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THE USE OF INTERTIDAL AREAS BY FORAGING WADERS: CONSTRAINTS ON THE EXPLOITATION OF FOOD RESOURCES

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This research was funded by Fundação para a Ciência e a Tecnologia (FCT) through a PhD grant (SFRH/BD/16991/2004) and the research projects POCTI/BSE/47569/2002 and PTDC/MAR/66319/2006.

“I find it both depressing and amusing that so many of our intellectual efforts, though masquerading attempts to understand nature, are really anodynes for justifying our hopes and calming our fears.”

(Stephen Jay Gould - An urchin in the storm)

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Resumo

Capítulo 1: Introdução geral

As aves limícolas são dos mais diversos e amplamente distribuídos grupos de aves. Muitos dos seus membros são migradores de grandes distâncias, nidificando nas regiões árcticas e sub-árcticas durante o curto período do verão boreal e viajando depois para zonas húmidas costeiras espalhadas por todo o globo, onde passam o restante período do seu ciclo anual. Durante o período não reprodutivo grande parte das aves limícolas utiliza as áreas estuarinas como locais preferenciais de alimentação. A disponibilidade cíclica de vastas áreas de sedimentos entre-marés oferece a estas aves a oportunidade de se alimentarem sobre invertebrados bentónicos, que geralmente ocorrem em grandes densidades nestes sistemas. A utilização das áreas entre-marés coloca às aves limícolas muitos desafios e dificuldades que serão examinados em detalhe ao longo desta tese. Será dada particular ênfase aos factores susceptíveis de limitar a exploração dos recursos alimentares pelas aves limícolas.

Capítulo 2: A invernada no Sul da Europa

Durante o inverno boreal as aves limícolas distribuem-se ao longo de uma vasta variação latitudinal, deste as regiões próximas ao círculo polar Árctico até aos limites sul de África, América do Sul e Australásia. O estuário do Tejo é uma das áreas de invernada mais importantes para estas aves no Corredor Migratório do Atlântico Leste, mas tal como muitas outras localizadas nas latitudes mais baixas deste corredor migratório, é relativamente pouco estudada. Nesta tese estão incluídos dois estudos abrangentes sobre a ecologia de invernada de aves limícolas no estuário do Tejo. No primeiro é examinada a dieta, selecção de presas, selecção de habitat e comportamento alimentar do pilrito-de-peito-preto (*Calidris alpina*). Esta espécie é a mais comum, e uma das menos estudadas, das aves limícolas que usam as zonas entre-marés do estuário do Tejo como local de alimentação. Verificou-se que na dieta dos pilritos-de-peito-preto estão incluídas algumas presas comuns às regiões norte europeias, mas outras, com particular importância energética, são exclusivas dos estuários sul europeus. Verificou-se também que as áreas entre-marés de sedimento vasoso constituem o habitat mais importante para alimentação desta espécie durante o inverno. O segundo estudo consiste numa análise macro-espacial do uso das áreas

entre-marés do estuário do Tejo por aves limícolas e outras aves aquáticas. Cerca de 73% da área entre-marés do estuário foi prospectada com o objectivo de determinar as densidades de aves em alimentação. Foi também recolhida informação sobre um conjunto de variáveis ambientais relevantes para a alimentação das aves. A análise destes resultados mostrou que o tempo de exposição dos sedimentos e a sua granulometria são os factores mais relevantes para a escolha dos locais de alimentação pelas aves estuarinas.

Capítulo 3: A exploração dos recursos alimentares

A modelação preditiva da distribuição das aves limícolas nas zonas entre-marés é ainda dos objectivos últimos na maioria dos estudos actuais sobre estas aves. Contudo, é também uma tarefa de enorme exigência, dadas as importantes lacunas no conhecimento sobre o modo como estas aves exploram os seus recursos alimentares. Nesta tese foram estudadas as relações entre as aves limícolas e as suas presas a uma escala espacial reduzida. Foi demonstrado que a existência de uma fina camada de água sobre os sedimentos influencia a disponibilidade à superfície dos invertebrados-presa dos pilritos-de-peito-preto. De facto, verificou-se que esta espécie captura diferentes presas nos microhabitats com e sem água superficial. Verificou-se também que a dificuldade de captura dos sifões do bivalve *Scrobicularia plana*, a sua presa com maior valor energético, força as aves inexperientes a alimentar-se no microhabitat onde existe maior disponibilidade de presas alternativas, com menor valor energético (o gastrópode *Hydrobia ulvae*). Com o objectivo de compreender as capacidades de percepção do pilrito-de-peito-preto, foi ainda realizada uma experiência onde se manipulou a abundância das presas enterradas em áreas experimentais de várias dimensões. Foi demonstrado que estas aves são muito pouco eficientes na detecção de agregados de presas com dimensão inferior a 1 m^2, mas melhoram as suas capacidades de detecção com o aumento do tamanho do agregado e também com o aumento da densidade de presas. Estes resultados mostram que mesmo em ambientes entre-marés com grande abundância de invertebrados, aspectos particulares na relação predador-presa podem restringir fortemente a quantidade de recursos alimentares disponíveis para as aves limícolas.

Capítulo 4: A alimentação nocturna

Uma das maiores lacunas no estudo da ecologia das aves limícolas diz respeito à sua alimentação nocturna. Estas aves gastam aproximadamente metade do seu tempo de alimentação durante a noite. No entanto muito poucos estudos foram conduzidos neste período devido às limitações técnicas para observar o seu comportamento alimentar em situações de reduzida luminosidade. Nesta tese é descrito um equipamento de visão nocturna que combina uma câmara de vídeo digital comum com iluminadores laser de infravermelhos de alta potência. Este equipamento demonstrou ser adequado para conduzir observações nocturnas a grande distância, sendo uma solução económica e eficiente para o estudo do comportamento dos animais durante a noite. Com este equipamento foi possível quantificar os parâmetros de alimentação das aves limícolas a distâncias desde cerca de 60 até mais de 200 metros. A sua utilização permitiu estudar pela primeira vez os efeitos da poluição luminosa na alimentação nocturna das aves limícolas. Foi demonstrado que em zonas com iluminação artificial as espécies com estratégias de predação visual aumentam as suas taxas de alimentação e espécies que alternam entre estratégias visuais e tácteis exibem preferencialmente estratégias visuais de alimentação. Mesmo os alfaiates (*Recurvirostra avosetta*), considerados predadores exclusivamente tácteis, aumentam a frequência de tentativas visuais de captura de presas à superfície do sedimento em locais iluminados. Para a maioria das espécies estudadas, estas mudanças das técnicas de alimentação expressaram-se numa maior frequência de captura de presas, o que indica que a iluminação artificial melhora a eficiência alimentar das aves limícolas durante a noite.

Capítulo 5: Discussão geral

Muitas populações de aves limícolas encontram-se presentemente em declínio à escala global. A grande pressão humana sobre as suas áreas de alimentação nas zonas entre-marés é apontada como uma das causas mais importantes para esse declínio. Nesta tese foram identificadas as principais áreas de alimentação de aves limícolas e outras espécies de aves aquáticas no estuário do Tejo. Foi também estudada com grande detalhe a utilização das áreas entre-marés do estuário do Tejo pelo pilrito-de-peito-preto, uma das espécies em acentuado declínio no Corredor Migratório do Atlântico Leste. Estes resultados podem ser utilizados para aumentar os níveis de protecção das áreas importantes para aves limícolas no estuário do Tejo e

para o delineamento e implementação de medidas específicas de conservação nessas áreas. Por outro lado, vários dos factores susceptíveis de limitar ou beneficiar a exploração dos recursos alimentares pelas aves limícolas foram aqui estudados em grande detalhe. Esta informação tem grande potencial para o desenvolvimento de medidas específicas de gestão e conservação das populações de aves limícolas num futuro próximo.

Palavras-chave: alimentação nocturna; áreas entre-marés; aves limícolas; comportamento alimentar; constrangimentos alimentares; disponibilidade de presas; estuários; estuário do Tejo.

Abstract

1. The life cycle of long-distance migratory waders is marked by an extended non-breeding period during which they congregate in highly productive intertidal areas across the globe. Waders face many challenges and difficulties while foraging in intertidal areas, and some of these will be examined in detail along this thesis. Particular emphasis will be given to the factors that constraint the exploitation of food resources by waders.

2. During the boreal winter waders disperse along a large latitudinal range. The Tagus estuary is one of the most important wetlands for waders in the East Atlantic Flyway, but like many areas located at lower latitudes in this flyway, is sparsely studied. This thesis includes two baseline studies on the wintering ecology of waders in the Tagus estuary. The first specifically addressed the foraging ecology of the dunlin (*Calidris alpina*), the most abundant and one of the less studied waders in the intertidal areas of the Tagus estuary. It was found that, in Tagus estuary, dunlins forage upon some invertebrate species that are also consumed in northern latitudes. However, some other invertebrates, with particular energetic importance for dunlins, seem to be exclusive prey from southern European latitudes. The second study examines the macro-scale use of intertidal areas by waders and other shorebirds at the Tagus estuary. It was found that the exposure period of intertidal sediments and their granulometry constitute the main factors driving the large scale selection of foraging areas by those bird species.

3. Predicting the distribution of waders in intertidal areas is still a major goal in current studies on waders, but this is a particularly difficult task due to the limited knowledge of how waders exploit their food resources. In this thesis, the small spatial scale relationships between waders and their invertebrate prey were examined. It was found that predator avoidance behaviour of some locally abundant prey can compromise their use as food by the less experienced waders. Also, by manipulating the distribution of buried prey, it was found that foraging dunlins have low efficiency to find prey aggregated in small patches. Both studies demonstrated that, even in an environment with high abundance of prey, particular aspects of the predator-prey relationships may restrict the amount of food resources available for waders.

4. One of the major gaps in the study of the ecology of waders concerns nocturnal foraging. Nocturnal foraging represents about half of the total foraging period in most

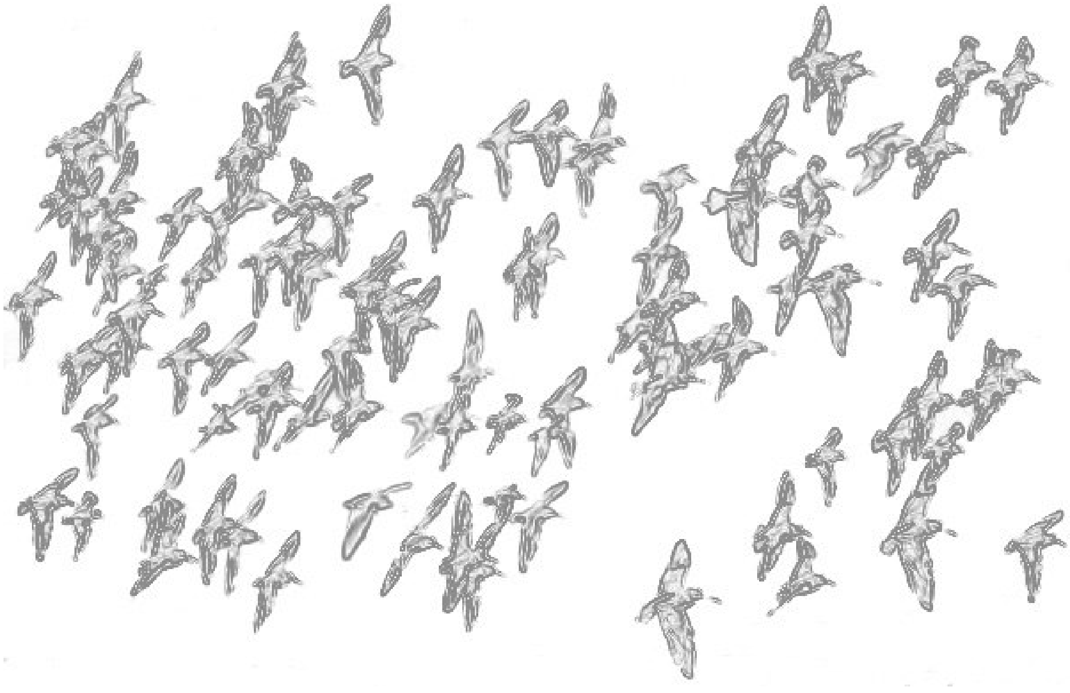
wader species and yet very few studies were conducted during the night, mostly due to the technical limitations to observe waders foraging in the dark. In this thesis is presented an efficient long-range night vision system, combining a regular camcorder and high power infrared laser illuminators. Using this equipment it was possible to quantify several parameters of wader nocturnal foraging activity at distances from ca. 60 to more than 200 meters. This equipment also allowed studying for the first time the effect of light pollution on the nocturnal foraging of waders. It was found that artificial light caused a change in the behaviour of all studied wader species, and also that most of them improved their foraging efficiency.

5. Many wader populations are currently declining at a global scale and the high human pressure that currently affects their intertidal foraging areas has been pointed out as one of the major causes for this decrease. Some of the results included in this thesis can have immediate utility for the management of waders using the intertidal areas, such as the identification of the most important foraging areas for waders in the Tagus estuary. The findings in this thesis also enlarged our knowledge on the factors that constraint or benefit the exploitation of food resources by waders in intertidal areas, and have high potential to be used in the development of specific measures for managing wader populations in the near future.

Key-words: estuaries; foraging behaviour; foraging constraints; intertidal areas; prey availability; nocturnal foraging; Tagus estuary; waders.

CHAPTER 1

GENERAL INTRODUCTION



Waders: travelling between hemispheres

Waders are one of the most diverse and widespread group of birds. Their members are included in the Order Charadriformes, which is subdivided into 12 Families and comprise more than 200 species (Hayman et al. 1986). Because most of them are associated with coastal wetlands, they are commonly referred as “shorebirds”, though other aquatic birds are also included in this designation.

Waders are best known for their spectacular migrations. Every spring, massive numbers travel from wetlands spread across the globe to breed in the Arctic Circle during the boreal summer and return then to their wintering grounds. Many species traverse more than 10,000 km in this annual circuit (van de Kam et al. 2004b). Some undertake the longest non-stop migratory flights known in birds, frequently surpassing 5000 km (Pennycuick and Battley 2003, Gill et al. 2005). The preparation for such long flights involves remarkable physiological adaptations. Before takeoff birds store large amounts of fat, frequently over 30% of their body weight (Piersma and van Brederode 1990). Their muscles and heart increase in size and their liver, stomach and intestine, less important organs during flight, reduce (Piersma and Gill 1998).

During such migrations waders use a network of stopovers to rest and restore the energy spent in their long flights. Some important stopovers are strategically used in periods of high productivity. For instance, during the spring migration half a million waders stop at the Delaware Bay in the USA to feed on horseshoe crab (*Limulus polyphemus*) eggs during their short spawning period (Clark et al. 1993). However, many of the stopovers are small wetlands with low numbers of waders along the year but receiving considerable numbers in very short periods during migration (Skagen et al. 2008).

At the breeding grounds, waders can take advantage of long daylight period, great abundance of food and fewer pathogens and parasites (Mendes et al. 2005, Buehler and Piersma 2008). However, in the breeding season waders face one of the most important challenges in their annual cycle, producing offspring during the very short arctic summer. After arriving to the breeding grounds, typically in May, waders have to establish a territory, perform courtship, mate, lay and incubate eggs, and take care of the young. All is completed in less than two months, when the food supplies start to decline, and adult birds begin their southern migration, followed by the juveniles a few weeks later (Cramp and Simmons 1983).

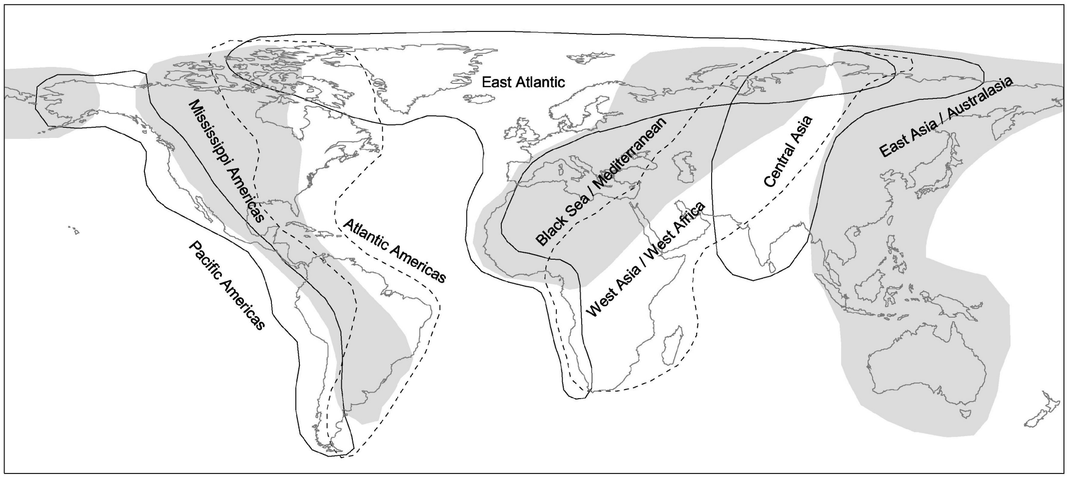


Figure 1.1. The eight broad flyways of waders (adapted from Boere and Stroud 2006).

Together, stopovers, wintering and breeding sites form a pathway called flyway. There are eight recognized major flyways worldwide (Figure 1.1, Boere and Stroud 2006). The East Atlantic Flyway is one of the largest and the best known concerning the number of birds involved and sites used. Approximately 15 million waders use this migratory route linking the breeding grounds located in Canada, Greenland, Iceland, Siberia and northern Europe to wintering grounds in Western Europe and Africa (Stroud et al. 2004).

The investigation included in this thesis was conducted in the Tagus estuary, one of the most important wetlands for waders in the East Atlantic Flyway during the non-breeding season. A detailed description of this period of the annual cycle of waders and a characterization of the Tagus estuary will be provided in the following sections of this introduction.

The non-breeding season: waiting for the low tide

During the non-breeding season most waders congregate to forage in tidal wetlands of temperate and tropical regions. Here their life is ruled by the rhythms of the tides. Normally twice a day, the receding tides expose large intertidal areas, allowing birds to feed extensively on the wealth of invertebrates hidden in the sediments. In order to avoid interspecific competition while exploiting the intertidal food resources, waders became specialized to forage in a large diversity of prey and foraging conditions. For instance, longer legs are adequate to forage in flooded habitats, such as tidal pools or at the tidal edge, larger feet allows to forage in softer sediments, and larger eyes facilitates foraging by sight in low light conditions (van de Kam et al. 2004c). Perhaps the most remarkable trait of their foraging adaptations is the extraordinary diversity in the morphology of their bills (Figure 1.2). From the curved bill of the avocet, specialized in sweeping the sediments and retaining small invertebrates, to the dagger-like bill of the oystercatcher, used to open thick bivalve shells, waders bills exhibit all kinds of specializations (Barbosa and Moreno 1999, van de Kam et al. 2004c). In a closer look, wader bills are provided with a high density of mechanoreceptors allowing them to perceive invertebrate vibrations under the sediments (Gerritsen and Meiboom 1986, Nebel et al. 2005).

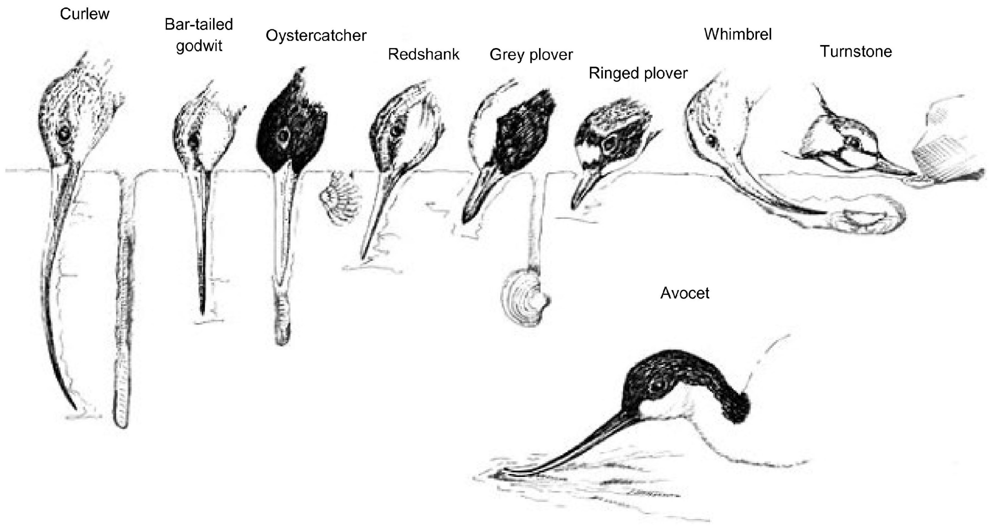


Figure 1.2. Bill shapes of common waders in European region (available at http://www.studentmag.acsedu.com/Articles/Seabirds-and-Waterbirds.aspx)

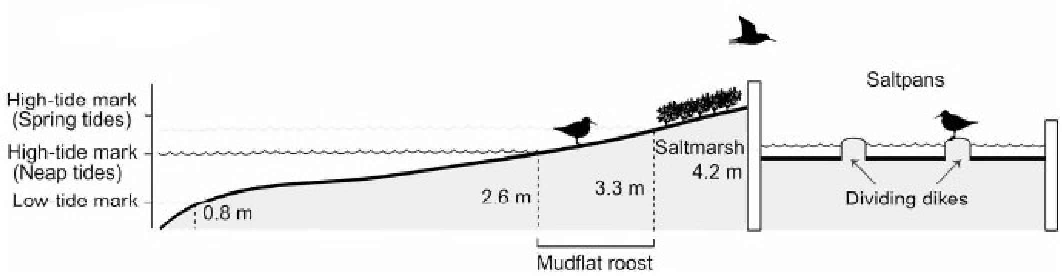


Figure 1.3. Representation of high tide roosts in relation to tidal height (from Rosa et al. 2006).

Because of the high dynamics of tides, waders are forced to be in constant movement between the upper flats, exposed for long periods, and the lower flats, exposed only at low tide. This causes a strong effect on their densities in intertidal flats; while they are very concentrated during the first stages of the tide, at low water level they disperse through the vast intertidal landscape (Burger et al. 1977, Granadeiro et al. 2006). Besides the concentration effect, some waders tend to follow the tide edge, presumably to take profit from a higher activity of invertebrates at the surface of sediments (Granadeiro et al. 2006, Rosa et al. 2007).

At the high tide waders are pushed away from the intertidal flats to the upper shore, where they roost in high concentrations at particular sites, such as saltpans or close to the saltmarsh (Figure 1.3). However, for those who were less efficient in foraging during the low tide or in periods of high energetic demands such as migration, the high tide period cannot be wasted resting. Instead, these birds forage in saltpans, rice fields or grasslands to satisfy their energetic needs (Velasquez and Hockey 1992, Smart and Gill 2003). The high concentrations of birds in the high tide roosts are also very attractive for predators such as raptors and carnivore mammals (Whitfield 1985, Rosa et al. 2006). Besides the risk of predation, the disturbance effect of predators upon roosting waders can involve considerable energetic costs due to flight alarms and vigilance (Rosa et al. 2006).

Most studies on wader ecology were conducted in non-breeding grounds. There are two main reasons for this: (1) the non-breeding period corresponds to approximately 10 months of the annual cycle of waders; (2) during this period waders are present in most wetlands of the temperate regions, where most human population is established. However, non-breeding grounds are also under much greater human pressure than the arctic and sub-arctic breeding regions. In fact, human population is often concentrated along the coastline, and large cities were built close to estuaries and coastal wetlands traditionally used by waders. Therefore, preserving wader populations greatly depends on increased efforts in research and management in their non-breeding areas.

The Tagus estuary: importance for waders and general characterization

The Tagus estuary covers about 320 km^2 being the largest estuary in Iberia and one of the largest in Western Europe. It is also one of the most important wetlands for waders in the East Atlantic Flyway (Stroud et al. 2004). The northern part of the estuary (ca. 142 km^2) was classified as Natural Reserve in 1976 by the Portuguese Government and a larger area of 450 km^2, including intertidal areas and surrounding land, was designated as a Special Protection Area for Birds under European Union legislation in 1988 (Figure 1.4b). During the winter the Tagus estuary regularly holds ca. 60,000 waders (estimated during the 90s), including important percentages (over 1%) of the geographical populations of avocet (*Recurvirostra avosetta*), grey plover (*Pluvialis squatarola*), black-tailed godwit (*Limosa limosa*) and dunlin (*Calidris alpina*) (ICNB winter counts compiled in Dias 2008, Stroud et al. 2004). Particularly, the wintering numbers of avocets frequently exceed 10% of the western European population (Stroud et al. 2004, Dias 2008). The Tagus estuary is also important as stopover for many waders migrating from/to wintering areas in Western Africa, although the numbers involved during this stage have still not been evaluated for the large majority of wader species (Stroud et al. 2004). It has been recently estimated that 15 to 25% of the western European population of black-tailed godwit regularly uses the Tagus estuary during their northern migration (Lourenço and Piersma 2008).

The Tagus estuary is characterized by extensive mudflats that cover most of the 97 km^2 of intertidal areas, and only some areas in the inner estuary close to the main channels present coarser sediments. There are also large banks of shells of dead oysters, a species that practically went extinct in the 70s due to contamination with TBTs released by heavy industries installed in the margins of the estuary (Figure 1.4a, De Bettencourt et al. 1999). Saltmarsh covers large areas along the northern margin of the estuary, but also small areas at the more urbanized southern part of the estuary (Figure 1.4a). At the upper shore there is a considerable area of saltpans, remnants of an intensive activity of salt exploitation that declined after the 70s (Figure 1.4a, Rufino and Neves 1992). Most saltpans are now abandoned but some are being converted to aquaculture. The margins of the estuary are strongly humanized along the right margin, particularly near Lisbon, but also at the southern part of the left margin (Figure 1.4b).

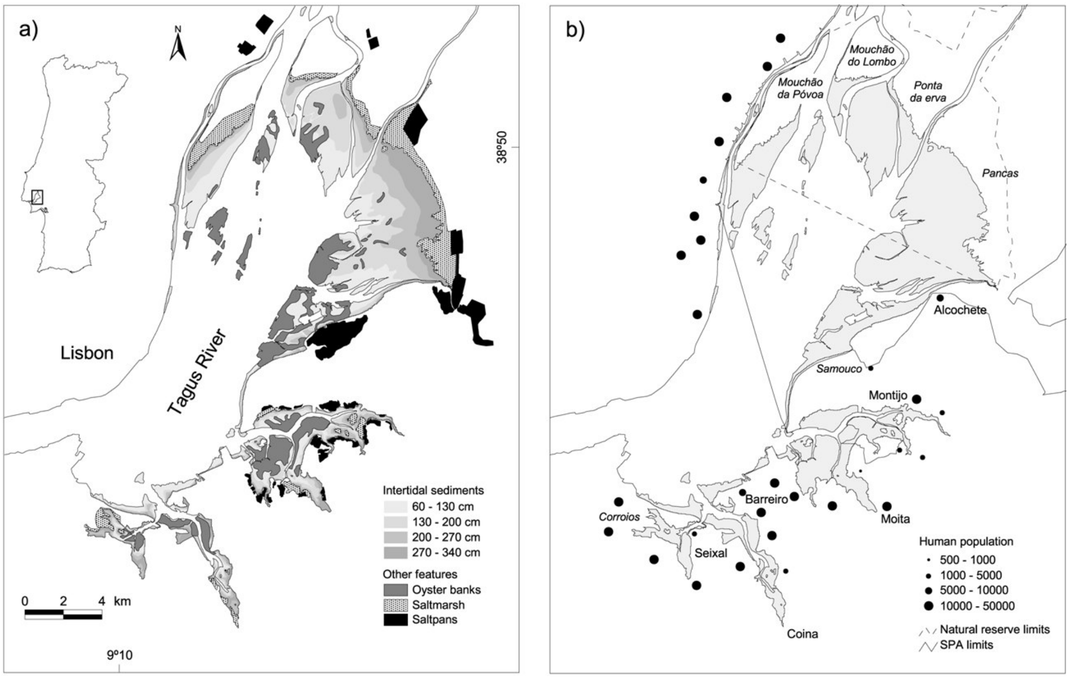


Figure 1.4. (a) Main features of Tagus estuary intertidal areas and near shore. Intertidal sediments were classified according to the bathymetry. (b) Human population in the close proximity of intertidal areas, and SPA and Natural Reserve limits.

The major human impacts occur in these humanized areas and include heavy industrial pollution, domestic pollution, land reclamation and artificialization of the estuarine margins (Rosa et al. 2003).

Several studies were carried out on the different components of the Tagus estuarine community, mostly since the 80s (see Brotas 1995, Cabral 1998, Caçador et al. 2007, and Sousa-Dias and Melo 2008 for general information on microalgae, fish, saltmarsh and macroalgae, respectively). Benthic invertebrate community was first described by Calvário (1984) for the different types of estuarine sediments. More recent studies conducted by Rodrigues et al. (2006) showed that small annelids dominate the benthic community in abundance and diversity while the bivalve *Scrobicularia plana* strongly dominates the biomass. Other abundant species, known as important prey for waders, included the polychaete *Hediste diversicolor*, the gastropod *Hydrobia ulvae*, and the isopod *Cyathura carinata*. The bird community was extensively studied by Moreira (1995b) who provided the first studies on the diet and foraging behaviour of most wader species and evaluated the role of the bird community on the estuarine food web.

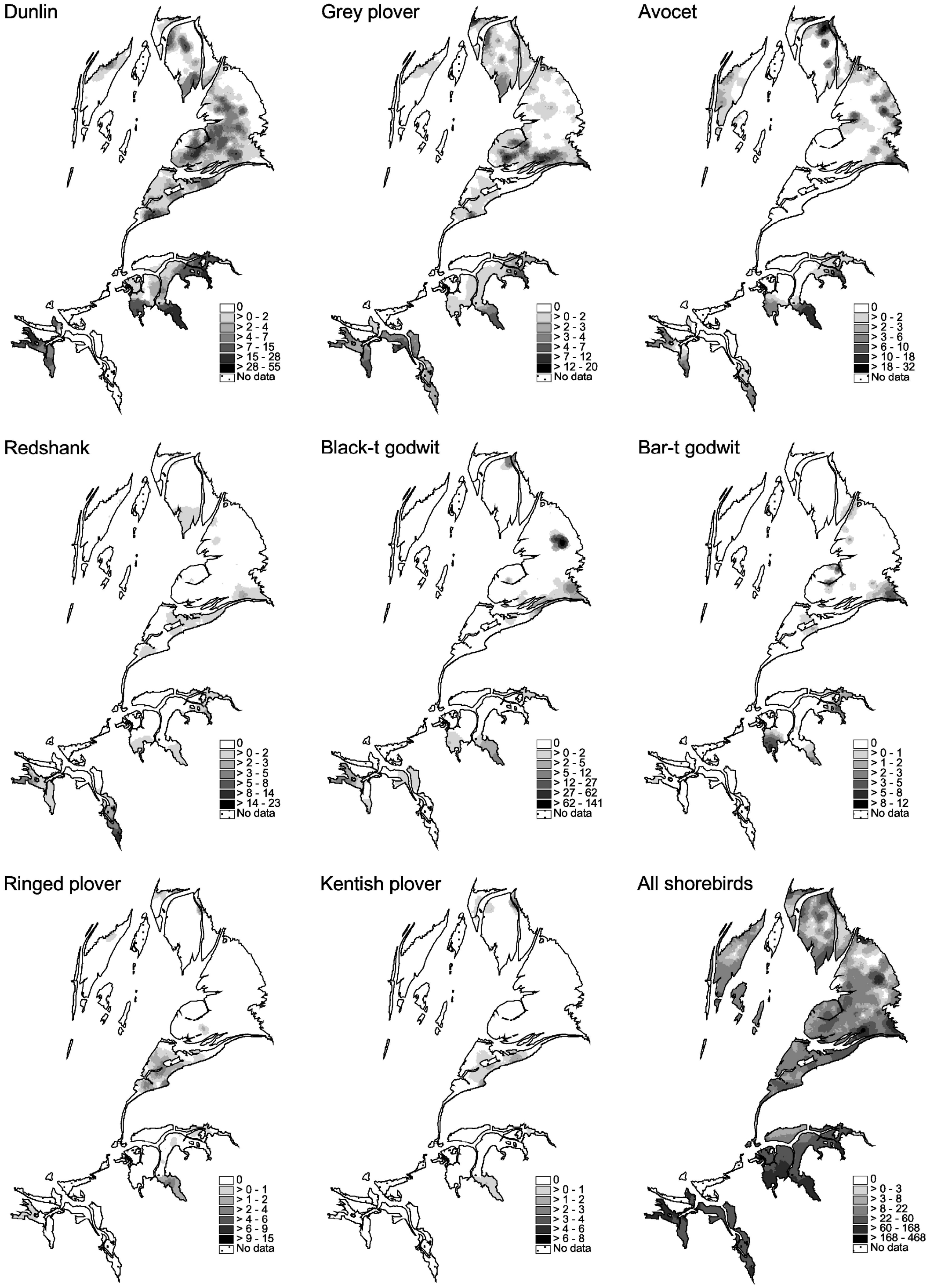


Figure 1.5. Low-tide distribution of shorebirds wintering in the Tagus estuary. Colour gradients represent the number of birds by hectare; "all shorebirds" include all bird species using the intertidal flats. See the last paper of chapter 2 for details on the field survey.

More recently, much research was done on diverse aspects of wader ecology in the Tagus estuary, including studies on foraging behaviour (e.g. Dias et al. 2009), night foraging (e.g. Lourenço et al. 2008), prey activity (e.g. Rosa et al. 2007) and migration (e.g. Lourenço and Piersma 2008). Concerning the distribution of shorebirds among their foraging intertidal areas, the first large scale survey was conducted by Teixeira (1985), and in 2002 and 2003 we conducted two other surveys with a much higher resolution. The distributions of the most important species of waders are presented in Figure 1.5 and a more detailed analysis is included in the last paper of chapter 2.

Outline of the thesis

This thesis includes six papers, published or submitted for publication in peer-reviewed scientific journals of ecology and ornithology, which made original contributions in three subjects of current wader ecological research: the winter ecology of waders at southern Europe; the exploitation of food resources by waders in intertidal areas; and the nocturnal foraging of waders. Each of these subjects is here presented in a separated chapter, provided with an overview where I revisited the general aspects of the subject and the particular aspects related to the investigation conducted in the papers. Finally, a general discussion is presented in the last chapter, in which the most important results that came out from the papers are discussed and the major conclusions are delineated.

The papers had fundamental contributions from several researchers that made part of the research team on wader studies of the Centro de Biologia Ambiental of Faculdade de Ciências da Universidade de Lisboa leaded by Dr. José Pedro Granadeiro and Prof. Jorge Palmeirim. However, I declare that in all papers included in this thesis I was deeply involved and/or had a leading role in its conception, execution, analysis and writing.

The papers included in this thesis, including the authors and the scientific journals where they were published, are listed below.

Santos, C. D., Granadeiro, J. P. and Palmeirim, J. M. 2005. Feeding ecology of dunlin *Calidris alpina* in a southern European estuary. Ardeola 52: 235-252.

Granadeiro, J. P., Santos, C. D., Dias, M. P. and Palmeirim, J. M. 2007. Environmental factors drive habitat partitioning in birds feeding in intertidal flats: implications for conservation. Hydrobiologia 587: 291-302.

Santos, C. D., Palmeirim, J. M. and Granadeiro, J. P. Choosing the best foraging microhabitats: individual skills constrain the choices of dunlins. Submitted for publication.

Santos, C. D., Saraiva, S., Palmeirim, J. M. and Granadeiro, J. P. 2009. How do waders perceive buried prey with patchy distributions? The role of prey density and size of patch. Journal of Experimental Marine Biology and Ecology 372: 43-48.

Santos, C. D., Lourenço, P. M., Miranda, A. C., Granadeiro, J. P. and Palmeirim, J. M. 2008. Birds after dark: an efficient and inexpensive system for making long-range observations at night. Journal of Field Ornithology 79: 329-335.

Santos, C. D., Miranda, A. C., Granadeiro, J. P., Lourenço, P. M., Saraiva, S. and Palmeirim, J. M. Effects of artificial illumination on the nocturnal foraging of waders. Submitted for publication.

CHAPTER 2

WINTERING AT SOUTHERN EUROPE

Overview

During the boreal winter waders spread along a large latitudinal range. In the East Atlantic Flyway, wintering grounds range from the Danish Wadden Sea to estuaries and coastal lagoons at the extreme of South Africa (Figure 2.1, Hockey et al. 1992). Along this range of latitude, waders are subjected to distinct conditions of temperature, weather, day length and food availability (van de Kam et al. 2004b). Although the advantages of being close to the breeding grounds are obvious, wintering further north involves much higher maintenance energetic costs. In fact, at the northern extreme waders can almost duplicate their daily energy expenditure when compared with those wintering at lower latitudes (Castro et al. 1992, Kersten et al. 1998). Weather conditions at the northern latitudes during the winter can be extremely severe. Temperatures can get cold enough to freeze large areas of intertidal flats, thus in addition to the high thermostatic costs waders can also be prevented from foraging efficiently during long periods (Camphuysen et al. 1996, van de Kam et al. 2004b). This has been shown to cause high mortality among wintering waders (Camphuysen et al. 1996, Mitchell et al. 2000) and also to force birds to move further south during such periods (van de Kam et al. 2004b). In order to survive in such harsh and unpredictable conditions, waders wintering in northern areas have to store far more fat reserves than their southern counterparts (Figure 2.2, Dugan et al. 1981, van de Kam et al. 2004b).

Wintering further south also involves considerable costs. Long-range migrations can be very expensive energetically (Drent and Piersma 1990) and can cause mortality or contribute to low breeding success (Morrison et al. 2007). In addition, wintering areas at low latitudes have very high densities of birds (Hockey et al. 1992), but relatively low abundance of food (Wolff et al. 1993), which might result in a strong competition for food resources. In fact, birds wintering in West Africa exhibit particularly low fattening rates when compared with those at higher latitudes (Zwarts et al. 1990b). This may also explain why young birds wintering in low latitudes delay their first return to the breeding grounds (Hockey et al. 1998).

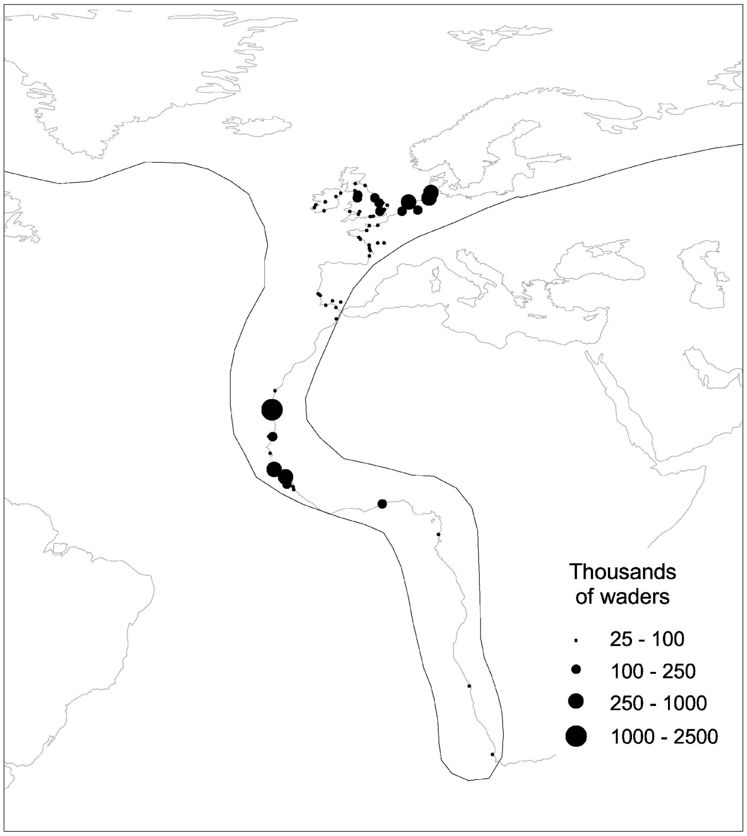


Figure 2.1. Important wetlands for wintering waders in the East Atlantic Flyway. Data from midwinter counts during the 90s (available in Stroud et al. 2004).

The reasons why waders migrate further south are still subject of discussion. Some of the reasons are probably related to historical traits (Sutherland 1998). For instance, the Banc d'Arguin, the most important wintering area in the East Atlantic Flyway, has evolved from a large delta complex (Hanebuth and Lantzsch 2008), probably with much higher carrying capacity than today. However, the lack of baseline information for most of the south wintering areas also limits our comprehension of migratory behaviour. In fact, there is a huge disproportion between the number of studies on the foraging ecology of waders conducted in the north European wintering areas and those conducted in southern Europe and African wintering areas.

This chapter includes two baseline studies on the wintering ecology of waders at the Tagus estuary, one of the most important wintering areas for waders in the southern European region. The first paper addresses general aspects of the foraging ecology of dunlin (*Calidris alpina*) in the Tagus estuary. The dunlin is the most abundant wader species in the intertidal areas of this estuary, with a regular wintering population of ca. 14,000 individuals, and it was also one of the less studied wader species. This paper describes diet, prey selection, foraging behaviour and habitat selection of this species, and also presents a detailed revision of its wintering foraging ecology along its wintering range. The second paper includes a large scale survey of shorebird densities and environmental variables covering ca. 73% of the intertidal area of the Tagus estuary. The data was used to describe the spatial distribution of the most abundant species and to investigate the most important environmental factors influencing their distribution.

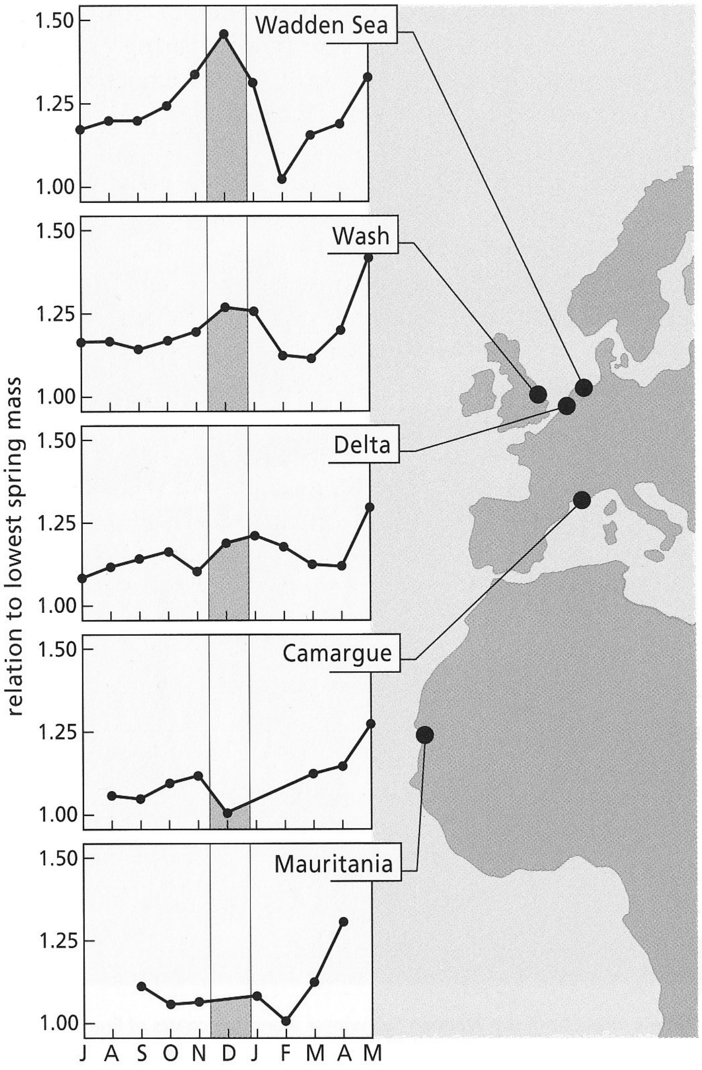


Figure 2.2. The mass cycles of dunlins on different wintering grounds (from van de Kam et al. 2004b).

Feeding ecology of dunlin *Calidris alpina* in a southern European estuary

Abstract

The feeding ecology of dunlin (*Calidris alpina*) wintering in southern European wetlands is poorly known. The aim of this paper is to describe the diet, prey selection, foraging habitat selection, and feeding behaviour of wintering dunlins, and interpret this information in the light of the current knowledge on the feeding ecology of this species. The study was carried out in the sediment flats of the Tagus estuary, Portugal, which is the largest estuary in Iberia, and harbours large numbers of wintering waders. Diet of dunlin was investigated using dropping analysis. Foraging habitat selection was studied using bird counts and behavioural observations, in sectors located on different types of sediment. The abundance of invertebrates in the sediment was sampled to evaluate prey availability and to interpret patterns of habitat selection by the birds. Scrobicularid bivalves and the gastropod *Hydrobia ulvae* were the most consumed prey items, followed by the isopod *Cyathura carinata* and insects. Prey species with higher biomass, such as *Hediste diversicolor* and Scrobicularid bivalves were preferred. The smallest and largest sizes of some important prey species were avoided. Dunlins showed a clear preference to forage in muddy, rather than sandy, sediments. Overall pecking rates were similar in all types of sediment, but deep probes were more frequent in softer mud. Some of the staple prey of dunlin in Tagus estuary are also abundantly consumed in northern latitudes. However, other prey species important in northern Europe are here replaced by similar and locally common species. In the Tagus, estuary dunlins feed upon a broad spectrum of invertebrate species, but show clear patterns of selection of prey species and sizes. Dunlins prefer to forage on muddy substrates, probably because their main prey are more abundant and accessible here than in harder, sandier, substrates.

Introduction

The dunlin (*Calidris alpina*) is the most abundant wader within the East Atlantic Flyway, with an overall population of more than 2 million individuals (Smit and Piersma 1989).

During the non-breeding season this population is distributed along the coastline from West Africa to northwest Europe (Cramp and Simmons 1983). Hockey et al. (1992) demonstrated that density of waders during the non-breeding season increases from northern to southern latitudes. The reason for this phenomenon has been discussed but is still poorly understood (e.g. Zwarts et al. 1990c, Hockey et al. 1992). Since waders are often limited by their food resources (e.g. Desholm 2000), it might be expected that invertebrates would show similar gradients. However, latitudinal gradients on invertebrate assemblages are much less obvious. Existing evidence indicates enormous variation in the density, biomass, availability and annual production of invertebrates at different latitudes (e.g. Warwick and Ruswahyuni 1987, Kalejta and Hockey 1991, Piersma et al. 1993). Nevertheless, the existent knowledge is unbalanced along the latitudinal gradient since most of tropical and sub-tropical areas are almost unknown. Also, the majority of the invertebrate studies are not focused on evaluating food supply for the birds, providing only rough measurements of invertebrate availability, such as overall biomass or density.

The feeding ecology of wader species is also not well studied along their non-breeding distributions. In the case of the dunlin most studies on the feeding ecology have been conducted on the European north Atlantic coast (e.g. Worrall 1984, Kelsey and Hassall 1989, le V. dit Durell and Kelly 1990, Mouritsen and Jensen 1992, Nehls and Tiedemann 1993, Mouritsen 1994, Dierschke et al. 1999). Conversely, there are only a few studies about this species in the southern European and African coasts. In fact, we only found three published studies on the feeding ecology of dunlin in this region (Barbosa 1996, Lopes et al. 1998, Luís et al. 2002). The lack of information on feeding ecology of waders and on their food resources in the southern region of their wintering distributions is still limiting our comprehension of the amazing migration of waders.

In this study we examined the feeding ecology of dunlin in the Tagus estuary (Portugal) during the winter. The Tagus estuary is one of the largest European wetlands and harbours a regular winter population over 14,000 dunlins. We analysed the diet, prey selection, habitat selection and feeding behaviour and interpreted this information in light of the current knowledge on the feeding ecology of this species.

Methods

Study area

Field-work was carried out in the southern margin of the Tagus estuary, Portugal (38º45'N, 8º59'W) in the winter of 2000/2001. The study site was a 2.3 km long stretch of tidal flats, gradually changing from sand at the western end, to mud at the east. During the spring tides (amplitude > 2.7 m), these tidal flats remain exposed for approximately three hours. Such areas are particularly important for foraging dunlins, supporting some of the highest densities in the whole estuary (Moreira 1995b, Rosa et al. 2003).

Three 1.5 ha (100x150m) plots were marked using stakes in each of the sediment types available: sand, mixed sediments and mud. The classification of sediments was based on the analysis of six sediment samples collected in each of the nine plots (laboratory procedures followed Buchanan 1984). Mean (± SD) percentage of weight of silt (particles < 0.063 mm) was 7.1 ± 4.8 (n = 18), 24.4 ± 8.2 (n = 18), and 79.1 ± 24.7 (n = 18) for sand, mixed sediments and mud, respectively.

Table 2.1. Equations used to estimate the size and the ash-free dry weight of invertebrate species. APL: antero-posterior length (mm); TL: total length (mm); TW: total width (mm); CL: cephalic length (mm); CTL: cardinal tooth length (mm); ML: mandible length (mm); AFDW: ash-free dry weight (mg). [1] Equation used for both *Abra* sp. and small *S. plana*; [2] equation used for large *S. plana*. [a] present study; [b] Masero et al. (1999); [c] Zwarts and Blomert (1992); [d] Zwarts and Wanink (1993); [e] Marques et al.(1994).

Species	Equation	Explained variance	Sample size	Range	Source
Scrobicularia plana/Abra sp.	$APL=22.94CTL+0.40$	0.98	60	1.9-19.3	[a]
Hydrobia ulvae	$TL=2.35TW-0.34$	0.96	134	0.5-2.6	[a]
Hediste diversicolor	$TL=40.173ML-3.4225$	0.98	41	25-95	[b]
Scrobicularia plana/Abra sp.[1]	$AFDW=0.013APL^{2.23}$	0.97	17	0.5-13	[a]
Scrobicularia plana[2]	$AFDW=0.008APL^{2.87}$	>0.995	158	12-45	[c]
Cerastoderma edule	$AFDW=0.012APL^{2.97}$	>0.995	1351	1-42	[c]
Hydrobia ulvae	$AFDW=0.0154TL^{2.61}$	0.92	28	1.8-5.3	[a]
Corophium volutator	$\ln AFDW=2.8\ln TL-5.244$	0.994	526	2-10	[d]
Cyathura carinata	$AFDW=19.0549CL^{2.71815}$	0.964	800	1-12	[e]
Hediste diversicolor	$\ln AFDW=2.208\ln(TL/10)-0.898$	0.996	3586	10-130	[d]
Nephtys hombergii	$\ln AFDW=2.017\ln(TL/10)-0.183$	0.962	263	20-120	[d]

Invertebrate sampling

The composition and abundance of the invertebrate fauna was determined from three to six sediment cores (86.6 cm^2, 30 cm deep) taken randomly in each plot in January 2001. The upper 5 cm of the cores was separated and sieved through a 0.5 mm mesh, and the remaining fraction was sieved through a 1 mm mesh. All invertebrates were separated from the sediment and stored in 70% alcohol.

Specimens in good condition were measured using a calliper or a stereomicroscope with a reticular eyepiece. Small worm species, less than 10 mm long, were not measured. Regression analysis was used to relate size and ash-free dry weight (AFDW). These relationships were constructed for *Hydrobia ulvae* and small scrobicularids (*Scrobicularia plana* and *Abra* sp. were pooled) using individuals collected in the study plots. For the remaining species, we used relationships available in the literature (see Table 2.1). To measure AFDW for small scrobicularids and *H. ulvae*, the specimens were grouped into size classes, dried to constant weight (48 h at 60ºC) and then incinerated in a muffle furnace (2 h at 500ºC). The samples were weighed after drying and again after incineration, and the AFDW was calculated as the difference between dry weight and ash weight. The shells of the bivalves were removed before drying. *H. ulvae* was incinerated with shell, but we subtracted 12.5% from the AFDW, which were assumed to approximately represent the organic fraction of the shell (Dekker 1979). The average AFDW was also determined for some abundant small worm species, namely for *Alkmaria ramniji*, *Tharyx* sp., *Streblospio shrubsolli*, Oligoqueta and Nematoda. A considerable number of individuals (over 40) of each species were grouped in 1 to 3 samples and processed as described above, to determine the individual AFDW.

The AFDW per m^2 was calculated by multiplying the mean density of each species by its mean AFDW, obtained directly (for small worms) or estimated from the size (for all other species).

Dropping analysis

One hundred droppings (separated in individual vials) were collected monthly between January and March 2001 from the eastern side of the study area. The collection was carried out during the rising tide, when the birds were concentrated close to the coast.

Bird flocks were observed for at least 30 min prior to the collection of droppings, to reduce the possibility of collecting droppings with remains coming from outside of the study area. Flocks were then followed at a short distance, and only fresh droppings were collected. The shape of the droppings and the footprints around them helped us to separate between the droppings produced by dunlins and by other species. Only 2% of the birds present in the area were small waders that produce droppings that can be confused with those of dunlins.

Diet analysis was based on the frequency of occurrence of prey in droppings. Although this procedure may result in an underestimation of prey types that leave few identifiable remains in the faeces, it is the most widely used technique for dietary analysis in waders. In any case, most of the invertebrates available in the study area are known to leave detectable remains in the droppings (see le V. dit Durell and Kelly 1990).

Droppings were examined with a stereomicroscope, and prey species were identified using all possible diagnostic remains such as shell fragments, mandibles, exoskeletons, and acicules. A sub-sample of each dropping was examined under a microscope (at 400x magnification) to search for polychaete setae, which were subsequently identified using a reference collection and published literature (e.g. Fauvel 1977, Ramberg and Schram 1983, Chambers and Garwood 1992).

The setae and acicules of annelids and hairs of insects found in microscopic analysis were used to record the presence of the item in the diet, but were not used in calculations of the frequency of occurrence. As these structures are particularly numerous, it is likely that remains of one prey will be released in the faeces for a long period, resulting in an overestimation of its occurrence.

Invertebrate size and AFDW were estimated from the size of some remains found in the droppings (cardinal tooth of scrobicularids, shells of *H. ulvae* and mandibles of *Hediste diversicolor*) by using the relationships shown in Table 2.1. The sizes of ingested *H. ulvae* were measured directly, in the case of intact shells, or estimated from the width of partially broken shells.

Due to the difficulties in distinguishing the remains of *S. plana* from *Abra* sp., we grouped these species in a single diet item, referred hereafter as *S. plana*/*Abra* sp.

Prey selection

Prey type and size selection were determined by comparing results of the analysis of droppings with the abundance and size of invertebrates found in sediment cores.

Densities of feeding dunlins differed among the study plots. Therefore, the invertebrate samples were stratified according to bird density, to ensure that invertebrate abundances used for comparison were representative of what was used by birds within the study area. A subset of cores was randomly selected such that the total number of cores per sediment type was proportional to bird abundance. This procedure assumes that droppings collected from the eastern side of the study area result from feeding activity over the entire study area. Observations of flock movements during the study confirm that this assumption was valid.

Prey type selection was determined using the Manly-Chesson preference index (Chesson 1983), described as

$$\alpha_i = \frac{r_i / p_i}{\sum_{j=1}^{m} r_j / p_j}, \qquad i = 1, \ldots\ldots, m,$$

where α_i is the preference for prey *i* when *m* prey are available, r_i is the relative abundance of prey *i* in diet, and p_i is the relative abundance of prey *i* in sediment. This preference index varies between 1, if the diet consists entirely of one food item, and 0, if the food item is absent from the diet. Values of $\alpha > 1/m$ indicate positive selection and $\alpha < 1/m$ indicate negative selection. This index considers only relative abundances of prey species, so it is possible to compare the abundance of invertebrates in the sediment assessed by sediment samples with the prey abundance in diet obtained from dropping analysis. Differences from null selection ($\alpha = 1/m$) were tested following Manly (1974). This procedure involves the estimation of the variance and the calculation of the statistic (G) (defined as the difference between the obtained value of α and the hypothesized α for null selection, divided by the standard deviation). This statistic is then tested against a standard normal distribution. The frequency of occurrence was used as a descriptor of the abundance of invertebrate species, both in the sediment and in the diet. Droppings collected between January and March were grouped, to perform the analysis of prey type selection, in order to increase the statistical power of the comparisons. This analysis did not cover species that do not leave detectable remains in droppings or that could only be detected by the presence of setae or acicules. Nematodes, nemertini, oligochaetes, large bivalves (> 13 mm), and several polychaete species were therefore excluded. The presence of insects in the diet, together with the absence of insects in intertidal sediments, may indicate that insect remains were probably retained for a long time in the digestive tract of the birds, so we also excluded these prey from the analysis. Size selection was performed only for the two main prey types, *S. plana*/*Abra* sp. and *H. ulvae*, because there was no sufficient data for the other prey species. Only droppings collected in January were used in this analysis.

Bird counts and feeding behaviour

Dunlins feeding in the plots were counted twice a month (during the spring tides) between November 2000 and April 2001. To control for potential tidal variation in the number of birds present within the plots (see Burger et al. 1977, Nehls and Tiedemann 1993), we divided the counting period (± 1 h from the low tide) into three equal sub-intervals. Each plot was counted preferentially only once within one of different sub-intervals, in each counting day. In each month all plots were counted at least twice in each sub-interval.

The foraging rate of dunlins was recorded during 1 min intervals in all types of sediment, using a 20-60x telescope. Pecks were assigned to three classes according to the penetration of the bill in the sediment: superficial pecks (bill inserted ca. 0-1 cm into the sediment), median probes (half bill inserted; ca. 1-2 cm) and deep probes (whole bill inserted; ca. 2-3 cm). Stitching behaviour was rarely observed and so it was not considered in the analysis. To minimize the possibility of sampling the same individuals more than once, each plot was only visited once in the same day and no more than 8 individuals were observed in each plot, each day. All birds observed within the same plot were chosen ensuring a minimal distance of 20 m from the previously observed bird, or moving the field of vision of the telescope in the opposite direction of the flock movement.

Means are presented ± SE and statistical procedures followed Sokal and Rolf (1995).

Table 2.2. Density (individuals per m^2 ± SE), size (± SE, in mm), and ash-free dry weight (AFDW - g per m^2) of invertebrates found in the study plots (sample size in parentheses). Densities in the three sediment types were compared with a Kruskal-Wallis test (ns: non-significant; * p < 0.05; ** p < 0.01; *** p < 0.001), followed by a Dunn test (superscript with identical letters indicates non-significant difference at p > 0.05).
Individuals with broken shells were excluded.

Species	Density					Size	AFDW
	Sand	Mixed	Mud	H	Total		
	(n=16)	(n=13)	(n=17)		(n=46)		
Mollusca							
Abra sp.	150±65	231±88	72±23	1.0 ns	146±35	2.1±0.2(26)	0.01
Cerastoderma edule	41±18	9±9	7±7	4.3 ns	20±7	19.4±4.9(6)	3.08
Scrobicularia plana	102±25^{a}	195±30^{ab}	332±58^{b}	13.6**	208±28	27.1±2.3(53)	-
S. plana <13 mm$^{\#}$	61±18	62±21	144±45	2.2 ns	90±19	8.9±0.6(24)	0.17
S. plana >13 mm$^{\#}$	20±15	98±22^{a}	144±26^{a}	14.5***	85±15	42.2±0.5(29)	31.94
Hydrobia ulvae	9633±3750	1688±454	1516±272	2.1 ns	4564±1449	1.5±0.04(333)	0.35
Crustacea							
Corophium volutator	14±10	44±21	14±10	2.4 ns	23±8	4.0±0.8(4)	0.01
Cyathura carinata	313±57^{a}	249±60^{a}	72±31	14.3***	211±32	8.5±0.6(34)	1.65
Polychaeta							
Alkmaria ramniji	7±7^{a}	418±158^{b}	188±110^{ab}	14.5***	186±63	-	0.003
Capitela capitata	231±100^{a}	62±38^{ab}	0^{b}	11.7**	103±40	-	-
Glycera tridactyla	27±13^{a}	0^{a}	0^{a}	7.3*	10±5	-	-
Hediste diversicolor	34±17	9±9	0	4.9 ns	15±7	32.9±21.2(4)	0.24
Nephtys hombergii	14±10	9±9	14±10	0.2 ns	13±5	49.3±12.2(4)	0.31
Polydora ciliata	7±7	44±16	36±20	4.4 ns	28±9	-	-
Pygospio elegans	618±248^{a}	98±39^{ab}	29±22^{b}	11.3**	266±97	-	0.003
Streblospio shrubsolli	8825±2316^{a}	9701±2147^{a}	3183±830	13.6**	7110±1132	-	0.08
Tharyx sp.	414±209^{a}	3749±707	917±379^{a}	19.3***	1532±324	-	0.07
Nemertini	0	0	36±22	5.9 ns	13±8	-	-
Nematoda	679±189	18±18^{a}	7±7^{a}	27.4***	259±82	-	0.0003
Oligoqueta	245±112	1954±578^{a}	729±159^{a}	14.6***	896±201	-	0.01

Results

Invertebrate abundance

The invertebrate fauna was numerically dominated by three species: the gastropod *H. ulvae*, and the polychaetes *S. shrubsolli* and *Tharyx* sp. However, these species only contributed 1% to the overall invertebrate biomass (AFDW, Table 2.2). There were also a few other species that were very scarce in the study area (occurring in densities < 100 individuals per m^2) that contributed virtually nothing in terms of biomass. Large individuals of *S. plana*, ranging 35-50 mm, clearly dominated the assemblage in terms of biomass, representing ca. 85% of the overall AFDW.

Different assemblages were found in the three studied types of sediment. *S. plana* and oligochaetes tended to be more abundant in muddy sediments, whereas nematods, *Capitela capitata*, *Pygospio elegans*, *Cyathura carinata* and *S. shrubsolli* were more abundant in sandy sediments (Table 2.2).

Diet composition

Nine different prey were found in droppings during the winter (Table 2.3). The bivalves *S. plana*/*Abra* sp., and the gastropod *H. ulvae* were the most frequently consumed prey, but the isopod *C. carinata* and insects were also regularly found in droppings. Five species of annelids were detected, but the frequency of occurrence was not calculated in those where only setae were found (see methods).

The sizes of ingested prey were determined only for *S. plana*/*Abra* sp., *H. ulvae*, and *H. diversicolor* due to the absence of measurable structures for the other prey (Table 2.3). Studies with knot (*Calidris canutus*) demonstrated that small shells of *H. ulvae* remain undamaged after digestion more often than larger ones, thus creating a bias on the size estimated from droppings (Zwarts and Blomert 1992, Dekinga and Piersma 1993). However, we did not find a significant difference between the size of intact shells and the size estimated from partially broken shells (Mann-Whitney test, U = 5183, p = 0.61, 137 broken shells and 79 intact shells), which indicates that in this case the digestion was not size selective.

Table 2.3. Winter diet of dunlins. Frequency of occurrence was calculated as the % of droppings with prey present (n = 244 droppings). Mean size (± SE, range in parentheses, in mm), and the corresponding ash-free dry weight (AFDW) (in mg) are indicated for species that could be measured. Droppings without any identifiable prey (ca. 19%) were excluded.

Prey	Freq. occurrence	Size	AFDW
Mollusca			
Hydrobia ulvae	39.3	1.8±0.03(0.8-3.4); n=216	0.07
Scrobicularia plana/Abra sp.	49.6	7.1±0.1(2.3-12.4); n=169	1.03
Crustacea			
Cyathura carinata	26.2	-	-
Polychaeta			-
Hediste diversicolor	5.3	37.8±3.2(9.1-66.4); n=34	7.68
Nephtys hombergii	0.8	-	-
Polydora ciliata	Present	-	-
Streblospio shrubsolii	Present	-	-
Oligoqueta	Present	-	-
Insects	23.4	-	-
Non-identified.	2.9	-	-

Prey selection

Among the invertebrates preyed by dunlins, *S. plana/Abra* sp. and *H. diversicolor* were the preferred prey while *H. ulvae,* and *C. carinata* showed lower values of selectivity (Table 2.4).

Only a narrow range of the available sizes of *S. plana/Abra* sp. were consumed by dunlins. In fact, the size of the shells found in the sediment and in the diet was significantly different (Mann-Whitney test, $U = 1140$, $p < 0.05$, $n = 74$ for sediment and 40 for droppings). Dunlins preferred specimens ranging 4-10 mm and avoided both smaller and larger individuals (Figure 2.3). Roughly the same pattern of selection was observed in *H. ulvae* (Mann-Whitney test, $U = 15685$, $p < 0.0001$, $n = 333$ for sediment and 163 for droppings). Nevertheless, *H. ulvae* larger than 3 mm were not abundant in the sediment.

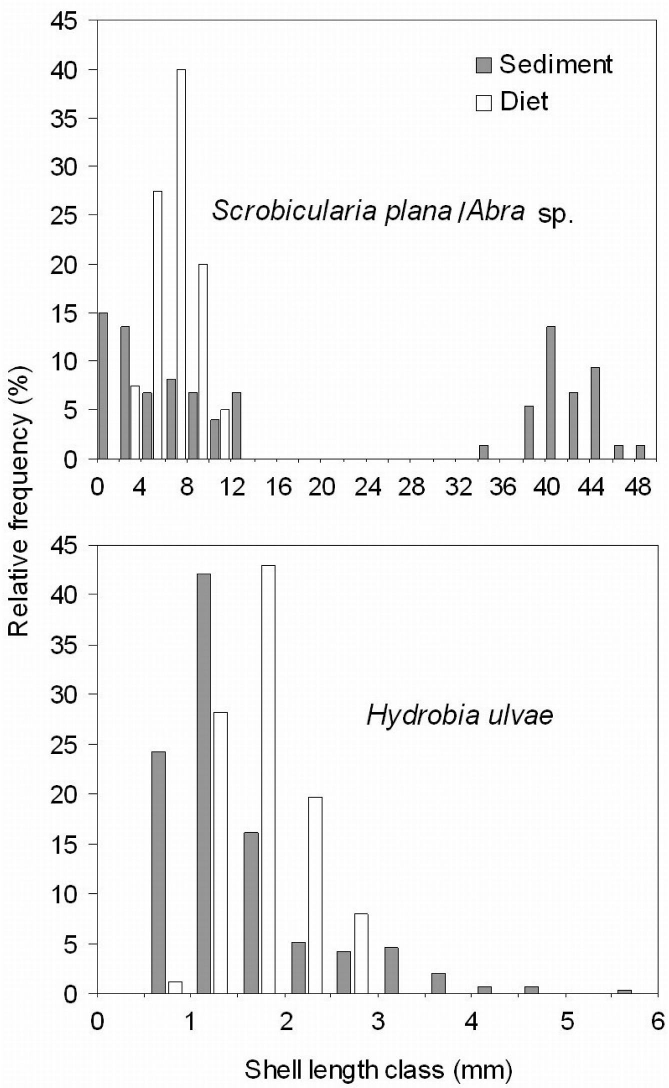


Figure 2.3. Size frequency distribution of *S. plana*/*Abra* sp. and *H. ulvae* found in the sediment and in the droppings of dunlin. Only the droppings collected in January were used. Sample size: *S. plana*/*Abra* sp., n = 74 in sediment, n = 40 in droppings; *H. ulvae* n = 333 in sediment, n = 163 in droppings.

Dunlin distribution and feeding behaviour

The densities of feeding dunlins were higher in muddy sediments (16.0 ± 1.6 birds.ha^{-1}, n = 101), followed by mixed sediments (9.8 ± 0.8 birds.ha^{-1}, n = 119), and sandy sediments (2.3 ± 0.3 birds.ha^{-1}, n = 106). Densities of birds on muddy and sandy sediments showed roughly the same temporal pattern (Figure 2.4), but there was an increase on the relative importance of mixed sediments during March and April (Figure 2.4). In fact, there were significant differences among months in the densities of birds, sediment types and their interaction (Repeated measures ANOVA with sediment type as independent factor; month effects, $F_{5,20} = 6.9$, $p < 0.001$; sediment effects, $F_{2,4} = 58.5$, $p < 0.01$; interaction effects, $F_{10,20} = 2.5$, $p = 0.04$; counts made on the same month were pooled).

Table 2.4. Prey selection by dunlins. Abundance of prey in sediment and in diet is represented by frequencies of occurrence (% of samples with the prey present). Selection is represented as α-1/m, such that 0 represents null selection, negative values indicate negative selection, and positive values indicate positive selection (see methods). The values of α were compared with the expected value for null selection using the G statistic (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Large *S. plana* (> 13 mm) present in sediment samples were excluded.

Prey	Sediment (n=29)	Diet (n=244)	Selection	G
Mollusca				
Scrobicularia plana/Abra sp.	75.9	49.6	0.170	5.3***
Hydrobia ulvae	100	39.3	0.045	2.1*
Crustacea				
Corophium volutator	17.2	0	-0.143	-
Cyathura carinata	58.6	26.2	0.071	2.6**
Polychaeta				
Glycera tridactyla	3.4	0	-0.143	-
Hediste diversicolor	10.3	5.3	0.104	2.0*
Nephtys hombergii	10.3	0.8	-0.105	-

The pecking rate was similar in all sediment types (Kruskal-Wallis test, $H = 0.33$, $p = 0.85$; $n = 119, 140, 111$ for sand, mixed sediments and mud, respectively; overall mean, 37.0 ± 26.3 pecks.min^{-1}). However, there were significant differences among sediment types in the rate of superficial pecks, median probes and deep probes (Kruskal-Wallis test; superficial pecks $H = 29.9$, $p < 0.0001$; median probes $H = 82.1$, $p < 0.0001$; deep probes $H = 180.7$, $p < 0.0001$). In sandy substrate, almost all pecks were superficial, while in mixed and muddy sediments a substantial part of the pecks were median or deep probes (Figure 2.5).

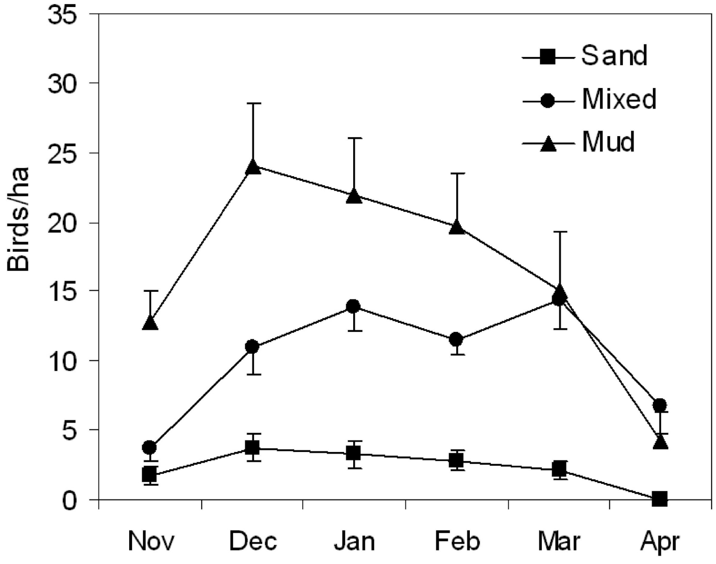


Figure 2.4. Phenology of dunlin in the three sediment types. Symbols represent mean densities and vertical lines their SE. N = 18 except for a few samples of November (mud = 16, mixed = 26) and December (mud = 13, mixed = 21, sand = 16).

Discussion

Diet composition

The species *H. ulvae* and *H. diversicolor* have been reported as the main prey of dunlin along the east Atlantic coast (Davidson 1971, Fuchs 1975, Goss-Custard et al. 1977, Worrall 1984, le V. dit Durell and Kelly 1990, Mouritsen 1994, Lopes et al. 1998, Luís 1998, Dierschke et al. 1999) and were also frequently taken by dunlins in the Tagus estuary. The consumption of these prey across this latitudinal range is probably related with their wide distribution and not with a selective feeding behaviour of the birds. Other invertebrate species frequently consumed by dunlins in northern Europe, like *Macoma balthica* and *Corophium volutator* (Davidson 1971, Goss-Custard et al. 1977, Worrall 1984, le V. dit Durell and Kelly 1990, Mouritsen 1994, Dierschke et al. 1999), are almost absent in south Europe, so they are replaced in the diet by species more common in southern latitudes such as *S. plana*/*Abra* sp. and *C. carinata* (Moreira 1995b, Lopes et al. 1998, present study). Spionids, oligochaetes, *Nephtys* spp. and insects have also been reported in the dunlin diet elsewhere (Fuchs 1975, Goss-Custard et al. 1977, Lifjeld 1983, Worrall 1984, le V. dit Durell and Kelly 1990, Mouritsen 1994, Lopes et al. 1998, Luís 1998, Dierschke et al. 1999).

The individuals of *S. plana*/*Abra* sp. consumed by dunlins in the Tagus estuary were much larger than the *M. balthica* consumed in the Severn estuary (Worrall 1984). In fact, the maximum size of *M. balthica* consumed by dunlins in the Severn estuary was

7-8 mm (Worrall 1984), whereas we observed the consumption of 12 mm *S. plana*/*Abra* sp. The shells of juvenile *S. plana* are very fragile, and thus we believe that these large individuals were probably *S. plana* that were smashed prior to ingestion. We also observed the consumption of *H. diversicolor* about 1.5 times larger than those preyed upon in northern Europe (Goss-Custard et al. 1977, Worrall 1984, Dierschke et al. 1999). In contrast, the individuals of *H. ulvae* consumed by dunlins in the Tagus estuary were about 1.5 times smaller than those consumed in northern Europe (Goss-Custard et al. 1977, Worrall 1984). The consumption of relatively small *H. ulvae* has also been reported from Mondego estuary, Portugal (Lopes et al. 1998). However, these north-south differences could be related with different availabilities on the invertebrate sizes between the places compared, and not with different feeding behaviour.

Prey selection

In the Tagus estuary, dunlins feed upon a broad spectrum of invertebrate species, but following clear patterns of selection of prey species and of prey size. The most preferred prey were those with higher biomass, such as *H. diversicolor* and *S. plana*/*Abra* sp. Small size invertebrate species and the smallest individuals of some important prey species were avoided. Previous studies demonstrated that the smallest sizes of *H. diversicolor* (Worrall 1984, Dierschke et al. 1999), *M. balthica* and *H. ulvae* (Worrall 1984) were rarely taken by dunlins, despite their abundance in foraging areas.

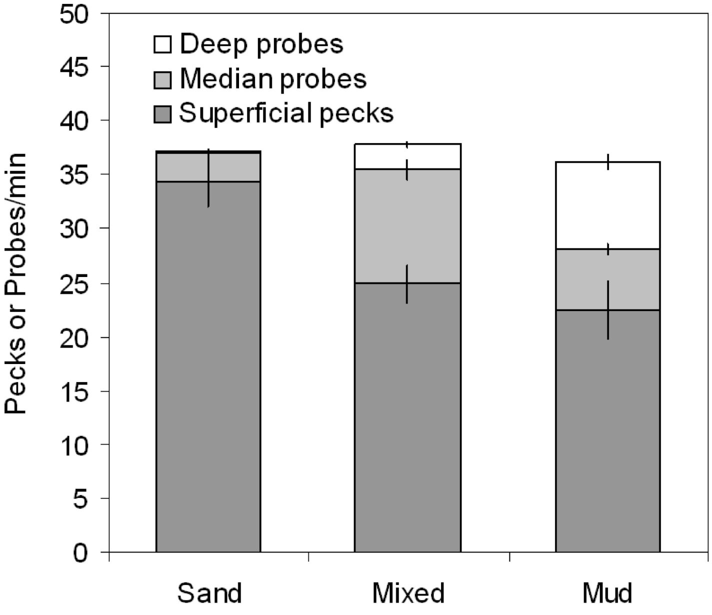


Figure 2.5. Pecking rate of dunlin, separated by classes of peck depth, in the three sediment types. Values represent mean ± SE of 119 observations for sand, 140 for mixed and 111 for mud.

Our results indicate that the lower limit of the prey size differs between prey and is probably established by their profitability. In fact, dunlins seem to ignore small *S. plana*/*Abra* sp. that have the size of preyed *H. ulvae* (Figure 2.3). It seems likely that *H. ulvae* is more profitable than *S. plana*/*Abra* sp. of the same size because their availability on the surface of the sediment allows birds to take them at a high rate.

The absence of *S. plana* larger than 13 mm in the diet of dunlins is explained by an inability to swallow such large specimens. However, dunlins are likely to consume siphons of large *S. plana*. These invertebrates are very abundant in the study area and siphon cropping seems to be a common feeding behaviour in other waders (Zwarts 1986, Moreira 1995b). However, siphons do not leave identifiable remains in droppings, so the importance of *S. plana* is probably underestimated by our analysis.

Habitat use

In this study, we observed that dunlins prefer muddy sediments as feeding areas during the winter, which agrees with observations made by other authors for the Tagus estuary (e.g. Granadeiro et al. 2004) and for several locations in eastern north Atlantic coast (e.g. Wadden Sea, in the Netherlands, and The Wash, in England; Kelsey and Hassall 1989, Nehls and Tiedemann 1993). Nevertheless, there are some geographical and seasonal variations on the habitat preference of dunlins. The winter densities of dunlins in Banc d'Arguin (Mauritania) were similar in both sandflats and mudflats (Zwarts et al. 1990c). In the Wadden Sea, dunlins prefer muddy substrates in winter and spring but appear to have no clear preference in summer and autumn (Nehls and Tiedemann 1993). Moreira (1995b) also observed seasonal variation in habitat selection of dunlins in the Tagus estuary. Given that dunlins are generalist, it is likely that they change their feeding habitat in response to different conditions of accessibility, availability, and profitability of invertebrates.

The observed preference for muddy substrates in the study area is probably related to two factors: prey abundance and prey detectability. In fact, *S. plana* is not only more abundant in muddy substrates but is probably also more easily detected there than in harder, sandier, substrates. Mouritsen and Jensen (1992) demonstrated that sediment penetrability improves the probability of detecting buried prey by dunlins. Our focal observations of feeding dunlins revealed that most bivalves and large worms were located by probing, and that probing was more frequently used on muddy areas.

Therefore, these observations indicate that detection efficiency may play an important role in the selection of habitat by dunlins.

Latitudinal gradients of birds and invertebrates

Densities of dunlins clearly increase from northern to southern latitudes along their non-breeding distribution within the East Atlantic Flyway (Table 2.5). This pattern is also observed at a global scale pooling the density of all wader species (Hockey et al. 1992). Several studies discuss this phenomenon but their conclusions are still limited by the insufficient information on the food availability for birds (e.g. Zwarts et al. 1990c, Hockey et al. 1992).

Table 2.5. Densities of dunlins during the winter and biomass of invertebrates in some of the most important sites for wintering dunlins in the East Atlantic Flyway, based on published literature. [a] Meltofte et al. (1994); [b] Zwarts and Wanink (1993); [c] Eybert et al. (2003); [d] Deceuninck and Mahéo (2000), only counts 1993-1999; [e] Estimated from Landsat images, freely available at http://glcfapp.umiacs.umd.edu; [f] Rufino and Costa (1993), Costa and Rufino (1994, 1996a, 1996b, 1997); [g] Present study; [h] Sprung (1994), biomass from all habitats was pooled; [i] Pérez-Hurtado and Hortas (1992); [j] Masero et al. (1999), biomass from February and March samples was pooled; [k] Hockey et al. (1992); [l] Dakki et al. (2001); [m] Piersma et al. (1993); [n] Wolff et al. (1993), intertidal area excluded Sebkhas; [o] Zwarts et al. (1998a, 1998b).

Site	Latitude (ºN)	Intertidal area (ha)	Number of Dunlins	Density (Dunlins.ha^{-1})	Invertebrate biomass (AFDW.m^{-2})
Wadden sea, Netherlands	53	114,100 [a]	56,013 [a]	0.5	94.1 [b]
Mont Saint Michel Bay, France	49	24,000 [c]	29,394 [d]	1.2	13.3 [c]
Tagus estuary, Portugal	39	9,719 [e]	14,449 [f]	1.5	37.9 [g]
Ria de Faro, Portugal	37	5,183 [e]	18,397 [f]	4.7	18.1 [h]
Cadiz Bay, Spain	36	3,915 [e]	12,176 [i]	2.3	44.7 [j]
Merja Zerga, Morocco	35	2,200 [k]	25,704 [l]	11.7	22.6 [m]
Banc d'Arguin, Mauritania	19	49,250 [n]	947,743 [o]	19.2	17.0 [n]

We compiled information on the invertebrate biomass along the wintering distribution of dunlins within the East Atlantic Flyway, and did not detect any clear latitudinal trend. (Table 2.5). Moreover, the two sites with the highest densities of birds (Merja Zerga, Morocco and Banc d'Arguin, Mauritania) presented much lower biomass of invertebrates than the Dutch Wadden Sea, which has the lowest densities of birds. However, the lack of clear patterns in this compilation of data has to be interpreted with care because of data insufficiencies.

A major problem with the available data is that food availability is not necessarily correlated to the overall biomass of invertebrates. This study demonstrated that only part of the invertebrates present in the sediment are actually exploited by the dunlins, not only because their selective behaviour but also because sediment characteristics seems to limit the exploitation of their prey.

The evaluation of food availability is further complicated by the fact that in most studies sampling schemes are very limited in terms of space and time covered. Additionally, size and burying depth of invertebrate species is rarely presented. Long-term studies on the invertebrate availability for waders reveal large seasonal and annual variation in abundance, size and burying depth of invertebrates (e.g. Zwarts and Wanink 1993). Also several studies have shown that invertebrates present patchy distributions (e.g. Thrush 1991), which are rarely taken into account in the sampling schemes.

The global populations of many wader species are currently decreasing (BirdLife International and European Bird Census Council 2000, Stroud et al. 2004). Although most of the important wintering areas have been identified, the evaluation of their food resources for waders is still missing, particularly for tropical and sub-tropical areas. It is generally recognized that because most waders are migratory, conservation plans at a flyway scale are necessary for the preservation of these birds. In this context, baseline knowledge (as diet and availability of food resources) in the least studied wintering areas is of major importance for the conservation of wader populations.

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

Abstract

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

Introduction

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

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

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

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

Methods

Study area

This study was carried out in the Tagus estuary, Portugal (38º 45’N, 09º 02’W; Figure 2.6). In this estuary the tides are semi-diurnal, with an amplitude ranging from 1 to 3.8 m in neap and spring tides, respectively. The sediments are relatively diverse, but most of the area consists of mudflats and oyster banks (Calvário 1984). About 97 km^2 of sediment flats are exposed at low water during an ordinary spring tide (0.6 m). In 1988, the Tagus estuary was designated as a Special Protection Area for Birds (covering about 450 km^2 of intertidal areas and surrounding land), under European Union legislation, and part of it is also classified as Nature Reserve since 1976.

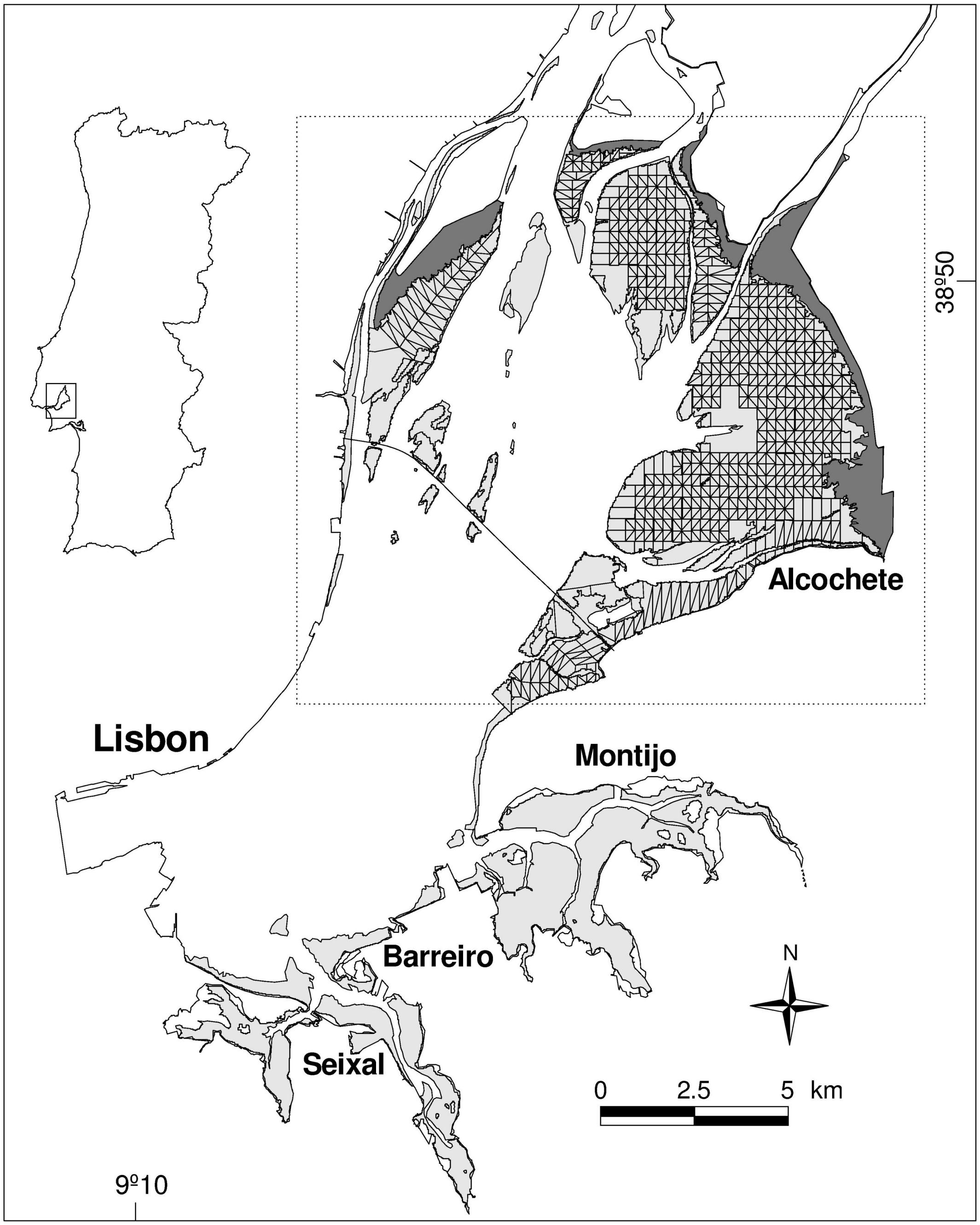


Figure 2.6. The Tagus estuary and location of the study area (dotted square). Dark grey areas represent salt marsh, and light grey areas represent intertidal flats.

Bird counts

Low-tide bird counts were carried out from December to mid-March in both 2002 and 2003. They covered all the intertidal areas from the marsh or coastal edge to the low water mark. In 2002 we were not able to count the southern portions of the intertidal flats of the estuary (Figure 2.6). Therefore the data analysed in this study refers only to the large sediment flats located north of Montijo, which comprise about 73% of the total intertidal area (Figure 2.6).

In the inner parts of the estuary (away from the coastline, see Figure 2.6), we marked the counting sectors using a grid of canes placed with the help of a GPS. The total area counted during a single day consisted of a rectangle of 2.5 km x 1.2 km (300 ha). In this large area, the individual counting sectors had a surface of about 3.75 ha and were generally triangular shaped (Figure 2.6). The center of the area was reached by boat during the receding tide and at low water two observers slowly walked in opposite directions along a transect on the edge of the sectors. Each observer walked ca. 3 km during each count and recorded the number of birds feeding in the ca. 40 triangular sectors.

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

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

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

There were some differences between years in the exact boundaries of some of the sectors. In order to combine the data obtained in 2002 and 2003, we started by determining the geographical coordinates of the centroids of all 2002 and 2003 sectors in the GIS. We then defined a fixed regular grid of plots measuring 230 m * 140 m (3.22 ha) over the entire study area against which we projected the (centroids of the) sectors counted both in 2002 and 2003. These regular plots (hereafter called quadrats) were approximately of the same area of our counting sectors, and thus were the best grid approximation of our sampling scheme. The density of birds in each quadrat was calculated as the average of the centroids lying within the limits of the quadrats. After applying this procedure to data collected in 2002 (1069 quadrats) and 2003 (1114 quadrats), we overlapped (and averaged where appropriate) the quadrats from the two years, resulting in a final dataset consisting of 1239 quadrats.

Environmental and GIS variables

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

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

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

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

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

Data analysis

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

Table 2.6. Densities (number of birds per 10 ha ± SD), frequency of occurrence (Freq.: expressed as the proportion of sectors where the species was detected), and total number of birds counted in the Tagus estuary during the surveys carried out in 2002 and 2003. Species are sorted by their average density.

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

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

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

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

Results

Number of birds in the estuary and between-year variability

Overall, in our study area we counted ca. 28,000 birds in sectors covering 59.4 km^2 in 2002, and ca. 20,800 birds in 58.6 km^2 in 2003. The densities of avocet (*Recurvirostra avosetta*), black-tailed godwit (*Limosa limosa*) and flamingo (*Phoenicopterus ruber*) decreased substantially from 2002 to 2003, whereas the number of dunlins (*Calidris alpina*) followed the inverse trend (Table 2.6). In both years dunlin was the most abundant species, with an average count of ca. 8000 birds. The density of lesser black-backed gulls was very similar in both years, and in average this was the second most abundant species. A few species occurred in very low densities (< 0.1 birds per 10 ha), such as the curlew (*Numenius arquata*), whimbrel (*Numenius phaeopus*), curlew sandpiper (*Calidris ferruginea*), and these are not listed in Table 2.6.

The correlation between the densities recorded in quadrats containing data from both 2002 and 2003 varied among species. Lesser black-backed gull, little egret (*Egretta garzetta*), redshank (*Tringa totanus*), Kentish plover (*Charadrius alexandrinus*), ringed plover (*Charadrius hiaticula*), black-headed gull (*Larus ridibundus*), dunlin, sanderling (*Calidris alba*) and grey plover (*Pluvialis squatarola*) showed significant correlation between the densities in both years (Spearman r: range 0.12-0.40, all $p < 0.05$), whereas the remaining 9 species showed little concordance between years (Spearman r: range 0.01-0.02, all non-significant). Establishing larger sectors (by duplicating the length and width of each quadrat, i.e. multiplying the area of the quadrats by four) and averaging the density estimates from neighbour sectors did not produce a very substantial improvement in these correlations. In fact, only two more species [turnstone (*Arenaria interpres*) and bar-tailed godwit (*Limosa lapponica*)] achieved marginal significances between their distribution in 2002 and 2003. The between-year agreement was not related with the density of the species (Spearman $r = -0.2$, $n = 18$, n.s.), but it was positively correlated with their frequency of occurrence (Spearman $r = 0.48$, $n = 18$, $p < 0.05$).

Species association and relationship with environmental factors

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

The structure of bird assemblage was examined using a CCA, and the results of the analysis are shown in Table 2.7. The canonical axis I and II (explaining respectively 52.3% and 18.4% of the variance, Table 2.7) ordinated the species along two gradients: (1) exposure period, mainly responsible for the separation of avocet, black-tailed godwit and flamingo and (2) mud content of the sediment, where dunlins occupy the muddiest sites and sanderlings the most sandy areas (Figure 2.7). Axis III accounted for 11.8% of the variance and mainly separated sites according to the relative amount of algae and oyster beds (Figure 2.7, Table 2.7). The environmental variables were able to explain ca. 12% of the variability of the bird scores.

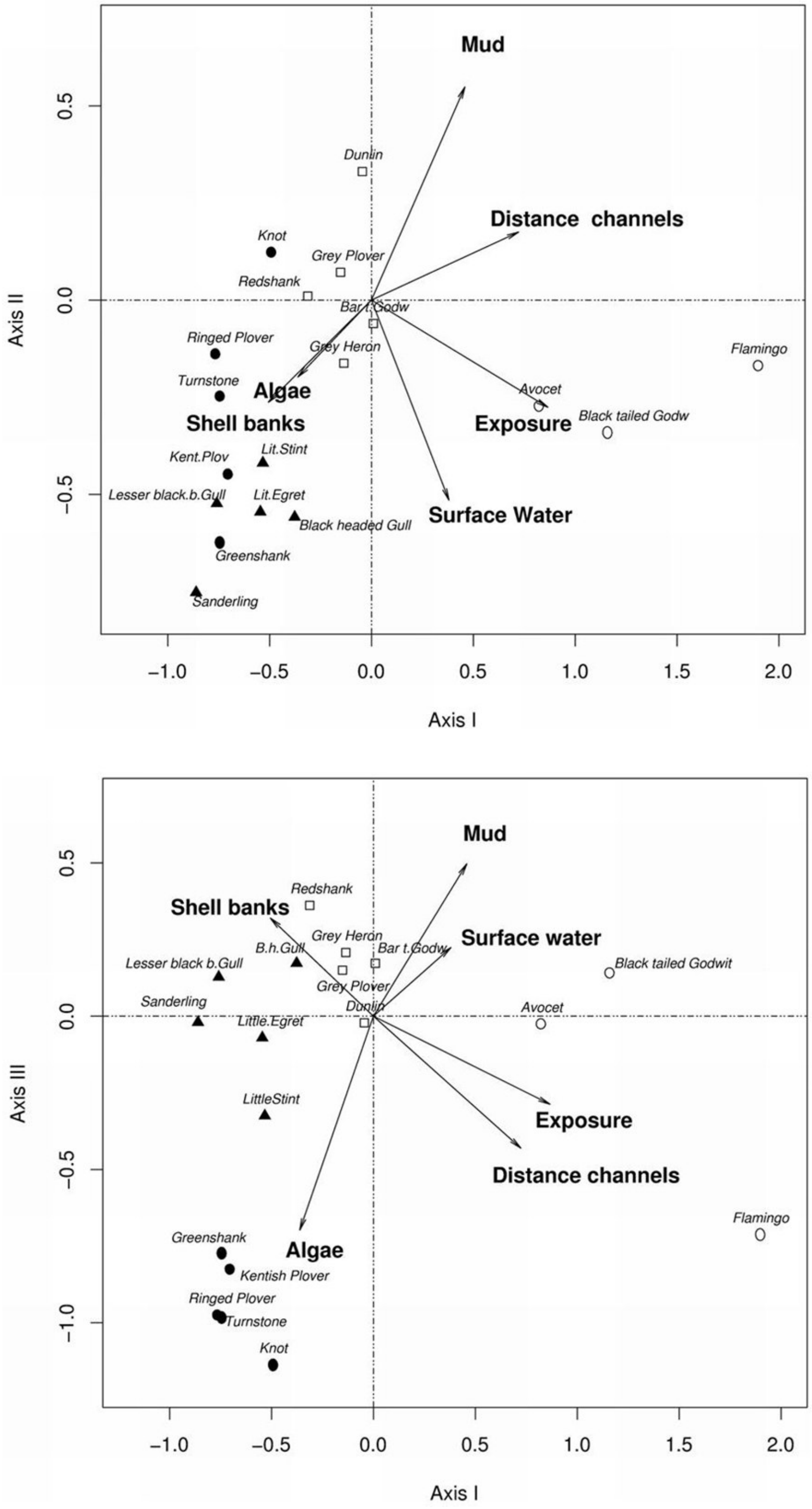


Figure 2.7. CCA ordination diagrams based on the (log-transformed) bird density data and (centred and scaled) environmental and GIS variables. Axis I, II and III accounted for 52.3%, 18.4% and 11.8% of the variability that could be explained by the environmental variables, respectively. Symbols represent species clusters, defined according to their relative distance in the CCA space (for explanation, see text).

Table 2.7. Summary statistics of the Canonical Correspondence Analysis (sum of all eigenvalues = 0.574).

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

A cluster analysis revealed four main groups: Group 1, comprising the flamingo, black-tailed godwit and avocet; Group 2, which includes the Kentish plover, greenshank (*Tringa nebularia*), knot (*Calidris canutus*), ringed plover and turnstone; Group 3, with lesser black-backed gull, sanderling, black-headed gull, little egret and little stint (*Calidris minuta*); and Group 4 comprising dunlin, redshank, grey plover, bar-tailed godwit and grey heron (*Ardea cinerea* Figure 2.8). Although the flamingo represents a separate group in the dendrogram (Figure 2.8), its position in relation to the gradients of the CCA supports the inclusion in the group formed by the avocet and black-tailed godwit (Figure 2.7). The environmental characteristics of quadrats where each group occurred are listed in Table 2.8.

The groups showed distinct distributions in the estuary, with Group 4 being relatively widespread whereas all the other groups showed a much more localized occurrence (Figure 2.9). The patterns of distribution of these groups were significantly different, as assessed by the Jaccard similarity coefficient (all pairwise comparisons $p < 0.01$).

Discussion

Comparison between years and with previous work

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

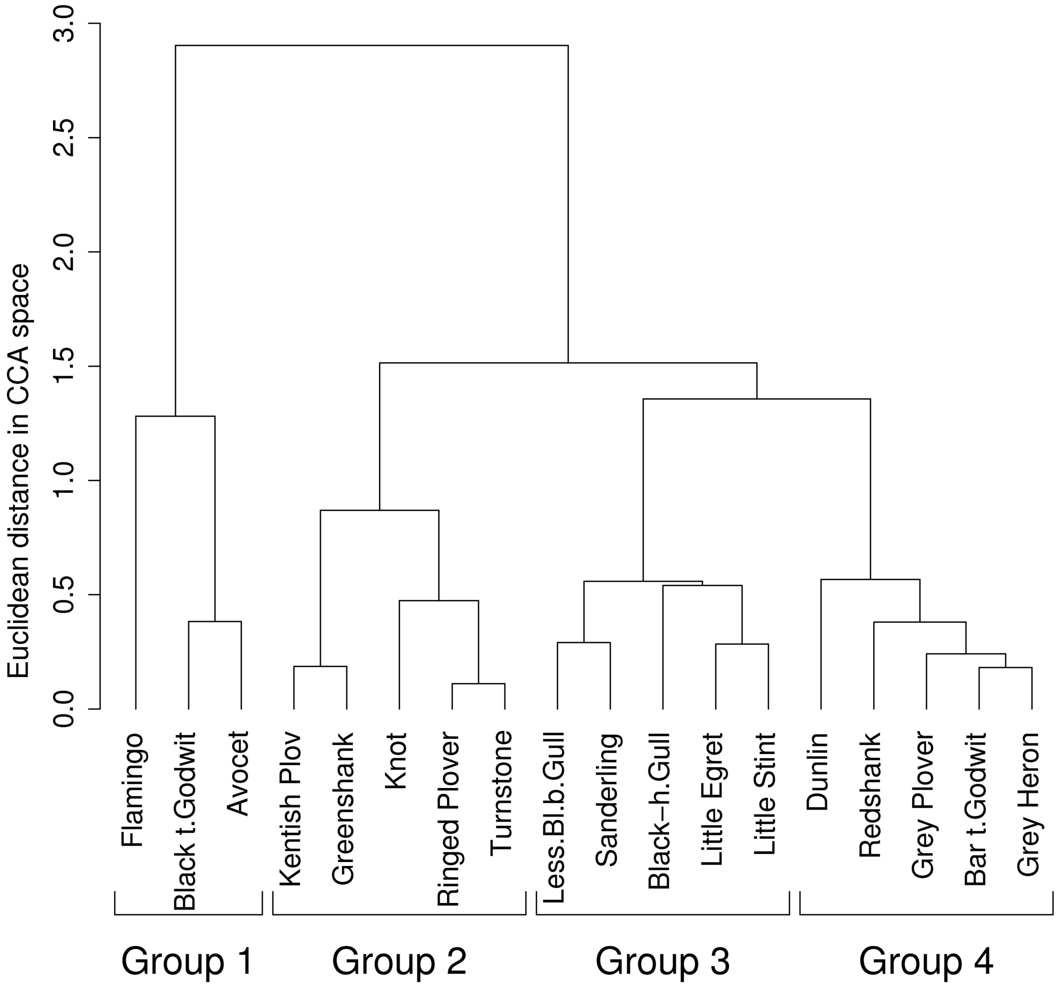


Figure 2.8. Dendrogram (based on euclidean distances and UPGMA algorithm, Gauch 1982) representing the similarities among species in the space defined by the first three axis of the CCA (see Methods).

Table 2.8. Summary of environmental characteristics (means ± SE) in the areas of occurrence of each group of species (sample sizes are indicated in parenthesis). Group 1: flamingo, black-tailed godwit and avocet; Group 2: Kentish plover, greenshank, knot, ringed plover and turnstone; Group 3: lesser black-backed gull, sanderling, black-headed gull, little egret and little stint; and Group 4: dunlin, redshank, grey plover, bar-tailed godwit and grey heron.

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

We did not carry out counts in the extensive salt marsh area located in eastern part of the estuary (Figure 2.6). Our observations showed that the vast majority of the birds fly directly from the high-tide roosts to the exposing sediment flats, bypassing the vegetated marsh areas, so we believe that any numbers that may have remained in the salt marsh represented a very small fraction of the birds feeding in the estuary.

The only complete low water count of shorebirds feeding in the Tagus estuary was carried out in the winter 1981/1982 (Teixeira 1985). In spite of the time separation of the two counts and of methodological differences (very large sectors, some of which counted by airplane), our results for most species are quite similar to those of Teixeira (1985). The most pronounced differences between the two sets of data relates to the numbers of *Larus* gulls and avocet. Teixeira (1985) counted 19,570 black-headed gulls in the winter 1981/1982, a total many times higher than what we observed. The same is true for lesser black-backed gull and avocet, with 12,900 and 10,280 birds counted by Teixeira (1985) and ca. 3500 and 3400 recorded in this study, respectively (Table 2.6). We can not exclude the possibility that the differences are due to a real reduction of the numbers of birds of these species wintering in the estuary. However, there is evidence that at least part of the differences are due to changes in the preferred foraging areas, which may have shifted to sediment flats located in the southern end of the estuary, not included in the counts reported in this study (Figure 2.6). Counts that we made in 2003 in this area resulted in 10,250 lesser black-backed gulls, 3800 black-headed gulls and 1479 avocets, and Moreira (1999) also reported a high abundance of the three species there. Nonetheless, the level of discrepancy found in our study is not unexpected, given the high interannual variability in bird numbers, their high mobility and the likely variation in the abundance of their prey, a factor well known to affect the birds distribution (Wolff 1969, Goss-Custard and Yates 1992, Zwarts et al. 1992, Yates et al. 1993).

Factors affecting the distribution of the bird assemblage

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

A substantial proportion of the variance of our data derived from the high preference of the flamingo, black-tailed godwit and avocet (Group 1) for areas with high exposure period (Figure 2.7, Table 2.8). This is consistent with previous observations of the influence of the exposure period in the distribution of several species, both in the Tagus estuary (Moreira 1993, Rosa et al. 2003, Granadeiro et al. 2004) and elsewhere (e.g. Yates et al. 1993, Scheiffarth et al. 1996). However, we can not rule out the possibility of a strong influence of the location of the high-tide roosts in the bird densities (rather than the exposure period alone), because these two variables were (inversely) correlated in the estuary.

Most sectors occupied by species of Group 1 were located in the higher reaches of the estuary, close to the salt marsh and hence generally away from the main channels (Figures 2.7 and 2.9, Group 1). These sectors consisted primarily of muddy sediments most of which retaining a thin layer of water (Table 2.8). A permanent water coverage is important to maintain the feeding efficiency of species like the flamingo and avocet (Moreira 1995d, Zweers et al. 1995).

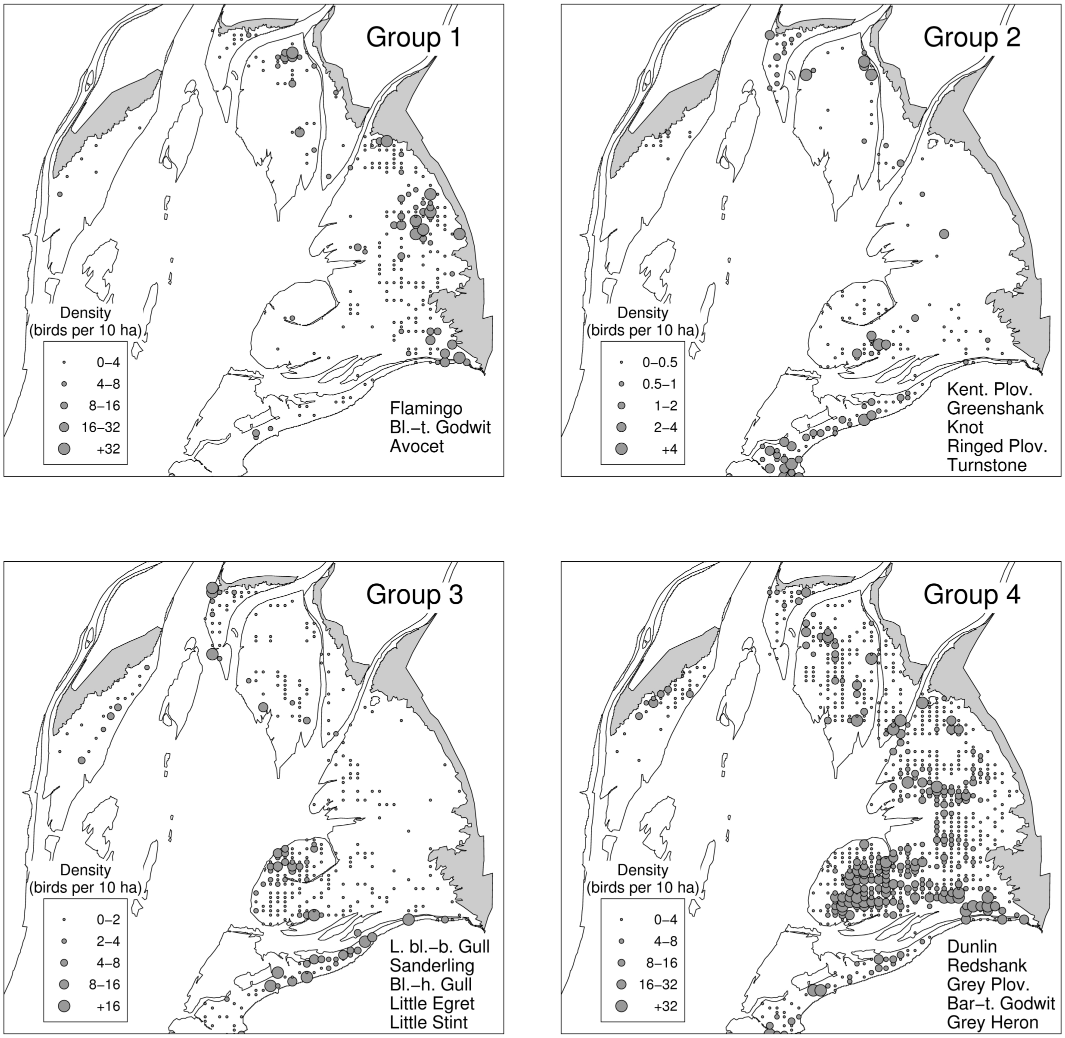


Figure 2.9. Joint distribution of the four groups of species identified in the CCA. Densities (in birds per 10 ha) are represented on a logarithmic scale.

The remaining species were aligned along a gradient of mud content, which is very clear in the joint plots of axis I and II (Figure 2.7). Dunlins (Group 4) preferred the muddiest sediments while gulls, greenshank and sanderling (Group 3) occurred in the sectors with coarser sediments, many of which were associated with shell banks. These data are consistent with previous observations in the Tagus estuary (first paper of this chapter, Moreira 1993, Granadeiro et al. 2004). In fact, sediment composition is a well known factor affecting distribution of shorebirds. It influences both the type and abundance of invertebrate prey (Wolff 1969, Evans 1979, Yates et al. 1993), and the access of birds to this prey for example, through penetrability and sediment wetness (Goss-Custard and Yates 1992, Mouritsen and Jensen 1992).

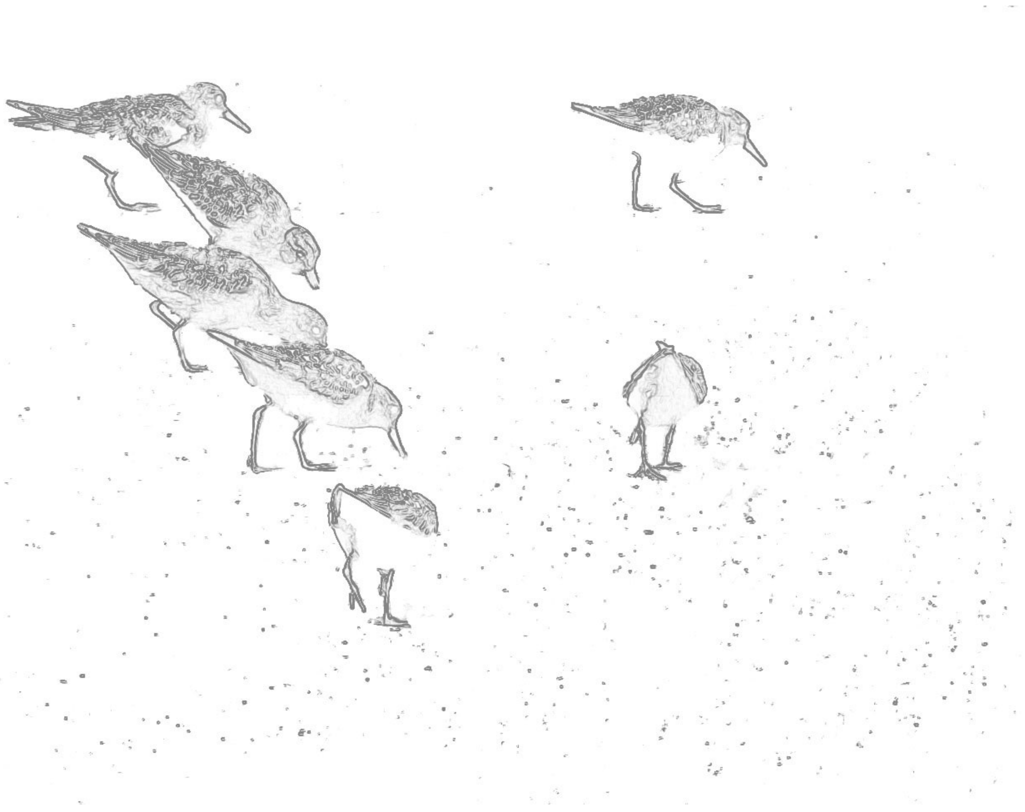
Two groups of species could be defined in the sectors with coarser sediments, which were mainly separated by the relative amount of macrophyte coverage and of shell banks (Table 2.8). Greenshank, Kentish plover, ringed plover, knot and turnstone (Group 2 in Figure 2.8) were more abundant in areas with higher density of macrophytes (generally with less dense shell banks), whereas *Larus* gulls, sanderling, little egret and little stint (Group 3) preferred areas with less macrophytes but a comparatively higher shell bank coverage (Table 2.8).

Species in Group 4 (dunlin, grey plover, redshank, bar-tailed godwit and grey heron) were located close to the centre of CCA plot, which indicates that they occur in a large variety of conditions, and thus show no marked preference along the gradients previously described. In fact, this is the group of species most widely distributed, occurring both in coastal and inner areas of the estuary (Figure 2.9) and in the average conditions of the entire estuary (Table 2.8).

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

CHAPTER 3

EXPLOITING FOOD RESOURCES



Overview

Foraging ecology is perhaps the most studied of all fields in wader ecology, and in the last decades a large number of papers were published on this subject. This field of study has gained a particular interest after the development of the Optimal Foraging Theory. In its most basic form, this theory postulates that foraging choices of organisms are aimed to maximize their long-term energy intake (MacArthur and Pianka 1966, Fretwell and Lucas 1970, Charnov 1976). In other words, organisms behave in such a way as to find, capture and consume food containing the most calories while expending the least amount of energy possible doing so. After an initial stage of mostly descriptive foraging studies, optimal foraging models became an interpretive tool for researchers to understand animal distributions. Four decades after the original conception of MacArthur and Pianka (1966), Optimal Foraging Theory has suffered major improvements and additional models were established (see Stephens et al. 2007 for a revision). However, explaining the distribution of animals in relation to their food resources is still on of the most important goals in the current ecological science.

In the case of waders, most distribution models lack predictability (e.g. Yates et al. 1993), mostly because the distribution of their invertebrate prey is highly variable (Zwarts and Wanink 1993), but also because there are still a number of gaps in the fundamental knowledge on how waders are related to their invertebrate prey.

This chapter is focused on small-scale relationships between waders and their food resources. The habitat selection models for waders are known to be severally affected by spatial scale (Colwell and Landrum 1993). At small-scale, waders exhibit particularly weak relationships with the distributions of their invertebrate prey (Kelsey and Hassall 1989, Wilson 1990). This is probably because invertebrates are subjected to frequent redistribution due to depletion and settlement (Underwood and Chapman 1996, Rosa et al. 2008), and also because individual birds depend particularly of their own foraging efficiency being little affected by the foraging decisions of the bird flock (Clark and Mangel 1984). However, a closer look to the individual behaviour of birds in relation to their prey can help to explain their distribution patterns at a much larger spatial scale.

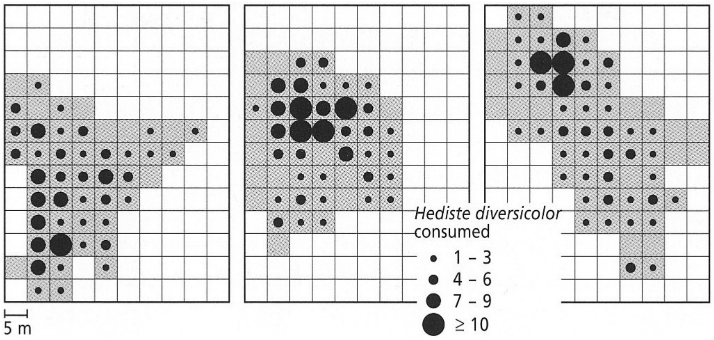


Figure 3.1. Prey captured by a curlew, within his territory, in three successive days (from van de Kam et al. 2004a).

There are several aspects that we should consider when studying small-scale relationships between birds and invertebrates: (1) intertidal invertebrates present aggregated distributions and waders exploit them accordingly (Figure 3.1, Thrush 1991, Dias et al. 2009); (2) only a small fraction of the invertebrates present in intertidal areas represents harvestable prey for waders (Figure 3.2, Zwarts and Blomert 1992); (3) the activity of invertebrates at the surface of sediments and their burying depth affects their detection rate by waders (Zwarts and Blomert 1992); (4) the invertebrate activity at the surface depends on the characteristics of the microhabitat, in particular of the superficial water (Rosa et al. 2007); (5) sediment characteristics, such as penetrability, can physically constrain the foraging of waders (Quammen 1982).

The first paper of this chapter examines how dunlins (*Calidris alpina*) exploit microhabitats in mudflats. Mudflats are among the most important feeding areas during non-breeding periods for many wader species and comprise a substantial micro-scale heterogeneity promoted by the differential drainage of the sediments. Since superficial water is known to affect the superficial activity of invertebrates (Rosa et al. 2007), it was hypothesised that patches with or without superficial water may have different use by foraging waders.

The second paper examines the importance of perceptual constraints faced by dunlins when exploiting buried prey. The perceptual constraints in foraging animals have been pointed out as a major issue regarding observed deviations from classic optimal foraging models (e.g. Gray and Kennedy 1994, Spaethe et al. 2001). Waders are likely to have a particularly limited perception of the distribution of their buried prey. In a field experiment, foraging dunlins were exposed to different scenarios of prey density and aggregation, and their efficiency to forage in each circumstance was examined.

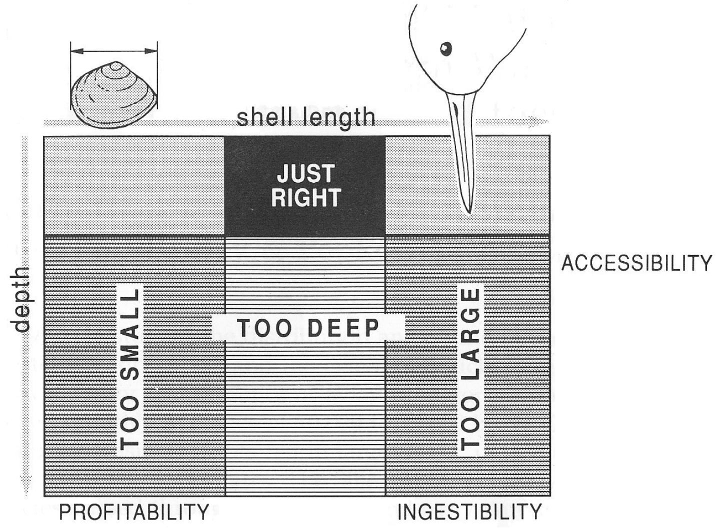


Figure 3.2. What represents harvestable prey for a knot with a bill 3.5 cm long and a gape about 7 mm wide? Some prey may be too small to be profitable, others are too large to be ingested, and prey of all sizes may be buried too deeply (from Piersma 1994)

Choosing the best foraging microhabitats: individual skills constrain the choices of dunlins

Abstract

Estuarine mudflats are among the most important foraging grounds for waders during non-breeding periods and present a complex mosaic of shallow pools and dry areas during the low tide. Little is known about how waders use such microhabitats for foraging but that may be determinant for their exploitation of estuarine food resources and ultimately affect their acquisition of energy during the non-breeding season. In this study we carried out close-range focal observations of dunlins (*Calidris alpina*) foraging in this patchy environment and determined their foraging parameters in each microhabitat. Birds foraging in wet patches mostly targeted the siphons of the bivalve *Scrobicularia plana* while in dry patches they mostly fed on mudsnails (*Hydrobia ulvae*). The visibility of prey at the surface, rather than their abundance in the sediments, explained the differences in prey selection. Feeding on dry patches provided 40% less energy intake than using wet patches, but still many birds extensively used this poor microhabitat. Because siphons retract quickly when the sediment is disturbed, birds often failed to catch them, and we found that those that failed more often tended to spend more time foraging on mudsnails in dry patches to ensure some energetic intake. The lack of skills at catching siphons can represent a major foraging constraint for dunlins wintering in the Tagus estuary, probably forcing them to forage during the high tide to achieve their daily energetic requirements and/or prevent them from undertaking their pre-breeding migration in due time. Therefore, improving skills in siphon capturing can constitute an important challenge for dunlins wintering in Tagus estuary.

Introduction

Estuaries are complex ecological systems where factors such as tides and currents shape the distribution of sediments and generate a multiplicity of intertidal habitats for living organisms (McLusky 1971). The diversity of habitats in the estuarine environment is more noticeable at a large scale, because it includes features as distinct as oyster beds and mudflats, but at a micro-scale there is also a considerable heterogeneity in intertidal areas (Thrush 1991, Underwood and Chapman 1996). The occurrence of small scale features, such as drainage channels, tide pools, macroalgae and shells generate very distinct microhabitats for organisms, particularly for invertebrates (e.g. Lopes et al. 2000, Lourenço et al. 2005, Rosa et al. 2007). Those in turn have the potential to determine the distribution of other animals higher up in the trophic web such as fish and waders (e.g. Blaber and Blaber 1980, Piersma et al. 1995, Gill et al. 2001).

Waders can respond directly to variations in abundance of their prey in different microhabitats by concentrating their foraging efforts in richer microhabitats (Lourenço et al. 2005), but their foraging can also be constrained by abiotic characteristics. For instance, low penetrability of sediments was shown to be a major constraint for the foraging of waders (e.g. Quammen 1982). Also, the presence of water on the top of sediments can promote the superficial activity of some invertebrate species, thus increasing their availability for waders (Rosa et al. 2007).

Mudflats are important foraging grounds for waders during non-breeding periods (e.g. Burger et al. 1997, Moreira 1999) and present a complex mosaic of shallow pools and dry areas caused by differential drainage of the sediments. The way waders use this matrix of microhabitats is poorly known but can raise important issues concerning their exploitation of intertidal food resources and ultimately affect their acquisition of energy during non-breeding periods.

In this study we conducted focal observations of dunlins (*Calidris alpina*) foraging in shallow pools and dry areas that are made available in mudflats during the low tide. We specifically addressed the following questions: (1) Do dunlins select particular mudflat microhabitats? (2) Is microhabitat use determined by the availability of prey? (3) How is microhabitat exploitation by dunlins related to their energy acquisition?

Methods

Study area, dunlins and microhabitats

This study was carried out in the mudflats West of Alcochete (38º45’N, 8º59’W), at the southern margin of the Tagus Estuary, Portugal. During the winter, the Tagus estuary holds about 14,000 dunlins that use primarily mudflats as foraging areas (see the first paper of chapter 2). Densities of foraging dunlins in the study area reach 20 birds per ha, which is among the highest observed in all the estuary (see the first paper of chapter 2). Mudflats in the study area are exposed for approximately three hours during spring tides (amplitude > 2.7 m), and the receding tide leaves a complex matrix of shallow depressions covered by a thin water film (less than 0.5 cm thick) and areas of completely drained sediments. These two microhabitats (hereafter wet and dry patches) present a patchy distribution, where individual patches usually do not exceed a few square meters. This microhabitat structure seems to stabilize about 30 min after the retreat of the water and at low tide peak (± 1 hr) both microhabitats cover approximately the same area.

Bird observations

During January and early February 2006 we video-taped 105 randomly chosen dunlins foraging on intertidal mudflats for periods of 1 min. All recordings were conducted in spring tides within ± 1 hr around low water time. No recordings were carried out on windy days since this could affect microhabitat structure and the behaviour of birds. Recordings were made using a MiniDV digital camcorder (NV-DS15, Panasonic) with a 20x optical zoom, which was further extended with a 1.4x lens converter. Birds were filmed with maximum optical magnification (28x) and at very close distance (from 9 to 37 meters, mean = 21, distances estimated from recordings, see the first paper of chapter 4 for details). Birds were rather numerous and flocks moved constantly along the shoreline generally in the same direction, so it is highly unlikely that pseudoreplication significantly affected our data.

Estimation of foraging parameters

Video sequences were downloaded to a computer and played back in slow-motion to record foraging parameters and prey collected in each microhabitat. Birds that spent less than 10 seconds of the focal observation in a single microhabitat were not considered in the estimates of foraging parameters for that microhabitat.

We recorded the following foraging parameters: pecking rate (pecks per min); probe rate (probes per min); siphon attempt rate (attempts to capture *Scrobicularia plana* siphons per min); and prey capture rate (prey per min). The attempts to capture siphons were easy to distinguish from regular pecks and probes because it involved long searching periods during which the bird kept the head up looking for siphons, followed by quick strikes to capture them, frequently with abrupt changes in the walking direction. Prey taken by dunlins included *Hydrobia ulvae* (mudsnail), *S. plana* siphons, *Hediste diversicolor* (ragworm), small worms (less than 1 cm long) and *Cyatura carinata* (isopod). In birds feeding on mudsnails using a pecking strategy it was difficult to observe all captures, because of the small size of mudsnails and the high rate of pecking. However, based on the closer observations, we estimated intake rate of mudsnails to be similar to pecking rate, an expected outcome since mudsnails are relatively easy to collect from the surface of the sediment. Also, the exact identification of small worms was not possible in the focal video-recordings, so we examined 50 dunlin droppings collected in intertidal areas under a microscope (400x magnification) to search for setae that allowed the identification of worms consumed (see the first paper of chapter 2 for details).

Energy intake rates were estimated (in mg of ash-free dry weight – AFDW) by summing the energetic content of each prey ingested, and were calculated separately for each bird and for both microhabitats. Energetic content for most prey was obtained in the first paper of chapter 2. The energetic content of siphons preyed by dunlins was not established for the study area, so we estimated mean size of collected siphons from 28 capturing events observed in the closest 27 recordings, and then calculated their energetic content from their size using the equation proposed by Moreira (1995a).

The efficiency of individual birds capturing siphons, their most profitable prey, was estimated by dividing the number of successes by the number of capture attempts. This parameter was estimated only for birds that made a minimum of four capture attempts.

Estimation of invertebrate abundance and surface availability

In order to estimate invertebrate abundance in each microhabitat, 20 sediment cores (86.6 cm^2, 30 cm deep) were collected in wet and dry patches. Only one sample was taken per individual patch. The top 4 cm of each sediment core was separated and sieved through a 0.5 mm mesh, while the remaining part was sieved through a 1 mm mesh. Only half of the top 4 cm sediment samples were processed due to the relatively high abundance of invertebrates. Invertebrates were stored in 70% ethanol and taken to the laboratory to be identified and counted.

The density of visible invertebrates from a “dunlin’s point-of-view” was obtained in both microhabitats by filming the surface of the sediments. The camcorder (described above) was placed obliquely with the lens 8 cm above the sediment (i.e. the height of the eyes of foraging dunlins) and covering a field of view ranging from 6 to 37 cm from the camcorder lens. This distance corresponds to the maximum distance walked by a dunlin when attempting to catch a siphon, as identified from the abrupt changes in walking direction, followed by a capture attempt (based on 20 observations). We filmed 14 wet and 13 dry patches, alternating between them, within ± 1 hr around the low water time. The camcorder was left filming unattended for 5 min in each patch after we left the site, to avoid any disturbance caused by the operator. Invertebrates re-establish their normal behaviour at the surface 2 or 3 min after being disturbed. Therefore, only a video sequence of 3 seconds, set at the fourth minute of each recording, was visualized to count visible prey. Only mudsnails and siphons were observed at the surface of the sediment. Siphons were counted within the whole viewing window of recordings. Mudsnails were counted in a smaller viewing window (10 cm range), since mudsnail feeding is conducted by dunlins at a much shorter distance.

Table 3.1. Foraging parameters and energy intake of dunlins using dry and wet patches (mean ± SE). Mann-Whitney tests (U) compare parameters between microhabitats, significant differences are indicated by ** ($p < 0.01$) and *** ($p < 0.001$).

	Wet n=93	Dry n=59	U
Foraging parameters (per min.)			
Siphon attempts	10.7±0.6	3.9±0.8	4324***
Probes	12.5±1.8	19.6±2.4	1941**
Mudsnails/pecks	22.2±4.4	82.2±10.2	1348***
Siphons	5.0±0.4	1.6±0.4	4262***
Small worms	0.6±0.2	2.7±0.5	1814***
Ragworms	0.1±0.0	0.2±0.1	2744
C. carinata	0.1±0.1	0.2±0.1	2804
Energy intake			
Energy intake (mg AFDW per min.)	26.6±1.7	15.9±1.7	3809***
Mudsnail contribution (%)	20±4	61±6	1402***
Siphon contribution (%)	75±4	28±6	2850***

Results

Feeding behaviour, diet, and energy intake in wet and dry microhabitats

Dunlins showed distinct foraging behaviour and fed on different prey in the two microhabitats. Birds targeted siphons much more frequently in wet patches, while pecking and probing were significantly more frequent in dry patches (Table 3.1). Consequently, birds captured siphons more frequently in wet patches, whereas mudsnails and small worms were more frequently captured in dry patches (Table 3.1).

The energy intake rate was significantly higher in wet than dry patches (Table 3.1). Siphons and mudsnails together represented the bulk of the biomass ingested by individual birds in both microhabitats (95% and 89% in wet and dry patches, respectively). However, the contribution of these prey for the overall ingested biomass differed greatly between the two microhabitats. In fact, while siphons represented the most important part of the ingested biomass in wet patches, mudsnails dominated in dry patches (Table 3.1).

Dropping analysis revealed that worm prey included ragworms and *Tharyx* sp., the latter being almost twice as frequent as the former. However, neither of these prey contributed significantly to the ingested biomass in the studied microhabitats. Apart from polychaete remains, only shell fragments of mudsnails were found in droppings.

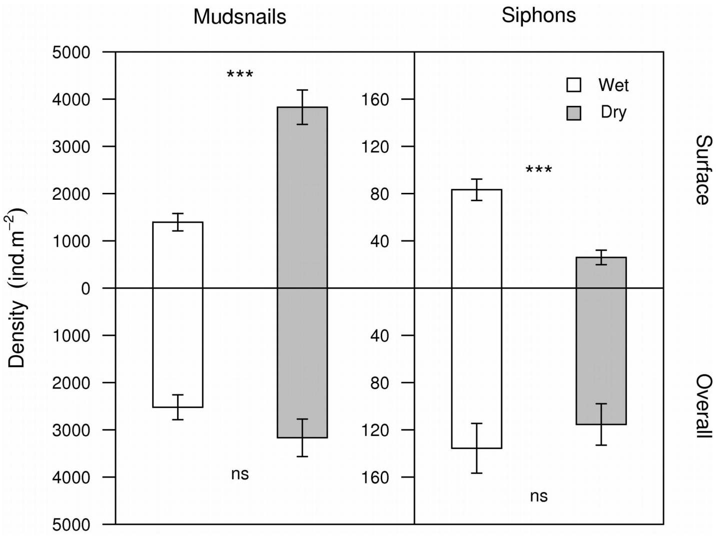


Figure 3.3. Densities (mean ± SE) of the main invertebrate prey visible at the surface and in the column of sediment, in wet and dry patches. Mann-Whitney tests compare invertebrate densities between microhabitats; ns indicates $p > 0.05$ and *** $p < 0.001$.

Table 3.2. Invertebrate densities (ind per m^2 ± SE) in samples of the top and bottom layers of sediment, in wet and dry patches. Mann-Whitney tests (U) compare densities between microhabitats, significant differences are indicated by * ($p < 0.05$).

	Top (0-5 cm)			Bottom (5-30 cm)		
	Wet n=10	Dry n=10	U	Wet n=20	Dry n=20	U
Main prey						
Mudsnails	2523±264	3170±398	155			
Adult *S. plana*				136±21	116±18	853
Small bivalves (<13mm)						
Abra sp.	58±20	92±20	154			
Juvenile *S. plana*	58±18	98±28	171	9±5	9±5	800
Crustaceans						
C. carinata	17±10	6±6	220	12±6	9±5	820
Large worms (>10mm)						
Adult ragworms				12±6	23±9	738
Nephtys hombergii				9±5	14±6	760
Small worms (<10mm)						
Alkmaria ramniji	17±10	6±6	220			
Juvenile ragworms	248±40	156±34	263			
Oligoquets	1010±196	1455±190	124*			
Streblospio shrubsolli	2627±276	3637±295	113*			
Tharyx sp.	3926±476	3886±387	194			

Invertebrate abundance and availability in wet and dry microhabitats

We found no differences in prey densities between microhabitats, as accessed by core sampling (Table 3.2). Among all invertebrates, only oligoquets and *Streblospio shrubsolli* showed significant differences between microhabitats, both being more abundant in dry patches (Table 3.2).

Mudsnails showed higher density at the surface in dry patches (Figure 3.3), similar to that obtained with core sampling, while it decreased to about half in wet patches (Figure 3.3). Siphons showed an opposite pattern being more available at the surface in wet than in dry patches (Figure 3.3). In both microhabitats only part of the *S. plana* buried in the sediment had their siphons exposed at the surface (Figure 3.3).

Efficiency in capturing siphons and relationship with microhabitat use

In average, dunlins only caught siphons in 48% (sd = 23.8%, n = 84) of their attempts. Birds showing higher efficiency in capturing siphons (i.e. a higher percentage of successful attempts) tended to spend less time in dry patches (Figure 3.4a) and reduced the number of crossings over dry patches while foraging (Figure 3.4b).

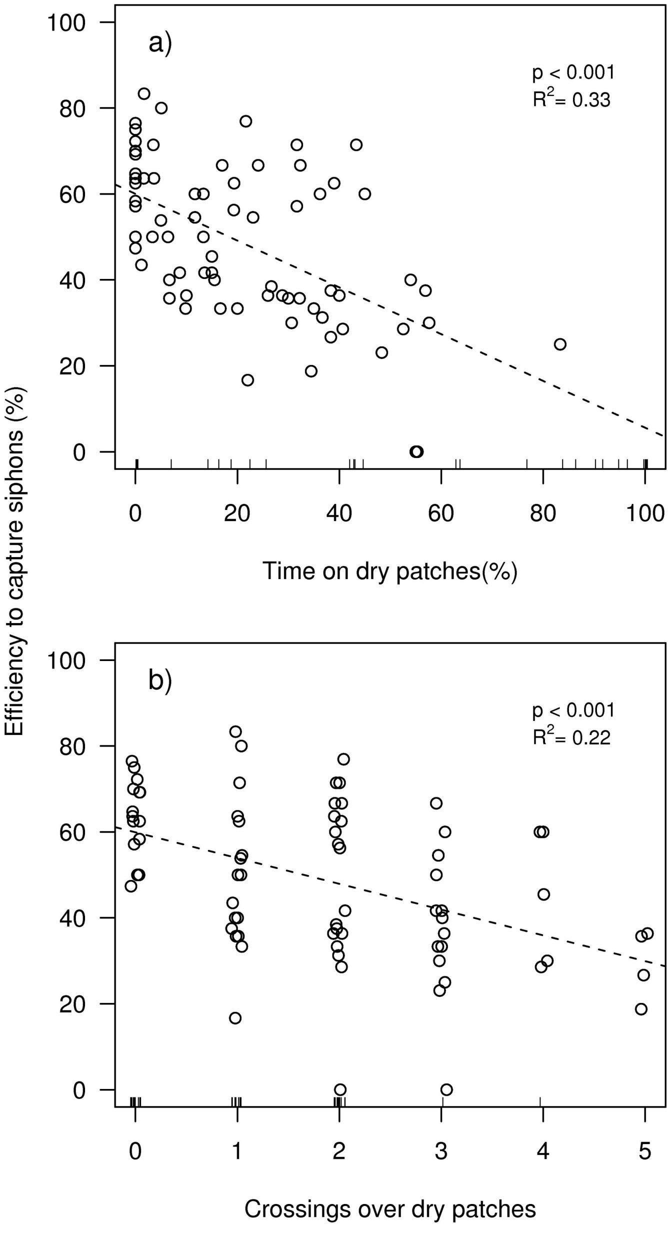


Figure 3.4. (a) Relationship between the percentage of time spent in dry patches by dunlins and their efficiency to capture siphons (percentage of successful attempts) and (b) relationship between the number of crossings of dry patches by focal birds and their efficiency to capture siphons. Rugs in x-axis represent birds that did not try to capture siphons or tried less than 4 times. Points were slightly jittered to improve readability in (b).

Discussion

Dunlins use wet and dry microhabitats differently

In this study we demonstrated that foraging dunlins adopted different foraging strategies and exploited prey at different rates in both studied microhabitats. Previous studies have already reported different patterns of use across other intertidal microhabitats by dunlins and other wader species, those including differences in bird density and in foraging behaviour (e.g. Kelsey and Hassall 1989, Mouritsen and Jensen 1992, Lourenço et al. 2005).

Here we showed that dunlins tend to forage mostly by siphon cropping in wet patches while in dry patches they mostly targeted mudsnails and small worms. These differences in prey selection determined the energetic intake of dunlins in these microhabitats. In fact, feeding on wet patches provided 1.7 times the energetic intake of dry patches. Most of the ingested biomass in dry patches came from mudsnails, while in wet patches siphons made by far the largest contribution. Dunlins also fed on small worms in dry patches despite their small contribution for energy intake. This might balance the ingestion of a large quantity of indigestible shell material from mudsnails, which is known to cause a significant digestive bottleneck (van Gils et al. 2005). It is worth noting the absence of small bivalves in the diet of dunlins, which were been shown to be a primary prey item in a previous study conducted in the same area (first paper of chapter 2). However, during the current study small bivalves were less abundant than before, probably due to weak recruitment.

Does prey distribution explain differences in use of microhabitats?

Prey densities, as obtained by ordinary core sampling, did not differ between microhabitats, even considering only the upper layer of sediments, accessible to dunlins. Similar results were obtained in previous studies of microhabitat use by dunlins, using the same methodology (Kelsey and Hassall 1989, Mouritsen and Jensen 1992). However, we found substantial differences in the density of prey visible at the surface of the sediment between microhabitats. Since birds were foraging mainly by sight, the perception of prey and thus the birds' foraging strategies should be sought in relation to the fraction of visible prey rather than with their abundance in the column of sediments.

Adult *S. plana* were present in quite similar densities in both studied microhabitats. However, the density of their siphons at the surface of sediment was much lower in dry than in wet patches. A previous experimental study showed that *S. plana* not only reduce the exposure of their siphons at the surface in dry sediments, but also reduce their sweeping rate (Rosa et al. 2007). Both factors reduce the visibility of siphons at the surface, which explains why dunlins fed on siphons mostly in wet patches. In contrast, mudsnails were more visible in dry sediments, because in wet patches they tend to burrow slightly in the top layer of the less compact sediments. In wet patches only about half of the mudsnails were actually visible, which could cause a reduction in the intake rates that may compromise their use as food for dunlins.

Why do dunlins also use the less profitable microhabitat?

Birds using dry patches got 40% less energy intake than those using wet patches, apparently due to a lower availability of *S. plana* siphons. Still, 6% of foraging dunlins used exclusively dry patches preying mostly on mudsnails, and 21% used them over 50% of their foraging time. Therefore, one may think these birds were wasting their time foraging in this low profitable microhabitat. However, in contrast to mudsnails, siphons are difficult to capture because they retract quickly when the sediment is disturbed, and in fact dunlins failed to catch them in 48% of their attempts. Therefore, it seems that collecting siphons at profitable rates requires skills that may be not attainable by all birds. In fact, we showed that the use of dry patches by dunlins tended to increase with their inefficiency to collect siphons, suggesting that inefficient birds are forced to feed in dry patches, where mudsnails were more abundant, to ensure some energetic intake. In contrast, birds that were efficient capturing siphons seemed to optimize their catch by walking along wet patches without stepping on dry patches.

The existence of differential foraging proficiencies among individual waders using the same available resources has been found to be frequently associated with age, where younger birds tend to have lower foraging proficiencies (e.g. Goss-Custard and le V. dit Durell 1987, Hockey et al. 1998). A clear age-related dietary segregation was also reported in dunlins staging in the southern Baltic Sea during the post-breeding migratory season (Dierschke et al. 1999). In that area, juvenile birds have been found to feed almost exclusively on mudsnails while adults feed on ragworms. Ragworms are much higher in energetic value but also require greater foraging skills to capture. We were not able to age our focal birds, but it is nonetheless interesting to note that the percentage of first winter birds captured with mist-nets in the closest high-tide refuge (16%, Afonso Rocha, unpublished data) was quite close to that of birds using mostly dry patches, suggesting those might be first winter birds.

The consequences of inexperience

The inefficiency in preying siphons may represent a significant energetic constraint for dunlins wintering in the Tagus estuary because *S. plana* clearly dominates the invertebrate biomass (Rodrigues et al. 2006). In fact, birds feeding exclusively on mudsnails and small worms at the observed rates would only obtain 85% of their daily energetic needs (estimate of DEE provided in van de Kam et al. 2004a), even if feeding throughout both daily low tides (diurnal and nocturnal). Such birds are probably forced to feed during high tide in order to achieve their daily energetic requirements (Velasquez and Hockey 1992, Smart and Gill 2003) and/or they would be unable to store enough fat during the winter to perform the pre-breeding migration (Summers et al. 1995, Hockey et al. 1998). However, it is also probable that inexperienced birds improved their foraging efficiency over the winter, as reported in oystercatchers (*Haematopus ostralegus*, Goss-Custard and le V. dit Durell 1987). If this is the case, learning how to capture siphons can constitute a most important challenge for dunlins wintering in Tagus estuary and probably in many other southern European estuaries.

How do waders perceive buried prey with patchy distributions? The role of prey density and size of patch

Abstract

Foraging animals are often constrained by their limited perception of the distribution of their food resources. Waders are likely to face such constraints when foraging on buried prey in intertidal sediment flats. Here we examined the extent of perceptual limitations of dunlins (*Calidris alpina*) to find patches experimentally enriched with their preferred prey, the ragworm (*Hediste diversicolor*). Patches of different sizes and with different prey densities were established in areas used by foraging dunlins to examine the effect of these two variables on the patch detection ability by dunlins. We found that most dunlins did not notice the high ragworm densities while crossing the enriched patches, presumably because they were often using a visual foraging strategy. Birds that detected the enriched patches changed their foraging strategy to feed on the available ragworms and that improved their energy intake rate by 2.9 times. In general, birds detected more easily larger and richer patches, but they seldom detected the smallest patches (0.25 m^2), even if highly enriched. The detection of enriched patches seemed to rely exclusively on tactile search, and it seems likely that a single contact with ragwoms induced the increase of tactile attempts resulting in the patch recognition. We demonstrated that waders face perceptual constraints in exploiting buried prey with patchy distributions, particularly when prey are aggregated in very small patches. This foraging constraint may have important energetic consequences at times of food scarcity or high energetic demands, and may help to explain the often reported lack of fine scale correspondence between distribution of foraging waders and that of their invertebrate prey.

Introduction

Animal foraging is ruled by a trade-off between acquiring energy from food resources and spending energy exploiting it. Classic foraging theory predicts that foragers are able to make foraging decisions that maximize their long-term rate of energy gain (MacArthur and Pianka 1966, Fretwell and Lucas 1970, Charnov 1976). A fundamental assumption of most foraging models is that animals have a complete knowledge of food distribution in the environment, based on which they can decide optimally (Gray and Kennedy 1994). However, empirical research showed that sensorial capacity of animals to evaluate the abundance of their food resources is frequently limited (e.g. Gray and Kennedy 1994, Tyler and Clapp 1995, Spaethe et al. 2001). Perceiving the foraging environment can be therefore a major constraint for making accurate foraging decisions, and ultimately can have important consequences in energy acquisition.

Waders foraging in intertidal flats have limited perception of the abundance of food resources because most of their prey are hidden in the sediments (Piersma et al. 1996). The mechanisms used by waders to find buried prey are diverse. To some extent, waders can use visual cues left by prey at the surface of sediments, but in general they mostly depend on the tactile information gathered by mechanoreceptors present in their bills (Gerritsen and Meiboom 1986, Piersma et al. 1998). Instead of getting an immediate picture of abundance of their prey, waders need to spend some time foraging to get sample information, upon which they have to make a judgement about the quality of the habitat (van Gils et al. 2003). Intertidal invertebrates are usually distributed continuously, but with patches of high abundance embedded in a matrix of lower abundance (Thrush 1991, Legendre et al. 1997). In addition, most wader species forage upon several invertebrate species that are available in the intertidal sediments (first paper of chapter 2, Goss-Custard et al. 1977), which increases the complexity of their foraging environment. Thus, one may think that waders forage in a landscape with high variability of feeding opportunities, in which their perception of food distribution can play a major role. In this scenario, it is important to understand how waders perceive their foraging environment. Are they able to recognize good quality food patches within a matrix of lower habitat quality? How concentrated should the food resources be and how large should the food patches be to become noticeable for birds in feeding activity? Answering those questions can help to clarify if waders make full use of the available resources, and shed light on our understanding of how waders use intertidal habitats.

In this study, we used dunlins (*Calidris alpina*) and ragworms (*Hediste diversicolor*) as a predator-prey model to examine the role of perception in the foraging of waders. Ragworms are a preferred prey for dunlins in many estuarine areas worldwide (first paper of chapter 2, Worrall 1984, Dierschke et al. 1999). We created enriched patches of ragworms in intertidal areas used by foraging dunlins, and examined their efficiency in finding these patches. We hypothesised that both density of ragworms and patch size influence this efficiency, so we manipulated both variables in the experiments.

Methods

Study site, dunlins and ragworms

This study was conducted in the intertidal flats west of Alcochete (38º45'N, 8º59'W), in the southern margin of the Tagus Estuary, Portugal. The study area is dominated by mudflats and is exposed for approximately three hours during spring tides (amplitude > 2.7 m). During Winter, dunlins forage on these flats in densities ranging from 10 to 25 birds per ha (first paper of chapter 2), usually in flocks that move along the shoreline. Ragworms are a highly preferred prey for dunlins in the Tagus estuary, but are relatively scarce in the study area (ca. 5 individuals per m^2; first paper of chapter 2).

Experimental set-up

From February to March 2006 and January to February 2007, we experimentally increased densities of ragworms in quadrats set in intertidal flats. The enriched patches were created in all combinations of three levels of ragworm density (200, 400, and 800 ragworms per m^2) and three levels of patch size (0.25, 1, and 4 m^2). Each trial began by setting two to 10 enriched patches in one to three lines perpendicular to the coastline (Figure 3.5). Enriched patches within each line were set at least 5 m apart, and lines were separated by at least 50 m. Since dunlins move mainly along the coastline, this arrangement reduced the likelihood of a given individual to contact with more than one enriched patch. Live ragwoms were obtained from a local commercial bait dealer, and used at most two days after being collected. During low tide, ragworms were carefully seeded by hand in the sediment following an approximately uniform distribution. A large wood plate was used as a support during seeding, to avoid reworking the sediments or leaving any significant markings that could attract to or deter birds from the experimental patches. Bird observations started on the day after seeding and did not extend for more than four days in the same enriched patches. When the observation period finished both the enriched patches and the adjacent intertidal areas (used as control, see Figure 3.5) were sampled to estimate the postexperiment ragworm densities. Five to 20 sediment cores (86.6 cm^2, 30 cm deep) were collected in the enriched and control areas (the number of cores depending on the size of the areas). The sediment cores obtained from the enriched patches were split in three layers, top 5 cm, 5-10 cm and 10-30 cm deep. Samples from the same area were pooled and sieved locally through a 1 mm mesh, or 0.5 mm for top 5 cm layers. Ragworms were stored in 70% ethanol and taken to the laboratory, where they were counted and measured. Also, we evaluated the density of ragworm holes at the surface of the sediment by counting them in a sub-area (0.25 m^2) of the enriched patches at the end of each experiment. The full procedure was repeated until we achieved at least three replicates of all combinations of density and patch size, and until a minimum of 30 birds were filmed in each combination.

Bird observations and data processing

Focal recordings were carried out from the shore using a MiniDV digital camcorder (NV-DS15, Panasonic) with a 20x optical zoom, which was further extended with a 1.4x lens converter. Typically, two observers were positioned in two distinct viewpoints each aligned with three enriched patches (Figure 3.5). Birds were filmed as they entered the control area and until they left the enriched patch (Figure 3.5). After that the birds were observed through binoculars until they left our range of vision. Birds that returned to enriched patches were not filmed. Birds that only crossed a small fraction of the enriched patches (less than its width) were also excluded. The limits of the enriched and control areas were marked with short sticks in each corner, and were clearly visible in all videos. The 0.25 m^2 patches were filmed using an automatic recording system, due to the comparatively lower frequency of birds crossing the experimental areas. The system was composed by four mini board-cameras connected to a quad multiplexer that recorded the video signal of all cameras simultaneously into a portable video recorder (full details of the equipment are provided in Rosa et al. 2007). The cameras were mounted on 2 m poles, 6 m away from the enriched patches, and the field of view of each camera encompassed one enriched patch and the control areas around it. Video sequences were downloaded and analysed in a computer to obtain foraging parameters of birds crossing control and enriched areas. We quantified the following parameters: time spent foraging (in seconds); pecking rate (pecks per minute); probe rate (probes per minute); and step rate (steps per minute). The recordings obtained with the board-cameras did not allow the distinction between probes and pecks, and so these parameters were not quantified.

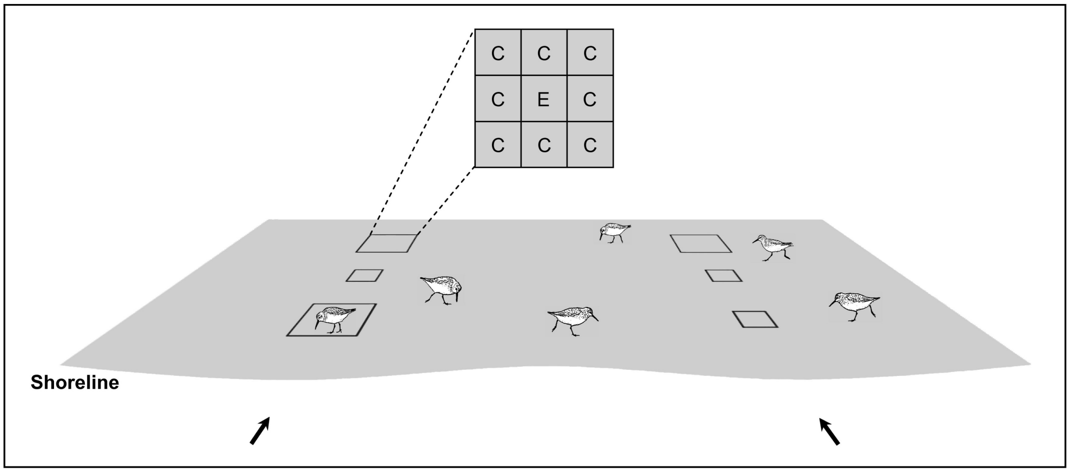


Figure 3.5. Diagram representing the sampling scheme. Arrows indicate viewpoints, “E”, and “C” indicate enriched and control areas, respectively.

Birds were considered to have detected the enriched patches if their residence period was comparatively longer than in control areas. To identify these birds we plotted the amount of time birds spent in the enriched patches against the time spent in the control areas. In general, individuals not detecting ragworm enrichments should spend about the same amount of time in both areas and so they should lie along a $y = x$ relationship, within an interval of natural variability due to different individual behaviour and velocity of progress in intertidal areas (see Figure 3.6). The limits of natural variability were set at a distance of the largest negative residual (Figure 3.6). In contrast, birds that detected the enriched patches should slow down and so were expected to spend an above-average period in treated areas.

To estimate the possible energetic gain of feeding in the enriched areas, we used recordings of birds that spent at least 1 minute feeding on those areas and were obtained close enough to observe all prey being ingested (n = 18). In addition, we made similar close-range video recordings of 105 birds feeding in non-enriched areas. All these recordings were visualized in a computer to obtain the frequency and type of prey ingested. Energy intake rate was estimated for birds feeding inside and outside the enriched areas by multiplying the mean frequency of capture of each prey and their respective energetic content (in mg of ash-free dry weight – AFDW). Prey energetic content was obtained in the first paper of chapter 2 for *Hydrobia ulvae* (gastropod), *Cyathura carinata* (isopod) and small worms, and from Moreira (1995b) for *Scrobicularia plana* (bivalve) siphons. For ragworms preyed inside the enriched patches, we used mean size of ragworms that could be reached by dunlins (present in the top 5 cm layer of sediment), and for those preyed in natural environment we used the size obtained in the first paper of chapter 2. In both cases their energetic content was estimated from the size using the equation proposed by Moreira (1995b).

Statistical analysis

We used log-linear models to seek for dependency relationships between detection of enriched patches by dunlins, ragworm density, and the size of the patch. Data was summarized in a multiway contingency table including the following categories: detection of the enriched patch by dunlins (detected or not); patch size (0.25, 1 or 4 m^2); and ragworm density (200, 400 or 800 individuals per m^2). Data from replicates were pooled. In this approach the null hypothesis is that all three variables are mutually independent, and the alternative hypothesis is that there are dependency relationships among variables. We built the independence model and the models with all combined interactions between variables, and compared those with the saturated model (which includes all interactions between variables) using the likelihood ratio test statistic (G^2). We selected the simplest model that did not differ significantly from the saturated model. All computations were performed using the freely available statistical software R (R Development Core Team 2005).

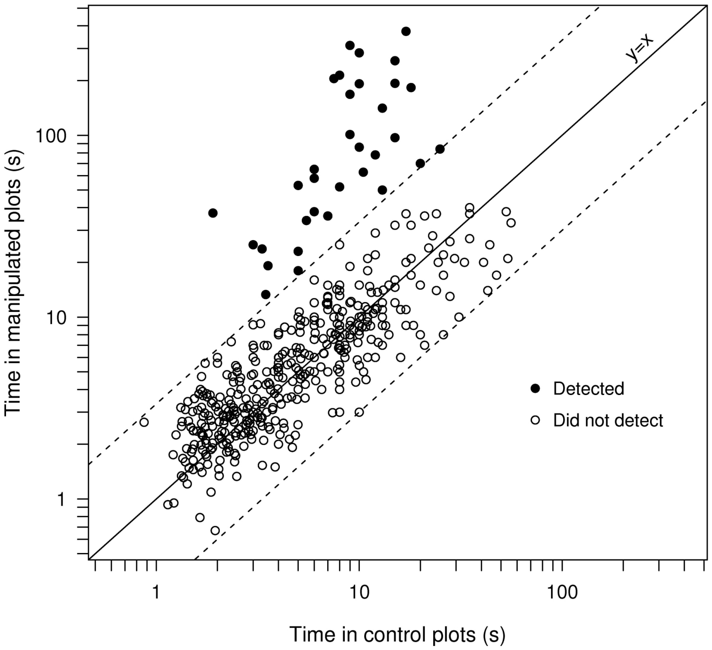


Figure 3.6. Decision criteria for classifying dunlins that detected enriched patches (marked as solid points). Individuals were considered as not having detected the enriched patches if lay along the $y = x$ relationship, within intervals set at the distance of the largest negative residual. Individuals were considered to detect enriched conditions if positioning above the upper interval line (for explanation, see methods).

Means are presented with standard error across the text otherwise it is stated. Bonferroni corrections were implemented whenever multiple two sample tests were used.

Results

Ragworm densities in experimental patches

At the end of the experiments enriched patches had lost on average 29% (SD = 18.5) of the ragworms that had been placed there. This loss was similar across patches with different sizes and ragworm densities (two-way ANOVA: ragwom density effect, $F_{2,28}$ = 0.42, p = 0.66; patch size effect, $F_{2,28}$ = 0.40, p = 0.68). Also, the loss of ragworms was not correlated with the duration of the experiment (Spearman r = 0.09, n = 29, p = 0.86), thus we assumed that this loss corresponds to ragworms that either died or left enriched patches shortly after the seeding. Densities of ragworms in the control areas were 10.5 ± 2.8 individuals per m^2, and had no relationship with the density of the corresponding enriched patches (Spearman r = 0.23, n = 33, p = 0.099). Ragworms showed a vertically structured distribution in the sediments. Most individuals occupied the 5-10 cm and the 10-30 cm layers of the sediment (38 and 56% respectively) and only 6% were the top 5 cm of the sediment. The number of ragworm holes at the surface of sediment showed a strong linear relationship with ragworm density (r^2 = 0.84, n = 27, p < 0.001, slope = 0.9 ± 0.1).

Table 3.3. Behavioural parameters of dunlins in enriched and control areas, according to their response to manipulated feeding conditions. Mean ± SE, number of focal birds (n), and paired Mann-Whitney test statistics (for peck and probe rate) or Student-*t* test statistics (for step rate), are indicated for each case. Significant comparisons are indicated by *** (p < 0.001, after Bonferroni correction).

	Did not detect				Detected			
	Control	Enriched	n	Statistic	Control	Enriched	n	Statistic
Peck min^{-1}	12.8±1.3	13.3±1.1	225	6233	21.3±3.7	16.7±1.7	27	201
Probe min^{-1}	21.8±1.0	21.8±1.0	225	11615	26.1±3.1	53.1±2.4	27	12***
Step min^{-1}	206.8±3.9	203.2±3.7	404	0.83	171.1±11.4	74.3±6.1	33	8.79***

Detection of enriched patches

Only 8% of the birds detected ragworm enrichments, remaining substantially longer in enriched patches than in corresponding control areas (Figure 3.6). These birds significantly increased their probe rate and decreased their step rate in the enriched areas (Table 3.3), and consumed exclusively ragworms. Also, 15% of these birds showed aggressive behaviour against birds passing close to the enriched patch. In contrast, no differences were observed in any of the behavioural parameters of the remaining birds (Table 3.3), and these were never seen ingesting ragworms in enriched patches.

Detecting and non-detecting birds differed in their foraging behaviour before contacting with enriched patches. Birds detecting ragworm enrichments were pecking at a higher rate (Mann-Whitney test with Bonferroni correction: U = 1991, p = 0.006) and had a lower step rate (Student-t test with Bonferroni correction: t = 3.0, p = 0.01) in control areas, as compared to birds not detecting the ragworm enrichments.

Birds foraging in enriched patches ingested 0.5 ± 0.1 ragworms per minute, corresponding to 49.9 ± 8.2 mg of AFDW per minute. The energy intake rate in non-enriched areas was 17.4 ± 1.1 mg of AFDW per minute, and diet was mainly composed by *H. ulvae* and *S. plana* siphons, representing 85% of the ingested biomass. Ragworms represented only 9% of the ingested biomass in non-enriched areas.

Table 3.4. Log-linear models for dunlins exposed to manipulated conditions. Individuals were cross-classified based on detection of the enrichment (Dt: detected or not), size of the patch (Si: 0.25, 1 or 4 m^2), and density of ragworms (De: 200, 400, 800 ind.m^{-2}). Degrees of freedom (d.f.), likelihood ratio test statistics (G^2), and p-value, are indicated. Low p-values indicate discrepancy between model and the full model (lack of fit). Testing parameters of the best-fitting model are in bold.

Models	d.f.	G^2	p-value
Independence	12	40.7	<0.001
All two way interactions	**4**	**3.5**	**0.484**
Dt x Si + Dt x De	8	22.4	0.004
Dt x Si + Si x De	6	13.3	0.038
Dt x De + Si x De	6	14.2	0.028

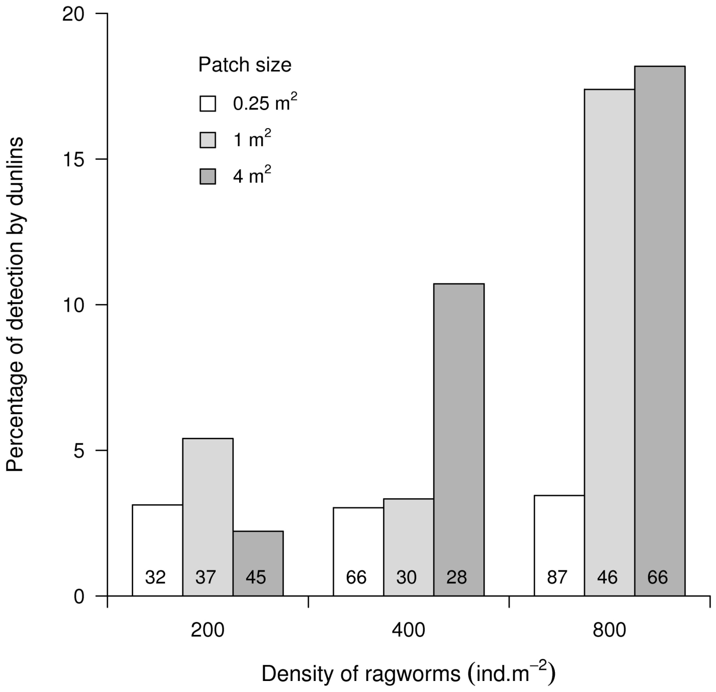


Figure 3.7. Effects of patch size and densities of ragworms on the percentage of birds that detected enriched patches. There were significant log-linear associations between both variables, and between each of them and the detection of patches by birds. The overall number of individuals observed is indicated inside the bars.

Detection rates across densities of ragworms and patch size

Log-linear analysis showed a significant dependence between the ability of dunlins to detect an enriched patch, the density of ragworms and the size of the patch (Table 3.4). The best model included the all two-way interactions, and the inclusion of the three-way interaction did not produce a significantly better model (Table 3.4). The removal of any of the two-way interactions produced poorly fitted models (Table 3.4). In fact, the percentage of birds that detected enriched patches tended to rise with the increase of both density of ragworms and patch size (Figure 3.7). However, there was a clear interaction between these two factors. In the smallest patches (0.25 m^2) the percentage of detection was below 4% for all ragworm densities (Figure 3.7). In 1 m^2 patches this percentage was also low for densities of 200 and 400 ragworms per m^2, but increased to 17% in patches of 800 ragworms per m^2 (Figure 3.7). Finally, in the 4 m^2 patches the percentage of detection increased gradually with the density of ragworms, reaching to 18% in patches with 800 ragworms per m^2 (Figure 3.7).

Discussion

In this study we demonstrated experimentally that foraging dunlins face perceptual constraints when exploiting buried prey in their foraging intertidal environment. Most of the birds that crossed the enriched patches did not recognize the improvement in the feeding conditions. In contrast, birds that did find the enriched patches changed their foraging strategy to feed on ragworms, thereby increasing their energy intake rate by almost a factor of 3. We also showed that such constraints depend on the foraging strategy used by the birds and on the characteristics of the food patch, particularly on prey density and on size of the patch. These issues will be discussed below, together with the mechanisms of patch recognition. Finally, we will discuss the implications of these findings for the understanding of how waders exploit food resources in intertidal areas.

Influence of foraging strategy in patch detection

Dunlins are known to use different foraging strategies to search for different prey species within the same foraging area (Kelsey and Hassall 1989, Mouritsen 1994). Birds that noticed the enriched patches were behaving differently from those birds that did not detect such patches. In fact, the observations made just before birds entered the enriched patches demonstrated that these birds walked slower and pecked more often, which certainly increased the likelihood of contacting with buried ragworms or their cues.

These results suggest that the low detection of enriched patches reflected the use of a dominating visual foraging strategy by the majority of foraging birds. In fact, most dunlins in the study area were preying upon *S. plana* siphons and *H. ulvae*, which are mostly located by sight (Moreira 1995b). Presumably, the use of a dominant visual strategy to feed on prey available at the surface of the sediments may have reduced their capacity to detect buried prey, which was mostly found by tactile searching. Nevertheless, it is unlikely that higher detection rates due to a more tactile foraging strategy would produce different patterns of detection across increasing food densities and patch size.

The influence of prey density and patch size on patch detection

In general, birds were more prone to detect larger and richer patches. However, these two factors were found to interact in determining patch detection. There was little detection of the smallest enriched patches regardless of the density of ragworms. This was probably related with the low number of feeding attempts (pecks or probes) done while crossing such patches. In fact, birds that did not detect ragworm enrichments made an average of just 1.3 feeding attempts in those patches, which is likely to be insufficient to detect an increase in the density of prey. Previous experiments also found other waders species to be unable to detect 0.25 m^2 patches that were kept enriched with buried prey for over a month (Cummings et al. 1997), which supports the idea that waders have in fact limited ability to recognize very small patches of buried prey.

In addition, the detection of medium (1 m^2) and larger (4 m^2) patches enriched with 800 ragworms per m^2 was similar. This indicates that at least for birds using a more tactile foraging strategy, 1 m^2 may represent the threshold of area for detecting such density of ragworms.

The mechanisms of patch recognition

The sensorial mechanisms used by waders to detect individual prey have already been described (e.g. Gerritsen and Meiboom 1986, Nebel et al. 2005), but the mechanisms used to recognize a patch of high density of buried prey within a matrix of lower density of prey are poorly understood. When foraging on sediment flats, what information do waders use to recognize that they hit a patch rich in buried prey?

Our study suggests that birds do not rely on visual cues to detect a high abundance of buried prey. In fact, a high amount of ragworm holes was clearly visible in the surface of the sediment, even in the smallest and least enriched patches, and yet birds failed to recognize them. Instead, birds seemed to depend on discrete tactile foraging attempts to become aware of the high density of ragwoms. Given the low number of probes (4 per m^2) it seems likely that a single contact with a ragworm (even without involving a capture) would trigger further tactile attempts resulting in a positive feedback mechanism eventually leading to patch recognition. In fact, it has been demonstrated that tactile waders increase their foraging effort in the close vicinity of a place where a prey was captured (Dias et al. 2009), which indicates a patch recognition reaction to the capture of a single prey.

Implications of perceptual constraints to the foraging of waders

We demonstrated that dunlins face perceptual constraints in exploiting buried prey with patchy distributions, particularly when prey are aggregated in very small patches. While such perceptual constraints may depend on the foraging behaviour of waders and vary across wader species and prey being used, the inefficiency to find small aggregates of buried prey seems to be a common trait as it was demonstrated previously for several wader species (Cummings et al. 1997). It is difficult to evaluate the relevance of such foraging constraints due to the lack of information on the small scale patchiness of their prey, but some studies found that intertidal invertebrates are often arranged in patches of less than 1 m^2 (e.g. Reise 1979, Schaffner 1990). One may also expect that, when small patches of prey are common and temporally stable, birds will show some level of adaptation to exploit those patches. In fact, it was demonstrated that distance between patches influences their exploitation by birds (Vahl et al. 2007). However, if invertebrate distribution is less predictable, one may expect that waders will frequently miss small prey aggregates due to perceptual limitations. This may cause an increase in the efforts to find prey, or force birds to redirect their search to alternative prey, potentially less profitable. Either way, birds will experience reduced foraging efficiency (Hinsley 2000, Berec et al. 2003), which could be a relevant issue in periods of food scarcity and/or high energetic demands.

The results presented here can also help to understand the effects of spatial scale on the strength of the relationship between the distribution of birds and invertebrates in the estuarine environment. In fact, the limited ability to perceive small-scale concentrations of prey will deteriorate the correlations between the fine scale distribution of birds and that of their invertebrate prey, which has been observed in several studies (e.g. Kelsey and Hassall 1989, Wilson 1990). Conversely, large-scale relationships will be comparatively less affected and in fact the empirical evidence support this idea (Colwell and Landrum 1993). Factors other than the perception of abundance of prey by individual birds may determine the large scale distribution of waders on their foraging sediment flats. Those include previous knowledge of habitat quality, which is facilitated by the higher stability of invertebrate densities at large spatial scale (Morrisey et al.

1992, Underwood and Chapman 1996), and information exchanged between individual waders due to flocking behaviour (Clark and Mangel 1984).

Field studies on wader foraging ecology usually assume that the densities of foraging birds should relate directly with “crude” invertebrate densities, but in addition to measuring the abundance of buried prey, it is important to understand their spatial structuring, as this can limit their availability for waders. This is particularly important when trying to establish carrying capacity of feeding areas. The availability of food resources for waders can be dramatically overestimated if we assume that overall biomass is fully available (Zwarts and Wanink 1991, Coleman 2008). One should keep in mind that the way we sample prey availability may not necessarily reflect how waders perceive their foraging environment.

CHAPTER 4

FORAGING AT NIGHT

Overview

The nocturnal activity has been traditionally attributed to a minority of bird species or groups commonly known as nocturnal birds. However, among waders and other shorebird species, night foraging behaviour seems to be a common trait (McNeil et al. 1992). Although there are no reports of species foraging exclusively at night, many forage regularly both in daylight and at night (McNeil et al. 1992). Until recently, the nocturnal behaviour of waders was largely unknown due to the technical limitations of observing them in the darkness. This scenario has changed after the development of night vision equipments. However, most commercial night vision equipments have low zoom power or/and are extremely expensive. Studying the foraging behaviour of waders in the field, even during the day, requests observation equipments with high magnifying capacity because waders normally do not tolerate the presence of humans closer than a few tens of meters (Lafferty 2001). In order to study the nocturnal foraging behaviour of waders it was developed an observation equipment that was adequate to night vision and had a magnification capability similar to that of the equipments used to observe wader foraging behaviour during day-time. In the first paper of this chapter is provided a technical description of such equipment and an objective evaluation of the efficiency of this system to study the nocturnal foraging behaviour of waders.

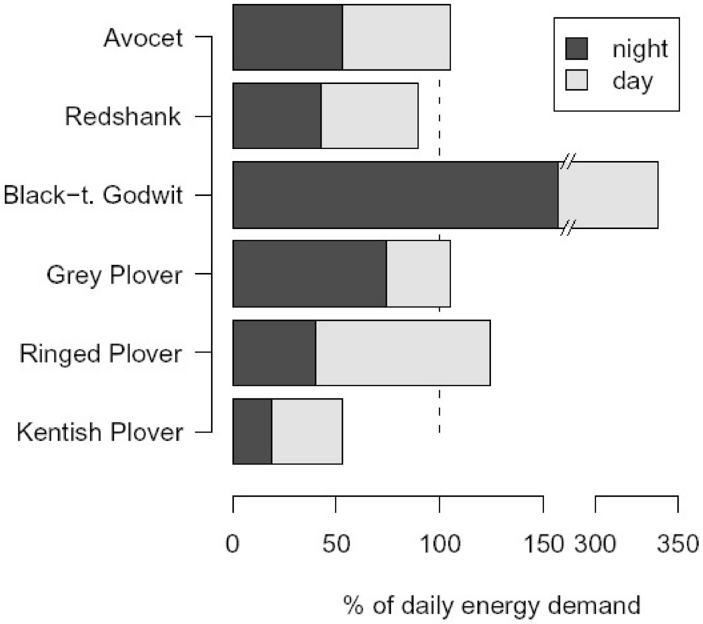


Figure 4.1. Relative energetic importance of day and night foraging for waders in the Tejo estuary. The vertical dashed line represents the estimated daily energetic demand (from Lourenço et al. 2008).

There are two main hypotheses explaining the night foraging behaviour in waders and other shorebirds: (1) the “supplementary hypothesis” which states that night feeding occurs when day-time feeding has been inadequate to meet the birds’ energetic requirements; and (2) the “preference hypothesis” which states that birds prefer to feed at night because it provides the most profitable, or safest, feeding opportunities (McNeil et al. 1992). In waders foraging in tidal areas, nocturnal foraging is largely seen as a complement of diurnal foraging. In fact, most species are known to obtain a larger fraction of their energy requirements during the day (Figure 4.1, Dodd and Colwell 1996, Lourenço et al. 2008). Moreover, waders are known to increase their nocturnal foraging activity in pre-migrating periods, when the energetic demands are higher (Zwarts et al. 1990a, Kalejta 1992). Nevertheless, there are some wader species particularly well adapted to forage during the night. Plovers in particular possess large eyes and high retinal rod:cone ratios, allowing them to forage by sight even in low light conditions (Rojas et al. 1999). For those species the preference hypothesis can be applied, in particular when disturbance or predation are higher during day-time (Lourenço et al. 2008).

It is evident that light can be a very important constraint for waders foraging at night. Even for the most tactile species, vision can be important for identifying cues of prey at the surface of sediments or for choosing feeding areas (Gerritsen and Meiboom 1986). Most wader species, plovers included, decrease foraging attempts and consequently prey intake rate at night, and some that use visual foraging during the day are forced to forage tactilely at night (Robert and McNeil 1989, Lourenço et al. 2008). Moreover, there is evidence that moonlight has a beneficial effect on the nocturnal foraging of waders. In fact, waders react to moonlight by increasing their feeding rates and/or using more visual search than in darker nights (Turpie and Hockey 1993, Dodd and Colwell 1998).

In the second paper of this chapter it is investigated how foraging waders respond to the artificial illumination that currently affects many estuaries and coastal wetlands. Light pollution has gained enormous proportions in the last decades, and presently affects a large portion of the globe (Figure 4.2). Although it is expectable that light pollution affects the nocturnal foraging of waders, this was never examined before.

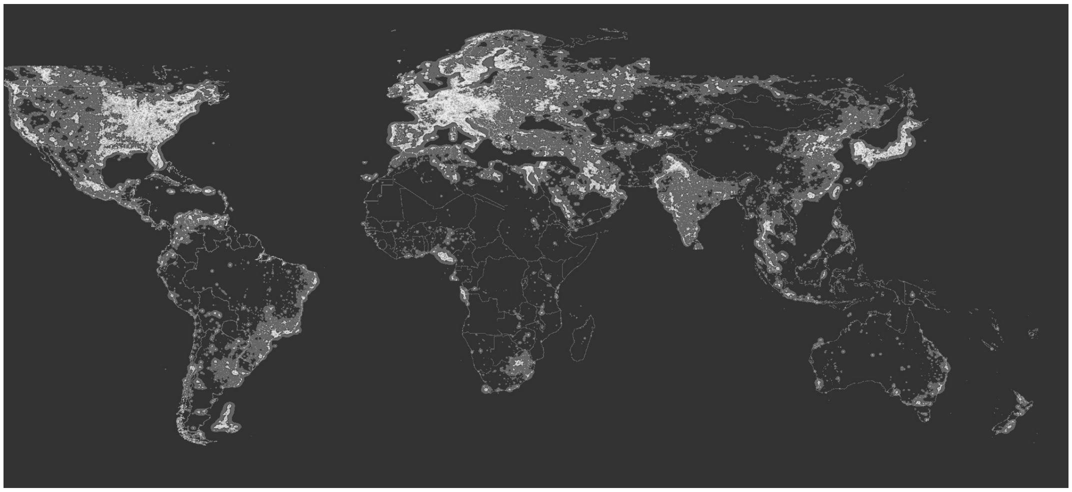


Figure 4.2. Artificial night sky brightness at sea level in the world. The map has been computed for the photometric astronomical V band, at the zenith, for a clean atmosphere with an aerosol clarity coefficient K = 1. The calibration refers to 1996–1997 (from Cinzano et al. 2001).

Birds after dark: an efficient and inexpensive system for making long-range observations at night

Abstract

The ability of investigators to study the behaviour of animals at night is often limited by the difficulties of making observations in the dark, particularly at a distance. Indirect techniques, such as radio tracking, generally produce limited behavioural data, and most night-viewing equipment tends to be both inefficient for making long-range observations and expensive. We describe a long-range night vision system consisting of a camcorder and infrared laser illuminators. We tested the performance of this system by comparing our ability to quantify the foraging behaviour of waders during the day and at night. Distance thresholds for detecting ingestion of prey and for identifying them were similar during the day and night for all species, and we found no differences between distances of observations made during the day and night in prey capture and ingestion and ability to identify prey for any focal species. At night, we were able to quantify all foraging parameters for all species at distances up to 59 m, and to count pecks and steps at distances greater than 200 m for some species. The observation system we describe can be further improved by using camcorders with higher optical zooms or more powerful infrared laser illuminators. Because of its efficiency and relatively low cost, this system has the potential for being useful in many other applications that require long-range observations of animals at night.

Introduction

Many animals are active at night, but information about their nocturnal behaviour and ecology is often limited by the difficulties of making observations in the dark. Some investigators have attempted to solve this problem by using indirect techniques, such as radio tracking (Whittingham 1996, Lewis et al. 2005) and examining traces of activity, such as tracks or footprints (Lernen and Freeman 1985, McCurdy et al. 1997). However, the amount and quality of the information collected using such indirect methods is limited. Night vision devices that use light enhancement, or image intensifiers, are an alternative that allow direct observation of nocturnal behaviour, and they have been used by many investigators (Robert and McNeil 1989, Klinka and Reimchen 2002, Rohweder and Lewis 2004). However, most of the best third or fourth generation image intensifiers are expensive and have low zoom power, restricting their use for long-range observations. Night vision devices that use thermal infrared radiation are promising for some applications, but are more expensive than the last-generation image intensifiers. In addition, their ability to detect animals in complex habitats is limited (Ditchkoff et al. 2005) and they are less useful for observing ectotherms because they depend on thermal IR radiation emitted by their bodies (Kuwae 2007).

The Charge-Coupled Devices (CCD) of camcorders that capture images are highly sensitive to reflected near-infrared (IR) radiation (not to be confused with thermal IR). However, in normal mode, this radiation is blocked by an IR filter between the lens and the CCD. To increase the sensitivity of camcorders to IR light, several models now include a switch that displaces the IR filter. This allows more IR radiation to reach the CCD, and extends the capacity of camcorders to work under low light conditions. Some can even record in complete darkness, thanks to built-in IR illuminators (usually a high-power IR light-emitting diode, or LED), but only at short range (about 3 m). IR illumination has the advantage of being largely invisible to vertebrates, but its short-range limits field observations.

The lack of long-range IR illumination is a major constraint for the use of camcorders as night-viewing devices, but illumination can be provided using laser IR illuminators. Lasers produce a narrow beam of concentrated light that can illuminate even distant animals. Observers can then take advantage of the zooming capacities of camcorders and make observations using the viewfinder or built-in screen while simultaneously recording. If enough IR light is provided, image quality can be quite good, even in complete darkness.

Here we describe and evaluate the performance of an inexpensive system to make long-range night observations using a camcorder and a pair of IR laser illuminators. We present the results of an objective evaluation of this system's efficiency in a study of the nocturnal foraging behaviour of waders.

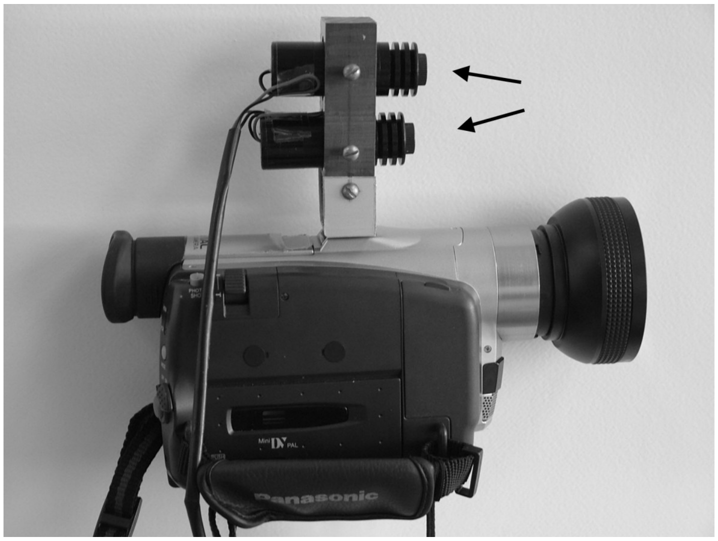


Figure 4.3. Night vision system consisting of a camcorder with IR laser illuminators (pointed by arrows).

Methods

From late January to early May 2005, five species of waders were video-taped during both day and night while foraging on intertidal flats of the Tagus Estuary, Portugal (38º42'N, 09º01'W). Thirteen areas of intertidal flat ranging in size from 1 to 7 ha were visited on consecutive day/night low tides during spring tides (amplitude above 2 m). Taping was conducted between 7:30 and 15:30 during the day and between 19:30 and 3:30 at night, within ± 3.5 hr of low tide. Randomly chosen birds were taped for 2-min periods and then were followed by another observer to reduce the chances of taping the same individuals. Taping sessions ranged from 2 - 50 min (mean = 19 min) in duration. Within each area, birds were filmed from the same locations (n = 1 to 3 depending on the area) during both day and night.

Recordings were made with a MiniDV digital camcorder (NV-DS15, Panasonic, Osaka, Japan) with a night view (0 lux) mode that displaces the IR filter from the path of the light reaching the camcorder CCD. This camcorder has an 800,000-pixel resolution and a 20x optical zoom that was further extended with a 1.4x lens converter. At night, we used the camcorder's night view mode, with long-range illumination provided by two IR laser diode modules (RLDB808-350-3, Roithner LaserTechnik, Vienna, Austria). Used primarily for industrial applications, these modules also work well as IR illuminators, with peak emission at 808 nm, output power of 350 mW, a life of more than 5000 hr of use (according to the manufacturer), and a focusable collimating lens that can be used to adjust the beam angle. The module operates with 3 V direct current, so we used two

1.5 V D-size alkaline batteries that lasted for about 3-4 hr with good illumination. The two IR illuminators were attached to the camcorder hot shoe with the aid of a custom-made adapter (Figure 4.3).

IR radiation becomes harmless to the eyes of birds beyond a range of just a few meters because the lens of the modules spreads the laser beam, and the amount of incident radiation per unit area quickly drops. Even so, birds were never taped at distances closer that 15 m for safety reasons. The illuminators emit a tiny amount of visible radiation that produces a faint red glow visible from a distance when looking directly at the illuminator. After systematically turning the IR illuminators on and off, we did not notice any abnormal behaviour by the birds in response to the presence of the glow and so did not attempt to eliminate it. However, this glow can be eliminated by placing an IR pass filter in front of the lasers. Nocturnal light levels varied with moon phase, cloud cover, and proximity to artificially illuminated areas, but this variation had no apparent effect on the performance of our night vision system.

Video sequences of foraging waders were downloaded to a computer and played back to determine number of pecks, steps, and prey ingested per minute of observation (i.e., prey intake), and, when possible, type of prey ingested. Our observations of the types of prey taken by waders in our study matched those reported in previous studies in the same area (first paper of chapter 2, Moreira 1996), and included the following locally abundant species: *Scrobicularia plana* (bivalve), *Hediste diversicolor* (polychaete), *Carcinus maenas* (crab), and *Hydrobia ulvae* (gastropod). Therefore, we identified and categorized prey as: (1) polychaetes (mainly *H. diversicolor*), (2) *S. plana* siphons, (3) juvenile *S. plana*, and (4) *C. maenas*. Prey size varied considerably, ranging from juvenile *S. plana* (ca. 7 mm) to large *H. diversicolor* (ca. 8 cm). Smaller prey, such as *H. ulvae* (ca. 0.5 to 3.5 mm), were also taken, but would have been frequently missed in our observations and so were excluded from analysis. Prey were identified based on shape, size, and behaviour. Both polychaetes and siphons have worm-like shapes, but siphons can be easily distinguished by the absence of any movement when captured. Juvenile *S. plana* have an elliptical shape and were taken after deep searches in the sediment. *C. maenas* were captured at the surface of sediment and their crab shape made their identification quite straightforward.

Table 4.1. Maximum distances (in m) at which we were able to quantify wader foraging behaviour during the day and using the night vision device at night. Intervals represent the approximate maximum distance for observing behaviour. For categories where the foraging parameter could be determined for all video-taped birds, the maximum distance at which observations were made is presented. Bird length (from bill tip to tail tip, in cm) is provided for comparison (following Cramp and Simmons 1983).

Species	Bird	Prey intake		Identifying prey		Steps	Pecks	Sample size	
	length	Day	Night	Day	Night	Night	Night	Day	Night
Kentish plover	15-17	>135	92-93	66-69	59-62	>114	>114	33	54
Ringed plover	18-20	95-173	107-113	88-95	91-92	>218	>218	54	131
Dunlin	16-20	73-83	64-67	54-56	60-62	>92	>110	34	90
Grey plover	27-30	171-179	143-149	149-152	137-143	>332	>332	66	63
Redshank	27-29	108-111	108-111	104-108	86-89	>156	>156	81	74

All foraging parameters were categorized as either 0 or 1 (0 if the parameter could not be estimated and 1 if it could) so the effect of distance on the quality of observations could be examined. To estimate distances, we established a relationship between distance and size on the computer screen using a 22-cm ruler video-taped at several reference distances (range = 20 - 120 m). This relationship was then standardized relative to the body size of each species, allowing us to estimate distance based on the size of the birds on the screen.

Figure 4.4. Captured frames from video recorded using our night vision system. A ringed plover at 25 m (top) and a grey plover at 85 m (bottom) during daylight (left) and at night (right).

We evaluated the performance of this system for studying wader foraging behaviour at night by comparing the distance thresholds for observing behaviour during the day and night. We also compared the distribution of diurnal and nocturnal observations of each behavioural parameter over a gradient of distances using a Kolmogorov-Smirnov test. We did not include ringed plovers (*Charadrius hiaticula*) in these comparisons because they tended to forage further from the coastline (where observers were located) at night. This would have result in significant differences due to the spatial distribution of the individuals and not to visibility.

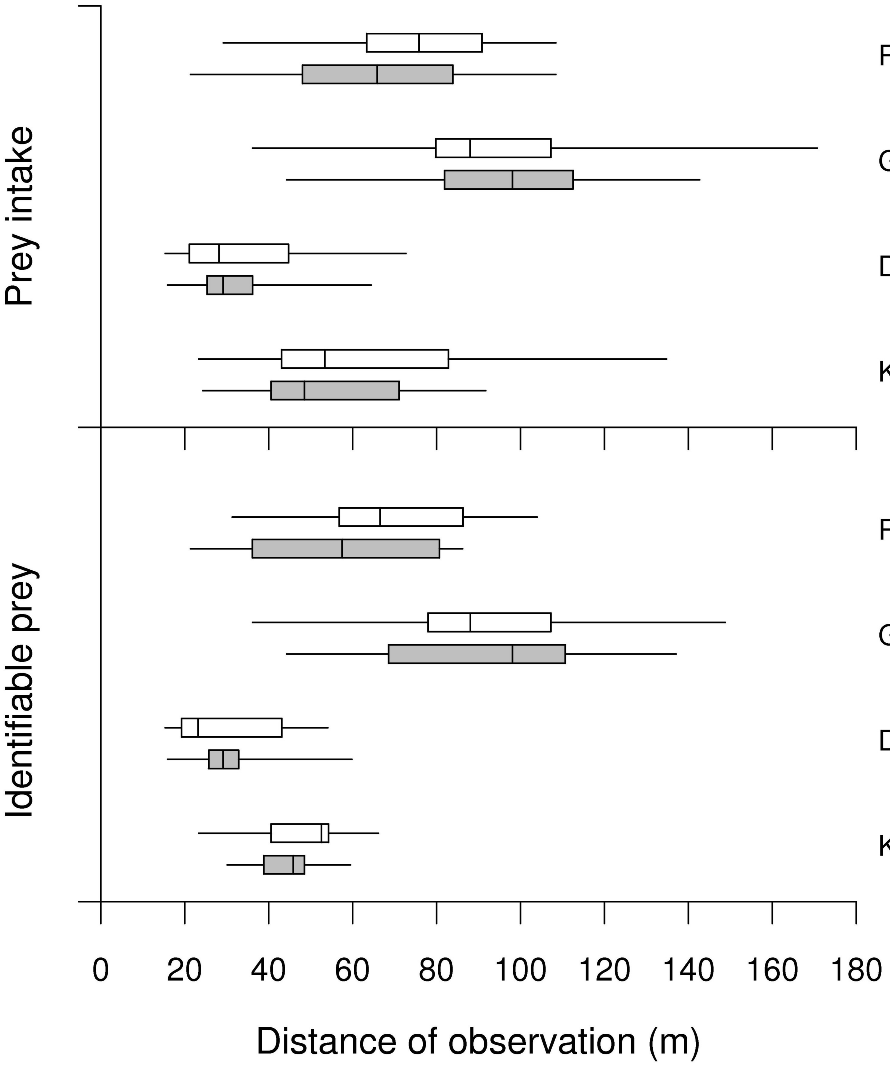


Figure 4.5. Distribution of observations of prey intake and identifiable prey at various distances during the day (white boxes) and at night (grey boxes). Boxes represent interquartile range and median; whiskers extend to the data extremes.

Results

We made 680 video clips of focal birds, including 412 at night. At night, all foraging variables (number of pecks, steps, prey intake, and identifiable prey intake) could be determined for all species at distances up to 59 m from the observer (Table 4.1, Figure 4.4), and the number of steps and pecks could be quantified a greater distances. For some species, we were able to accurately quantify the number of steps and pecks from more than 200 m away (Table 4.1). The distance threshold for observing prey ingestion and identifying prey was similar during day and night, or only a few meters less at night (Table 4.1). We found no differences between distances of observations made during the day and night in prey intake and ability to identify prey for any focal species (K-S test; $p > 0.05$ in all cases, Figure 4.5).

The size and feeding behaviour of focal species influenced the distance at which we were able to observe prey intake and identify prey. Among species of similar size, we were able to determine these parameters at greater distances for visual predators, including grey plovers (*Pluvialis squatarola*), ringed plovers, and Kentish plovers (*Charadrius alexandrinus*) because they typically moved more slowly and made fewer feeding attempts than more tactile species, such as dunlins (*Calidris alpina*) and redshanks (*Tringa totanus*, Table 4.1, Figure 4.5).

Discussion

Our system allowed us to quantify the foraging behaviour of waders at night, with no differences between day and night in the distances at which we were able to observe prey intake and identify prey items. We were also able to determine the number of steps and pecks at night for all birds filmed, even for birds filmed at distances greater than 200 m.

IR-sensitive video cameras have been used for monitoring animal behaviour in low light conditions at close-range (Rodrigues and Palmeirim 1994, Stake et al. 2004, Sabine et al. 2005). However, using long-range IR laser illuminators and an IR sensitive camcorder with 20x optical zoom and a 1.4x lens converter, we were able to make long-range observations at night. Observations at even greater distances may be possible because some currently available camcorders have 35-40x optical zooms. However, we recommend careful comparison of the night-viewing sensitivity of different camcorder models because we found substantial differences among them. Consulting the manufacturer’s specifications may be useful for selecting camcorders with better sensitivity on the near IR emission peak frequency of the laser.

We found that images became increasingly grainy and lost detail with increasing distance. Adding more IR light is the solution for this problem and can be achieved either by using more IR modules or more powerful ones. The modules we used had an output power of 350 mW, but more powerful ones are available (although stronger lasers pose greater risks for the eyes). However, it is important that the peak frequency of the laser is close to 808 nm; shorter wavelengths produce more visible light and longer wavelengths are further from the peak of sensitivity of the camcorder CCD and would result in poorer illumination. It is also important to choose a laser module with adjustable beam angle.

At close-range, laser diodes can cause serious damage to eyes. Investigators should be aware of laser safety and local regulations, and always check the instructions that accompany laser modules. Instructions may vary among models, but, in any case, one must never look into the laser beam, even briefly, to determine if it is emitting. A camcorder should always be used to check for illumination. One should be particularly careful around mirrored surfaces that may reflect the beam into the eyes, and in the close presence of people or animals. This equipment should not be left unattended in places accessible to people or animals, and it should be set with the highest beam divergence that puts sufficient light in the target area. Users must keep in mind that IR radiation is not visible, so batteries should be disconnected when the illuminator is not in use.

The system we used was relatively inexpensive. The laser modules cost $170 (US) each (in 2005), and camcorders with night-viewing capability and a good zoom typically cost a few hundred dollars (US). In addition to being cheaper, our system also permits greater magnification than possible with image intensifiers. Also, many image intensifiers come with low-power IR illuminators and, as a result, some investigators using image intensifiers have had to use additional IR illuminators (Klinka and Reimchen 2002, Rohweder and Lewis 2004), increasing overall cost. Our system allowed us to observe and quantify the foraging behaviour of waders at night and, by producing high quality recordings at relatively low cost, should provide other investigators with the opportunity to study, at long-range, the nocturnal behaviour of many other animals.

Effects of artificial illumination on the nocturnal foraging of waders

Abstract

Large areas of natural and semi-natural habitats are exposed to artificial illumination, from adjacent urban areas and roads. Estuarine and coastal wetlands are particularly exposed to such illumination, because shorelines often are heavily utilized by man. However, the impact of artificial illumination on the waders that forage in these highly-productive habitats is virtually unknown. We evaluated the effects of artificial illumination on the nocturnal habitat selection and foraging behaviour of six wader species with different feeding strategies: three visual foragers, two species that alternate visual and tactile strategies (mixed foragers), and one tactile forager. We quantified the number of birds and their foraging behaviour at sites affected and not affected by streetlights, and also before and after illuminating experimental sites. Areas illuminated by streetlights were used more during the night by visual foragers, and to a lesser extent by mixed foragers, than non-illuminated areas. Visual foragers increased their foraging effort in illuminated areas, and mixed foragers changed to more efficient visual foraging strategies. These behavioural shifts improved prey intake rate by an average of 46% in visual and mixed foragers. Artificial illumination causes shifts in the distribution of foraging waders, but this may draw them to degraded areas close to urban centres, and potentially raises their exposure to predators. Also, it allows for a substantial increase in foraging efficiency, but this could have consequences on the populations of estuarine invertebrates. Our results suggest that artificial illumination should be investigated as a tool in the management of highly-threatened populations of waders, although more research is also needed to clarify the potential negative impacts of illumination on the estuarine ecosystem.

Introduction

Since the invention of electric lighting, the night-time environment has changed dramatically on a global scale. Recent research on nocturnal sky brightness has shown that two-thirds of the world's populated areas are above the threshold set for light pollution, which corresponds to a first quarter moon in unpolluted areas (Cinzano et al. 2001).

Artificial illumination can have dramatic consequences on animal populations. Each year, large numbers of migratory birds are attracted to and often collide with lighthouses, large buildings, and other illuminated structures (Jones and Francis 2003). Hatchling sea turtles (Tuxbury and Salmon 2005) and fledgling seabirds (Le Corre et al. 2002) become disoriented by artificial lights while attempting to reach the sea for the first time, and many eventually die due to injuries, starvation or predation.

On the other hand, some animals can benefit from artificial illumination. Nocturnal predators may improve their visual skills due to illumination (Jetz et al. 2003), or feed upon concentrations of insects attracted by artificial lights (Rydell 1991, Heiling 1999). Some diurnal animals, like passerines and falcons, also are known to extend their daily activity into the night under artificially-improved light conditions (e.g. Derrickson 1988, Negro et al. 2000). The effects of these behavioural changes on ecological systems are largely unknown, and constitute a new and important focus of research in ecology (Longcore and Rich 2004).

Estuaries and coastal wetlands are among the habitats most exposed to artificial illumination, due to the frequent development of urban centres and industrial areas in their vicinity. In general, these areas are almost devoid of vegetation and other obstacles, so artificial light can propagate great distances, thereby affecting areas that are far from the source of illumination. These habitats are also of great importance for waders, particularly during the winter and migratory periods. During these periods, the foraging activities of these birds largely are determined by the tidal cycles (e.g. Granadeiro et al. 2006). In general, intertidal areas are exposed by the ebbing tide twice each day, allowing birds to feed extensively on the wealth of invertebrate prey that become available. This cyclic availability of food forces most estuarine waders also to forage during nocturnal low tide periods to fulfil their high daily energy requirements (e.g. McNeil et al. 1992, Lourenço et al. 2008). Waders use different foraging strategies during the day than they do at night, presumably as a consequence of the limited availability of light. Waders that use vision to detect their prey reduce their pecking rates at night (Kalejta 1992, Rohweder and Lewis 2004, Lourenço et al. 2008). Other species, capable of switching between tactile and visual searching, become more tactile at night (Robert and McNeil 1989, Rompré and McNeil 1996). Also, several species forage more actively on moonlit than on darker nights (Pienkowski 1982, Turpie and Hockey 1993, Dodd and Colwell 1998), which reinforces the importance of ambient light during nocturnal foraging.

This evidence suggests that light level is a limiting factor for waders foraging at night. Consequently, one might predict that artificial illumination would improve their foraging activities. In fact, in areas close to urban centres or major roads, artificial illumination can cause a substantial increase in ambient light, exceeding that resulting from a full moon. Such a change in environmental conditions has the potential to influence wader foraging behaviour, intake rate, choice of foraging areas, and even their role in estuarine food chains. Considering the increasing spread of artificial light around estuaries and the great dependence of waders on these geographically-restricted environments, it is important to understand how this factor impacts foraging waders. Strikingly, very little is known about this phenomenon (but see Sitters 2000).

In this study, we tested whether artificial illumination influences nocturnal habitat selection and foraging behaviour among waders, and quantified this influence. Specifically, we addressed the following questions: (1) Do waders prefer to forage in artificially illuminated intertidal areas at night? (2) Do they change their normal nocturnal foraging behaviour in these areas? And (3) if they do change their foraging behaviour in illuminated areas, do these changes improve their prey intake rates? Since wader species with different foraging strategies may not respond in the same way to artificial light, we studied three visual foragers, one tactile forager, and two species that switch between these two strategies (hereafter, termed mixed foragers). To address these three questions, we used two different approaches. We (1) compared nocturnal habitat use and foraging behaviour of birds at sites exposed and not exposed to streetlights and (2) conducted an experiment in which we recorded nocturnal foraging behaviour of birds after artificially manipulating the existing levels of illumination. The potential ecological implications of the results are discussed.

Methods

Study area

This study was conducted at the southern margin of the Tagus Estuary, in Portugal (Figure 4.6). The Tagus Estuary is among the largest wetlands in Western Europe, holding over 50 000 waders during non-breeding periods. It also is a key stopover during migration periods. The intertidal areas cover about 97 km^2 and are dominated by mudflats, although there also are extensive dead oyster beds and sandy flats. The tides are semi-diurnal, and their amplitude ranges between 1.0 and 3.8 m from neap to spring tide, respectively.

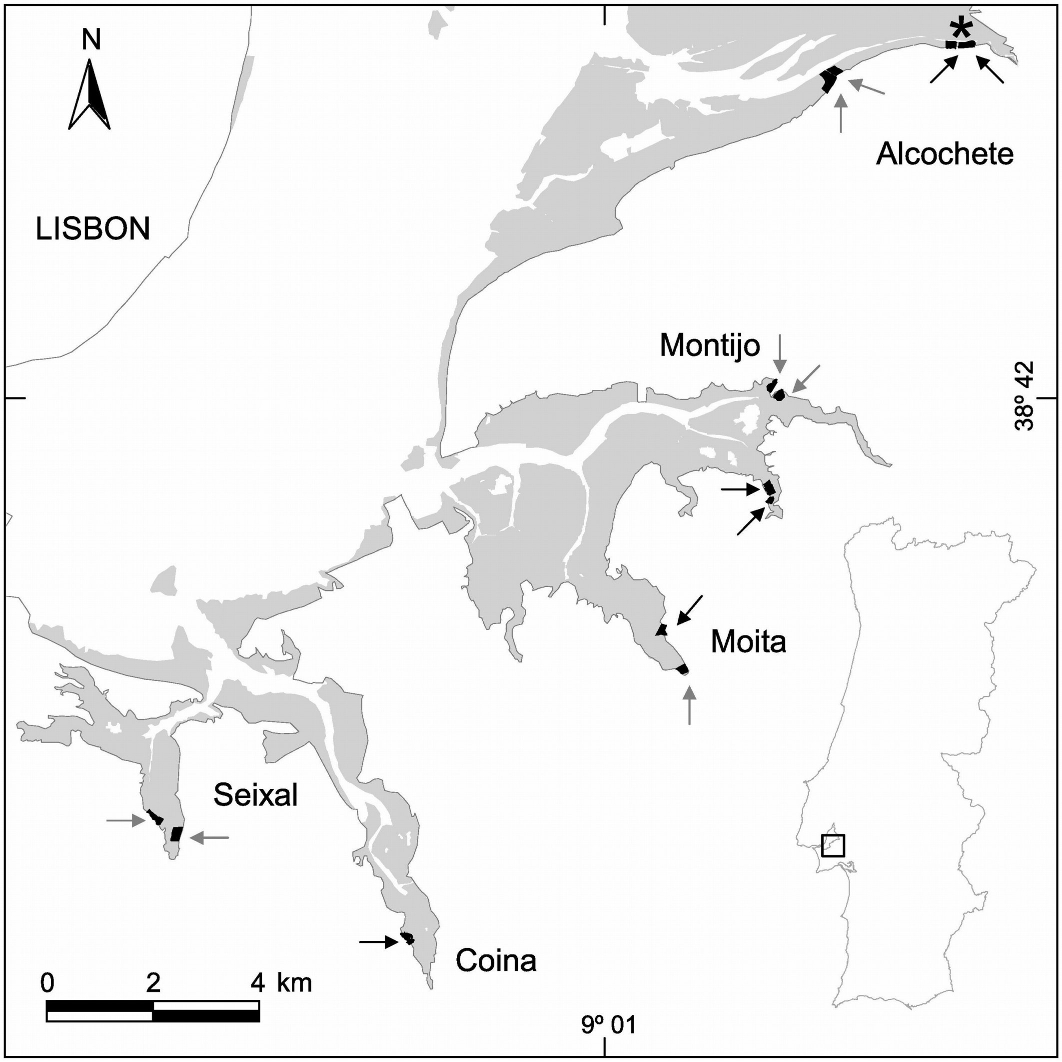


Figure 4.6. Study area at the southern margin of the Tagus Estuary (Portugal), with intertidal flats represented in grey. Black areas represent sectors affected (grey arrows) and not affected (black arrows) by streetlights. Asterisk indicates the location where light-manipulation experiments were conducted.

Comparisons of areas affected and not affected by streetlights

We selected 13 intertidal sectors of 1 to 7 ha, all with similar sediment characteristics, in areas known to hold high densities of feeding waders during the day (usually over 10 birds per ha). Seven of these sectors were located close to streetlights, whereas the remaining six sectors were far from any direct source of artificial illumination (Figure 4.6).

In each sector, we measured light levels with a light-meter (337, Center Technology Corp., Taipei, Taiwan) to the nearest 0.01 lux. During new moon nights, we carried out one to three transects (depending upon the distribution of streetlights along the coast) perpendicular to the coast, and recorded light measurements at the ground level at 30 m intervals. The light levels ranged between 0.18 and 0.71 lux in illuminated sectors, and were virtually nil in non-illuminated sectors. The light levels in illuminated areas corresponded to 1.8 to 7.1 times the levels recorded during a full moon on a clear night (ca. 0.1 lux).

Between late January and early May 2005, we counted birds foraging in each sector and conducted behavioural observations. We visited all sectors during spring tides, with a fortnight periodicity, hence comprising periods of new and full moons. This procedure meant that our observations were balanced to coincide with the main lunar phases.

Experimental manipulation of illumination

In early March 2006, we demarcated four sectors of ca. 0.5 ha in a non-illuminated intertidal area (Figure 4.6). In two of these sectors, we set up three 500 W and two 300 W halogen floodlights. The floodlights were mounted on top of 4 m poles, which we set 15 m apart and supplied with an AC 220 V current. The light levels provided by the floodlights (measured as described above) represented an increase of ca. 0.74 lux relative to baseline illumination (0 lux during a new moon).

We kept the lights on for two weeks, and carried out behavioural observations in the second week, in both illuminated and non-illuminated sectors. After that period, we switched the floodlights between the illuminated and non-illuminated sectors, and repeated behavioural observations. This procedure enabled us to observe birds in the same areas under illuminated and non-illuminated conditions, thereby eliminating any potential site-specific biases. We did not count birds in these experimental sectors because sector areas were small and consequently, bird densities were highly variable.

Observation device

Counts and focal observations during the night were conducted using a digital camcorder (NV-DS15, Panasonic, Osaka, Japan), with night vision capability and a 20x optical zoom, coupled with two custom-made 350 mW infrared laser illuminators (RLDB808-350-3, Roithner LaserTechnik, Vienna, Austria). This setup allowed us to observe and film the birds from a distance of up to 300 m in the absence of light and without disturbing their behaviour (full details are provided in the first paper of this chapter). The quality of the image provided by this equipment mostly was determined by the amount of light provided by the laser illuminators. Therefore, there were virtually no differences in the quality of the films obtained in illuminated and non-illuminated sectors, and consequently no bias in the number of birds counted or in the data obtained during the behavioural observations that could be attributed to ambient light (see the first paper of this chapter).

Wader counts

Sectors affected and not affected by streetlights were counted 7 to 11 times during the night and again on the following day at the same tidal stage, to avoid variation in bird densities due to the tidal cycle. To enable for comparisons between sectors, we calculated an index of nocturnal preference, representing the percentage difference between the number of birds counted during the night and the following day in the same sector:

$$\textit{Nocturnal preference index} = \frac{\textit{No. birds night - No. birds day}}{\textit{No. birds night + No. birds day}} \times 100.$$

Potential index values thereby range from 100 (when birds are present only at night) to -100 (when birds are present only during the day), and the value is 0 if the same number of birds are counted at night and during the day. We compared index values obtained at illuminated areas to those at non-illuminated areas using permutation tests

(Efron and Tibshirani 1993). Permutation data sets (n = 1000) were created by randomly re-sampling (with replacement) the original data, and these sets used to construct the distribution of the test statistics (difference of means). The p-value was the quantile of the original statistic in that distribution. All computations were performed using the statistical software R (R Development Core Team 2005).

Ringed plovers (*Charadrius hiaticula*) and Kentish plovers (*Charadrius alexandrinus*) proved to be difficult to distinguish during the night at a distance, so we pooled them as *Charadrius* spp.

Behavioural observations of foraging waders

As stated above, we obtained foraging behavioural data for six wader species demonstrating different feeding strategies: three visual foragers (ringed plover, Kentish plover, and grey plover, *Pluvialis squatarola*), one tactile forager (avocet *Recurvirostra avosetta*) and two mixed foragers (dunlin, *Calidris alpina*, and redshank, *Tringa totanus*). Focal birds foraging inside the study sectors were chosen randomly and then filmed for 2 minutes. To avoid filming the same bird more than once, a second observer followed the previously-filmed birds. Video sequences were downloaded and visualized on a computer. We quantified the following parameters: prey intake rate (prey per minute) for all species; pecking rate (pecks per minute) and step rate (steps per minute) for visual foragers and avocets; and sweeping rate (sweeps per minute) only for avocets.

We only measured prey intake rate on a subset of recordings taken close enough to ensure reliable results. Nonetheless, the capture of a few small prey could have been missed, so this parameter should be interpreted conservatively as the rate of capture of large prey, rather than as an absolute feeding rate. Because of small sample sizes for this parameter, we pooled the datasets from the streetlight comparison and the experimental manipulation of illumination.

Redshanks and dunlins used both tactile and visual foraging strategies. Therefore, we quantified their foraging behaviour by determining the proportion of birds using either strategy. An individual bird was considered to be using a tactile versus a visual strategy if it spent at least 90% of the observation period using that strategy. Stitching and sweeping were the typical tactile strategies of dunlins and redshanks, respectively.

Results

Influence of artificial illumination on the choice of nocturnal feeding site

The nocturnal preference index was significantly higher in sectors affected by streetlights for visual foragers (grey plover and *Charadrius* spp.) and for dunlin (Figure 4.7). Hence, these species were more abundant at night in illuminated sectors, after corrected by their respective daily abundances on these sectors. In contrast, redshank and avocet did not exhibit any noticeable trend in the nocturnal preference index between sectors affected and not affected by streetlights (Figure 4.7).

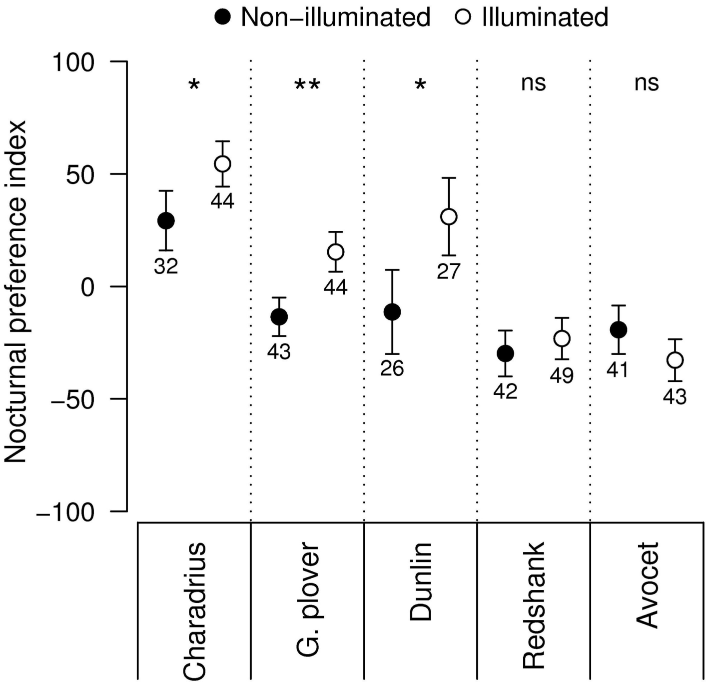


Figure 4.7. Nocturnal preference index (mean ± SE) in sectors affected and not affected by streetlights. This index represents the percentage difference between the number of birds counted during the night and the following day within the same sector (see Methods). Results of one-tailed permutation tests are indicated: ns $p > 0.05$; * $p < 0.05$; ** $p < 0.01$. Sample sizes are indicated below the points.

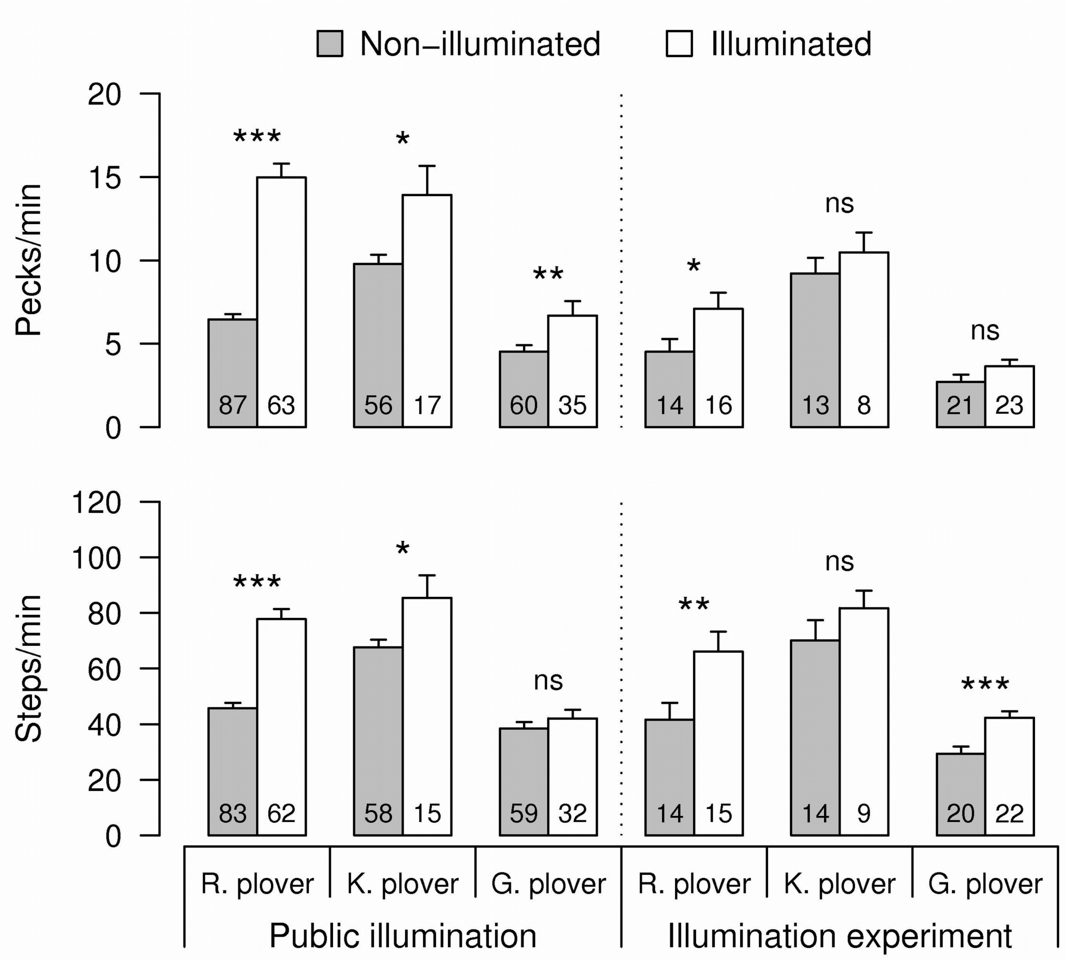


Figure 4.8. Feeding parameters of visual foragers (mean + SE) in sectors illuminated and non-illuminated by streetlights (left) and by experimentally-set floodlights (right, see Methods). Results of one-tailed Student-*t* tests are indicated: ns $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Sample sizes are indicated inside the bars.

Influence of artificial illumination on nocturnal foraging behaviour

Foraging activity was greater in visual foragers (ringed, Kentish and grey plovers) in sectors affected by streetlights than in those that were not affected, as we observed significantly higher pecking rates for all species and stepping rates for *Charadrius* spp. (Figure 4.8). We observed similar trends in the light manipulation experiments, although the differences were not always statistically significant (Figure 4.8).

The percentage of mixed foragers (dunlin and redshank) using a visual strategy at night was higher in sectors affected by streetlights and in experimentally-illuminated sectors, when compared with their darker counterparts (Figure 4.9). The difference in the proportion of birds using visual and tactile strategies was significant for all comparisons.

The avocet (tactile forager) exhibited significantly higher pecking and sweeping rates, and a lower stepping rate in sectors affected by streetlights (Figure 4.10). For pecking and stepping rates, we observed trends in the same direction in the experimental light manipulations, although none was statistically significant (Figure 4.10).

Prey intake rates were significantly higher in illuminated sectors for Kentish plovers, grey plovers and dunlins, and seemed to reveal a similar, but non-significant, trend for ringed plovers (Figure 4.11).

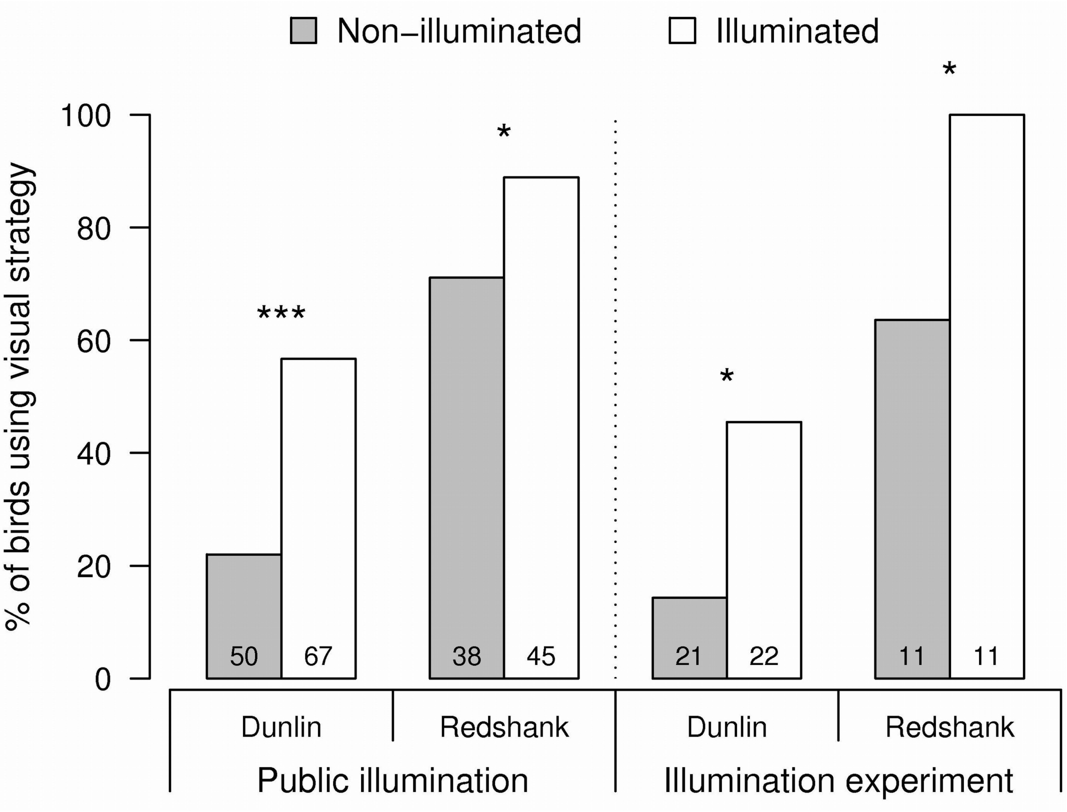


Figure 4.9. Percentage of mixed foragers using visual strategies in sectors illuminated and non-illuminated by streetlights (left) and by experimentally-set floodlights (right, see Methods). Results of one-tailed Fisher exact tests, comparing the proportion of birds using visual and tactile strategies, are indicated: * $p < 0.05$; *** $p < 0.001$. The overall number of individuals observed is indicated inside the bars.

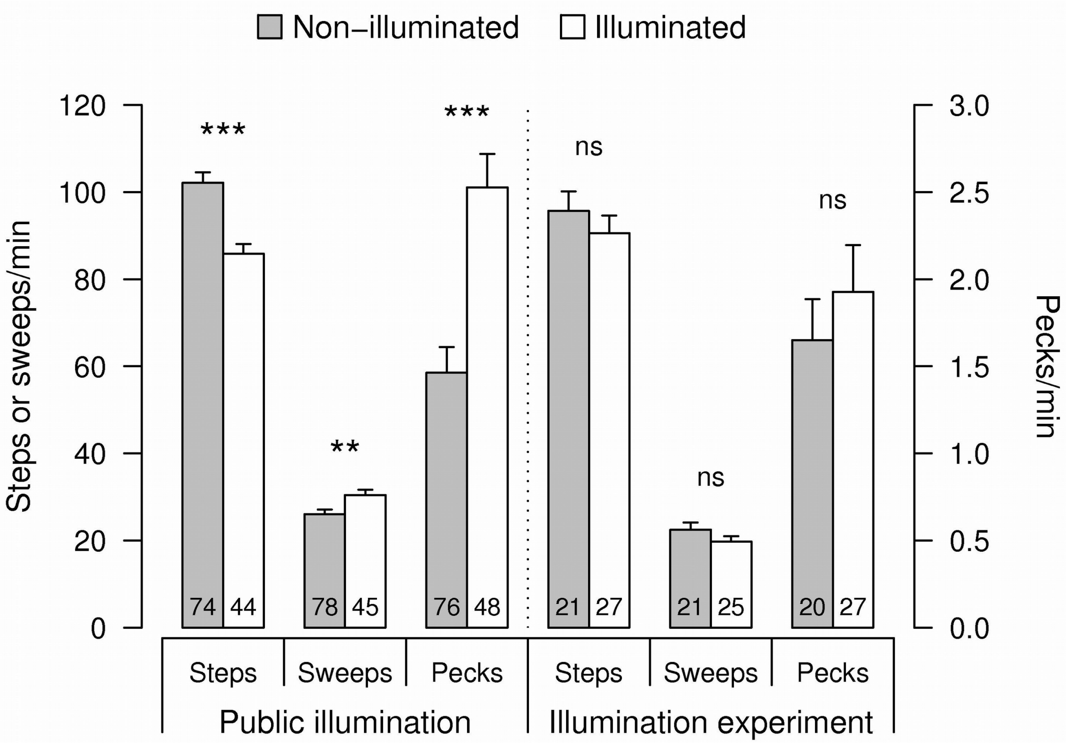


Figure 4.10. Feeding parameters of avocets (mean + SE) in sectors illuminated and non-illuminated by streetlights (left) and by experimentally-set floodlights (right, see Methods). Results of one-tailed Student-*t* tests for Steps and Sweeps, and one-tailed Mann-Whitney tests for Pecks are indicated: ns $p > 0.05$; ** $p < 0.01$; *** $p < 0.001$. Sample sizes are indicated inside the bars.

Discussion

Artificial illumination influences the nocturnal foraging site selection of waders

Areas illuminated by streetlights were used more during the night by foraging waders than non-illuminated areas. In fact, the nocturnal preference index was 20% higher in illuminated than in non-illuminated areas across all studied species. This preference was particularly marked in visual foragers and dunlins. These results are consistent with the behavioural data that we collected, which demonstrate that these waders are able to take advantage of the extra illumination to improve foraging. They also are consistent with data collected on willets (*Catoptrophorus semipalmatus*), which show that moonlight influences foraging site selection. This species generally is restricted to tactile foraging at night but on moonlit nights, it moves to areas where can feed visually on the abundance of fiddler crabs (Uca cumulanta, Rompré and McNeil 1996).

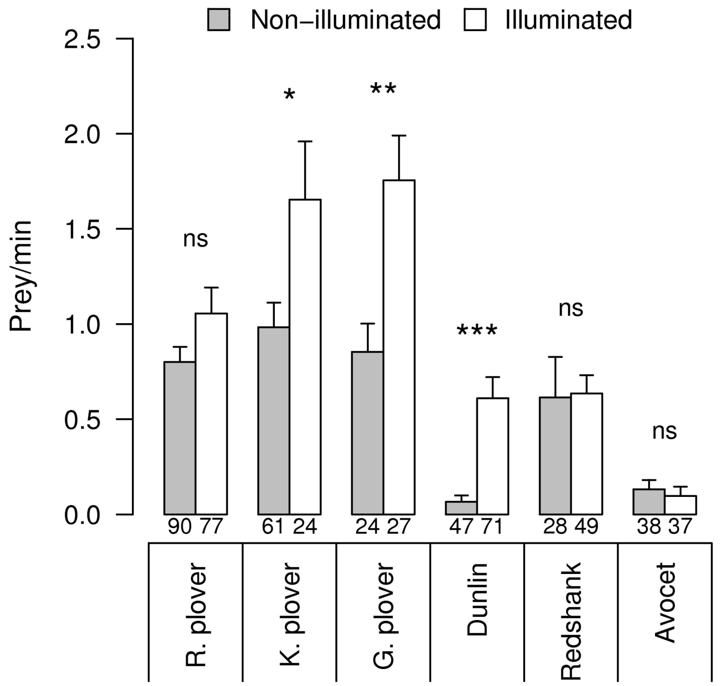


Figure 4.11. Prey intake rate (mean + SE) in sectors illuminated and non-illuminated. Results of one-tailed Mann-Whitney tests are indicated: ns $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). Sample sizes are indicated below the bars.

The consequences of this nocturnal habitat switch in waders due to artificial illumination could be very important, particularly in estuaries close to major urban and industrialized regions. In these areas, artificial illumination is likely to constitute an important factor driving the nocturnal habitat selection of foraging waders.

Waders changed their foraging behaviour under artificial illumination

Both visual and mixed foragers changed their nocturnal foraging behaviour under conditions of artificial illumination. Visual foragers exhibited a general increase in their feeding activity parameters. Pecking rates increased in all species in areas affected by streetlights, as well as step rates in *Charadrius* species. These results were consistent with those obtained in the experiments using artificially-manipulated light levels. The direction of the observed changes in foraging parameters was the same as that reported in day/night and moonlit/moonless behavioural comparisons (e.g. Turpie and Hockey 1993, Rohweder and Lewis 2004, Lourenço et al. 2008). In these studies, as natural light became scarcer, visual foragers decreased their feeding activity by reducing their pecking and stepping rates.

Dunlins and redshanks, which usually adopt a tactile feeding behaviour at night (Goss-Custard 1969, Mouritsen 1993), increased their visual foraging under illuminated conditions. In fact, the proportion of birds using a visual strategy was much greater in areas illuminated by streetlights, and in areas where light levels had been experimentally increased. The most likely explanation for the change in the behaviour of these species in illuminated areas is the enhanced prey visibility resulting from the increase in light intensity. This could increase predatory opportunities considerably, resulting in an intensification of feeding activity, as observed in the plover species, and in a switch to visual strategies, as observed in dunlins and redshanks.

Avocets are mostly tactile foragers, so we had not expected that their foraging activity would be much influenced by artificial illumination. However, in the presence of streetlights, we observed a substantial increase in pecking rates and, to a lesser extent, sweeping rates, as well as a decrease in stepping rates. Such behavioural changes suggest that avocets use a more visual strategy in illuminated areas. In fact, pecking is assumed to be a visual strategy of avocets (Moreira 1995c), while the observed decrease in step rates could be a consequence of a more focused, visually-aided search for prey or their cues. Also, it has been shown that avocets reduce nocturnal foraging activity on very dark nights (Hötker 1999), which supports the conjecture that the absence of light can represent a constraint for foraging, even for this primarily tactile forager.

Artificial illumination increases the nocturnal prey intake rate of waders

Visual and mixed foragers demonstrated higher prey intake rates in illuminated areas. Even in species for which this was not statistically significant, the direction of the difference consistently corroborated this conclusion. In fact, if we pool all the data for all species, the increase in prey intake rate under illuminated conditions is 43% (46% if we exclude the avocets). A positive correlation between prey intake rate and overall illuminance (artificial and lunar) also has been observed in oystercatchers (*Haematopus ostralegus*, Sitters 2000).

Our findings support the concept that artificial illumination can be beneficial for several wader species; and that the magnitude of the increase in prey intake is not negligible. In fact, for some species, the gains are so substantial that it seems likely that under certain circumstances, artificial illumination may help them to overcome periods of high energy demand.

Ecological and management implications

Artificial illumination caused a considerable increase in the use of tidal areas by waders, and an average increase of 43% in prey intake rate across all studied wader species. Such a shift in the way waders use their foraging areas in intertidal areas, and in their predatory success, may have important ecological consequences.

Waders are among the most important estuarine predators and can exert significant impacts upon invertebrate communities (e.g. Szekely and Bamberger 1992, Goss-Custard et al. 2002). Artificially illuminating an area may result in a substantial increase in prey consumption, which may depress its invertebrate densities. In contrast, non-illuminated areas may experience reduced levels of invertebrate consumption. Such changes can impact various components of the estuarine food chain including fishes as well as species at the lowest trophic levels (e.g. primary producers, meiofauna).

An additional consequence of artificial illumination relates to the attraction of foraging waders to areas near well-lit urban areas. In fact, birds may be exposed to greater disturbance and higher pollutant loads in these areas. Both factors are known to produce detrimental effects on birds (e.g. Hill et al. 1997, Stephenson 1997). Finally, birds attracted to well-lit areas may be more vulnerable to predators, both because areas close to the coast have a higher density of wader predators (Cresswell 1994), and because nocturnal predators may improve their predatory success under illuminated conditions (Mougeot and Bretagnolle 2000).

It is worth noting that we only demonstrated that artificial illumination results in local shifts within foraging areas. However, we cannot exclude larger-scale effects, such as the movement of birds to better lit estuaries. If such a situation occurs, the ecological consequences of artificially increasing ambient light may be greater than suggested here.

While we demonstrated that the artificial increase of ambient light in estuaries has substantial implications in the foraging ecology of waders, particularly for visual and mixed foragers, we did not determine if its overall impact is positive or negative for the wader populations. In fact, the observed increases in prey intake rate may not compensate for the potential disadvantages of concentrating near well-lit urban areas, disadvantages which were not addressed in our study. In addition, it should be noted that we only evaluated situations of relatively low-intensity illumination, so our results should not be extrapolated to situations involving high-power and/or flashing illumination. Consequently, we do not see in our results an argument to deregulate the control of artificial illumination in important wader feeding areas. However, our findings do suggest that artificial illumination of foraging areas affects wader foraging parameters and, thus it is worth investigating its potential as a tool in the management of highly-threatened populations of waders that are dependent upon intensive management.

CHAPTER 5

GENERAL DISCUSSION

General discussion

In the previous chapters of this thesis many aspects on how waders use their foraging intertidal areas were addressed, and the specific objectives and conclusions were extended in each study. In this chapter I will highlight the most important findings and the new approaches that came out from those studies, and discuss their implications for the conservation of wader populations. Finally, I will pass through some of questions that are still in open and give a personnel perspective of the directions for future research in wader ecology.

Foraging constraints in the exploitation of food resources

In this thesis, particular attention was given to the factors that constraint the exploitation of food resources by waders. In chapter 3, it was showed that foraging dunlins (*Calidris alpina*) have limited perception of the distribution of their buried prey. In fact, dunlins exhibited a reduced ability to find patches with high prey density with less than 1 m^2, and the same was observed in larger patches with lower density of prey. These results indicate that there are thresholds in the density of prey and in the size of a food patch below which waders are unlikely to find and exploit their prey due to perceptual limitations. This greatly restricts the amount of food resources available for waders at the scale of an estuary, and also explains, at least partly, the weak relationships between the abundance of waders and that of their prey at the very low spatial scales (e.g. Kelsey and Hassall 1989, Wilson 1990).

Also, it was found that the presence of a thin layer of water over the intertidal sediments plays a crucial role in the availability of prey for dunlins foraging by sight. In fact, in sediments with superficial water, more *Scrobicularia plana* siphons were visible at surface, while in dry sediments mudsnails (*Hydrobia ulvae*) were more conspicuous. Dunlins responded to the availability of prey at the surface of sediments by consuming more siphons in wet sediments and more mudsnails in dry sediments. However, the consumption of these two prey also resulted in very distinct rates of energy intake. By far siphons represent a higher energetic reward for dunlins and are much easier to digest than mudsnails (van Gils et al. 2005). Nevertheless, siphons are difficult to catch because they retract quickly when the sediment is disturbed. By measuring the efficiency of birds in catching siphons it was found that birds that spent more time foraging upon mudsnails were those with low performances capturing siphons. Once again it was demonstrated that even in environments with high abundance of prey, particular aspects of the predator-prey relationships may restrict the amount of food resources available for waders.

Finally, in chapter 4 it was demonstrated that light is a limiting factor for waders foraging at night. In the presence of artificial light, all studied wader species exhibited foraging strategies closer to those observed during the daylight. Visual predators, such as plovers, increased their foraging rates in the presence of artificial light, while mixed predators, that can use both tactile and visual strategies, preferred to use a visual strategy. Even avocets (*Recurvirostra avosetta*), normally considered exclusively tactile predators, reacted to the presence of artificial light by increasing the attempts to catch prey visually at the surface of the sediments. For most species, the observed changes in foraging strategies resulted in higher prey intake rates, which indicate that light can greatly improve their foraging efficiency during the night.

New approaches in the study of waders

One of the major gaps in the study of the ecology of waders concerns their nocturnal foraging. Nocturnal foraging represents about half of the total foraging period in most wader species and yet few studies were conducted during the night, mostly due to technical limitations to observe waders foraging in the dark (McNeil et al. 1992). No studies on nocturnal habits of waders had ever been conducted in the Tagus estuary, and so addressing this theme represented a major challenge. However, data on nocturnal foraging would allow to estimate accurate rates of daily energy acquisition of waders, which represents the most basic information to compare the Tagus estuary as wintering area for waders to other areas along the East Atlantic Flyway. Furthermore, it would allow studying factors with potential important influence in the foraging ecology of waders and that had never been studied, such as artificial light. However, the night vision equipments that had been used before to directly observe waders foraging at night proved to have insufficient resolution to observe parameters such as prey intake, or to identify prey while being ingested. In addition, the last generations of night vision equipments are extremely expensive, and still share the same limitations to observe waders foraging at a distance with the most basic equipments. In the first paper of chapter 4 it is described and tested a long-range night vision system combining a regular camcorder and high power infrared laser illuminators. Regular camcorders are highly sensitive to reflected near-infrared radiation, still their use as night vision devices was limited by the reduced IR illumination that is reflected by distant objects. Thanks to the recent development of high power IR lasers, it was possible to provide additional IR illumination at very long-distance, and thus to explore the high zoom power of camcorders for making long-range observations during night-time. This system proved to be very efficient to observe foraging parameters of waders at night at considerable distances, and can certainly be useful in other studies that require long-range observations of animals at night.

Throughout this thesis it was also demonstrated that field experiments can be very useful approaches to test specific hypothesis in the study of the foraging ecology of waders. Like captivity experiments, such approaches allow to isolate and test factors of interest in relatively controlled conditions, but have the advantage of being conducted in the natural environment, hence ensuring that no effects of enclosure influence the behaviour of animals. In the last paper of chapter 3, it was showed that manipulating the density of prey in patches was an efficient way to observe dunlins foraging in different scenarios of food availability, and thus to investigate their perceptual limitations in the exploitation of food resources. Using this approach, experimental patches could be established in the same foraging habitat, thus avoiding different habitat characteristics to influence the response of birds. Similarly, in the second paper of chapter 4, after demonstrating that birds behaved differently in areas affected and not affected by streetlights, artificial illumination was experimentally added in areas previously not affected by any kind artificial light. This experiment allowed to compare the nocturnal foraging behaviour of birds before and after the light was added in the same foraging areas, thus ensuring that no site-specific factors would affect the results.

Finally, in this thesis it was showed that video recording can be a very efficient tool to sample wader and invertebrate behaviour, allowing to analyse a wide range of parameters with a precision that would otherwise be impossible to attain. In the first paper of chapter 3, particular emphasis was given to using video recording to sample prey availability, as an alternative to the classic methods based on sediment core sampling. In fact, for wader species that forage by sight, the visibility of prey at the surface of sediments corresponds to the most realistic measure of their availability. Using video recordings of the sediment surface, this availability can be estimated with higher precision and lower logistic effort than with sediment core sampling.

Relevance of the findings for the conservation of wader populations

Many wader populations are currently declining at a global scale (BirdLife International and European Bird Census Council 2000, Stroud et al. 2004). This conclusion resulted from an intense effort in censusing wader populations at their breeding and wintering grounds in the last decades. However, only in a few cases the specific reasons for the observed decline are known (e.g. Gill et al. 2007, Niles et al. 2009). Conserving wader populations is a particularly difficult task because the effectiveness of conservation initiatives depends on a profound knowledge of their ecology at breeding, wintering, and stopover areas. While wader populations are relatively well studied and are being monitored in some areas within their range of distribution, in most flyways there is a critical lack of baseline information (Stroud et al. 2004). In particular, on the East Atlantic Flyway, the areas located in southern Europe and along the West African coast are considerably less studied than those located at northern Europe.

In the first paper of chapter 2 it is provided the most complete data set for dunlins wintering in southern Europe, including their diet, prey selection, foraging behaviour and habitat choice. Despite being the most abundant wader in the East Atlantic Flyway, some populations of dunlin are currently in sharp decline, in particular those wintering in southern regions of this flyway (Stroud et al. 2004). It was found that, in Tagus estuary, dunlins forage upon some invertebrate species that are also consumed in northern latitudes. However, some other invertebrates, with particular energetic importance for dunlins, seem to be exclusive prey from southern European latitudes. The last paper of chapter 2 includes the first detailed description of the large scale distribution patterns of waders at the Tagus estuary. In this study, the main foraging areas for waders in the Tagus estuary were established, and the main factors driving the selection of those areas were identified. This information was important to conduct other studies addressing the roles of specific factors relevant for the conservation of waders (e.g. Lourenço et al. 2005, Dias et al. 2006b), and can be used as baseline against which future surveys can be compared. Moreover, together with the high tide counts at roosts, the foraging distribution of shorebirds in the Tagus estuary constitutes a complete database to be used by stakeholders and managers in order to increase the level of protection of the most important areas for shorebirds, and to implement specific conservation measures in those areas.

More specific factors but with high potential to be used in conservation and management of wader populations were analysed in chapters 3 and 4. In the two papers of chapter 3 it was showed that a considerable part of the food resources present in estuarine areas may not be available to waders. In fact, buried invertebrates can be present at densities that are too low, or they can be aggregated in patches that are too small to be detected and exploited by waders. Also, the predator avoidance behaviour of some abundant prey can compromise their use as food for the most inexperienced waders. These results show that subtle relationships between waders and their prey can bias our evaluation of the carrying capacity of estuarine areas for waders. Based on this sort of information, areas with optimal conditions for foraging can be identified and their level of protection can be increased, and specific management measures can be implemented at less valuable areas to increase their potential as foraging grounds for waders.

In the last paper of chapter 4 it was demonstrated that the presence of artificial light can improve the night foraging conditions of waders. In fact, waders foraging at night improved their foraging strategies and consequently their prey intake rate under illuminated areas. Although the effects of artificial illumination still need to be evaluated for other species and groups across the estuarine community, artificial illumination can potentially be used to manage highly threatened populations of waders.

Some answers, more questions

Perhaps one of the most intriguing questions that came out from this thesis is why are the densities of waders so low in the Tagus estuary? This fact is clear from the table 2.5 for dunlins, but it also applies to other wader species (compare table 2.6 with data provided by Hockey et al. 1992). Wader densities in the Tagus estuary, and in other wintering areas of southern Europe, are similar to those found in northern Europe, but much lower than those observed in north and west Africa. As discussed in chapter 2, the main reasons proposed to explain the high densities of waders in the lowest latitudes of their non-breeding range include more stable climatic conditions, that allow waders to spend less maintenance energy, and more predictable food resources (Hockey et al. 1992). Compared to northern Europe, the climatic conditions in the Tagus estuary during the winter are reasonably stable, mean temperatures range between 8 and 16 ºC, and events of high mortality of waders due to low temperatures were never observed. The invertebrate biomass in the Tagus estuary is much higher than that found in West Africa (see table 2.5), and high densities of *Scrobicularia plana* provide an abundant and predictable source of siphons that is exploited by almost all wader species (Moreira 1995b, Rodrigues et al. 2006). Moreover, wintering at the latitude of the Tagus estuary reduces the migration distance to/from breeding grounds in the Arctic, which results in considerable energetic savings (Hockey et al. 1998). So, why is not the Tagus estuary the “land of plenty” for waders? A biased perspective of invertebrate availability can partly explain this riddle. In fact, as demonstrated in chapter 3, the presence of high abundance of invertebrates does not necessarily means high availability of food for waders. Particular aspects concerning the behaviour of invertebrates can tremendously reduce the amount of food resources available for waders.

However, to what extent should we expect waders to optimize the choice of their wintering sites? How much of the observed patterns of wader distribution is predetermined by historical traits? Fidelity is among the most prominent phenomena in wader ecology (Warnock and Takekawa 1996, Burton 2000, Leyrer et al. 2006) and can represent an optimal strategy for surviving when foraging conditions are stable in long-term. In fact, it might be better for waders to regularly use the same places, if can meet there their energetic requirements, than wasting energy looking for better places to forage. However, maintaining some plasticity in the choice of foraging areas and exploring of new foraging sites may also help waders to survive if foraging conditions change drastically. As discussed previously, major changes in wader distributions were already observed to respond to extremely harsh weather in the northern wintering grounds (van de Kam et al. 2004b). However, large numbers of waders preferred to stay in their regular wintering grounds and challenged those adverse conditions (Camphuysen et al. 1996, Mitchell et al. 2000).

For most wader species, it is still difficult to draw a general picture of which are their main constraints at the scale of a flyway. Future research should seek for obtaining baseline information on the foraging conditions in the less studied areas used regularly by waders, including amount of food resources available, levels of disturbance and predation impacts. The quality of foraging areas for waders can also be pragmatically accessed measuring physiological indicators of stress in birds (Wikelski and Cooke 2006). Maintaining regular counts of waders in their main wintering areas will be crucial to ascertain population changes. But monitoring efforts should be extended to migratory periods, when wader populations are particularly vulnerable and much less information is available. New methods of tracking technology, such as satellite tracking and the use of automatic radio tracking stations, can be a great help in achieving that goal (Drent et al. 2006, Rogers et al. 2006). Those can also be very useful to investigate the role of night foraging in the ecology of waders (van Gils and Piersma 1999). These steps will help to understand the causes of the declines in waders and to undertake efficient measures to conserve their populations.

Agradecimentos

Em primeiro lugar gostaria de agradecer aos meus orientadores, Jorge Palmeirim e José Pedro Granadeiro, pela orientação desta tese. Ao Prof. Palmeirim agradeço o entusiasmo pelo meu trabalho, as suas boas ideias e por ter apoiado também as minhas. Agradeço-lhe também o esforço e dedicação na leitura dos meus artigos até ao mais ínfimo detalhe. Ao Zé Pedro agradeço a boa disposição e o espírito positivo com que orientou esta tese, o pragmatismo nas decisões difíceis e a facilidade em transformar os tímidos avanços em grandes vitórias. Tive a oportunidade de testemunhar o entusiasmo com que abraçou esta complexa tarefa de construir um grupo de investigação nas limícolas. É para mim um grande privilégio trabalhar com o Zé Pedro e fazer parte desse grupo.

Gostaria de agradecer às muitas pessoas que fazem e fizeram parte da equipa das limícolas, que já conta com quase uma década! Queria destacar o grande contributo para esta tese da equipa dos noctívagos: a Catarina, o Pedro e a Andreia. Durante muitas noites de inverno trocámos a cama quente pelo frio gélido do estuário, tempos difíceis... Destaco também o contributo dos exploradores do Tejo profundo: o Zé Pedro, a Maria, a Ana Tavares, o Ricardo e a Teresa. Juntos calcorreamos o estuário, dos cavalos aos mouchões, passando pelo pé de galinha para lhe cravar uma bandeira do Sat-tagis. Devo também um agradecimento especial à Sara, que me acompanhou em boa parte desta tese. Agradeço-lhe o esforço, a dedicação e o espírito de sacrifício. Foram muitos vídeos analisados, muitos cores arrancados e muitas minhocas minúsculas identificadas.

Gostaria de agradecer aos muitos voluntários e amigos que participaram no trabalho de campo desta tese. Em particular à grande equipa do plantio da minhoca, o Dejone, a Joana, a Iris, a Taia, o Pef, a Catarina e o Ricardo Lima. Foi talvez das partes mais complicadas deste doutoramento, e de maior loucura também… Agradeço também aos meus amigos Zé, Vasco, Isra, Pef e Dejone, que muitas vezes me acompanharam ora no trabalho nocturno ora a arrancar um ou outro core.

À Reserva Natural do Estuário do Tejo agradeço todo o apoio logístico prestado durante o trabalho de campo.

Agradeço aos revisores dos meus artigos e desta tese: a Maria, a Susana, o Pedro, a Catarina, a Ana Rainho e a Sofia. Special thanks to Adam Fudickar, Michele Boyles,

Jim Wilson and Jeanne Hammond who were very kind in proofreading some of my papers.

Aos meus companheiros de laboratório: as Anas (Leal e Rainho), a João e o Tiago, agradeço por me terem apoiado e animado, sobretudo nestes últimos meses quando a inspiração me faltava.

Ao meu amigo Isra agradeço por ter sido o ouvinte diário das frustrações e de algumas euforias também. Força parceiro, és o próximo…

Agradeço a toda a equipa do projecto da Amazónia, em particular à João por me ter desafiado a participar no projecto. Foi sem dúvida uma grande oportunidade e uma pausa revitalizante no meu doutoramento. Que saudades dos tempos a bordo do Uacari…

Ao meu amigo Gante, agradeço por me ter puxado também prós peixes e por me ter ajudado a descodificar um bocadinho das ferramentas da genética.

Ao Dejone e à Joana agradeço por tantas vezes me terem dado guarida e carapaus nestes últimos meses de escrita, quando a vontade de fazer jantar me faltou.

Agradeço aos meus amigos das jantaradas no Sô Lucian: o Isra, o Vasco, o Zé, o Dejone, o Pef, o Pedro, o Rafael e o Gante. Foram uma boa parte da minha vida social durante este doutoramento.

À minha família agradeço todo o apoio e o orgulho exagerado que têm em tudo aquilo que faço.

À Catarina por tudo…

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