ARS. We also found strong evidence that this species is able to adapt its fine scale movement in response to previous knowledge of the distribution pattern of its prey.

Chapter 6

Does traditional shellfishing affect foraging by

waders? The case of the Tagus estuary (Portugal)

6. Does traditional shellfishing affect foraging by waders? The case of the Tagus estuary (Portugal)

6.1. Abstract

Estuarine intertidal flats are often exploited by humans and waders since they provide food, particularly shellfish. This raises important conservation issues. Waders can be affected by shellfishing activities in multiple ways, such as a reduction of the available shellfish, disturbance by the presence of shellfishers on their feeding areas, and changes in micro-habitat, due to sediment reworking. In this study we quantified the impact of traditional shellfishing on waders in the Tagus estuary. Particularly attention was given to hand-raking of clams *Scrobicularia plana*, which constitutes most of the consumed food by waders.

Shellfishers did not cause a relevant depletion of clams for waders; they removed less than 0.3% of its total production and focused on size classes that were usually not taken by birds. Hand-raking caused temporary changes in the vertical distribution and availability of invertebrate prey in the sediment. However, this did not affect the bird's feeding rates, presumably because prey availability remained above the threshold at which intake rates are expected to decline. The presence of shellfishers in the birds foraging areas potentially affects waders by keeping them away from foraging areas, but even the most affected species lost less than 10% of their foraging grounds due to this factor. Overall, we conclude that the current low harvesting levels of shellfishing are compatible with the preservation of the estuary as a key site for waders. Nevertheless, simulations showed that traditional shellfishing could have much greater potential to affect waders through disturbance than through prey removal. The results for the Tagus show that even small harvest rates, representing a

negligible loss of food for waders and potentially considered sustainable by shellfish managers, could have a great impact on waders due to increased disturbance. This effect of disturbance likely occurs in most estuaries and should be taken into consideration when planning shellfish harvesting in important wader feeding areas.

6.2. Introduction

Shellfisheries represent a very important economic activity in many estuaries worldwide, but may conflict with the conservation of these habitats of great natural value. High-intensity mechanical shellfishing, usually carried out during high-tide, can substantially reduce the populations of bivalves, and consequently the availability of food for birds foraging during low-tide (Piersma et al. 2001; Camphuysen et al. 2002; Atkinson et al. 2003). On the other hand, traditional shellfishing, usually carried out manually during low-tide, tends to be less extensive thus causing less damage to shellfish populations. However, the presence of shellfishers can result in disturbance to the birds that feed on the sediment flats (e.g. Stillman et al. 2001). Additionally, both methods can have significant impacts on the sediment composition (Piersma & Koolhaas 1997) and consequently on non-target invertebrates (e.g. Ferns et al. 2000; Kaiser et al. 2001; reviewed by Collie et al. 2000) and on the birds that prey upon them (Masero et al. 2008).

The Tagus estuary is one of the most important staging areas for waders in the East Atlantic Flyway (Stroud et al. 2004), and it is an internationally important site for avocet *Recurvirostra avosetta* and black-tailed godwit *Limosa limosa* (Stroud et al. 2004; Granadeiro et al. 2007). Shellfishing is a very common activity in this estuary, particularly the traditional hand-raking. In fact, it is not unusual to see hundreds of hand-rakers and bait-diggers working simultaneously on some intertidal flats of the

Tagus. One of the main target species is the clam *Scrobicularia plana,* which is the most abundant benthic invertebrate, and represents more than 86% of the invertebrate biomass (Rodrigues et al. 2006). This species is also the most important prey for the waders on this estuary, contributing more than 50% of the biomass consumed during winter (Moreira 1997). Despite the ecological and economic importance of this resource, it is currently unknown whether shellfishing significantly affects the clam's population. It is also unclear if the presence of shellfishers on the intertidal flats during low-tide significantly disturbs the feeding birds, reducing their access to important foraging areas. Manual shellfish harvesting, similar to that taking place in the Tagus estuary, is common in many estuaries throughout the World. Since the sediment flats of these estuaries are often critical feeding habitat for large numbers of waders, and many of these are currently under threat, it is important to understand the impacts of this economic activity to manage it properly.

In this study we analysed the impact of traditional shellfishing on several species of waders. We examined three potential effects: 1) the decrease of clam availability for waders; 2) the disturbance caused by the presence of shellfishers in the intertidal feeding areas, and 3) the impact of sediment reworking on non-target invertebrates and on the foraging efficiency of birds.

6.3. Methods

Study Area

The study was carried out in the Tagus Estuary, Portugal (Fig. 6.1). Intertidal flats cover about 97 km^2, and are mainly composed of muddy areas and dead oyster beds (Granadeiro et al. 2007). Tides are semi-diurnal, with an amplitude that ranges

between 1 to 3.8 m during neap and spring tides, respectively. Hand-raking of clams takes place throughout the year in many areas of the estuary; bait-digging is also a common activity, particularly on the sandiest flats.

Number of shellfishers and quantification of the removal of clams

The intertidal area of the estuary was divided into 17 sectors (Fig. 6.1), which were visited approximately once every fortnight during spring and neap low-tides, from March 2005 to May 2006. Overall 10 weekend and 14 weekday surveys were carried out, during which we recorded the number of shellfishers and bait diggers. We also registered the type of organism being harvested, which could be easily determined from a distance. To obtain an estimate of the mean number of shellfishers present during the year in each sector, we averaged the number of shellfishers observed in each survey, and weighted these values by the number of surveys carried out in each season, and by the proportion of weekends and weekdays in a year.

Shellfishing in the Tagus estuary is mostly an informal activity, so there are no official records of the amount of clams collected. Therefore, we estimated the overall harvest by multiplying the total number of shellfishers by an estimate of the average number of clams removed by each shellfisher, which we obtained from focal observations of the shellfishers (N=42 shellfishers observed during 5 min periods, evenly distributed throughout the annual cycle). The removal rate (number of clams removed per minute by each shellfisher) was then multiplied by the total amount of time available for shellfishing throughout the year. Available time was based on daytime low-tide periods. To our knowledge, there is no nocturnal shellfishing activity in the Tagus.
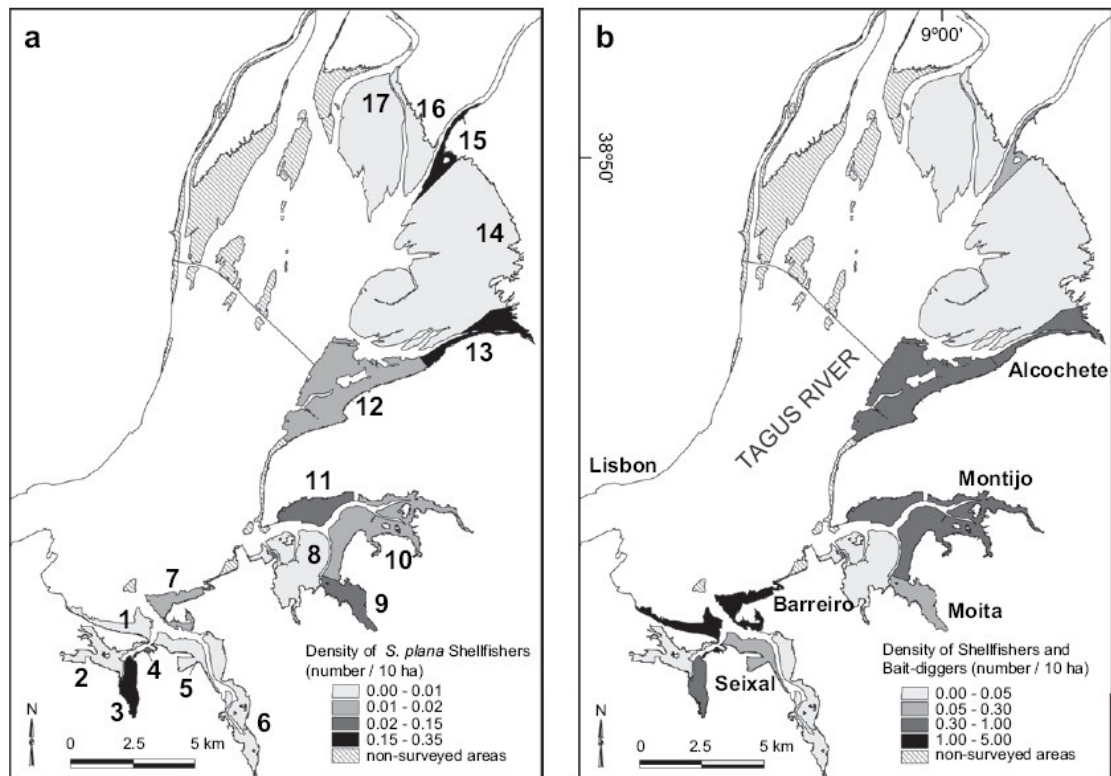
Figure 6.1. Distribution of harvesting effort of (a) clam shellfishers and (b) all shellfishers (including clam shellfishers) and bait-diggers in the intertidal flats of Tagus estuary. Numbers identify each study sector.

We compared the size classes harvested by shellfishers with those consumed by the two wader species that prey upon entire clams in the Tagus estuary: the black-tailed godwit and the dunlin *Calidris alpina*. These two species are responsible for 99% of the clam biomass consumed by waders (Moreira 1997). The mean length of the clams removed by shellfishers (maximum shell length) was estimated by measuring a sample of 226 clams collected by several harvesters. Size classes consumed by black-tailed godwit and dunlin in the Tagus estuary were obtained from the literature (Moreira 1995c and Santos et al. 2005, respectively).

The biomass (ash-free dry weight - AFDW) removed by the shellfishers was estimated using alometric equations (Moreira 1995c). We calculated the annual harvest (in percentage) as the biomass of clams collected annually by the shellfishers in

relation to the secondary production of clams. The latter value was based on the annual invertebrate production in Tagus (ca. 853 kJm^{-2}year^{-1}; Moreira 1997), 86% of which corresponds to clams (Rodrigues et al. 2006), and assuming that 1 g of AFDW corresponds to 20.92 kJ (McLusky 1981).

Disturbance caused by the shellfishers at the bird feeding areas

The disturbance caused by human presence in the bird's feeding areas was expressed as a percentage of habitat affected. We assumed that birds were displaced from a circular area around each disturber (shellfisher or bait-digger) present in the feeding grounds (disturbed area = π*(flight distance)^2); Smit & Visser 1993; Stillman et al. 2001). Flight distance of each species (i.e. the distance at which birds take flight when disturbed) was obtained from the literature (Smit & Visser 1993; Boer & Longamane 1996; Fitzpatrick & Bouchez 1998; Lafferty 2001; Burton et al. 2002; Thomas et al. 2003). Whenever more than one estimate was available for any given species, we averaged the values. In species for which we could not find flight distance estimates (black-tailed godwit, avocet, knot *Calidris canutus* and ringed plover *Charadrius hiaticula*), we estimated this parameter using a linear regression model of the flight distance and body mass of known species (Blumstein et al. 2005). These species were oystercatcher *Haematopus ostralegus*, kentish plover *Charadrius alexandrinus*, grey plover *Pluvialis squatarola*, sanderling *Calidris alba*, dunlin, bar-tailed godwit *Limosa lapponica*, curlew *Numenius arquata* and redshank *Tringa totanus*. Body masses were obtained from Cramp and Simmons (1983) and flight distances are shown in Table 6.1. The equation obtained was: flight distance = 37.14+0.18*body mass (R^2=0.85; P=0.001; N=8). Given that the flight distance of each species varies with factors such location, time of year, habituation, and availability of alternative feeding areas (Gill et al. 2001a; Mori et al. 2001; Stillman et al. 2001; Webb

& Blumstein 2005), we calculated the percentage of habitat affected in a range of values of flight distances (average ± 50%).

The mean number of disturbers in the bird feeding areas was calculated by averaging numbers by habitat (using a detailed map of main sediment areas, obtained from previous studies – Granadeiro et al. 2007) and season (see above), weighted by the density of birds (using data for the Tagus; Moreira 1995c). By doing this, we assumed that bird densities reflect the importance of each habitat and season for each species. The total area disturbed was computed as the sum of the areas affected by each disturber, i.e., we assumed that the areas did not overlap. This approach corresponds to the worst possible disturbance scenario, because disturbers can be closer than twice the radius of disturbance.

Impact of hand-raking on feeding behaviour of birds and on prey availability

To analyse the impact of hand-raking on the feeding behaviour of waders we compared their feeding rates on raked and adjacent non-raked (control) areas during the winter (February and March 2005). For this purpose we hand-raked for clams in mudflats located in the southern margin of the estuary (Sarilhos), known to sustain high densities of clams and birds (Lourenço et al. 2005). We raked about 2000 m^2 of mudflats, divided into smaller areas (approximately 100 m^2 each), to simulate the pattern produced by the hand-rakers in Tagus. All clams larger than 25 mm were collected. We quantified prey intake rates (number of prey consumed per minute) of black-tailed godwit and redshank, and the sweeping rate (number of sweeps per minute) of avocet by focal observations. The prey intake rate of redshanks could only be accurately recorded when birds were at close range (less than 80 m), due to the small sizes of their prey. Success rate of these birds was then estimated at 0.93±0.07

prey/peck, N=38, and used to calculate the number of prey taken by redshanks that were feeding further away. A total of 114 avocets, 103 black-tailed godwits and 54 redshanks were observed. Simultaneously, we counted the number of waders present in the experimental areas, in order to control for possible interference among birds due to high density levels (e.g. Yates et al. 2000). The average bird densities (black-tailed godwit: 8.71±1.08; redshank: 2.16±0.41; avocet: 10.81±0.95) were well below the threshold reported for bird interference (approximately 100 birds/ha in redshank – Yates et al. 2000 - and predicted to be more than 200 birds/ha in black-tailed godwit – Stillman et al. 2002; there is no evidence of interference among avocets – Moreira 1995c).

To quantify prey availability we collected ten cores of sediment (86.6 cm^2 x 20 cm deep), in both raked and control areas, immediately after hand-raking. A new set of ten cores was collected 15 days later. The top 5 cm of each core was split into 1 cm sections, and sieved through a 0.5 mm mesh. The remaining 15 cm of the core were sieved through a 1 mm mesh. All invertebrates were stored in 70° ethanol. All individuals in good condition were measured and their biomass (expressed in AFDW) was calculated using published equations (Appendix 1).

Prey items harvestable by avocets were all invertebrates found in the top 2 cm of sediment (Moreira 1995b). For black-tailed godwit all ragworms *Hediste diversicolor* larger than 20 mm and all clams *Scrobicularia plana* between 10 and 20 mm, regardless of their burying depth (Moreira 1994; Perez-Hurtado et al. 1997). For redshank, ragworms between 18 and 85 mm, mudsnails *Hydrobia ulvae* smaller than 4 mm, buried at less than 5 cm, and all clam siphons (Davidson 1971; Goss-Custard et al. 1977; Moreira 1996; Perez-Hurtado et al. 1997).

Simulating an increase in the number of shellfishers

We calculated the potential consequences of an increase of the number of shellfishers in mudflats. We simulated the loss of habitat and clam depletion for a range of values of shellfishers' densities. For this purpose, we assumed a constant proportion among the number of shellfishers on the various mudflats sectors. During the simulations we randomly allocated the shellfishers in the mudflats. We then calculated the area disturbed by the presence of shellfishers, as described in previous sections. We assumed that the area affected by two shellfishers could be closer than twice the flight distance, and hence would overlap. The area disturbed by each shellfisher varies among wader species, because it is a function of the corresponding flight distance. Therefore, we ran separate simulations for different flight distances. We only considered the flight distances of species that potentially occur on the muddy and sandy mud intertidal areas, the most common habitat on Tagus estuary. These included the avocet, grey plover, knot, dunlin, black-tailed godwit, bar-tailed godwit and redshank. For each value of shellfisher's density we also estimated the percentage of clams removed, using the approach described in the previous sections.

All spatial analyses were conducted in a Geographic Information System using the software Arcview 3.2 (ESRI 1999). Statistical computations were carried out using the R package (R Development Core Team 2005).

6.4. Results

Number of clams removed by the shellfishers on Tagus estuary

The most intensively exploited areas in the Tagus estuary (Fig. 6.1) tend to be near the coast and in the south eastern area of the estuary (i.e., around major urban centres).

The average density of shellfishers in the intertidal flats was 0.02 shellfishers/10 ha. Overall, they removed ca. 240 tons of clams *Scrobicularia plana* during a year, corresponding to an average daily harvest of 20.9 kg AFDW.

The size of the clams removed by the shellfishers varied between 32 and 53.5 mm (average: 41.49 ± 0.28 mm; N=226). There was a clear difference between the sizes removed by the shellfishers and those taken by the two main wader species that prey upon clams (Fig. 6.2).

Disturbance caused by shellfishers

The presence of shellfishers and bait-diggers on the intertidal flats during low-tide affected a relatively small proportion of the feeding habitat of the waders (Table 6.1). The most affected species was the black-tailed godwit, with less than 5% of its feeding habitat becoming unavailable due to disturbance. Even in the worst flight distance scenario considered (multiplying the published estimates by 1.5), less than 10% of the habitat of this species is affected (Table 6.1).
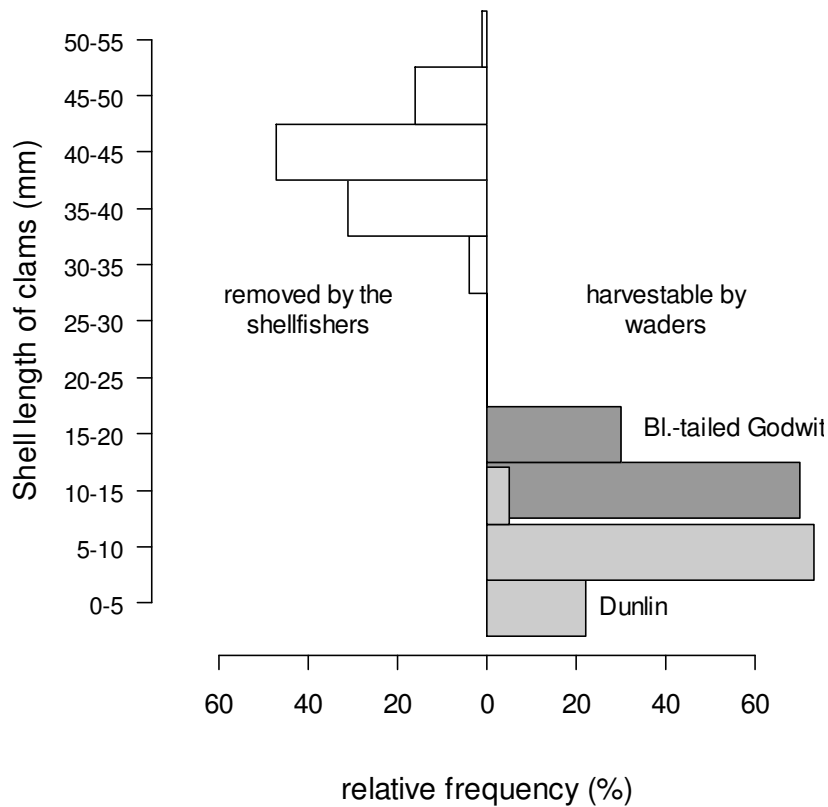
Figure 6.2. Size frequency distribution of clams *S. plana* removed by the shellfishers (left) and by the two main wader species that prey upon clams (right): black-tailed godwit (dark grey bars; values based on Moreira 1995c) and dunlin (light grey bars; based on Santos et al. 2005).

Impact of hand-raking on feeding behaviour and prey availability

Raking the sediment had a significant immediate impact on the vertical structure of the non-target invertebrates (Fig. 6.3). Top layers were more affected than deeper layers, and density was generally more affected than biomass. The vertical structure recovered rapidly during the following two weeks (Fig. 6.3), but even after this period it had not entirely returned to the original state.

Table 6.1. Impact of the presence of shellfishers and bait-diggers on the extent of feeding areas available to waders, expressed as the proportion of the habitat affected. Values between brackets correspond to ± 50% potential variation on the flight distance. (a) This study (see methods); (b) Lafferty (2001); (c) Boer & Longamane (1996); (d) Burton et al. (2002); (e) Thomas et al. (2003); (f) Smit & Visser (1993); (g) Fitzpatrick & Bouchez (1998).

Species	Flight Distance (m)	Source	Density of shellfishers and bait-diggers in their feeding areas (per 10 ha)	% of habitat affected
Avocet	82	(a)	0.06	1.2 (0.3-2.8)
Ringed plover	47	(a)	0.33	2.3 (0.6-5.2)
Kentish plover	30	(b)	0.21	0.6 (0.2-1.4)
Grey plover	85	(c), (d)	0.15	3.5 (0.9-7.8)
Knot	59	(a)	0.05	0.6 (0.1-1.3)
Sanderling	26	(e)	0.32	0.7 (0.2-1.5)
Dunlin	73	(d)	0.17	2.8 (0.7-6.3)
Black-tailed godwit	78	(a)	0.22	4.2 (1.1-9.5)
Bar-tailed godwit	107	(f)	0.01	0.6 (0.2-1.4)
Redshank	56	(d), (g)	0.20	2.0 (0.5-4.5)
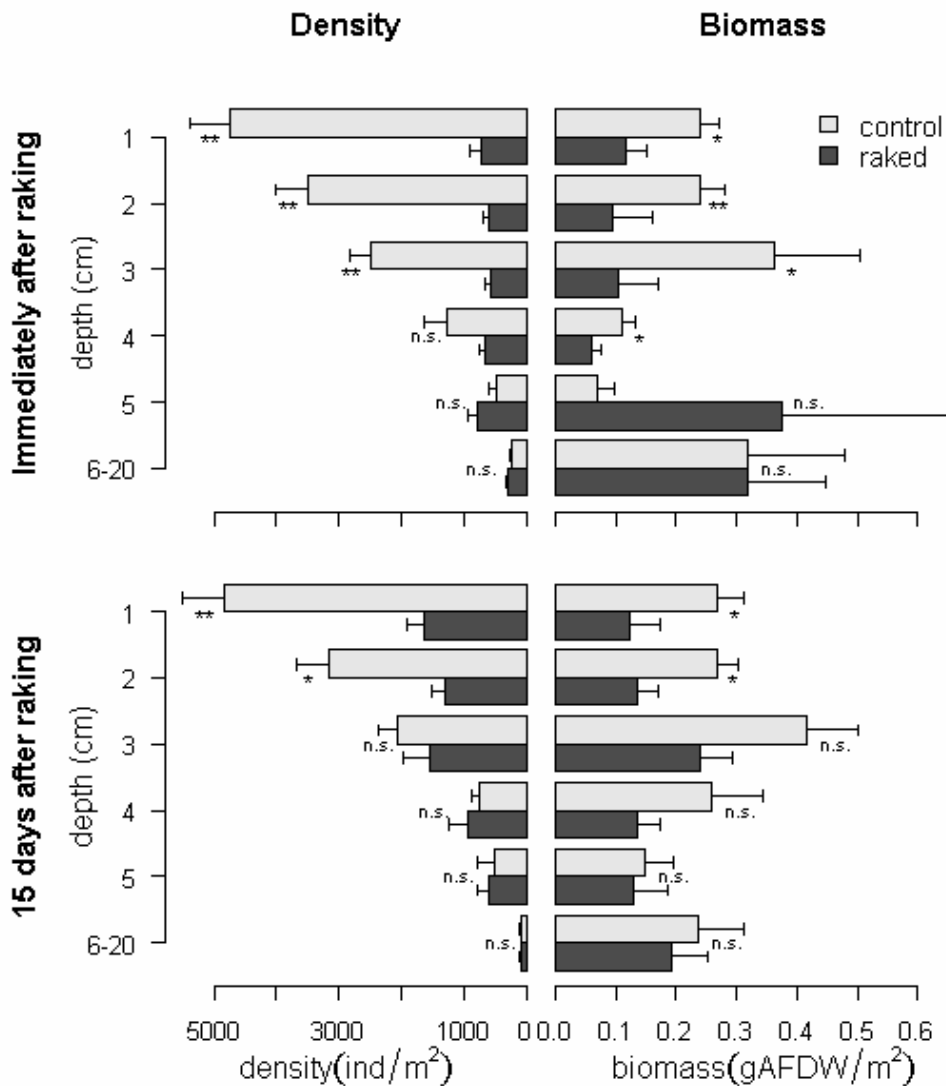
Figure 6.3. Density and biomass (means ± SE) vertical structure of non-target invertebrates on raked and control areas, immediately after raking and 15 days later. Symbols represent the results of Mann-Whitney tests: **: P<0.01; *: P<0.05; n.s.: P>0.05. Values of the "6-20 cm" layer were divided by 14, to allow the direct comparison with the other layers (see methods).

The density of prey harvestable by avocets dropped to 1/7 in raked areas, and was still less than half of the control value fifteen days later (Table 6.2). The available biomass for this species decreased to half after raking, showing almost no recovery two weeks later. The densities of prey harvestable by redshanks decreased to half after raking, but no significant differences were found on the biomass. The fraction

harvestable by black-tailed godwits (both density and biomass) did not change after raking (Table 6.2).

Despite these variations, there were no significant differences between the feeding rates of the studied species on raked and control areas (Table 6.3).

Simulating an increase in the number of shellfishers

The increase of the density of shellfishers had much more harmful impact on the habitat affected than on the percentage of clams removed, particularly for the species with larger flight distances (Fig. 6.4).

Table 6.2. Prey density (ind/m^2; Dens.) and biomass (AFDW/m^2; Biom.) on raked and control areas (means ± SE). P-values correspond to the results of Mann-Whitney tests.

		Immediately after raking			15 days after raking		
		Control	Raked	P	Control	Raked	P
Avocet	Dens.	8349±1131	1139±492	**<0.001**	8152±952	2956±385	**<0.001**
	Biom.	0.48±0.06	0.21±0.09	**0.005**	0.48±0.04	0.26±0.06	**0.005**
Bl.-tailed godwit	Dens.	139±38	230±49	0.198	335±80	277±77	0.560
	Biom.	1.31±0.63	3.28±1.56	0.225	2.53±0.57	1.47±0.54	0.140
Redshank	Dens.	2644±581	1132±142	**0.021**	2910±447	1189±129	**0.002**
	Biom.	1.62±0.22	1.61±0.46	0.393	1.59±0.38	1.31±0.28	0.631

Table 6.3. Feeding rate (prey/min or number of sweeps/min, for avocet; means ± SE) inside the raked areas and in adjacent control areas. Values between brackets correspond to sample sizes.

	Control	Raked	T-test
Avocet	34.80 ±0.66	35.66 ±0.89	t=0.78
	(76)	(38)	P=0.437
Black-tailed godwit	5.30 ±0.31	4.80 ±0.43	t=0.95
	(54)	(49)	P=0.347
Redshank	41.22 ±2.13	34.22 ±3.68	t=1.65
	(38)	(16)	P=0.112
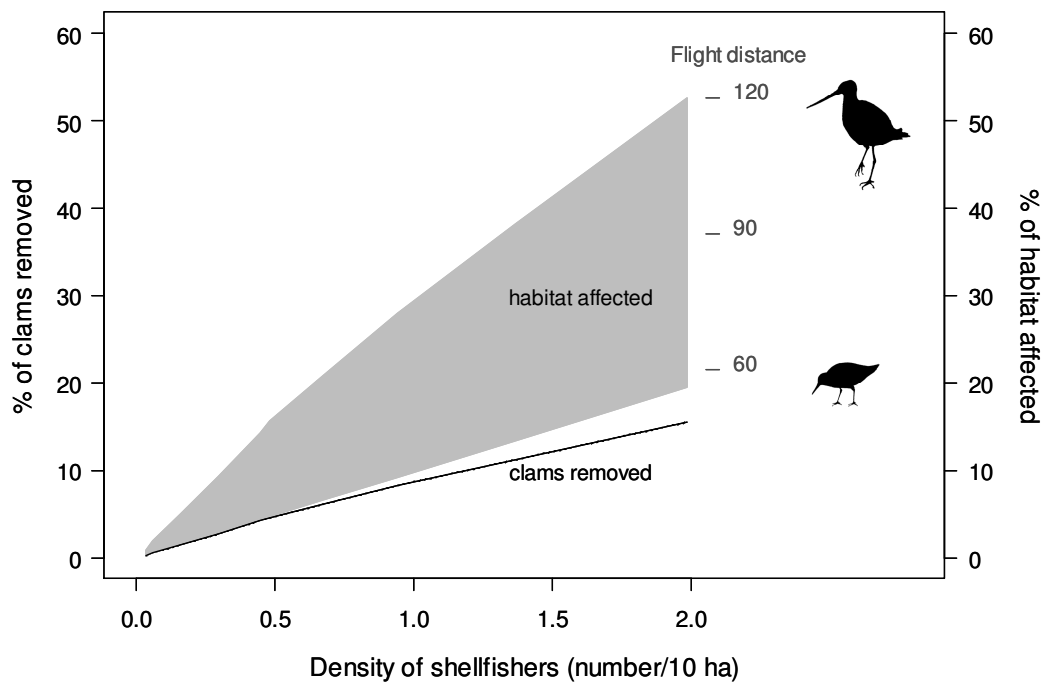
Figure 6.4. Percentage of clams removed (solid line), and habitat affected at several flight distances scenarios (grey area, inner scale), in relation to increasing shellfisher density. It is noticeable that the removal of even relatively small percentages of clams result in major losses of habitat, and that this impact is much more substantial for waders with greater flight distances.

6.5. Discussion

In this study we present the first data on the status of shellfishing in the Tagus estuary and on its potential impacts on waders. We addressed potential conflicts between shellfishers and foraging waders: the reduction of clam availability (competition for prey), the disturbance caused by human presence during low-tide (temporary loss of feeding habitat) and the reworking of the sediments (deterioration of feeding habitat). Previous studies have addressed this question in other estuaries, but to our knowledge none presented such an integrated approach (most of them focus on just one or two major type of effects - usually the combination of disturbance and shellfish depletion; e.g. Stillman et al. 2001; Goss-Custard et al. 2004).

Shellfishers do not compete with waders for clams in the Tagus estuary

Shellfishers remove around 7650 kg AFDW of clams during a year, which corresponds to less than 0.3 % of the annual secondary production of the estuary. This value is very low when compared with that removed by the bird community (approximately 8%; data from Moreira 1997). This suggests that the impact of the shellfishers on the availability of clams for birds is almost negligible. In addition, the size classes removed by people are not harvestable by waders (Fig. 6.2). Therefore, clam extraction could only affect the species that harvest clam siphons, such as the grey plover and the redshank (Moreira 1995c). However, we do not exclude the possibility of significant local effects, particularly in the intertidal flats near the main urban centres, where up to 3.7% of the clam biomass production is harvested (ca. half of that consumed by the birds).

Disturbance caused by the shellfishers on the waders

We quantified the effect of disturbance on the waders using the proportion of habitat affected by the human presence during low-tide. This approach assumes that the presence of people excludes the birds from feeding in a circular area around them, causing a temporary loss of habitat. For most species, less than 5% of the preferred habitat was affected by the presence of shellfishers. The largest effect involved the black-tailed godwit, but even in this case less than 10% of the habitat was disturbed (Table 6.1). The temporary loss of foraging area caused by disturbance may result in a significant increase of the bird density in nearby areas (Stillman et al. 2003; Goss-Custard et al. 2004). This may increase interference among foraging birds, due to prey depression (Yates et al. 2000) or kleptoparasitism (Triplet et al. 1999). At high densities, waders may significantly decrease their intake rate (above approximately 100 birds/ha, Durell et al. 2006), and ultimately may not be able to fulfil their daily energy requirements (Stillman et al. 2003; Goss-Custard et al. 2004). However, in the case of the Tagus, the likely increase in wader densities due to this cause would still be well below the levels required to produce any significant effects due to interference.

In addition to the loss of feeding area, the energy and time costs of commuting to another area may also represent a significant fraction of the daily energy costs of waders (West et al. 2002, 2003; Goss-Custard et al. 2006a). We did not analyse the magnitude of these impacts, but previous studies have shown that they are almost insignificant in similar scenarios (i.e., when bird densities are relatively low and the proportion of habitat affected is small; West et al. 2002).

Therefore, the impacts of the disturbance caused by the current levels of shellfishery at Tagus can be considered relatively small, particularly because the most inaccessible areas of the estuary remain undisturbed (Fig. 6.1). However, they can assume greater significance when acting together with other potential causes of loss of

intertidal flats, such those resulting from climate changes or habitat reclamation (Crooks 2004; Durell et al. 2006; West & Caldow 2006), or when associated with severe winters (Goss-Custard et al. 2006a). Birds can adapt their tolerance to human disturbance if the availability of habitat decreases (Gill et al. 2001a), but the combined effect of different sources of habitat loss may have severe impacts on their survival (Durell et al. 2006).

An alternative approach to evaluate the combined effects of multiple sources of habitat loss and disturbance is the development of a behaviour-based model (a model that simulates the behaviour of individual birds by optimizing rules that determine their daily energy requirements; e.g. Goss-Custard et al. 2004). This methodology has proved to be of great use to predict the impact of habitat changes and of shellfisheries intensification on wader winter survival (e.g. Stillman & Goss-Custard 2006; West & Caldow 2006). However, even the most recent simplified models (such as the MORPH – Durell et al. 2006) require a wealth of baseline data (such as the availability of prey in the various sediment flats and the natural winter mortality of prey and birds), that is still lacking for most estuaries. Our approach is less powerful in predicting the long term impacts on the survival of the populations, but since it is based on easily collectable data (overall bird abundances and shellfishery intensity), it is a simpler and quicker alternative for areas that have not been thoroughly studied.

Impact of hand-raking on feeding behaviour and prey availability

Raking the sediment disrupted the vertical distribution of the invertebrate community (Fig. 6.3). The slight recovery of the vertical distribution after two weeks was probably a result of an upward migration of the invertebrates, combined with colonization from neighbouring areas. The density of non-target invertebrates was

more affected than the biomass, which suggests that raking had more impact in the smaller invertebrates. On the other hand, the top layers were much more affected than deeper areas of the sediment. As a result, the shorebirds that prey upon the small invertebrates present on top layers suffered a major decline on the harvestable prey fraction (redshank and avocet). In fact, we found a significant decrease in the density of prey for avocets and redshanks and biomass (only for avocets) available immediately after raking, which was still noticeable two weeks later (Table 6.2). Despite this fact, none of these species showed a significant difference in their feeding rates (Table 6.3).

In most waders feeding on benthic invertebrates, the maximum intake rate is constrained by searching and handling times (Piersma et al. 1995; Goss-Custard et al. 2006b), reaching an asymptote above a given prey density threshold (following the Holling type II functional response model). This threshold is usually very low (less than 150 invertebrates/m^2), and it is strongly dependent on the body mass of the bird and the mean biomass of their prey (Goss-Custard et al. 2006b). Using the available equations to estimate the functional response (Goss-Custard et al. 2006b), we concluded that prey densities after raking were still well above the threshold densities that would depress intake rates. Therefore, it is not surprising that intake rates remained unchanged after raking.

However, prey density at the surface of the sediment is not the only factor that is likely to affect the foraging efficiency. The reworking of the surface sediment can also obstruct visual and tactile cues, thus affecting prey detectability (Shepherd & Boates 1999). We did not detect any variation in feeding rates that could be caused by reduced prey detectability. However, some wader species, particularly visual predators like plovers, could be more affected by this indirect effect of raking. Nevertheless, the total area affected by this reworking is very small when compared with the total available habitat for these species (*pers. obs.*). Therefore, we do not identify sediment reworking as a major problem for foraging waders.

Conclusion

We did not find any evidence that the current shellfishing effort in the Tagus estuary is causing any significant negative effect on waders. At a more local level, the impacts may be somewhat higher, and can result in reduced foraging areas and a decrease in food availability, particularly for species that prey upon clams' siphons. However, we believe that these impacts are well below the threshold that may affect the wintering survival of the birds, especially when compared with other estuarine areas where the shellfishing intensity is much higher (e.g. Goss-Custard et al. 2006a).

None of the three major potential negative impacts of shellfishing currently seems to be conservation problem in Tagus estuary. It is clear from our results that traditional shellfishing has much more potential to affect waders through disturbance than through the removal of prey. In fact, even small harvest rates that represent a negligible loss of food for waders, and may be considered sustainable by shellfish managers, will have a great impact on waders due to disturbance (Fig. 6.4). This should be taken in account in management plans of estuaries, especially when establishing quotas for the shellfish harvesting.

The methodology used in this study is simple to apply in other estuarine areas, and may provide a first approach to the problem of shellfisheries in similar situations. It can represent an alternative to the most recent individual-based models, which require a wealth of baseline information that is not available for most estuaries.

Appendix 1. Equations used to estimate the invertebrate biomass. TL - total length (mm); L_3 – Length of the prostomium, peristomium and the first setigerous; mm); AFDW – ash-free dry weight (mg); SL - shell length (mm); SLS - surface length of siphon (mm). (a) – P. Lourenço (unpublished data); (b) - Zwarts & Wanink (1993); (c) - Santos et al. (2005); (d) Zwarts & Blomert (1992); (e) Zwarts et al. (1994); (f) Moreira (1996); (g) R. Martins and M.P. Dias (unpublished data); (h) – C.D. Santos (unpublished data)

Species	Equation	R^2	n	Source
H. diversicolor	$TL=21.422 L_3^{1.4538}$	0.93	73	(a)
	$\ln AFDW = 2.208 \ln TL/10 – 0.898$	>0.99	3586	(b)
H. ulvae	$AFDW = 0.0154 SL^{2.61}$	0.92	28	(c)
S. plana/*Abra* sp. < 10 mm	$AFDW = 0.013 SL^{2.23}$	0.97	17	(c)
S. plana > 10 mm	$AFDW = 0.008 SL^{2.87}$	>0.99	158	(d)
S. plana siphons	$SLS = (0.09SL + 1.4)*10$	0.49	75	(e)
	$Log(0.842 AFDW) = 1.031 \log(SLS) – 0.783$	0.48	29	(f)
Cyathura carinata	$\log (AFDW)=2.5003 \log(TL)-5.6345$	0.99	213	(g)
Streblospio shrubsolii	AFDW/individual=0.0256	-	4044	(g)
Alkmaria ramniji	AFDW/individual=0.0159	-	44	(h)
Tharyx sp.	AFDW/individual=0.0448	-	415	(h)
Oligochaeta	AFDW/individual=0.0262	-	7327	(g)
Nematoda	AFDW/individual=0.0014	-	74	(h)

Chapter 7

General Discussion

7. General Discussion

In this thesis some of the main factors driving the movement and distribution of waders in low-tide sediment flats were analysed, giving a particular focus on their implications to the conservation of these species. In order to contribute to this major goal, several specific questions were addressed, whose main aims and conclusions were described in detail in the previous chapters. The present section consists in an integrated discussion of the major findings, in the light of the current knowledge on the ecology of waders during their non-breeding season.

Studying movement patterns of wintering waders at several scales: from meters to kilometres

The relative importance of the different abiotic and biotic factors to explain the distribution of animal is obviously linked with the scale at which the natural phenomena are observed (Wiens1989). In this thesis several temporal/spatial scales of analysis were considered: from a broader estuarine scale, by analysing the movement of the waders between feeding and roosting areas, to the immediate foraging decisions, that are taken in a matter of seconds. In between, an intermediate scale was studied by analysing the distribution of birds along the tidal cycle.

Some of the major factors driving the choice of foraging areas in an estuarine scale are well documented, and include the sediment type or the relative availability of prey (e.g. Goss-Custard et al. 1977; Moreira 1993a; Yates et al. 1993). Several other studies hypothesized the potential influence of the proximity of main roosting sites over the choice of the low tide feeding areas (Handel & Gill 1992; Scheiffarth et al. 1996;

Fox & Madsen 1997), but the first strong evidence of this link was given by the work presented in chapter 2. Additional recent studies conducted in other estuarine systems point to similar conclusions (Rogers et al. 2006a; Van Gils et al. 2006), and corroborate the importance of the maintenance of a network of good quality roosts in the vicinity of feeding areas. This evidence of a close relationship between feeding and roosting areas raises another relevant question: are birds choosing to feed close to the roosts or, conversely, to roost close to the feeding grounds? The answer to the question seems to be the relative availability of each type of habitat. In Tagus estuary, as probably in many estuaries, the availability of roosts is the limiting factor, so birds are constrained to feed close to the roosts.

Once chosen to feed in an intertidal flat located in the vicinity of the roost, waders have to make decisions at lower scales. For instance, they have to decide if they stay in the same foraging ground for the entire exposure period or, in contrast, if they explore different tidal flats as they became accessible during the tidal cycle. This question was studied in chapters 3 and 4. There was an obvious variation among species in what regards to their response to the movement of the tidal line: black-tailed godwit *Limosa limosa*, dunlin *Calidris alpina* and avocet *Recurvirostra avosetta* were considered as "tide-followers", whereas grey plover *Pluvialis squatarola*, bar-tailed godwit *Limosa lapponica* and redshank *Tringa totanus* as "non-followers". These variations proved to have large implications in the estimates of use of tidal flats with different exposure periods.

Finally, when waders are searching for prey, they have to make several fine scale decisions, as to speed up in order to maximize the exploited area (Speakman & Bryant 1993), or to slow down to detect less conspicuous prey (Gendron & Staddon 1984). This was addressed in chapter 5. The study of the fine-scale movement of waders presented here represents one of the first approaches to this question. More specifically, the "area-restricted search" (e.g. Benhamou 1992) was hypothesized to

describe the type of movements presented by waders. The results obtained by the analysis of more than 12 000 spatial positions showed that this only applies to tactile predators, like the black-tailed godwit.

Searching strategies and the importance of prey activity

The differences on the type of search presented by the several wader species (visual, tactile or sweep) have major ecological implications on the use of tidal flats, as shown in chapters 4 and 5. Generally, tactile species (as black-tailed godwits and dunlins), are more linked to the tidal edge. The causes for this bond are still unknown, but can be related with the peak of activity of their main prey, the clam *Scrobicularia plana*, during the first phases after tidal passage (Rosa et al. 2007). Prey activity also determines the fine-scale movements of the waders, and again it differs among species with different searching behaviour (chapter 5).

The major implications of the differences in the foraging behaviour between tactile and visual predators are probably in their overall pattern of exploitation of tidal flats: tactile species tend to use the plots more evenly, irrespective to their exposure period, while visual predators used more intensely the upper areas.

New approaches to the study of waders in tidal flats

Along this thesis a set of new methods was used to study some of the factors driving the intertidal use by waders. In chapter 3 it is shown that some established methods widely adopted in wader studies (the low-tide counts) can result in inaccurate

estimates of the relative use of intertidal areas within the estuary. An alternative methodology, with an equivalent sampling effort, was proposed.

Geographic Information Systems (GIS) proved to be of great value in approaching several aspects of the intertidal use by waders. They were used as a tool to study the large-scale movements between feeding and roosting areas (chapter 2), and also the fine-scale movement in a specific intertidal flat (chapter 5). GIS also contributed to gather a large amount of information related with sediment composition, tidal exposure, location of major roost sites, among many others, that have contributed to several analyses and illustrations of the results. Finally, GIS are the base of some of the new methodological approaches proposed here, as the evaluation of the potential impact of losing or creating new roosts for birds (chapter 2), the simulation of the major consequences of increasing shellfishers densities (chapter 6) or the geo-correction of behavioural data obtained by video-recording (chapter 5). Although all the data were collected in Tagus estuary, these new methods can be applied in many other estuaries worldwide, which share many of the same ecological constrains and conservation problems.

Major conservation implications

The major conservation implications of the study were addressed in each chapter, but some key conclusions can be drawn.

Current levels of shellfishing and other sources of human disturbance do not seem to constitute a major conservation problem in Tagus, mainly because large areas of tidal flats remain very difficult to reach (Fig 1.3). However, the human pressure in the most vulnerable areas is strongly increasing. For example, the construction of a new

bridge linking Lisbon to Alcochete had increased in ca. 50% the human population in the vicinity of some of the most important feeding and roosting areas for waders in Tagus estuary. As shown in chapter 6, the increase in disturbance levels can have serious impacts on some wader species, particular those that show larger flight distances such as black-tailed godwits. The recent governmental decision to construct the new Lisbon airport – the largest Portuguese airport – in the close vicinity of the Tagus estuary poses even more serious challenges to the bird conservation in this wetland, since it is most probable that the human pressure will continue to increase in the next decades. Moreover, this pressure is likely to be experienced more intensively in upper tidal flats (that provide the largest fraction of biomass required by birds; chapter 4) and supratidal habitats (as roosts).

The most immediate cause of concern with respect to wader conservation in Tagus estuary is probably the loss and degradation of roosts, as previously addressed (chapter 1). In the last few years, some of the most important roost sites in Tagus were lost. Chapter 2 showed that these losses can have serious consequences in the access of waders to the available foraging areas, and consequently to the carrying capacity of the estuary. Nowadays, some tidal areas are probably under used by birds because they are located too far from suitable roost sites. The situation can be easily solved by adopting correct management practices in the saltpans (particularly in those more strategically located, like Vasa-Sacos and Samouco), in order to improve their quality as roost sites for waders (Velazquez 1992; Warnock et al. 2002). Furthermore, the creation of a new refuge in the northern part of the estuary (see Fig. 2.1) would be of great use to compensate for the past losses of roosts in this area, as suggested by the modelling application developed in chapter 2.

The consequences of habitat deterioration on the wintering survival of waders are very difficult to predict. However, this is a key issue in conservation science, because winter survival is the only effective expression of the impact of changes in

wintering conditions in the population dynamics and, ultimately, on the survival of the species. Individual-based models, or behaviour-based models, are a recent tool for predicting the mortality rates on waders in their wintering quarters (e.g. Stillman & Goss-Custard 2006; West & Caldow 2006). These models are based on the assumption that individuals within a population always behave in order to maximize their own chances of survival (e.g. Goss-Custard et al. 2004), following the predictions stated by "Optimal Foraging" and "Game" theories (Stillman & Goss-Custard 2006). These models have proved to be of great value to evaluate the impact of habitat loss (Durell et al. 2005, 2006), disturbance (West et al. 2002; West & Caldow 2006) or shellfishing (Stillman et al. 2001, 2003; West et al. 2003; Caldow et al. 2004). However, its application requires a wealth of baseline data that is still lacking for most estuaries. This reinforces the need to continue to gather some basic information on the waders' ecology in Tagus, as well in other poorly known estuaries. In this context, the data related with foraging behaviour of birds (as those presented in chapters 4, 5 and 6) are of great importance.

Most of the waders that winter in the Tagus estuary are long-distance migrants that highly depend on the continued existence of staging areas along their flyways. The decline of the quality of these key sites, caused by habitat deterioration, is likely to have major implications for the reproduction and survival of these migrants (Gill et al. 2001c; IWSG 2003). In the light of the steep declines currently faced by several migratory wader species, there is a vital and urgent need for the development of internationally co-ordinated research initiatives to uncover reasons behind the declines (IWSG 2003), and also to ensure the effective appliance of the international agreements related with the protection of migratory birds (as the Bonn Convention).

Future work

Although the number of studies related with wader ecology in Tagus estuary had increased considerably in the last decade (e.g Granadeiro et al. 2004, 2007; Rosa et al. 2007, 2008; Santos et al. 2005, 2008), many questions are still to be answered and worth further investigation.

Probably the most critical issue (at least, concerning to the conservation of waders that use the EAF) is a correct assessment of Tagus importance as a staging area during the migration periods. Several aspects related with the migration ecology are still virtually unknown for Tagus estuary, as the magnitude of the migrating populations, the residence period of birds, the preferred foraging sites for refuelling and the rates of mass increase. This lack of knowledge is probably due to the huge amount of effort usually needed to correctly address those questions. However, advances in radio-tracking technology, like the use of Automatic Radio Tracking Stations (Van Gils & Piersma 1999; Rogers et al. 2006b), can be of great value to overcome those difficulties.

The knowledge about the main causes driving the apparent decline of some wintering wader populations, as grey plovers and dunlins (Fig. 1.5), is also of key relevance. Potential internal (as deterioration of wintering habitat quality) and external factors must be considered in future studies. External factors can be related to changes in habitat quality in other wintering and stopover sites, as well the population trends in breeding areas. Fortunately, most of the wetlands located in EAF are fairly well monitored (Stroud et al. 2004), and count data regularly published (e.g. Smit & Piersma 1989; Delany et al. 1999; Stroud et al. 2004). The maintenance of the current monitoring schemes (mid-winter counts) is also vital to detect changes in the use of Portuguese wetlands by aquatic birds.

The total area of tidal flats available for foraging varies by several-fold between spring and neap tides (Fig 1.3). Many lower estuarine flats that are intensively used during the spring low-tides (Granadeiro et al. 2007) remain submersed during the neap tides. This may represent almost half of the total low-tide time available for waders to gather food during the winter. The response of birds to these dramatic changes in the availability of their main feeding areas was never been addressed before, despite it obviously implications on the overall use of the estuaries by waders.

The results presented in chapter 2 clearly showed the importance of the location of roosts in the use of intertidal flats by dunlins. But are these findings applicable to other wader species? Evidences from other studies suggest that this is probably the case (Symonds et al. 1984; Warnock & Takekawa 1996; Drake et al. 2001; Rogers et al. 2006a), but the magnitude of such interactions has never been quantified in other species. The main causes of this tendency for feed close to the roost areas are still unknown, but are probably related to energy (and/or time) costs associated with the movements between feeding and roosting areas. If so, it can be hypothesized that species with higher flight costs (or more limited in their time budgets) should stay near to their roosts, and *vice-versa*.

Major conclusions

The results obtained in this thesis contributed to the knowledge of some of the major factors that affect the movements and distribution of waders in their intertidal feeding areas. The proximity to the main roosts sites and the exposure period of the tidal flats proved to be particular important to explain the use of these areas. These findings have obvious implications on the conservation of estuarine areas, highlighting the relevance of the maintenance of good-quality roosts, as well of upper sediment

flats. In the particular case of Tagus estuary, these two habitats are precisely the ones more vulnerable to the likely increase of human pressure, derived from the recent and predicted development in its close vicinity. The levels of disturbance are also expected to consequently increase, what may also strongly affect the use of tidal flats by the waders.

This thesis also presented a set of new methodological approaches to the study of wintering waders. Most of them were based in GIS, which proved to be, once again, of great use as a tool in ecological studies. The simplicity of some of these modelling approaches, as those presented in chapters 2 and 6, allows their application in many other estuarine systems worldwide.

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