

**Staging ecology of black-tailed  
godwits in Portuguese rice  
fields and correlations with  
breeding season events**



**rijksuniversiteit  
 groningen**

**faculteit wiskunde en  
 natuurwetenschappen**

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RIJKSUNIVERSITEIT GRONINGEN

**Staging ecology of black-tailed godwits  
in Portuguese rice fields and  
correlations with breeding season events**

Proefschrift

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geboren op 3 december 1980  
te Caldas da Rainha, Portugal

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*Mudam-se os tempos, mudam-se as vontades,  
Muda-se o ser, muda-se a confiança;  
Todo o mundo é composto de mudança,  
Tomando sempre novas qualidades.*

*Continuamente vemos novidades,  
Diferentes em tudo da esperança;  
Do mal ficam as mágoas na lembrança,  
E do bem, se algum houve, as saudades.*

*O tempo cobre o chão de verde manto,  
Que já coberto foi de neve fria,  
E em mim converte em choro o doce canto.*

*E, afora este mudar-se cada dia,  
Outra mudança faz de mor espanto:  
Que não se muda já como soía*

**Luís Vaz de Camões**

Paranimfen: Rosemarie Kentie  
Krijn Trimbos

## CONTENTS

<b>Chapter 1:</b> General Introduction	9
<b>Box A:</b> Introducing the rice cultivated landscape of the Tejo and Sado estuaries, Portugal	18
<b>Chapter 2:</b> Waterbird densities in South European rice fields as a function of rice management (published in <i>Ibis</i> , 151: 196-199)	23
<b>Chapter 3:</b> Stop-over ecology of Black-tailed Godwits <i>Limosa limosa limosa</i> in Portuguese rice fields: a guide on where to feed in winter (published in <i>Bird Study</i> , 55: 194-202)	39
<b>Chapter 4:</b> Population overlap and habitat segregation in wintering black-tailed godwits (in press in <i>Bird Study</i> )	55
<b>Chapter 5:</b> Site selection and resource depletion in black-tailed godwits <i>Limosa l. limosa</i> eating rice during northward migration ( <i>Journal of Animal Ecology</i> , 79: 522-528)	71
<b>Chapter 6:</b> Phenology, stop-over dynamics and population size of migrating black-tailed godwits <i>Limosa limosa limosa</i> at a key staging area, the Tejo and Sado rice plantations (published in <i>Ardea</i> , 98: 35-42)	87
<b>Chapter 7:</b> Repeatable timing of northward departure, arrival and breeding in black-tailed godwits <i>Limosa l. limosa</i> , but a surprising absence of domino effects	103
<b>Box B:</b> The different names of a migratory species	119
<b>Chapter 8:</b> General Discussion	123
<b>References</b>	137
<b>Summaries</b>	161
<b>Other Publications</b>	173
<b>Acknowledgements</b>	181
<b>Addresses of Co-authors</b>	187





# Chapter 1

## General Introduction

Pedro M. Lourenço

## Staging areas as critical steps in avian migration

Migration is a widespread phenomenon in nature. From the daily vertical migration of plankton life-forms, to the epic three generations long journey of the monarch butterfly *Danaus plexippus*; from the massive migratory movements of the wildebeest *Connochaetes gnou* in the African savannah to the trans-oceanic voyages of whales, the scale and complexity of wildlife migratory movements have always marvelled and puzzled man (Dorst, 1962; Alerstam, 1990).

A common feature associated with birds is their habit of migrating. The relatively low energy costs, in relation to the distance travelled, of locomotion by flight (Schmidt-Nielsen, 1972; Rayner, 1995), especially when compared with the speed of aerial journeys (Alexander, 1998), allow birds to perform long migratory journeys, not uncommonly on an intercontinental scale. Bird migration has long been seen as one of the main research fields in ornithology. Ornithologists have come a long way since Linnaeus, 250 years ago, suggested that swallows winter in the bottom of lakes and skylarks *Alauda arvensis* among the roots in holes in the ground (Alerstam & Hedenström, 1998a). Developments, like bird ringing, field identification, radio-tracking and, more recently, satellite tracking of individuals have been crucial for a better understanding of bird migration (Alerstam & Hedenström, 1998b).

For a migrant bird, the shortest distance between two points seldom is a straight line. There are constraints in terms of habitat availability on the migratory route, obstacles to cross and compromises to be made (Alerstam, 1990). On the course of a migration, animals must make decisions upon which depend their survival and breeding success. They must decide when to depart, they must decide whether to make the trip in one long jump or to stop along the way, and in each stop they must decide how long to stay (Jenni & Schaub, 2003; Schaub *et al.*, 2008). The migratory journey is often characterized by an alternation between flight, when distance is covered and energy is consumed, and fuelling when energy for the next flight stage is accumulated (Piersma, 1987; Alerstam & Hedenström, 1998a). In fact, the majority of time and energy spent during an entire migration episode are actually spent on the ground (Hedenström & Alerstam, 1997).

A large number of staging events allows birds to fly with smaller energy costs, as shorter flights require less fuel stores, so birds can complete them while flying with relatively lower weights (Piersma, 1987). However, increasing the number of stop-overs will extend the time spent on migration, in part due to the settling costs in each stop-over

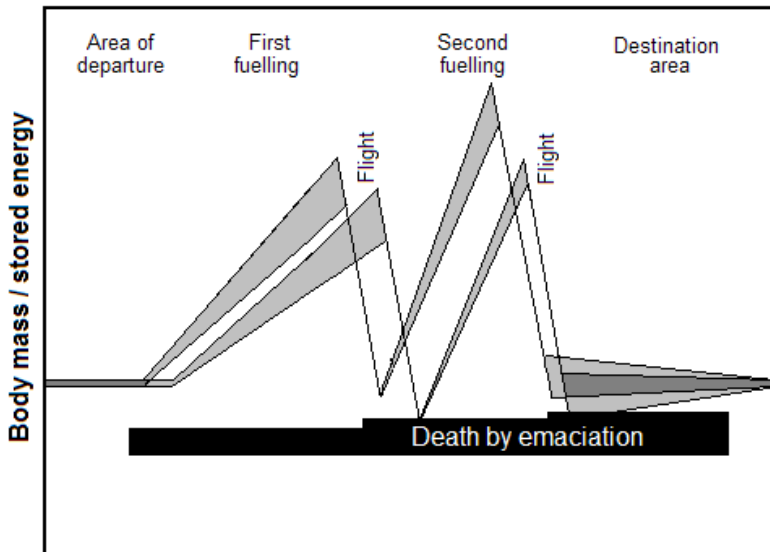
site (Alerstam & Lindström, 1990). Additionally, at some staging areas, birds will be faced with risks of predation (e.g. Moore *et al.* 1990; Ydenberg *et al.*, 2007) and parasitism (Figuerola & Green, 2000), to which they are virtually invulnerable during migratory flights (Gill *et al.*, 2009).

The trade-off between time-minimizing and energy-minimizing during migration has been subject of much discussion. Early arriving birds tend to have higher breeding success than late arriving birds (e.g. Myers, 1981; Smith & Moore, 2005; Drent *et al.*, 2006). Minimizing time spent on migration can thus benefit the breeding success of migrant birds. Minimizing the energy spent on migration will make it possible for birds to buffer the uncertainties in weather conditions and food availability during migration and upon arrival (e.g. Gudmundsson, 1991; Ebbinge & Spaans, 1995), and to meet the energetic demands of reproduction (Alerstam & Lindström, 1990). Using maximization models, Farmer & Wiens (1998) showed that birds may use different strategies during spring and autumn migration. Time-minimizing seems to have greater importance in spring migration as birds are time-limited by the need to arrive early at their breeding sites (Lindström & Alerstam, 1992).

Migratory staging periods are very important in the yearly cycle of migrant birds, conversely, knowledge of habitat requirements of migrants during stop-over is crucial for efficient conservation of medium- and long-distance migrants (Ens *et al.*, 1990; Chernetsov, 2006). Despite this, stop-over ecology is one of the least studied aspects of avian migration (Lindström, 1995). At staging sites, large numbers of birds gather in relatively confined areas, needing to quickly find enough food to replenish their energy stores. In these conditions, strong competition for food is likely to arise, with food sources becoming depleted by the intense foraging activity of large numbers of birds (Schneider, 1978; Nolet & Drent 1998; van Gils & Tijssen, 2007). The presence of many birds at the same spot will also attract predators, so predation risk is also an important limiting factor for the survival of birds during staging periods (Newton, 2006).

Birds will establish themselves at staging sites with the larger food supplies (Ottick & Dierschke, 2003; van der Graaf *et al.*, 2007) relative to other fitness-related habitat selection criteria (van Gils *et al.*, 2004), as the fuel deposition rates are closely correlated with the abundance, availability and quality of food (Piersma *et al.*, 2005; van Gils *et al.*, 2005; van Gils & Tijssen, 2007). In sites where birds can achieve higher intake rates, birds will be able to obtain the necessary stores for the next flight faster and, thus, be able to leave the staging site sooner. In fact, staging duration is negatively correlated with food

abundance (Russell *et al.*, 1992; Schaub, *et al.*, 2008), so the food availability at staging sites can have a very important impact on the speed of the whole migration. However, there is evidence of great individual variation within migrating populations, as many individuals fail to attain the maximum expected refuelling rates (Lindström, 2003), and fuel deposition rates may be locally lowered due to harsh weather conditions (Schaub & Jenni, 2000). Also, birds that arrive at their stop-over sites in worse condition tend to stay there for longer periods of time, as they require more food intake to achieve the necessary fuel loads for departure (Morris *et al.*, 1996; Yong & Moore, 1997). In some cases, when faced with unexpected unfavourable conditions, birds can decide to skip a staging site completely, probably hopping to find better conditions further ahead in their migratory route (Gudmundsson *et al.*, 1991; Kuenzi *et al.*, 1991). They can also strategically skip a staging site en route through the phenomenon of overloading (Gudmundsson *et al.*, 1991)



**Figure 1.1:** Graphical representation of the long-term domino effects in migration. Problems in the first and/or second refuelling episodes reduces the rates of mass gain and accumulation of energy stores (grey area) and the top speeds no longer occur. The accumulated energy stores no longer suffice and a proportion of birds may die from exhaustion and emaciation. Based on Fig. 7.5 in Piersma & Baker (2000).

The individual differences can reflect differences between the sexes or between adults

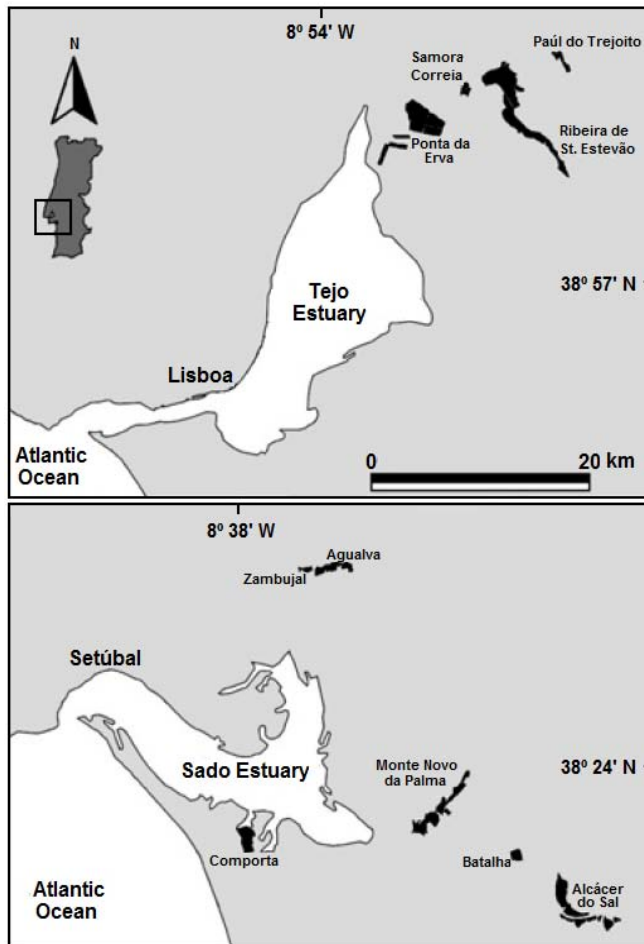
and juvenile birds, which may be explained by different competitive ability (Newton, 2006). Individual experience can also be an important factor on the foraging efficiency of the birds. On the other hand, body condition of the birds is also known to influence the foraging activity of the individuals, e.g. when lean birds achieve higher feeding rates than heavier birds (Yong & Moore, 1993; Moore, 1994). This may happen because lean birds are willing to face higher risks, using more dangerous feeding areas and spending more time foraging and less time looking for predators (Ydenberg *et al.*, 2002; Pomeroy *et al.*, 2006).

Slow fuelling rates may cause birds to suffer from the so called domino effect. Slow fuelling rates will lead to later departure times, causing birds to arrive later at the next stop-over and finding this second area already depleted, which will slow down the fuelling rates on that site, delaying the departure again, in a cascade of events that greatly reduces the overall speed of migration (Piersma, 1987). The same is true for body mass. Slower birds will have more difficulties accumulating the necessary energy stores at each step of the migration which will cause further delays and can have more drastic repercussions than simply reducing the speed of migration (Fig. 1.1). The inability to accumulate sufficient energy stores for the following flights will cause a proportion of birds to die from exhaustion and emaciation (Moore *et al.*, 1990; Piersma & Baker, 2000), and the risk of predation is higher in weaker birds (Bijlsma, 1990). Mortality is especially common after crossing great expanses of unusable habitats, like oceans or deserts (Strandberg *et al.*, 2009) or due to adverse weather conditions. Also, birds arriving with low body mass and trying to win back the mass and time delays might run a disproportionate high risk of infection by parasites or pathogens (Piersma & Baker, 2000).

The conditions found during the wintering and staging periods can affect the subsequent breeding season. Habitat quality can affect fuelling rates and consequently the individual timing of departure from the non-breeding grounds (Marra *et al.*, 1998) and arrival on the breeding grounds (Gill *et al.*, 2001a; Norris *et al.*, 2003). This can then influence breeding success as early arriving birds tend to have higher breeding success than late arriving birds (e.g. Hötter, 2002; Neto & Gosler, 2005; Smith & Moore, 2005). Furthermore, studies in snow goose *Anser caerulescens* and pink-footed goose *Anser brachyrhynchus* have shown a positive correlation between individual condition during migration and variables related to breeding success, like clutch size, egg volume, chick weight and egg laying date (Madsen, 1995; Bêty *et al.*, 2003; Drent *et al.*, 2003).

### A migrant that relies on rice fields during much of the year

The black-tailed godwit *Limosa limosa* is a medium sized wader (sub-order Charadrii). The species is divided into three subspecies. Both the continental (*L. l. limosa*) and the Icelandic (*L. l. islandica*) subspecies breed in Europe, while the eastern one (*L. l. melanuroides*) breeds in Asia (Delany *et al.*, 2009). The two European subspecies are segregated during the breeding season. The Icelandic godwits breed almost exclusively in Iceland, with a few pairs breeding in Norway and Scotland. The continental godwits breed in northern Europe, from the British Isles in the west to the Yenisey River in Russia in the east (Thorup, 2006; Delany *et al.*, 2009).



**Figure 1.2:** Map of the study areas, located around the estuaries of the Tejo and Sado rivers in the Portuguese western coast. The monitored rice field areas are presented in black.

The recent population trends of these subspecies are highly divergent: the continental population is declining severely, while the Icelandic population is undergoing a sustained increase (Gunnarsson *et al.*, 2005a; Gill *et al.*, 2007). The bulk of the *L. l. limosa* population breeds in The Netherlands (Thorup, 2006). The western part of this subspecies is believed to be isolated (Höglund *et al.* 2008), including birds that breed in The Netherlands, but also in Germany, Belgium, France, Sweden and Denmark. This western population will be the main focus of this thesis.

These birds mostly winter in western Africa, namely in Senegal, Gambia, Guinea-Bissau and Mali, where they use freshwater habitats, both natural marshes and man-made rice plantations (Beintema & Droost, 1986). They are early migrants and start northward migration as early as December. From December to March they stage in Iberia where they mostly use rice fields areas. The main rice field areas in Portugal, mostly around the Tejo and Sado estuarine areas in the central western coast (Fig. 1.2), are known to harbour very large concentration of godwits during migration (Beintema *et al.*, 1995; Lourenço & Piersma, in press a; Chapter 6). However, there is little information about their ecology in these areas, about their diet, about their habitat preferences and exact numbers. Also, the conditions found at these staging sites can be significant to the subsequent breeding season and to the birds' breeding success.

### **Birds and rice cultivation in Portugal and the world**

Human caused changes to the world's ecosystems have reached unprecedented levels. Nearly one half of the ice-free land mass of the Earth has been changed by human action, most of this transformed into agricultural land (Vitousek *et al.*, 1997). In recent years there has been great concern regarding agricultural land uses and their importance for the conservation of biodiversity (Pain & Pienkowski, 1997).

Wetland areas are one of the ecosystems most affected by agricultural encroachment. In many parts of the world, wetlands have been replaced by rice plantations which today represent 15% of the global wetland area (Lawler, 2001). Studies in all continents have proven their importance, particularly for waterbirds, which often use rice cultures as a substitute for natural wetlands lost to human development (Fasola & Ruíz, 1996; Elphick, 2000; Maeda, 2001; Richardson & Taylor, 2003; Blanco *et al.* 2006; Sánchez-Gusmán *et al.*, 2007). In the rice fields birds find invertebrate prey (Lawler, 2001), as well as plant remains and spilled rice grain (Trèca, 1994; Bird *et al.*, 2000).

**Table 1.1:** World rice production by continent. We present the yearly rice production (Mt), the land area used for this crop (x 1000 km<sup>2</sup>) and the percentage of the World's rice cultivated area present in each continent (FAOSTAT, 2009).

Continent	Production (Mt)	Land area (x1000 km <sup>2</sup> )	% Total area
Asia	584.6	1351.2	86.7
Africa	37.6	133.4	8.6
S America	22.1	49.3	3.2
C and N America	1.4	17.8	1.1
Europe	3.6	5.9	0.4
Oceania	0.2	0.6	0

Most of the rice production is concentrated in Asia, where well over a million square kilometres are covered by this crop (Table 1.1). Although Europe is a secondary player in rice production, significant areas, mostly in Southern Europe are used for rice cultivation. Here, the four main producers are Italy, Spain, Portugal and France. The extent of rice cultivation evolved in different ways in these countries in the last five decades. While in Italy and Spain there were significant increases, in Portugal and France the overall trend was negative (FAOSTAT, 2009).

In Portugal, rice farming goes back to the Middle Ages, when it was introduced during the kingdom of D. Dinis (1279-1325), but it only gained its current importance in the 1930s (Lains & Sousa, 1998). The area used for rice production peaked in the 1960s after which it had a negative trend, decreasing by almost 30% in the last 55 years (Lains & Sousa, 1998; FAOSTAT, 2009). Little information was available about the significance of Portuguese rice cultivations for resident and migratory bird species. Portuguese rice fields are known to harbour important numbers of egrets, herons and storks (Farinha & Trindade 1994), and are used by raptors, namely in the winter (Costa *et al.* 1993, Lourenço, 2009). However, the most important bird population using these rice fields is possibly the continental black-tailed godwit.

## Thesis aims and outline

After this general introduction, the main body of the thesis is composed by six chapters,



each composed of a research article, followed by a general discussion of the overall findings.

While starting this work, it became clear that much baseline information regarding the ecology of the bird community in the rice fields of southern Europe was not available in the literature. Therefore, the first chapters try to fill some of these gaps in our knowledge. In **Chapter 2** we describe the habitat preferences of the most abundant waterbird species present in the rice fields, and draw some conclusions regarding the conservation of avifauna in this agricultural habitat. In **Chapter 3** we take a similar approach to analyse in more detail the habitat preferences of black-tailed godwits in relation to rice field management, taking into account their diet and the abundance of the main food source – rice seeds. **Chapter 4** is a joint project with colleagues from the University of East Anglia, in which we unravel the issue of the habitat segregation between the two European subspecies of black-tailed godwits during the period when they overlap in Iberia.

The following chapters capitalize on this initial work to study some of the staging processes in our study population. In **Chapter 5** we analyse the role of resource depletion in the foraging site selection of black-tailed godwits using Portuguese rice fields, and determine how individual godwits decide when to leave a specific rice field and where to start foraging next. In **Chapter 6** we describe the phenology of the black-tailed godwit staging period in Portuguese rice fields and calculate the duration of this staging period for individual birds. We further estimate the total number of godwits using these areas during migration, which allows for a better evaluation of the significance of this staging area for the overall population. Using the density of individually marked individuals we estimate of the current size of the western population of *Limosa l. limosa*.

In **Chapter 7** we explore the repeatability in the timing of individual migratory and breeding schedules, and analyse the possible correlations between the timing of the staging period and the timing of arrival at breeding areas and the timing of breeding. Finally, in **Chapter 8** we integrate the findings of the previous chapters with current scientific knowledge on a general discussion.

### **Box A: Introducing the rice cultivated landscape of the Tejo and Sado estuaries**

The central part of the Portuguese western coast is characterized by two very large estuaries, where the rivers Tejo and Sado meet the Atlantic Ocean. Along the lower basins of these two rivers, the presence of flat terrain and the hydrological regime attracted the cultivation of rice soon after this crop became available in Europe. The current rice plantations are present in two different landscapes. Along the main valley of the Tejo and its last main tributary, the Sorraia, there are vast stretches of flat land, so irrigation channels span far beyond the river bed, serving a large area of crop fields including rice, maize, wheat, oats and other crops. There the rice fields cover large continuous areas of several hundreds of hectares (Fig. A.1).



**Figure A.1:** Flooded rice field in the flat low-lying areas north of the Tejo estuary.

Along the valleys of the Sado and its tributaries, and along the smaller tributaries of the Tejo, the rice fields occupy the small available patches between the river and the hills surrounding them. Here the rice fields are much smaller, often covering less than 100 ha, always close to the river and bordered by the cork oak and pine woods that cover the nearby hills (Fig. A.2).

Rice fields are a very seasonal habitat due to the cycle of rice cultivation. Sowing occurs early in the spring, after which the fields are kept flooded for most of the growing period. By the end of the summer the rice is maturing (Fig. A.3) and the water levels are

allowed to drop until the fields are dry in time for the harvest in October and November. From November to March there is no rice cultivation.



**Figure A.2:** Flock of godwits over a small rice field in Zambujal, Sado. The rice field is bordered by cork oak woods.



**Figure A.3:** Mature rice in September, in a rice field near Samora Correia, Tejo.

In this period the water levels vary between rice fields. In some areas the fields are

drained in order to burn the stubble, while in other areas the fields are flooded to facilitate the decomposition of the plant remains. Some fields are left unmanaged and the water level changes according to the amount of rainfall during the winter. In particularly wet winters some of the valleys are totally flooded. Before the next sowing season, the fields must be ploughed and leveled (Fig. A.4), but these actions can take place at any point during the winter, so some fields are already ploughed in December, while others are still covered with stubble in early March.



**Figure A.4:** Ploughing activities in a rice field near Monte Novo, Sado.

In most cases, rice fields have a strong human presence, even in the winter. This presence ranges from farms and farming activities in and around the rice fields, to roads with traffic, hunting for snipes and quails, and even built-up urban areas within a few hundred meters of the rice fields (Figs. A.5 and A.6). Despite all these sources of disturbance, the rice fields around the Tejo and Sado estuaries support a rich bird community, including grebes, cormorants, herons and egrets, storks, ibises, spoonbills, flamingos, ducks, birds of prey, rails, gulls, kingfishers, passerines and, of course, waders. During the winter, the black-tailed godwit is the most abundant bird species in the area. Large flocks of tens of thousands of these birds have been spotted even in rice fields bordered by urban areas (Fig. A.6).



**Figure A.5:** Rice fields adjacent to the town of Alcácer do Sal, Sado.



**Figure A.6:** Large flock of godwits (whole flock was estimated to include 26000 birds) in rice fields bordered by the town of Samora Correia, Tejo.



# Chapter 2

## **Waterbird densities in South European rice fields as a function of rice management**

Pedro M. Lourenço

Theunis Piersma

Ibis (2009) 151: 196-199

*Human activities are greatly changing the world's habitats and many natural wetlands have been drained or otherwise transformed for farming activities, like rice plantations. Some of these agricultural habitats are now of importance for the conservation of aquatic species that lost their natural environments.*

*We analysed how two aspects of rice field management (amount of water in fields and straw management), affected waterbird densities in these areas during the winter, using generalized mixed-effects models.*

*Both variables had a significant influence on the distribution of aquatic birds, with most species showing higher abundances in flooded fields rather than dry or moist fields. Some species showed higher densities in ploughed fields whereas others preferred fields where the stubble was left for burning; a few species had high densities in set-aside fields.*

*Having established that farming practices affect aquatic bird communities, and considering that rice fields today represent what were earlier extensive natural freshwater marshes, we conclude that correct management of these areas is essential to guarantee the conservation of waterbirds. Accordingly, we propose that simple management measures such as the flooding of fields and phased ploughing throughout the winter ensure conditions that are beneficial for both farmers and waterbirds.*



## Introduction

In recent years there has been great concern regarding agricultural land uses and their importance for the conservation of biodiversity (Pain & Pienkowski, 1997). Human caused changes in the world's ecosystems have led to a progressive substitution of natural habitats by artificial agricultural habitats, which today represent one third of the world's ice-free land area (Urban & Vollrath, 1984). Many wild species adapt to these new habitats. Examples are the agricultural meadows on which so many species of meadow birds now depend in northern Europe (e.g. Musters *et al.*, 2001), or the artificial cereal steppes that allow the survival of steppe land species, like the great bustard *Otis tarda* and the lesser kestrel *Falco naumanni*, in southern Europe (e.g. Pinto *et al.*, 2005; Rodríguez *et al.*, 2006).

Rice (*Oriza sativa*) cultivations represent today 15% of the world's wetlands (Lawler, 2001) and have been shown to be of great importance for aquatic birds in areas like southern Europe (Fasola & Ruíz, 1996), North America (Elphick & Oring, 1998; Elphick, 2000), Japan (Maeda, 2001) and West Africa (Tréca, 1994; Kuijper *et al.*, 2006). For many species, rice fields have replaced the original wetland habitats lost to reclamation and drainage. Rice fields function as temporary wetlands, with conditions changing drastically in the course of the year. In southern Europe, paddies are flooded in spring to prepare for seed plantation, during summer water levels are kept high and in September/October the paddies are drained to facilitate the harvest. During winter the water level in the rice fields depends on rainfall and agricultural management.

Birds can have a negative impact on rice plantations during the summer, as they eat seeds and trample the crops (Decker *et al.*, 1990; Tourenq *et al.*, 2001a). However, the presence of birds in flooded rice fields during the winter seems to enhance straw decomposition, thus providing direct economic benefits for farmers (Bird *et al.*, 2000; van Groenigen *et al.* 2003). Flooding attracts birds to the rice fields and speeds straw losses while reducing weed biomass in the paddies (Manley *et al.* 2005). That most birds, especially the northern migrants, use the rice fields in winter during their non-breeding season yields the possibility to create a situation that is beneficial in terms of both economics and biodiversity conservation.

Modernization of rice farming practices influences the conditions for waterbirds. In other farming systems, low intensity farming, with the maintenance of set-aside fields can be beneficial for some species (Bignal & McCracken, 1996; Blanco *et al.*, 1998), while better draining systems can eliminate wet winter rice fields that have been proven important

for aquatic birds (Day & Colwell, 1998; Elphick & Oring, 1998; 2003). In Portuguese rice fields, flooded fields seem to harbour the highest amounts of waste rice, an important food source for some birds (Lourenço & Piersma, 2008a; Chapter 3); however, some studies in North America contradicted this pattern, suggesting flooding fields reduces the amount of waste rice due to seed decomposition and germination (Stafford *et al.*, 2005; 2006). Changes in water levels and straw management can influence the use of rice paddies by birds (Day & Colwell, 1998; Elphick & Oring, 1998).

In order to understand how rice field conditions influence the bird species that use these agricultural habitats during the winter, we analysed the patterns of specific abundance on the bird community of the rice field areas around the Tejo and the Sado estuaries, Portugal, and related these to two rice paddy characteristics: (1) straw management and (2) presence of water.

## **Methods**

### *Study Area*

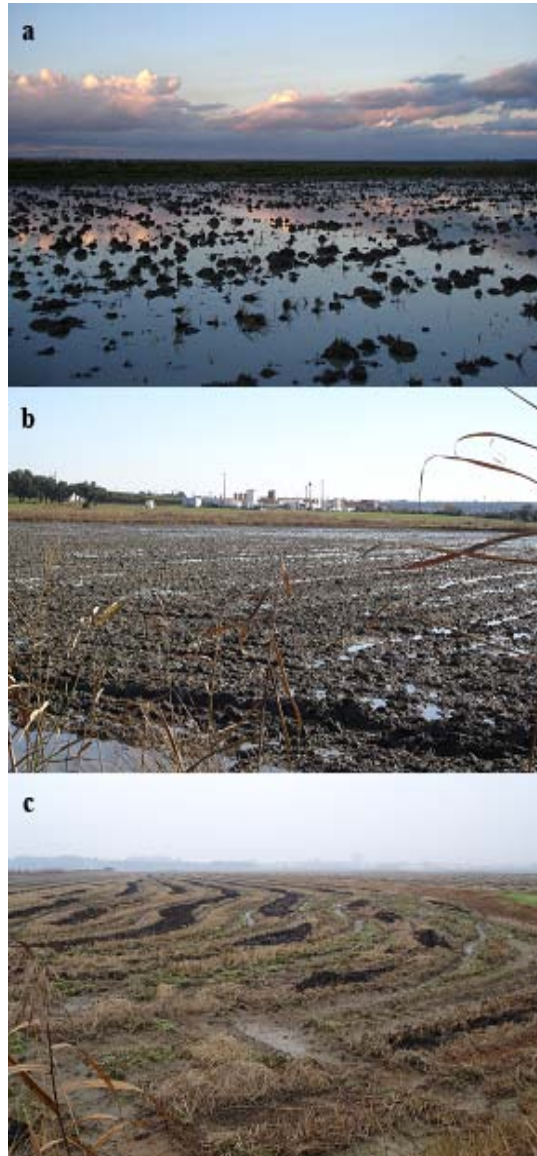
Although records of rice farming in Portugal go back to the Middle Ages, large scale rice production only started in the 1930s (Lains & Sousa, 1998), currently reaching over 25000 ha planted each year. Most of these areas are located around the estuaries of the Tejo (38° 57' N, 8° 54' W) and Sado (38° 24' N, 8° 38' W) rivers, and along the lower parts of their basins.

Field work took place in a number of areas around these two estuaries. In the Tejo we counted waterbirds in Ponta da Erva, Samora Correia, Ribeira de St. Estevão and Paúl do Trejoito; in the Sado estuary we counted Zambujal, Agualva, Monte Novo da Palma, Alcácer do Sal, Batalha e Carrasqueira (Fig. 1.2).

After the harvest, in September/October, stubble is left standing in the fields. During the following months, some farmers plough the fields, mixing the stubble with the soil; others leave it and later burn the stubble. The water level in the fields also differs between paddies, due to both rainfall and drainage, with some fields completely drying out, others remaining moist, with some water in parts of the field and ditches, and others remaining flooded. Finally, some fields are set-aside and unused for a whole year.

When bird censuses were performed, every paddy was characterized according to the stage of straw management: mature rice, standing stubble, ploughed fields and set-aside fields; and presence of water; flooded fields, moist fields, dry fields (Fig. 2.1). Later, the

size of each paddy was measured using aerial photography (Google Earth) and GIS software.



**Figure 2.1:** Examples of the three types of fields, regarding the amount of water in the paddies. a – flooded fields, b – moist fields, c – dry fields.

### *Bird censuses*

We randomly selected 120 rice paddies, representing over 10% of the total surface of the study areas (280 ha out of a total 2547 ha). Bird censuses were performed every two weeks, from October 2005 through March 2006, and in December 2006 and January 2007, always avoiding hunting days (Thursdays, Sundays and national holidays), when birds are constantly moving from field to field due to disturbance. The total number of counts in individual fields was 885.

During the census, all non-passerine birds present within the fields were counted. Birds disturbed from a field were included, but birds seen just flying over were excluded. When selecting random fields, we rejected adjacent paddies to avoid the risk of double counting birds that were flushed from a paddy during the census. To avoid any systematic biases due to regular movements of the birds, the order in which the fields were visited changed in each count.

### *Data analysis*

Census data were first converted into densities and then analysed fitting generalized mixed-effects models (Pinheiro & Bates, 2000) for each species. For these we used WET (amount of water in the field: dry/moist/flooded) and STR (stage of straw management: mature rice/standing stubble/ploughed field/set-aside) as fixed factors in the models, and EST (estuary: Tejo/Sado), SIT (each of the study areas around the estuaries), PAD (individual paddies within each area) and DAT (the Julian date in which the count was performed) as random factors, nesting PAD within SIT and SIT within EST, while DAT was nested within this nesting structure. To account for the temporal variation we used a type 1 autocorrelation structure (Box *et al.*, 1994) for the last random factor, DAT. This hierarchical structure solves the problems caused by serial correlation and heteroscedasticity. The multilevel regression approach provides extremely flexible variation for the error term structure, which enables us to test random effects, fixed effects and provides more robust models.

The Akaike Information Criterion (AIC) was used to select the best model for each species, and a pseudo  $R^2$  was calculated for the final models to assess the quality of the fit (Pinheiro & Bates, 2000). Finally, we used Tukey's HSD tests to evaluate differences between treatments in the variables that were included in the final fitted models. All computations were performed using the R software package.

## Results

### *Bird densities*

The most abundant species in the studied rice fields were waders, herons, egrets and storks. The densities were generally quite low, with a large proportion of counted fields being empty of birds. We detected a total of 37 non-passerine bird species, of which the 13 most common were used for further analysis (Table 2.1; Appendix 2.A).

Even within these 13 species, densities were generally below 1 individual per hectare. Extrapolating over the entire area of rice habitat, however, suggests that even these low densities would translate into hundreds or thousands of individuals of each species using the habitat (Table 2.1).

**Table 2.1:** The 13 most abundant non-passerine bird species present in our study plots. We present the densities  $\pm$  SE in individuals/10 ha and an estimate of the total number of individuals present in the entire study area, based on a total surface of 2547 ha. Taxonomic order based on del Hoyo *et al.* (1992; 1996).

Species	Density	Estimated total
Grey heron <i>Ardea cinerea</i>	$1.1 \pm 0.1$	284
Little egret <i>Egretta garzetta</i>	$2.4 \pm 0.3$	622
Cattle egret <i>Bubulcus ibis</i>	$0.3 \pm 0.1$	67
White stork <i>Ciconia ciconia</i>	$3.4 \pm 0.5$	854
Greater flamingo <i>Phoenicopterus roseus</i>	$2.0 \pm 0.1$	510
Black-necked stilt <i>Himantopus himantopus</i>	$0.5 \pm 0.2$	124
Pied avocet <i>Recurvirostra avosetta</i>	$3.4 \pm 2.4$	866
Lapwing <i>Vanellus vanellus</i>	$7.0 \pm 2.0$	1781
Common snipe <i>Gallinago gallinago</i>	$2.1 \pm 0.5$	540
Black-tailed godwit <i>Limosa limosa</i>	$15.2 \pm 5.4$	3848
Redshank <i>Tringa totanus</i>	$0.5 \pm 0.2$	136
Lesser black-backed gull <i>Larus fuscus</i>	$0.3 \pm 0.2$	83
Black-headed gull <i>Larus ridibundus</i>	$2.4 \pm 1.1$	631

### *Generalized mixed-effects models*

For five species, cattle egret *Bubulcus ibis*, black-winged stilt *Himantopus himantopus*, common snipe *Gallinago gallinago*, lesser black-backed gull *Larus fuscus* and black-

headed gull *Larus ridibundus*, none of the fixed factors were included in the final fitted models (Table 2.2). Straw management stage was included in the final fits for seven species, little egret *Egretta garzetta*, grey heron *Ardea cinerea*, white stork *Ciconia ciconia*, pied avocet *Recurvirostra avosetta*, northern lapwing *Vanellus vanellus*, black-tailed godwit *Limosa limosa* and common redshank *Tringa totanus* (Table 2.2). The amount of water in the paddies was also included in the final fitted models for seven species, including greater flamingo *Phoenicopterus roseus* for which it was the only fixed variable included in the final model (Table 2.2).

**Table 2.2:** Results of the regression analysis, for each studied species. For each species we indicate the fixed factors included in the final fitted model, and the pseudo  $R^2$  calculated for the model. A factor was not included when the AIC of the models that included them were less than two units lower than the AIC of the best fitting model.

Species	WET	STR	pseudo $R^2$
Little egret	X	X	0.49
Grey heron	X	X	0.38
Cattle egret			
White stork	X	X	0.25
Greater flamingo	X		0.31
Black-winged stilt			
Pied avocet	X	X	0.42
Northern lapwing	X	X	0.52
Common snipe			
Black-tailed godwit	X	X	0.59
Common redshank		X	0.22
Lesser black-backed gull			
Black-headed gull			

### *Habitat preferences*

Looking at our three explanatory variables, we found varying effects in different species. The amount of water in the rice fields was a significant factor for seven species, of which all showed higher densities in flooded fields (Table 2.3). The only variation from this norm was the little egret, which had similar densities in both flooded and moist fields, with

no significant distinction between the two (Tukey test:  $P > 0.1$ )

**Table 2.3:** Species preference for the amount of water in the fields. All densities are in birds/10 ha  $\pm$  SE. Presented results indicate the results of the Tukey HSD tests. \* -  $P < 0.05$ ; \*\* -  $P < 0.01$ ; \*\*\* -  $P < 0.001$ .

Species	Water in the field		
	dry	moist	flooded
Little egret	$0.3 \pm 0.1$	$2.4 \pm 0.3^{**}$	$4.3 \pm 0.6^{**}$
Grey heron	$0.3 \pm 0.1$	$1.1 \pm 0.1$	$1.9 \pm 0.1^{**}$
White stork	$0.3 \pm 0.1$	$2.8 \pm 0.4$	$8.1 \pm 0.9^{***}$
Greater flamingo	$0.0 \pm 0$	$0.0 \pm 0$	$11.4 \pm 2.5^{***}$
Pied avocet	$0.0 \pm 0$	$0.0 \pm 0$	$19.3 \pm 5.1^{**}$
Northern lapwing	$0.1 \pm 0.0$	$3.9 \pm 1.5$	$24.9 \pm 4.1^{**}$
Black-tailed godwit	$0.0 \pm 0$	$0.0 \pm 0$	$85.8 \pm 1.7^{***}$

The stage of straw management was a significant factor determining the densities of seven species (Table 2.4); among these, little egret, grey heron and white stork showed higher densities in standing stubble fields, although the latter had similar densities in set-aside fields (Tukey test:  $P > 0.1$ ).

**Table 2.4:** Species preference for different straw management stages. All densities are in birds/10 ha  $\pm$  SE. Presented results indicate the results of the Tukey HSD tests. \* -  $P < 0.05$ ; \*\* -  $P < 0.01$ ; \*\*\* -  $P < 0.001$ .

Species	Straw management stage			
	mature rice	standing stubble	ploughed field	set-aside
Little egret	$0.0 \pm 0$	$2.8 \pm 0.3^*$	$1.3 \pm 0.2$	$0.0 \pm 0$
Grey heron	$0.0 \pm 0$	$1.2 \pm 0.3^*$	$0.2 \pm 0.1$	$0.2 \pm 0.1$
White stork	$0.0 \pm 0$	$1.6 \pm 0.3^*$	$0.2 \pm 0.0$	$1.2 \pm 1.3^*$
Pied avocet	$0.0 \pm 0$	$0.0 \pm 0$	$15.7 \pm 2.9^{***}$	$0.0 \pm 0$
Northern lapwing	$0.0 \pm 0$	$0.9 \pm 0.3$	$0.6 \pm 0.2$	$20.1 \pm 8.1^{***}$
Black-tailed godwit	$0.0 \pm 0$	$0.9 \pm 0.3$	$66.6 \pm 1.2^{***}$	$0.0 \pm 0$
Common redshank	$0.0 \pm 0$	$0.1 \pm 0.0$	$2.1 \pm 0.4^{**}$	$1.9 \pm 0.2^{**}$

Pied avocet, black-tailed godwit and common redshank had higher densities in ploughed fields, but in the latter case there was no significant difference between the density in the ploughed and set-aside fields (Tukey test:  $P > 0.05$ ). Northern lapwing was the only species with the highest densities in set-aside fields.

## Discussion

The observed densities in our study areas ( $4.07 \pm 0.13$  birds/ha) are comparable to waterbird densities in nearby estuarine areas (4.72 birds/ha in Granadeiro *et al.*, 2007). This is consistent with the notion that rice fields are currently a very important habitat for aquatic birds (e.g. Fasola & Ruíz, 1996; Elphick, 2000). However, it is likely that this is also due to the poor situation in which the remaining natural wetlands are in many parts of the world, and rice fields are not truly a good alternative to natural wetlands, but more of a necessary compromise for wildlife that lost their native habitats (Lawler, 2001; Ma *et al.*, 2004). In fact, in areas where natural wetlands are still abundant and remain in good quality, like the French Camargue, bird densities in local rice fields are much lower than in natural areas (Tourenq *et al.*, 2001b).

Still, rice plantations currently represent 15% of the world's wetlands, and in many places are the only lasting habitats for aquatic birds (Elphick, 2000; Lawler, 2001). A correct management of these agricultural habitats thereby becomes imperative for the conservation of waterbirds. What advice on proper management can this study give? Most studied species were significantly affected by at least one of the tested variables. The few species whose densities were unaffected by these variables included cattle egret and the two species of gulls, which are known to be generalist species, using a large range of habitats and food sources (Moreira, 1995a; Richardson & Taylor, 2003; Tourenq *et al.*, 2004). In the case of snipe, they are known to use both wet and dry rice fields, being one of the few waterbirds that does so (Maeda, 2001). Also, snipes are very hard to sample accurately, and this species is the target of hunting in our study areas (pers. obs.), so human disturbance can be a very significant factor in their distribution. Black-winged stilts are mostly found in saltpans (Múrias *et al.*, 2002) and their densities in the rice fields were rather low, probably the reason behind the apparent lack of habitat preferences in the rice fields.

It is not surprising that the amount of water in the paddies is a significant variable determining the distribution of the studied species, which are mostly waterbirds. All seven species with this variable in the final fitted model showed higher densities in flooded fields.



Flooding rice fields has been shown to be important for aquatic birds in the Central Valley, California, where a higher abundance and diversity of aquatic birds is observed in fields that are flooded (Elphick & Oring, 1998; 2003) and the simple presence of open water areas was shown to be important for the bird community in Taiwan (Chan *et al.*, 2007). In our study areas, little egrets, grey herons and white storks are likely to be using flooded fields to hunt the introduced Louisiana crayfish *Procambarus clarkii*, which has quickly become an important food item for these birds (Correia, 2001) and is rather abundant in the rice fields (Marques & Vicente, 1999). Flamingos and avocets filter small invertebrates from the water or the upper layers of sediment (Moreira, 1995b; Arengo & Baldassarre, 2002) and thus require at least some water to forage, whereas black-tailed godwits forage on rice seeds which are mostly available in flooded fields (Lourenço & Piersma, 2008a; Chapter 3). Lapwings can use a wide range of habitats, including wetlands and dry cereal crops (Delgado & Moreira, 2000; Atkinson *et al.*, 2002), but in the present case show higher densities in flooded fields being virtually absent from dry fields.

The impact of ploughing on birds has been the topic of some discussion, with contrasting results in different studies. The bird community in Japanese rice fields seems to be negatively affected by ploughing (Maeda, 2001), perhaps due to a reduction in seed availability (Shimada, 1999), while in California small waders were more common in ploughed fields, but overall bird densities were lower (Elphick & Oring, 1998; 2003). Our results suggest indeed that waders prefer ploughed fields, an effect that might be explained by the fact that ploughed fields become levelled, and thus more similar to the mudflats where this species also forage. The lack of obstacles allows an early detection of possible predators, a condition favoured by waders (Cresswell, 1994). In the case of black-tailed godwits, which forage mostly on waste rice in Portuguese rice fields, the preference seems to be explained by higher rice grain abundance in ploughed fields (Lourenço & Piersma, 2008a; Chapter 3). The heightened abundance of storks, herons and egrets in standing stubble fields is probably due to lower biomass abundance of their invertebrate prey after human intervention in the fields (Marques & Vicente, 1999).

The high abundance of lapwings in set-aside fields is in accordance with what is known for these birds in drier habitats (Delgado & Moreira, 2000). Set-aside rice fields are also important for egrets and waders in Japan (Fujioka *et al.*, 2001) where the birds prefer these fields when they are flooded, like we found in this study for white stork, northern lapwing and common redshank.

### *Implications for conservation*

The data presented here suggests that rice field management is important for the conservation of waterbirds. Densities are affected by both the amount of water in the fields and straw management. Due to drainage and other human developments, rice fields became a last resort for many species of aquatic birds and, thus, management decisions will be of great importance for the conservation of these birds.

Maintaining part of the rice fields flooded throughout the winter seems to be the most advantageous measure for the bird community, as most species are more abundant in flooded areas. This measure would also be profitable for the farmers, as the activity of foraging birds in flooded rice fields increases straw decomposition, while reducing weed biomass (Bird *et al.*, 2000; van Groenigen *et al.*, 2003; Manley *et al.*, 2005).

As different species have different preferences, the ideal situation seems to be a mosaic of ploughed, standing stubble and set-aside fields. Ploughed fields seem to be the preferred situation for most waders, while storks, herons and egrets mostly use standing stubble fields. In order to maximize the ideal condition for birds, the best situation would be one where fields are ploughed, but ploughing is spread across the winter, in order to have standing stubble fields available throughout the season. The presence of some set-aside fields can also be advantageous, namely for northern lapwing, common redshank and white stork.

Although management of individual rice fields depends on their owners, most rice fields in the lower basins of the Tejo and Sado rivers are part of farming cooperatives. Additionally, rice production in these areas is strongly subsidized by the EU (GPPAA, 2006). This way, the current situation seems favourable for the application of management guidelines that can guarantee the conservation of aquatic birds, while ensuring the economic viability of rice farming. The Portuguese governmental authorities must take action among the farming cooperatives in order to implement environmental-friendly farming practices in the rice fields, guaranteeing the presence of flooded fields in the winter, the ploughing of the fields in the correct periods and ensuring the maintenance of rice plantations. EU financing can be used as warranty for farmers to commit to official management guidelines.

In conclusion, the best situation for aquatic birds wintering in rice fields is likely to be a mosaic of moist and flooded fields, with different water levels, most of which are ploughed, but where ploughing is spread across the autumn and winter. This can be achieved by a set

of management guidelines to be proposed to local farmer cooperatives that can create a state of affairs favourable for farmers and aquatic bird conservation.

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**Appendix 2.A:** Complete list of the 37 non-passerine bird species detected in the rice fields. Average densities in individuals/10 ha. \* Detected in less than 1% of the counts.

Species	Density
<b>CICONIIFORMES</b>	
Grey heron <i>Ardea cinerea</i>	1.1
Great white egret <i>Egretta alba</i>	*
Little egret <i>Egretta garzetta</i>	2.4
Cattle egret <i>Bubulcus ibis</i>	0.3
White stork <i>Ciconia ciconia</i>	3.4
Spoonbill <i>Platalea leucorodia</i>	0.3
<b>PHOENICOPTERIFORMES</b>	
Greater flamingo <i>Phoenicopterus roseus</i>	2.0
<b>ANSERIFORMES</b>	
Teal <i>Anas crecca</i>	*
Mallard <i>Anas platyrhynchos</i>	0.1
Pintail <i>Anas acuta</i>	0.1
<b>FALCONIFORMES</b>	
Black-shouldered kite <i>Elanus caeruleus</i>	*
Marsh harrier <i>Circus aeruginosus</i>	0.1
Hen harrier <i>Circus cyaneus</i>	*
Buzzard <i>Buteo buteo</i>	0.1
Kestrel <i>Falco tinnunculus</i>	*
<b>GALLIFORMES</b>	
Ring-necked pheasant <i>Phasianus colchicus</i>	*
<b>GRUIFORMES</b>	
Moorhen <i>Gallinula chloropus</i>	0.1
<b>CHARADRIIFORMES</b>	
Black-necked stilt <i>Himantopus himantopus</i>	0.5
Pied avocet <i>Recurvirostra avosetta</i>	3.4
Lapwing <i>Vanellus vanellus</i>	7.0
Grey plover <i>Pluvialis squatarola</i>	*
Jack snipe <i>Limnospiza minutus</i>	*
Common snipe <i>Gallinago gallinago</i>	2.1
Black-tailed godwit <i>Limosa limosa</i>	15.2
Curlew <i>Numenius arquata</i>	0.1
Spotted redshank <i>Tringa erythropus</i>	*
Redshank <i>Tringa totanus</i>	0.5
Greenshank <i>Tringa nebularia</i>	0.1
Green sandpiper <i>Tringa ochropus</i>	0.1
Wood sandpiper <i>Tringa glareola</i>	*
Common sandpiper <i>Actitis hypoleucos</i>	*
Little stint <i>Calidris minutus</i>	*
Dunlin <i>Calidris alpina</i>	0.1
Ruff <i>Philomachus pugnax</i>	*
Lesser black-backed gull <i>Larus fuscus</i>	0.3
Black-headed gull <i>Larus ridibundus</i>	2.4
<b>COLUMBIFORMES</b>	
Common Pigeon <i>Columba livia</i>	0.6





# Chapter 3

## **Stop-over ecology of black-tailed godwits *Limosa limosa limosa* in Portuguese rice fields: a guide on where to feed in winter**

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Theunis Piersma

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*Staging episodes are critical periods in the lives of migratory birds. Here we analyse habitat selection and quantify the diet composition of black-tailed godwits during their stop-over in Portuguese rice fields, an area used by a large portion of the continental European population *Limosa limosa limosa*, but about which precious little is known.*

*Using water level and agricultural management of the fields as variables, habitat selection was analysed by compositional analysis. Godwit diet composition was quantified by faecal analysis, and food abundance was sampled to explain the observed habitat selection.*

*We found evidence of higher use of flooded and ploughed paddies than expected from their relative abundance. These fields have the highest densities of buried rice kernels, which seem to be the main food source for back-tailed godwits.*

*Currently, godwits find good foraging areas in Portuguese rice fields, fuelling with rice kernels that are mostly found in flooded ploughed fields. Changes in rice farming, late ploughing and predicted decreases in rainfall add to future habitat losses. Yet, because of the man-made nature of their requirements, it should be possible to install relevant land-use practices that guarantee the availability of high quality stop-over habitats.*



## Introduction

In the course of a long migration, birds need to stop a number of times for refuelling, before continuing their journeys. The migratory journey is characterized by an alternation between flights, when distance is covered and energy is consumed and staging periods, when energy for the next flight stage is accumulated (Gudmundsson *et al.*, 1991; Alerstam & Hedenström, 1998a). In fact, most of the time and energy spent during an entire migration episode is spent on the ground (Hedenström & Alerstam, 1997). Migratory stop-overs are very important periods in the yearly cycle of migrant birds, with downstream consequences for survival, breeding success and demographics (e.g. Newton, 2006). As a consequence, knowledge of habitat requirements of migrants during stop-over is crucial for their conservation (Piersma & Baker, 2000; Chernetsov, 2006). Despite this, stop-over ecology has remained one of the least studied aspects of avian migration (Lindström, 1995).

The black-tailed godwit *Limosa limosa* is a long-lived, migratory bird. The continental European race *L. l. limosa* mostly breeds in agricultural grasslands in northern and eastern Europe, where it faces a serious population decline (Birdlife International, 2004), leading to the recent classification of the species as “Near Threatened” on the IUCN Redlist (IUCN, 2009). Although this decline is mostly blamed on habitat loss and changes in agricultural practices in the breeding areas (Beintema *et al.*, 1985; Beintema & Müskens, 1987), the failure of most conservation programs (Kleijn *et al.*, 2001; Kleijn & Van Zuijlen, 2004) suggests that this subspecies could be facing additional problems at other times during their annual cycle. Black-tailed godwits winter in West Africa in marshes, flooded plains and rice fields (Cramp & Simmons, 1983) and an important part of this population performs an extended stop-over in the Iberian Peninsula, during the pre-nuptial migration, where they mostly use rice fields as foraging habitat (Beintema *et al.*, 1995; Kuijper *et al.*, 2006). Little is known about their ecology in these areas other than that they seem to forage on rice kernels (Kuijper *et al.*, 2006).

Rice fields are considered a very important agricultural habitat for birds (Fasola & Ruíz, 1996; Elphick & Oring, 1998). In many cases rice fields are seen as substitutes for natural wetlands in places where drainage and other human developments forced birds away from their original habitats (Elphick, 2000; Lawler, 2001; Tourenq *et al.*, 2001b). However, the intensification of rice farming involves changes in the management of rice paddies, with consequences for their use by birds (Maeda, 2001; Elphick & Oring, 2003). In some areas the lack of economic incentives and European Union directives have lead farmers to

abandon rice fields or change them into cornfields (GPPAA, 2006), reducing the available habitat during stop-over.

In Portuguese rice cultures, most fields are harvested in September and October, after which the stubble is left standing for the following months. Most fields are left unmanaged throughout the winter, with the water level changing with rainfall, although in some areas fields are drained in order to keep the straw dry, after which it is burned. From December onwards, farmers start to plough the fields in preparation for the next sowing season, in April, with water levels mostly fluctuating with rainfall. Thus, a mosaic of flooded, wet and dry fields in different stages of management is found when godwits arrive in Portugal in late December.

Information on the stop-over ecology of black-tailed godwits is very limited, and a better understanding of their food and habitat preferences will allow an assessment of how rice farming practices affect the quality of their stop-over habitat. The present study aims to explain the patterns of use of rice fields by black-tailed godwits as a function of food preferences, food availability and rice field management, thus providing important guidelines for the management of these areas for black-tailed godwit conservation.

## **Methods**

### *Study site*

Field work took place in a number of rice plantations around the estuaries of the Tejo (38° 57' N, 8° 54' W) and Sado (38° 24' N, 8° 38' W) rivers (Fig. 1.2), located near Lisboa along the central western coast of Portugal. These are two of the main rice production areas in Portugal, with significance in the context of southern Europe (Lains & Sousa, 1998). Field surveys were performed during the black-tailed godwit stop-over period in the area from December 2005 through February 2006 and from December 2006 through February 2007.

### *Habitat selection*

In the course of the two winters, 120 randomly selected rice paddies were characterized according to type of straw management (standing stubble, ploughed fields, and set-aside fields) and water level (flooded fields, water in ditches, wet soil, and dry fields), to evaluate habitat availability. The same paddies were studied in both years, and represented over 10% of the total rice cultivated area (280 out of 2547 ha) that was monitored for godwit

presence. This habitat characterization was performed once every fortnight, thus yielding 10 samples in each paddy, five in each year, from the second half of December to the second half of February.

Several times per week we surveyed all 2547 ha for godwit flocks. Whenever a flock was detected, it was assigned to the rice paddy where it was found, which was also characterized as above. To determine if foraging black-tailed godwits used particular habitats selectively, we compared the proportion of godwit flocks observed in each habitat with the proportion of the respective habitats available each fortnight. Since proportions of habitat types always sum to 1 and are not inter-independent (unit-sum constraint; see Aitchison, 1986), we used compositional analysis to examine our data. This method renders the proportions independent and approximately normally distributed by log-ratio transformation based on one of the proportions as denominator, after replacing zero values with 0.01 (Aebischer & Robertson, 1992). Using multivariate analysis of variance and a suitable statistic (Wilk's lambda,  $\Lambda$ ), it is then possible to assess whether log-ratio differences (utilized - available) differ significantly from 0 (random habitat use) over all the periods. Finally, a rank of the habitats can be composed, based on the relative use of each type, taking also into account when different ranks represent statistically significant differences in the relative utilization of the corresponding habitat types (for more details see Aitchison, 1986; Aebischer & Robertson, 1992; Aebischer *et al.*, 1993; Tomé & Valkama, 2001).

#### *Food availability and diet*

In 2006, a group of 48 rice paddies, representative of the different management and water level conditions were sampled, using a flat shovel that was able to cut through the hard roots in the soil. Each sample was a 10x10 cm square, with a depth of roughly 12 cm, to correspond with the maximum bill size of an adult Black-tailed Godwit (Cramp & Simmons, 1983). In each paddy, four samples were collected in the beginning of the staging period, in order to estimate food availability for godwits before they could have any significant depletion effect on the fields. The four samples from each paddy were averaged and data was log-transformed before further analysis. Additionally, on eight occasions we collected paired soil samples in paddies recently used by godwits and in a randomly selected paddy within 500 m of the first, but where no godwits were observed. The latter were paddies where no godwits had been seen until the sampling date and, later observation

shown to have not been used at all during our study. Again, we collected four samples per paddy, which were averaged for analysis. All samples were sieved through a 1 mm mesh and all invertebrates and seeds were identified under a stereomicroscope.

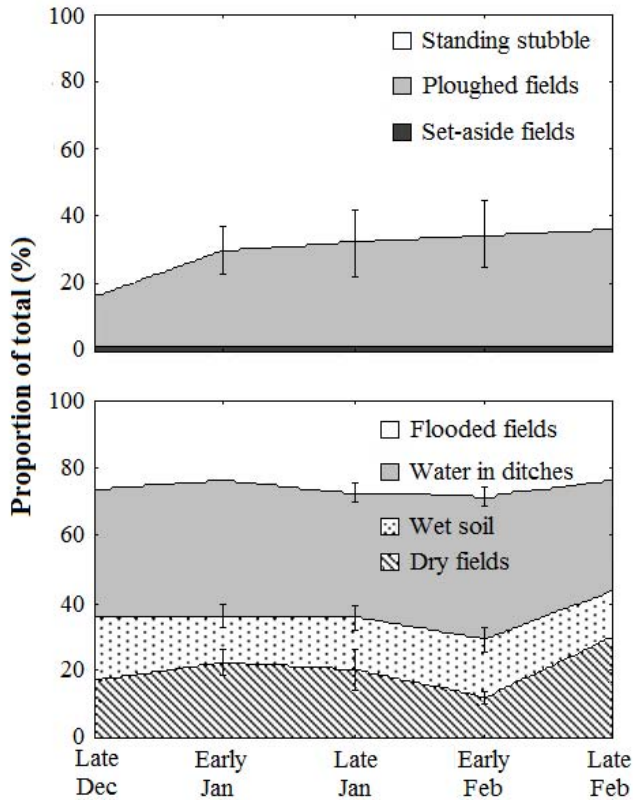
In fields that were not completely flooded, we were able to collect godwit faeces, which were stored in 70% ethanol until further analysis. These faeces were collected in paddies where very large groups of godwits had been foraging for several hours and so there was little chance of wrongly collecting faeces from other species, and each faeces was selected, based on size and appearance, to ensure no faeces of other species (e.g. gulls) were taken. A total of 79 individual faeces were sieved through a 63  $\mu$ m mesh and examined for food remains under a stereomicroscope. For most prey items it was possible to identify individual prey species in the faeces, but this was not the case for oligochaete worms, which were identified by the presence of chaeta in the samples. This poses a problem when trying to determine the proportion of the diet represented by each food type, but since the few samples where oligochaete chaeta were found had a very low number of chaeta (mean 34.2, range 5-66,  $n=5$ ) compared with the number of chaeta present in one oligochaete worm (mean 1078, range 624-1296,  $n=45$ ; Wroot, 1985), we assumed only one worm in each faeces.

## **Results**

### *Habitat selection*

As a consequence of farming activities and rainfall, the conditions in the rice fields varied over the course of the season. In both years we observed that the proportion of ploughed fields increased, as the farmers started preparing the rice paddies for the spring sowing, while the water level in the paddies changed in a more variable fashion, following the stochasticity of rain patterns (Fig. 3.1).

The habitat use of the black-tailed godwits showed a rather clear pattern (Fig. 3.2). Of a total of 205 observed flocks (92 in the first winter, 113 in the second winter), most were seen in ploughed and flooded fields. With respect to field type, the godwits occurred more often than expected in ploughed fields, secondarily using set-aside fields, while avoiding the more common standing stubble (Compositional Analysis:  $\Lambda=0.21$ ,  $P<0.01$ ). With respect to water level in the rice paddies, the godwits used flooded fields more than randomly expected, whereas all other water levels were used less than expected (Compositional Analysis:  $\Lambda=0.04$ ,  $P<0.01$ ). This pattern was maintained in both years.



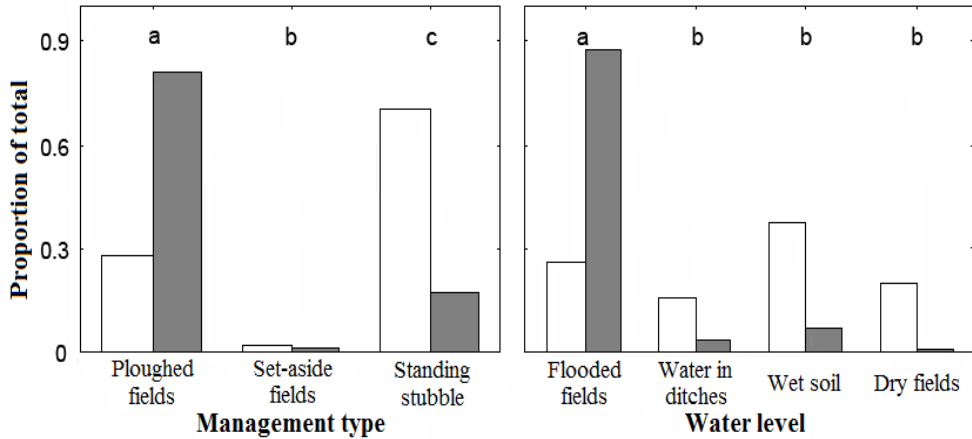
**Figure 3.1:** Variation in the availability of each management type and water level category along the stop-over period (n=120 per fortnight in each year). The sample period ranges from the second half of December to the second half of February and the percentages here presented result from the average of the two years, error bars represent  $\pm$ SE.

### *Food availability and diet*

Fifty-eight of the 79 faecal samples contained noticeable food remains. Rice kernels, found in 78% of the samples, were the most common food item. Otherwise we found gastropods, oligochaete worms, dysticid insects and the Louisiana crayfish *Procambarus clarkii*, but all of these were present in fewer than 15% of the samples (Tab. 3.1). Overall, rice kernels represented 94% of the food items identified.

Given these dietary preferences, we were then able to determine in which types of rice fields food was more abundant. The abundance of rice kernels varied sharply between different rice paddies, from locations with no rice to paddies with over 10000 kernels per

m<sup>2</sup>. This variation was related to the management type (Two-way ANOVA:  $F_{(2,48)} = 4.1$ ,  $P < 0.01$ ) and water level of the paddies (Two-way ANOVA:  $F_{(3,48)} = 5.4$ ,  $P < 0.01$ ) without significant interaction between the two factors (Two-way ANOVA:  $F_{(6,48)} = 0.77$ ,  $P > 0.1$ ).

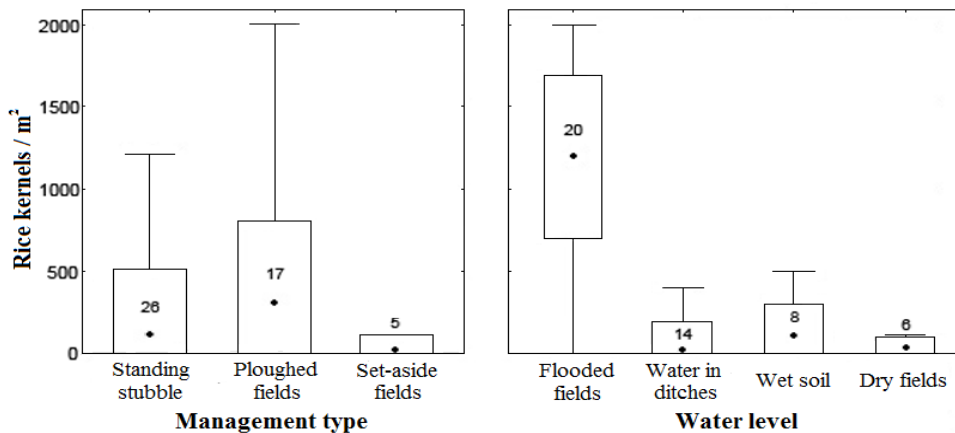


**Figure 3.2:** Habitat selection of black-tailed godwits in the rice fields. The white bars represent the proportion of rice paddies ( $n = 120$  per fortnight in each year) assigned to each management type or water level category; the grey bars indicate the proportion of godwit flocks ( $n = 205$ ) observed in each category. Note that the godwit flocks were detected in all of the study area and not only in the sub-sample of 120 paddies used to measure habitat availability. For each variable, godwit preference decreases from left to right, different letters indicate significant differences in the compositional analysis.

**Table 3.1.** Diet of black-tailed godwits during migratory stop-over in Portuguese rice fields. We present the proportion of faeces ( $n = 58$ ) where each food type was found (presence in faeces) and the proportion of the total number of identified food items ( $n = 453$ ) represented by each food type (proportion of diet).

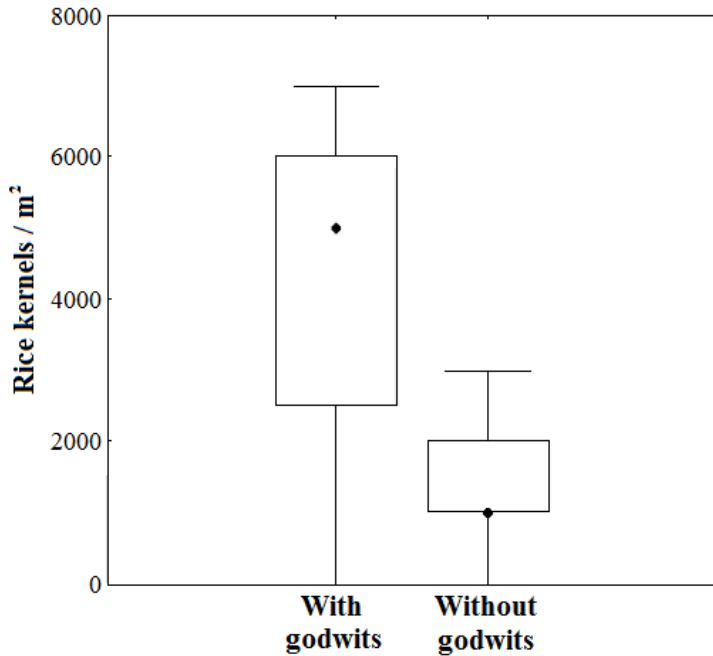
Food type	Presence in faeces	Proportion of diet
Rice kernels	0.78	0.94
Gastropoda	0.14	0.04
Oligochaeta	0.09	0.01
Distycidae	0.05	0.01
<i>Procambarus clarkii</i>	0.03	0.00

With respect to management type, we found that ploughed fields had on average the highest abundances of rice kernels, followed by standing stubble fields and finally the set-aside fields (Fig. 3.3). In relation to water levels, we found that flooded fields had by far the highest densities of rice kernels. However, post-hoc Tukey tests showed that in fields that were both flooded and ploughed, rice abundance was significantly higher than in any other, while ploughed fields with some water (wet fields or water in ditches) had significantly more rice than most other management types, even if flooded. Flooded fields of all management types tended to have more rice than fields with less water, although these differences were not always statistically significant. We found no statistically significant differences in the abundances of other food items between different management types and water levels.



**Figure 3.3:** Rice kernel abundance in the different rice field types. Both management type and water level were found to have a significant effect in rice abundance. Analysis based on 192 samples collected in 48 different rice fields. Number of fields sampled in each category is presented. The dots represent the median, the boxes are the 25-75% quartile and the whiskers indicate the 95% range.

These results suggest that the observed habitat selection is likely related to the abundance of rice kernels, the main food item for black-tailed godwits during stop-over. To further investigate this hypothesis, on eight occasions we collected paired soil samples in a field where godwits were seen foraging and in a random rice field within 500 m of the first, where no godwits were observed. Again, we found that rice abundance was significantly higher (Wilcoxon matched pairs test:  $Z=2.52$ ,  $P<0.05$ ,  $n=8$ ) in the paddies where black-tailed godwits were foraging (Fig. 3.4).



**Figure 3.4:** Differences in rice abundance between fields used by foraging godwits and other random fields. The paddies used by foraging flocks had significantly higher abundances of rice kernels. Analysis based on 64 samples collected in 8 pairs of rice fields. The dots represent the median, the boxes are the 25-75% quartile and the whiskers indicate the 95% range.

## Discussion

### *Habitat selection*

We found foraging black-tailed godwits to be very selective with respect to the type of rice field used. They clearly use flooded ploughed fields more often than expected, in opposition to dryer or unploughed land, although the latter are the most common rice field conditions. Their use of fields with the higher abundance of the main food item, rice kernels, confirms the common pattern that, during the non-breeding period, habitat selection is primarily driven by food availability (e.g. Nehls & Tiedemann, 1993; van Gils *et al.*, 2004; Lourenço *et al.*, 2005; Piersma, 2006).

Confirming suggestions by Beintema *et al.* (1995) and Kuijper *et al.* (2006), our faecal analysis showed that the main food items during the stop-over period are rice kernels. In fact, rice seeds represented over 90% of the food items found in the faeces. Other food



items, gastropods, oligochaetes and arthropods seem to be marginal in the diet. Black-tailed godwits wintering in rice fields in Senegal also fed on rice (Trèca, 1994), but black-tailed godwits are mostly carnivorous in habitats such as mudflats (Moreira, 1994), salt pans (Perez-Hurtado *et al.*, 1997) and grasslands (Beintema *et al.*, 1995). However, herbivorous foraging has been described for a closely related species, the Hudsonian godwit *Limosa haemastica* (Alexander *et al.*, 1996).

#### *Correlates of food availability*

Rice grains are accidentally spilled in the fields during the harvest, in September and October, staying in the fields during the following autumn, until the arrival of the godwits in late December and January. The water level and the management type affect the abundance of rice kernels in distinct ways. To some extent, flooded fields can cause loss of rice seeds due to decomposition, a factor that has been shown to be of great importance in the Mississippi Alluvial Valley (Stafford *et al.*, 2006). On the other hand, dry fields attract granivorous passerines (Elphick, 2004), which gather in flocks that quickly remove the spilled rice, hardly leaving any seeds in the soil by the time the godwits arrive (pers. obs.). This phenomenon also becomes clear in fields that become dry during the winter, due to drainage or lack of rainfall. In such fields, large groups of sparrows (*Passer* spp.) and finches (*Carduelis* spp.) were seen gathering to eat the rice that becomes available. Another source of depletion in drier rice fields are the rodents that feed on rice seeds and frequently become a pest to farmers (Rabiu & Rose, 2004; Brown & Tuan, 2005). Despite possible losses to decomposition, foraging by small granivores is likely to explain our finding that flooded fields have very much higher rice kernel abundances than fields with lower water levels. Thus, only fields that are flooded, or at least partially flooded throughout autumn and winter, are likely to be of interest to foraging godwits.

With respect to management type, the finding that ploughed fields have much higher rice kernel abundances than unploughed fields seems to explain the observed godwit habitat selection. Although we have no quantitative proof, we speculate that heightened rice abundances in ploughed fields are caused by the fact that a large part of the spilled grain is buried in the soil by the wheels of the harvesting machines, thus becoming inaccessible to the birds (and conversely inaccessible to our sampling) until the time when the fields are ploughed and the deeper soil layers are brought to the surface again by the tractors. Apparently, northward migrating black-tailed godwits find their ideal foraging habitat in

rice fields based on the amount of rice and, probably, on the depletive effect of other granivores on rice abundances. Different farming practices and water levels have an effect on these competitors, determining where the rice is, during and after godwit arrival. The question remains whether the waterbirds that are common in rice fields (Fasola & Ruíz, 1996; Elphick & Oring, 1998; Tourenq *et al.*, 2001b) could possibly reduce the food available. Of the species concerned, northern lapwings *Vanellus vanellus*, white storks *Ciconia ciconia*, black-headed gulls *Larus ridibundus*, little egrets *Egretta garzetta* and common snipes *Gallinago gallinago* (Lourenço & Piersma, 2009; Chapter 2), white storks and egrets forage extensively on the abundant Louisiana crayfish (Correia, 2001; Marques & Vicente, 1999) and the others also known carnivores (Lajmanovich & Beltzer, 1995; Moreira, 1995a; Tsachalidis & Goutner, 2002; Holland *et al.*, 2006). Our own study proves that typically carnivorous species can use rice grain as a seasonal food source; however, as all other bird species had very much lower densities, it is unlikely they can have a depletive effect on the food available for godwits.

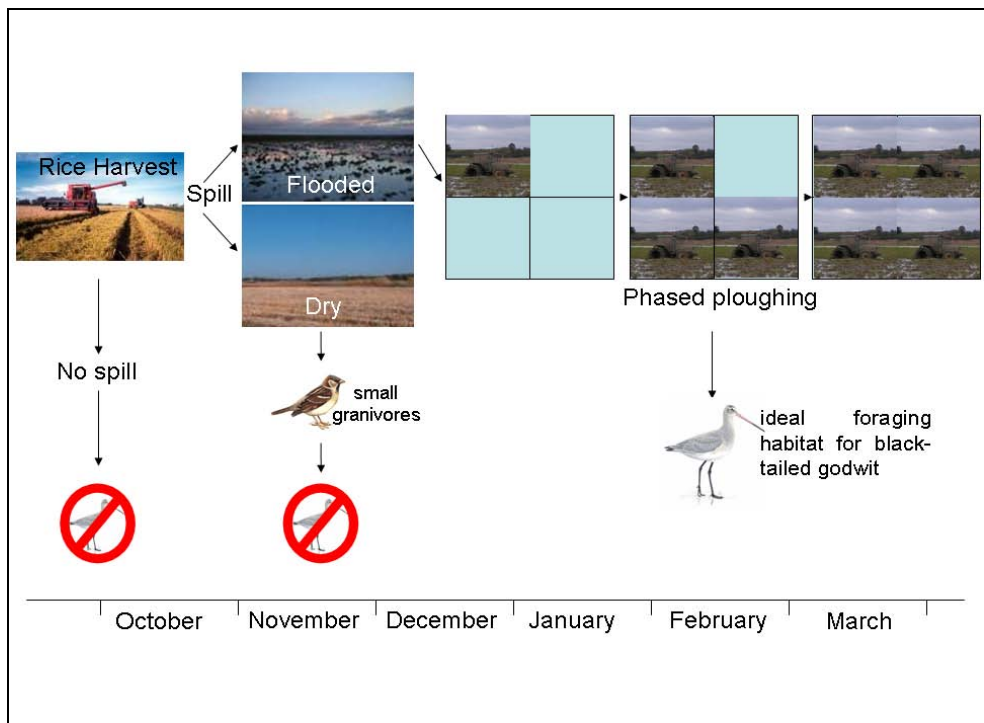
#### *Guidelines for modern godwit-friendly rice farming*

Food abundance and the activity of granivorous competitors probably determine where godwits can find food, but as man-made agricultural habitats, the conditions encountered by black-tailed godwits upon return from West Africa will depend on the decisions made by farmers and environmental managers. The modernization of rice farming frequently involves better drainage systems that allow farmers to keep their fields dry during winter (Shuford *et al.*, 1998; Elphick & Oring, 2003). This way, farmers can burn the stubble, quickly removing plant remains. However, as the activity of foraging birds in flooded fields accelerates decomposition, eliminating plant residues (Bird *et al.*, 2000), we can envisage a management scenario that does not cause air pollution and that is of benefit for both farmers and wild birds (Badarinath *et al.*, 2006). Instead of draining the fields, blocking field drainage to help retain rainwater, a management method suggested for rice fields in North America (e.g. Elphick & Oring, 2003; Manley *et al.*, 2005), is likely to also be beneficial in SW Europe, especially as rainfall is likely to decrease in the future (see below).

Ploughing is another way in which farmer influence habitat quality for black-tailed godwits. The timing of ploughing is crucial, as the birds stay in the area for a limited period

of time. If farmers only plough their fields in March, the godwits should already be on their way to the breeding grounds, missing that potential food source. Currently, there are no guidelines for farmers, who usually have other occupations during the winter, ploughing the fields when they have free time. Also, in more modern large scale rice cultivations, the fields are usually only ploughed later, shortly before sowing, and after the period of presence of the black-tailed godwits in Portugal (pers. obs.).

The implementation of more efficient harvesting methods can reduce the amount of spilled rice seeds, diminishing the rice available for godwits, but it is hard to estimate the extent of this impact. More serious is the substitution of rice fields by other crops, like maize, causing a serious reduction of available habitat for northward migrating black-tailed godwits.



**Figure 3.5:** Schematic illustration of how the management of rice fields can determine the quality of foraging habitat for black-tailed godwits. Early in the season, the presence of spilled rice and the flooding of the fields are essential for later godwit presence. During the staging period, phased ploughing of the fields is likely to create ideal conditions for foraging godwits by ensuring a continuous supply of fields in which grain is newly available.

Finally, there is another way in which human activities might affect the stop-over ecology of black-tailed godwits in Portugal. With increasing evidence of human caused global climatic change (e.g. Crowley, 2000), current climatic models for the Iberian Peninsula predict a decrease in rainfall (Goodess & Jones, 2002). Since rainfall determines the amount of water in many rice fields, especially the more traditional fields where most godwits are found, climatic changes can reduce the availability of high quality foraging habitat.

Since the ancestral natural wetlands where this bird used to forage are now mostly gone (Kuijper *et al.*, 2006), it is mandatory that rice fields are maintained in such conditions that allow black-tailed godwits to find food there. For this purpose we suggest fields should be kept flooded throughout the autumn and winter, at least part of the ploughing ought to take place between December and February (Fig. 3.5), and the substitution of rice fields by other crops must be avoided. Since most rice farming in the lower basins of the Tejo and Sado rivers is controlled by cooperatives of farmers, some of which closely associated with Portuguese governmental institutions, we encourage the Portuguese ministries of Agriculture and Environment to support the implementation of a set of environment-friendly farming practices in the rice fields, following the guidelines summarized in Fig 3.5. Additionally, since rice farming is highly dependent on EU funding (GPPAA, 2006), European financial incentives could be the best way of ensuring the willingness of farmers to manage their rice fields in a godwit-friendly fashion.

### **Acknowledgements**

We would like to thank all the land owners who allowed us to carry out field work in their properties, and Freek Mandema, Catarina Miranda and Carlos David Santos for help in the field. We also thank Nuno Lourenço for help sorting soil samples, and Chris Elphick and Jennifer Gill for many useful comments on the Chapter. This work was funded by the Portuguese “Fundação para a Ciência e Tecnologia” through grant SFRH/BD/21528/2005.





# Chapter 4

## **Population overlap and habitat segregation in wintering black-tailed godwits**

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Theunis Piersma

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Jennifer A. Gill

Bird Study (in press)

*Distinct breeding populations of migratory species may overlap both spatially and temporally, but differ in patterns of habitat use. This has important implications for population monitoring and conservation. We aim to quantify the extent to which two distinct breeding populations of a migratory shorebird, the black-tailed godwit (Limosa limosa), overlap spatially, temporally and in their use of different habitats during winter.*

*We use mid-winter counts between 1990 and 2001 to identify the most important sites in Iberia for black-tailed godwits. Monthly surveys of estuarine mudflats and rice-fields at one major site, the Tejo estuary in Portugal in 2005-2007, together with detailed tracking of colour-ringed individuals, are used to explore patterns of habitat use and segregation of Icelandic godwits L. l. islandica and the nominate continental subspecies L. l. limosa.*

*In the period 1990-2001, over 66000 black-tailed godwits were counted on average in Iberia during mid-winter (January), of which 80% occurred at just four sites: Tejo and Sado lower basins in Portugal and Coto Doñana and Ebro delta in Spain. Icelandic black-tailed godwits are present throughout the winter and forage primarily in estuarine habitats. Continental black-tailed godwits are present from December to March and primarily use rice-fields.*

*Iberia supports c. 30% of the Icelandic population in winter and most of the continental population during spring passage. While the Icelandic population is currently increasing, the continental population is declining rapidly and, although the estuarine habitats used by Icelandic godwits are largely protected as Natura 2000 sites, the habitat segregation means that conservation actions for the decreasing numbers of continental godwits should focus on protection of rice-fields and re-establishment of freshwater wetlands.*



## Introduction

Distinct populations of migratory species can overlap in space and time during the non-breeding season, a period when energetic demands are high at temperate latitudes (Wiersma & Piersma, 1994) and there may be intense competition for food. Overlapping populations of a species may differ in their use of habitats (Telleria *et al.*, 2001; Pérez-Tris & Telleria, 2002; Duijns *et al.*, 2008), but this has rarely been documented (Baker & Baker, 1973). In part, this might reflect different populations being difficult to identify in the field (Pérez-Tris *et al.*, 1999; Durell, 2000), particularly during the non-breeding season when ornamental traits are maintained at minimum levels. Habitat segregation in overlapping populations can have important conservation implications (Durell, 2000). Their description and analysis can potentially increase our understanding of key evolutionary and ecological processes, such as speciation and intra-specific competition (Newton, 2008).

In migratory waders (Charadrii), the majority of species are restricted to a few suitable habitats, which comprise only a very small area of each continent. Open habitats with low vegetation (e.g. wet grasslands and Arctic tundra) are typical breeding locations, while intertidal habitats and wetlands comprise the vast majority of the non-breeding habitats used by most species (van de Kam *et al.*, 2004). At the species level, waders display a remarkable diversity of morphological traits, which have been suggested to facilitate resource partitioning in response to inter-specific competition (Zwarts & Wanink, 1984). This adaptive radiation of body size, leg length and particularly bill shape in relation to different foraging strategies allows quite fine-tuned specialisation to harvestable food types, and may reduce the need for spatial, temporal or habitat-based segregation among species in this community (Baker & Baker, 1973; Zwarts & Wanink, 1984). However, this foraging specialisation may simultaneously limit the use of other habitats and associated food resources (Weller, 1999), and thus constrain the capacity for within-species habitat or resource segregation. Within-species spatial segregation has been reported between age classes and sexes (Goss-Custard & Durell, 1983; Cresswell, 1994) and between distinct breeding populations (Burton *et al.*, 2002). However, the extent to which populations concentrate their activity on different habitats is not often known (Baker & Baker, 1973; Newton, 2008). Without this information, protection and management of specific habitats may result in some populations being neglected. Identifying which populations might be constrained to particular habitats is therefore likely to be of importance in identifying conservation priorities for populations. This is particularly relevant for migratory waders as

many of the habitats on which they depend, such as estuarine flats and coastal wetlands, are currently heavily impacted by human activities both directly (e.g. through dredging, reclamation and over-harvesting of shellfish (Piersma *et al.*, 2001; van Gils *et al.*, 2006a)) and indirectly (e.g. through climate change impacts (Watkinson *et al.*, 2004)).

Here we explore the non-breeding spatial and temporal overlap between two distinct breeding populations of black-tailed godwits (*Limosa limosa*). The continental population, *Limosa limosa limosa*, has its core breeding areas in The Netherlands and winters from Iberia to West Africa (Gill *et al.*, 2002; Delany *et al.*, 2009). The smaller population of Icelandic black-tailed godwits, *Limosa limosa islandica*, breeds almost entirely in Iceland and winters across western Europe, from Britain and Ireland in the north, to Iberia and Morocco in the south (Prater, 1975; Gill *et al.*, 2002). Both *limosa* and *islandica* subspecies are present in Iberia during the non-breeding season (Stroud *et al.*, 2004) and both overlap considerably in size and morphology (Prater *et al.*, 1977). The recent population trends of these subspecies are highly divergent: the continental population is declining severely, while the Icelandic population is undergoing a sustained increase (Gunnarsson *et al.*, 2005a; Gill *et al.*, 2007). In Iberia, black-tailed godwits make extensive use of estuarine mudflats and rice-fields, and it has previously been suggested that there may be some habitat segregation between the subspecies (Moreira, 1994; Leitão, 1998). As the estuarine habitats are typically designated as Natura 2000 sites, while the rice-fields have no formal protection, habitat segregation could have important implications, particularly given the rapid decline of the continental godwit population for which loss and degradation of non-breeding habitat has been highlighted as a key issue (Gill *et al.*, 2007).

We use mid-winter counts to determine the most important sites for black-tailed godwits in the Iberian overlap zone. We then use recent intensive survey information to describe the spatial and temporal overlap and the patterns of habitat use of the two subspecies. As the subspecies are almost impossible to identify accurately in winter plumage (Gunnarson *et al.*, 2006a; Kuijper *et al.*, 2006), we capitalise on the recent development of extensive colour-ringing programmes on the breeding grounds for each population, to assess their degree of habitat segregation throughout the winter. We conclude by recommending appropriate monitoring and conservation measures for the species in Iberia.

## Methods

The most important sites for black-tailed godwits within the Iberian Peninsula were

identified based on census data compiled from national wetland surveys of Portugal and Spain, internal reports from governmental agencies, and published books and articles, covering the last three decades (e.g. CEMPA, 1982; Rufino & Neves, 1986; Rufino, 1993; Rufino & Costa, 1993; Costa & Rufino, 1994; 1996a; 1996b; 1997; Martí & del Moral, 2003). The majority of these counts originate from the pan-European waterbird survey scheme run by Wetlands International (Delany *et al.*, 1999; Gilissen *et al.*, 2001). Incomplete counts, either due to bad weather conditions or low spatial coverage, were excluded from analyses. January count data from Spain were only available between 1990 and 2001, thus the Iberia-wide analysis is restricted to this period.

Intensive field surveys of godwit use of different habitats took place in the winters of 2005-2006 and 2006-2007 at two major sites within Iberia: the Tejo (38° 57'N 8° 54'W) and Sado (38° 24'N 8° 48'W) lower basins in western Portugal. During the first winter (December 2005 to March 2006), the rice-fields of the Tejo lower basin were visited every fortnight and all black-tailed godwits counted. During the second winter (October 2006 to March 2007), both the rice-fields of Tejo and Sado and the estuarine areas of Tejo were searched systematically and black-tailed godwits were counted simultaneously at least once a month on both habitats. Nocturnal foraging of black-tailed godwits in this area is rarely recorded (Lourenço *et al.*, 2008), and so surveys were carried out during daylight hours only. Black-tailed godwit flocks were regularly scanned for colour-ringed individuals before and after each count during the second winter. Only flocks containing one or more colour-ringed godwits from known breeding population were considered for this analysis (total number of sightings of individually marked godwits = 380, total number of separate observations of flocks = 170).

Colour-ringed black-tailed godwits of the *islandica* subspecies have been caught and ringed either on the Icelandic breeding grounds (Gunnarsson *et al.*, 2005c; 2006b) or during post-nuptial migration on the Wash estuary (Gill *et al.*, 2001a) on the east coast of England (total number of colour-ringed Icelandic godwits = 1639). Black-tailed godwits of the *limosa* subspecies used in this study were caught and ringed during the breeding season (Roodbergen *et al.*, 2008; van den Brink *et al.*, 2008; Schroeder *et al.*, 2009a) in The Netherlands (total number of colour-ringed continental godwits = 384). Colour-ringing of these populations has taken place over several years, so the number of colour-ringed godwits estimated to be alive in the winter of 2006-07 was calculated from the annual totals (16-284 *islandica* colour-ringed each year between 1995 and 2006; 33 – 152 *limosa* colour-

ringed each year between 2002 and 2006) and published estimates of the survival rates for chicks during the first year of life (*islandica*: 50%; *limosa*: 54%) and annual survival rates for adults (*islandica*: 93%; *limosa*: 83%) (Gill *et al.*, 2001a, 2007; Roodbergen *et al.*, 2008). The ratio of marked birds from each population for the winter 2006-07 was then compared to the ratio of marked birds from each population in each habitat (mudflats and rice-fields) in that year, to assess the extent of habitat segregation between the populations and the proportion of godwits of each population using each habitat.

## Results

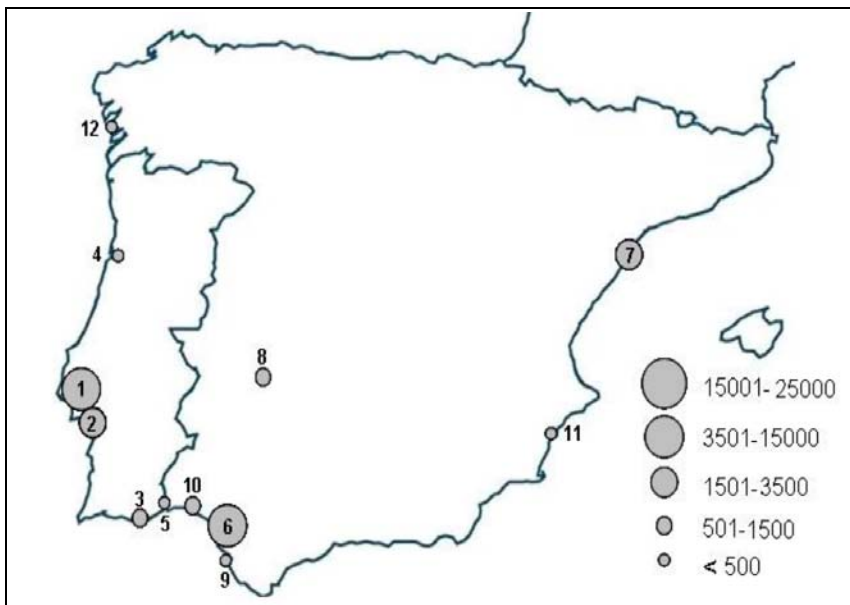
### *Key sites for black-tailed godwits in Iberia*

**Table 4.1:** January counts of black-tailed godwits on major sites in Portugal and Spain between 1990 and 2001. All sites with two counts > 500 individuals in any year are included, and also Umia-O Grove which has fewer birds but is regularly used. Site codes are given for spatial reference of each site on Fig. 4.1.

Site	Min.	Max.	Average	National(%)	Cumulative(%)	Code
<b>Portugal</b>						
Tejo estuary & rice-fields	1020	48980	23929	75.10	75.10	1
Sado estuary & rice-fields	241	20030	4331	13.59	88.69	2
Ria Formosa	551	4474	2455	7.71	96.41	3
Ria de Aveiro delta	356	5022	485	1.52	97.93	4
Castro Marim saltpans	174	1570	528	1.66	99.59	5
<b>Spain</b>						
Coto Doñana	5000	55190	24638	71.55	71.55	6
Ebro delta	0	4797	3474	10.09	81.63	7
Palazuelos rice fields	0	9026	2257	6.55	88.19	8
Cadiz Bay	0	4250	1139	3.31	91.49	9
Odiel marshes	102	722	381	1.11	92.60	10
Santa Pola saltpans	0	756	343	1.00	93.60	11
Complex Umia-O Grove	23	491	237	0.69	94.28	12

Between 1990 and 2001, Portugal supported an average of 30000 black-tailed godwits in January, with almost all occurring within just five distinct wetland sites (Table 4.1). The Tejo and Sado river basins alone held c. 88% of the total number of godwits recorded in Portugal between 1990 and 2001.

In Spain the situation is similar, with an average of 34000 godwits recorded in January between 1990 and 2001, and two sites, Coto Doñana and Ebro Delta, holding c. 81% of the godwits, although many more sites were used by the species over the census period. In some sites, such as Palazuelos rice-fields in Extremadura province and Odiel Marshes in Andalusia province, godwits were only recorded during the initial years of the census period, as no published counts have taken place there since 1995. However, during recent years J.A. Masero and co-workers have recorded numbers averaging about 24000 individuals during mid or late February on the recently developed rice-fields of Extremadura, making this a site of major importance for godwits in Iberia (Kuijper *et al.*, 2006; Sánchez-Guzmán *et al.*, 2007). Other sites, such as Santoña marshes, have had increasing numbers since 1994 (to a maximum of 300 in 2000) which are reported to have continued increasing since then (Navedo *et al.*, 2007).

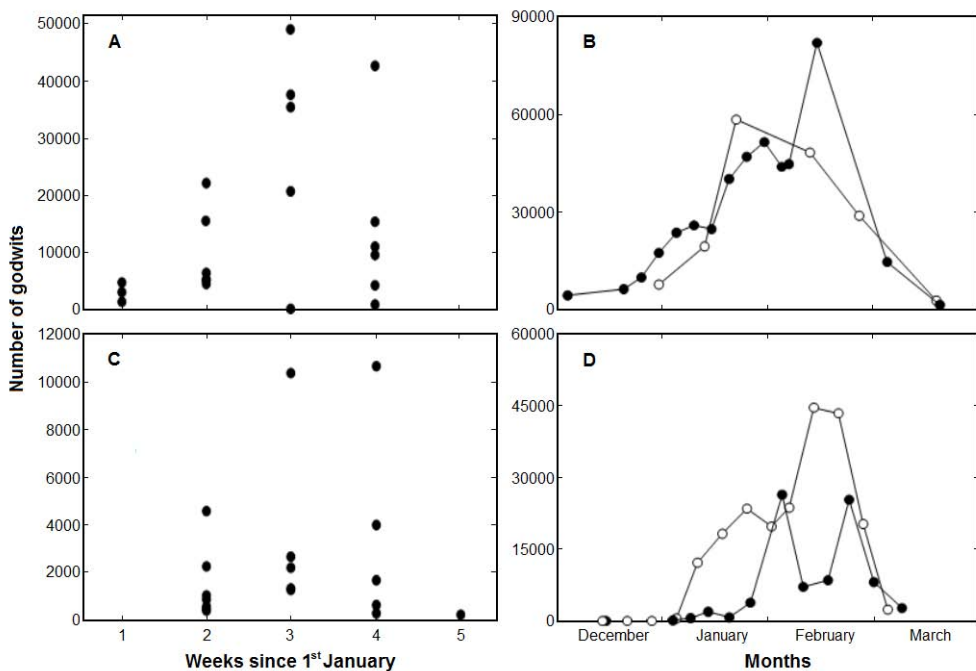


**Figure 4.1:** Location of important sites for black-tailed godwits in the Iberian Peninsula. Numbers refer to average January counts for the period 1990-2001. The eleven marked sites supported c. 95% of the total number of godwits in the region during this period.

In the Iberian Peninsula, the four most important sites for the black-tailed godwits (Tejo and Sado lower basins both on the west coast of Portugal, Coto Doñana in southern Spain and Ebro delta in eastern Spain, Fig. 4.1), all have large areas of two distinct habitats that are used by the species: rice-fields and estuarine mudflats (Martí & del Moral, 2003).

#### *Seasonal and geographic overlap of continental and Icelandic godwits*

During the northward migration from west Africa, continental godwits make an extended stop-over in Iberia from late December to early March (Lourenço *et al.*, in press a; Chapter 6). During this period, several thousand black-tailed godwits join the wintering flocks at the major Iberian sites using both the mudflats and the rice-fields. Consequently, at the start of January, there are typically fewer than 10000 godwits present on the Tejo and Sado lower basins, but numbers increase rapidly during January to over 50000 individuals (Fig. 4.2).



**Figure 4.2:** Variation in numbers of black-tailed godwits recorded in each of the first five weeks of the year between 1978 and 2006 at Tejo (A) and Sado (C), and at the Tejo lower basin during two consecutive winters 15 years apart: (B) 1991-1992 (filled circles) and 1992-1993 (open circles); (D) 2005-2006 (filled circles) and 2006-2007 (open circles).

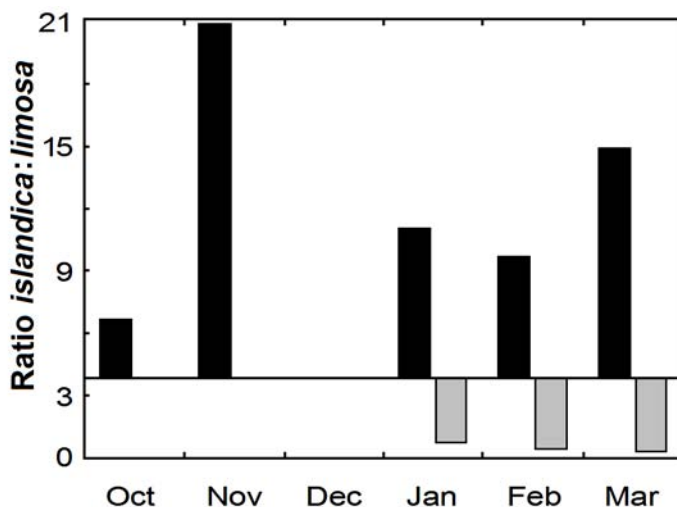
January counts vary greatly among years on the Tejo estuary (mean = 23929, SD = 16571, n = 11), Coto Doñana (mean = 24638, SD = 16008, n = 11) and Sado estuary (mean = 4341, SD = 5954, n = 11). On the Tejo estuary, the variance in counts is significantly lower during the first half of the month than during the second half (Brown-Forsythe Levene's test:  $W = 7.12$ ,  $p = 0.016$ ,  $n = 20$ , Fig. 4.2). The same does not apply to the counts in the Sado ( $W = 1.24$ ,  $p = 0.28$ ,  $n = 18$ ), probably due to the lack of any counts in the first week of January, but the high variance in counts in late January is also apparent at this site (Fig. 4.2).

The variation in counts at the Tejo and Sado lower basins (Fig. 4.2) is clearly a consequence of the timing of passage of the continental subspecies. Around 15000 *islandica* godwits (for which the total population size is c. 50000) are believed to winter in the whole of Iberia (Gunnarsson *et al.* 2005b). Thus the January counts in Iberia comprise a large proportion of continental godwits.

#### *Habitat segregation of continental and Icelandic godwits*

A total of 231 sightings of individually marked Icelandic and 149 sightings of individually marked continental black-tailed godwits were recorded on the mudflats and rice-fields of Tejo and Sado during the winter of 2006-07. The distribution of these godwits across habitats in each month varied greatly, with 1.7 to 5.5 times more colour-ringed Icelandic godwits than continental godwits using the estuarine mudflats (Fig. 4.3). By contrast, on the rice-fields, the number of colour-ringed continental godwits was 1.4 to 2.5 times higher than the number of Icelandic godwits (Fig. 4.3). The overall pattern of habitat segregation of the two populations is significantly different from an even distribution across the habitats, ( $\chi^2_3 = 281.16$ ,  $p < 0.01$ ), and only three of the 37 colour-ringed individuals that were recorded on more than one occasion were seen in both habitats.

Simultaneous counts of black-tailed godwits at the Tejo rice-fields and estuary depict the different patterns of use of these habitats (Fig. 4.4). While c. 3000 godwits are present on the mudflats throughout the winter period, counts on the rice-fields indicate that over 20000 black-tailed godwits are present during a relatively short period in January and February. The influx of continental godwits into the Tejo lower basin during January and February therefore appears to have little effect on the number of godwits present on the estuarine mudflats.

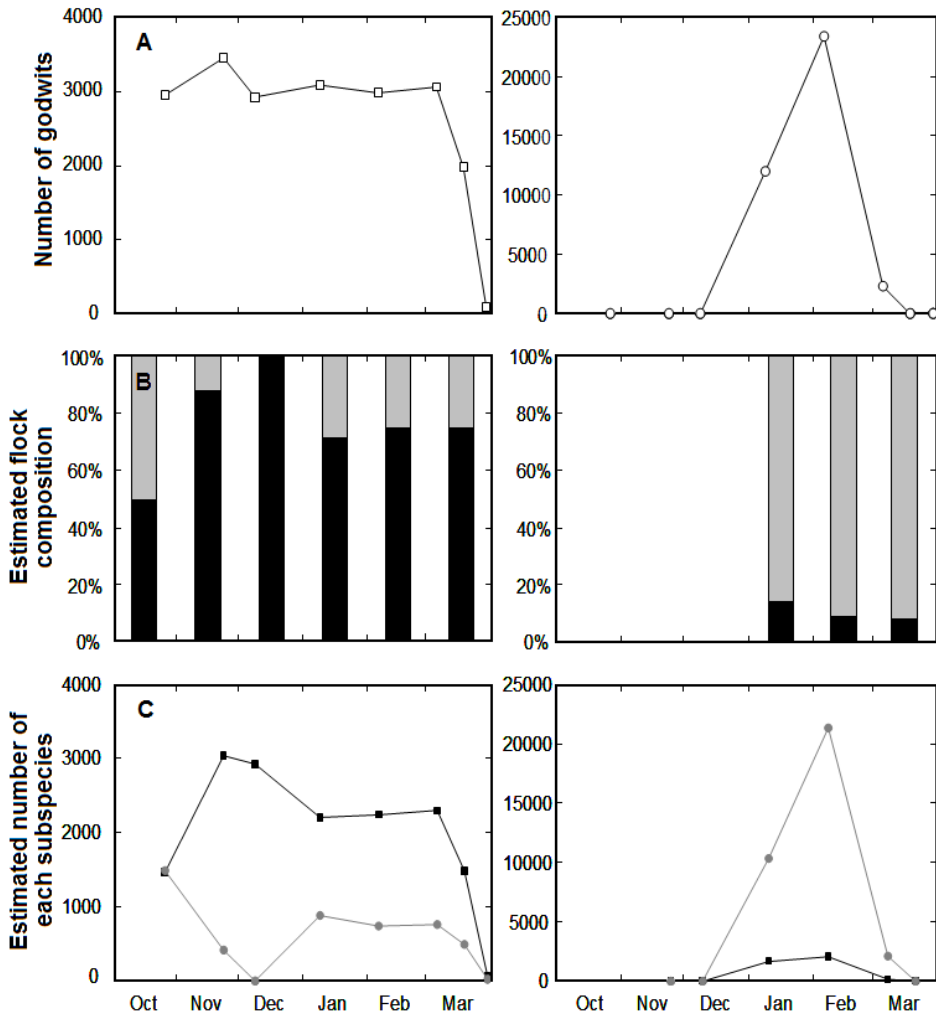


**Figure 4.3:** Monthly variation in the ratio of *islandica:limosa* colour-ringed black-tailed godwits on the estuarine mudflats (black) and the rice-fields (grey) of Tejo and Sado during 2006-2007. The horizontal line indicates the population-wide ratio of colour-ringed *islandica:limosa* estimated for the winter of 2006-2007 (ratio = 3.8). No colour-ringed continental godwits were recorded on the estuary during December, and no colour-ringed godwits were recorded on the rice-fields prior to January.

The monthly ratio of colour-ringed individuals from each population using each habitat during the winter was used to estimate the proportion of godwits from each population present on each habitat on a given month. On average, 76% of godwits on the estuarine mudflats are of the Icelandic population whereas 90% of godwits on the rice-fields are of the continental population. These proportions vary seasonally (Fig. 4.4), reflecting the phenology of both populations and the absence of rice-field usage prior to January. In October, the c. 3000 godwits on the estuary are estimated to comprise roughly equal proportions of both populations (Fig. 4.4) as some Icelandic godwits have not yet arrived and some continental godwits stop off on their way to west Africa. At this time of year the rice-fields areas are unharvested and too dry for godwits (Lourenço & Piersma, 2008a; Chapter 3). From November to January, only around 500-1000 continental godwits are estimated to occur on the estuary, together with an estimated 2000-3000 Icelandic godwits (Fig. 4.4). By contrast, the rice-fields are estimated to support more than 20000 continental



godwits in January but a maximum of only c. 1000 Icelandic godwits (Fig. 4.4).



**Figure 4.4:** Monthly variation on estuarine (left column) and rice-field (right column) habitats of (A) total numbers of black-tailed godwits on the Tejo lower basin during 2006-2007, (B) the proportion of colour-ringed Icelandic (black) and continental (grey) black-tailed godwits and (C) the estimated numbers of each subspecies present on each habitat throughout the winter.

## Discussion

Between 1990 and 2001, both Icelandic and continental black-tailed godwits in the Iberian Peninsula congregated on four major sites during the non-breeding season. Mid-winter counts show that the lower basins of Tejo and Sado in Portugal, together with Coto

Doñana and Ebro delta in Spain, held more than 80% of the black-tailed godwits recorded in Iberia between 1990 and 2001. All four sites contain a mosaic of estuarine mudflats and rice-fields with individuals from both populations being present on both habitats. However, in the Tejo there is clear habitat segregation, with Icelandic godwits primarily occurring on mudflats and continental birds primarily using rice-fields. This pattern of habitat segregation might occur throughout the main Iberian sites.

Individuals from both black-tailed godwit populations are present in Iberia from October until March, but the overlap is most apparent when the massive flocks of continental godwits (c. 15000 to 45000) arrive in the peninsula from late December, when the rice-fields become available (Lourenço & Piersma, 2008a; Chapter 3), to early March and join the overwintering flocks (c. 150 to 3000). It is noteworthy that comparison of peak counts in the Tejo lower basin during the early 1990s and 2005-07 indicates an approximately 50% decline in numbers of godwits in this area (Fig. 4.3). This reduction is consistent with the major declines in numbers of continental godwits in recent years (Gill *et al.*, 2007). Although counts made during the 1990s were carried out at dawn when godwits leave the estuarine roost towards the rice-fields and the later counts were made by visiting all the rice-fields during day time, this is unlikely to contribute significantly to the different numbers in the two time periods as all suitable rice-fields were surveyed during the more recent counts.

In more recent years, godwits have occurred in increasing numbers in the inland rice-fields of Extremadura, western Spain (Sánchez-Guzmán *et al.*, 2007). Our estimate of the proportion of Icelandic godwits on the rice-fields (c. 10%) is very similar to estimates from Extremadura (Masero *et al.*, 2009), despite those inland rice-fields having no estuarine habitats in close proximity. Icelandic godwits therefore do not appear to be common on rice-fields, even when no other habitat is available.

Although godwits of both subspecies occur on mudflats and rice-fields, there is a clear tendency for Icelandic godwits to use the estuarine mudflats and continental godwits to use the rice-fields as foraging locations (Moreira, 1994; Lourenço & Piersma, 2008a; Chapter 3). Given the morphological similarity of both subspecies, and the fact that some individuals move between the habitats, the reasons for this habitat segregation are not immediately obvious. Estuarine mudflats and rice-fields may provide structurally similar foraging conditions, as both comprise the soft, moist sediments that black-tailed godwits can probe to extract food items. However, whereas black-tailed godwits on estuarine

mudflats are ingesting animal prey (Moreira, 1994; Gill *et al.*, 2001b), godwits on the rice-fields forage almost exclusively on plant material, primarily rice seeds (Lourenço & Piersma, 2008a; Chapter 3). It is therefore possible that there is a physiological basis to the habitat segregation and that switching between habitats may incur several costs: (1) changing between animal and plant diets is likely to require modifications of the gastrointestinal tract to process such different food types (Piersma *et al.*, 1993; Dekinga *et al.*, 2001), and to assimilate different nutrients efficiently (e.g. protein versus carbohydrates and fibre) (Starck, 1999; Castro *et al.*, 2008; Santiago-Quesada *et al.*, 2009); (2) habitats with a higher saline load may require a larger salt gland (Staaland, 1967; Rubega & Oring, 2004), in order to excrete a more concentrated secretion, and thus tolerate higher salt loads (Staaland, 1967); (3) estuarine and freshwater habitats may differ in the prevalence of pathogens and parasites (Piersma, 1997; Mendes *et al.*, 2005) or levels of toxic chemicals (Tavares *et al.*, 2007), which may also require physiological adaptations and have longer-term implications for activation of the immune response or the bioaccumulation of toxic substances (Scheuhammer, 1991; Hanssen *et al.*, 2004).

Continental godwits use mostly freshwater habitats in the African winter grounds, particularly the rice-fields of Senegal and Guinea Bissau (Tréca, 1994; Gill *et al.*, 2007; Zwarts *et al.*, 2009). The costs associated with switching to a saline habitat, alongside an energetically demanding migratory flight between west Africa and Europe, may explain why continental godwits avoid estuarine mudflats in late winter. On departure from Iberia, both subspecies migrate to The Netherlands (and to a lesser extent eastern England) where the continental godwits breed and the Icelandic godwits refuel before migrating to Iceland (Gill *et al.*, 2007).

#### *Conservation implications of habitat segregation in distinct godwit populations*

The clear differences in habitat use and phenology of the two populations of black-tailed godwits in Iberia can inform targeted conservation and monitoring efforts. Firstly, although January is considered to be the month when migratory movements of waterbirds are less common (Martí & del Moral 2003; Stroud *et al.*, 2004; Delany, 2005), this is not the case in southwest Europe for this species. The extensive movement of continental godwits from Africa to Iberia during January and February results in huge variability in the mid-winter (January) counts. Effective monitoring of both godwit populations in Iberia therefore requires counting periods to be scheduled in accordance with the relevant

migration patterns, as counts in December or early January will largely comprise Icelandic godwits whereas counts in late January and February will also capture continental godwits. Secondly, the lack of any legal protection on more than 80% of the rice-field area in the lower basins of the Tejo and Sado rivers is of great concern given the huge proportion of the rapidly declining continental godwit population that depends on this habitat. Widespread drainage of wetlands has left rice-fields as virtually the only remaining freshwater habitat for foraging waders, and rice-fields are now of great importance for many species (Elphick 2000; Lourenço & Piersma, 2009; Chapter 2). Protection of key wetland sites (including rice-fields) in southern Europe and Africa is of critical importance in maintaining threatened populations that depend upon these habitats (Gill *et al.*, 2007; Lourenço & Piersma, 2009; Chapter 2).

Habitat segregation of overlapping breeding populations during winter might be more common than is currently known, and might have important implications for the conservation of other migratory species. Detailed studies on habitat use of overlapping populations are scarce but can inform the development of conservation policies. The present widespread decline of many wader species might also be influenced by threats to small patches of habitat with paramount importance for some species. This can be particularly acute for populations where conservation and habitat management actions already employed in some areas of the range have failed to reverse population declines, as is the case for breeding continental black-tailed godwits (Kleijn *et al.*, 2001). Without detailed studies on overlapping populations we are unaware of such events and thus unable to effectively protect these populations.

### **Acknowledgements**

We are grateful to Rui Rufino, Renato Neves and Vitor Encarnação for providing access to Tejo (1991/1992 and 1992/1993) and national counts respectively, developed by CEMPA/ICNB. José A. Masero, Rui Rufino, Simon Gillings and an anonymous referee provided very helpful comments on this chapter. The Dutch colour-marking work is coordinated by Jos Hooijmeijer of the University of Groningen and we thank him for all his efforts. This work was supported by funding from Calouste Gulbenkian Foundation and British Ornithologists' Union (JAA), Portuguese “Fundação para a Ciência e Tecnologia” (PML), a set-up grant of the University of Groningen (TP), the Arcadia Fund (WJS) and NERC (JAG).





# Chapter 5

## **Site selection and resource depletion in black-tailed godwits *Limosa l. limosa* eating rice during northward migration**

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*During migratory stop-overs, animals are under strong time stress and need to maximize intake rates. We examine how foragers react to resource depletion by studying the foraging ecology and foraging site selection of black-tailed godwits Limosa l. limosa staging in rice fields during their northward migration stop-over (Jan-Mar 2007).*

*We analysed godwit abundance and foraging behaviour, sampled the availability of rice in the fields, and used the functional response model to predict the giving-up density (GUD) of rice kernels when godwits should give up a rice field. Sightings of individually colour-marked birds were used to verify whether individuals moving between rice fields confirmed the predicted GUD.*

*Black-tailed godwit intake rates at different rice densities fitted Holling's functional response curve. The predicted GUD of rice necessary to balance allometric estimates of daily energy expenditure (DEE) and measured time budgets were confirmed by GUDs measured in the field.*

*Individually marked birds moved towards rice fields with higher rather than lower rice densities more often than randomly expected. These birds increased the measured intake rates after this move.*

*Godwit foraging caused a decrease in the rice density of individual fields during the stop-over period. Despite this, overall intake rates remained constant as godwits reacted to resource depletion by moving to a new foraging site as soon as their intake rate falls below the required levels to achieve DEE.*



## Introduction

During migratory stop-overs, animals gather in large numbers in relatively confined areas, needing to quickly find enough food to replenish their energy stores to continue their migratory journeys (Newton, 2006). Understanding staging strategies reveals much about migratory systems (Lindström, 1995). Interpreting how food availability shapes habitat use can provide great insights to what foraging decisions are behind the refined way in which migrants make the best of these critical staging periods.

In order to correctly assess the quality and availability of foraging habitat, an understanding of the processes underlying their foraging activity and resource use is necessary (Goss-Custard *et al.*, 2003; van Gils *et al.*, 2004). The carrying capacity of a given habitat unit primarily depends on food abundance and the degree to which losses are replenished. In the simplest approach, intake rates depend on the density of available food resources and the forager's functional response to these resources (Holling, 1959; Piersma *et al.*, 1995; van Gils *et al.* 2004). Functional response relationships predict an upper limit to intake rates, due to the necessary handling time spent on each food item. They also predict a decrease in intake rates at lower food densities, because a forager has a limited instantaneous area of discovery, thus spending more time to find each food item when density decreases. This relationship is described by the following equation (for more details see Holling, 1959; Piersma *et al.*, 1995):

$$\frac{N}{T} = \frac{aD}{1+aT_hD}$$

where  $N$  is the number of prey ingested,  $a$  is the instantaneous area of discovery ( $\text{m}^2.\text{s}^{-1}$ ),  $D$  is the food density ( $\text{m}^{-2}$ ),  $T$  is the total time spent foraging (s), and  $T_h$  is the handling time (s). A patch should be abandoned when the local intake rate falls below the required level to balance the current energy budget (Stephens & Krebs, 1986; Piersma *et al.*, 1995; van Gils *et al.*, 2004).

Ideal and free foragers would distribute themselves proportionally to the food abundance of each patch in what is known as an Ideal Free Distribution (Fretwell & Lucas, 1970; Sutherland, 1996). However, foragers frequently are not free and not ideal, as movements are never cost-free and the identification of relative resource availabilities will be constrained at some level (van Gils *et al.*, 2006b). Also, the metabolic cost of foraging might differ between patches, and different patches may vary in terms of predation risk,

both potentially causing “unexpected” situations where the individual fitness may be maximized by foraging in the patches with lower food abundance (van Gils *et al.*, 2004).

Foraging on non-renewable resources will eventually deplete food stocks, causing a decrease in the quality of a particular habitat unit (Vickery *et al.*, 1995; Gill *et al.*, 2001b; van Gils *et al.*, 2006b). Furthermore, when changes in the quality of the habitats occur, animals are faced with the decision to either stay at a site or to attempt to find a better one. The decision to move is believed to be based on the density of prey; the prey densities measured in the field after foragers give up on a unit of habitat are known as giving-up densities (GUD, Brown, 1988). Even when the information about the overall availability of food resources is not freely available to the foragers, it is possible that simple patch-leaving rules allow an optimal use of resources (Griffen, 2009). Such decisions are particularly important during stop-overs, when time is short, information is limited and the price for delays is paid in terms of reduced breeding success and even survival (Newton, 2006).

There are several accounts of migrants depleting food resources, both during the winter (e.g. Raffaelli & Milne, 1987; Rosa *et al.*, 2008) and at staging sites (e.g. Schneider & Harrington, 1981; Moore & Yong, 1991; Nolet & Drent, 1998; van Gils & Tijssen, 2007). However, this information alone does not imply that resource depletion has a negative effect on staging migrants. Foraging animals may increase foraging effort or simply move to better foraging locations to maintain required levels of food intake despite food depletion or competition (van Gils *et al.*, 2006b; Lewis *et al.*, 2008). Digestively constrained foragers can also respond by increasing the processing capacity of the digestive system (van Gils *et al.*, 2006a).

The black-tailed godwit *Limosa limosa limosa* is a long-lived migratory bird, breeding in northern Europe and wintering in Western Africa. During northward migration, large numbers of these birds stop-over in Iberia, where they forage in large flocks that gather in rice field areas (Kuijper *et al.*, 2006; Lourenço & Piersma, 2008a; Chapter 3). This concentration of animals in a relatively small number of sites, and the fact that they forage almost exclusively on spilled rice kernels (Lourenço & Piersma, 2008a; Chapter 3), enabled us to measure and correlate resource depletion, foraging activity, and site selection of staging migratory birds. This study aims to: (1) determine the extent to which black-tailed godwits deplete their food source during their stop-over in Iberia; (2) examine how resource depletion affects intake rates and the use of different foraging sites; (3) analyse whether birds move to better sites in response to resource depletion; and (4) understand

which foraging decisions could explain the observed site selection.

## Methods

Field work took place in the winter 2006-2007, in a number of rice field areas covering 2547 ha around the estuaries of the Tejo and Sado rivers (Fig. 1.2) on the Portuguese west coast (for more details see Lourenço *et al.*, 2009). All studied rice plantations were surveyed at least once per week during the staging period between late December and early March (Kuijper *et al.*, 2006). Only 11 rice fields, covering 28 ha, were used by the godwits and are part of our analysis. Whenever a godwit flock was found, the number of birds was counted and rice abundance was measured.

At each rice field, 15 birds were used for behavioural observations each week. These were randomly selected by using only every 100<sup>th</sup> scanned bird for focal observation. Each individual was observed for a maximum period of 120 s (birds observed for less than 60 s were excluded from further analysis) and the number of probes and swallows were counted. These were later converted into rates per minute. Probes were defined as periods when the bill was inserted in the sediment, a new probe only started after the bill tip had been out of the sediment. Food intake rates were defined as the number of swallowing movements following upward movements of the bill. Recent work in Spain showed that godwits always take only one rice seed at a time (J.A. Masero pers. comm.; Santiago-Quesada *et al.*, 2009), so we assume that each swallowing movement represents the ingestion of a single rice kernel. The proportion of each behaviour in a flock was scored in three categories (foraging, roosting and preening) in samples of 100 birds. In the last two weeks of the study (late February-early March), some flocks only had roosting and preening birds. These were excluded from the analysis as they probably represented birds that were ready to migrate; such birds may not forage because they are undergoing body composition changes in preparation for the long migratory flight (Piersma, 1998; Landys-Ciannelli *et al.*, 2003).

Rice abundance was measured in each rice field by collecting four samples at random locations using a flat shovel that was able to cut through the hard roots in the soil. At each field, samples were collected once per week since the first time a godwit flock was detected until one week after the godwits stopped using that field. Four fields were only sampled twice as they were used for a single week (fields 1, 2, 3 and 4) and the remaining fields were sampled three to six times. In three cases (fields 7, 9 and 10) we were unable to

sample every week and so the sampling frequency is more sparse. Each sample was a 10x10 cm square, with a depth of roughly 12 cm, to correspond with the maximum bill size of an adult black-tailed godwit (Schroeder *et al.*, 2008). The coefficient of variation between each set of four samples averaged  $0.56 \pm 0.27$ , so we believe this sampling effort was sufficient to precisely characterize local rice densities in each occasion. One field had extremely high rice densities, as it was not harvested due to a flood. This field was excluded from the rice depletion analysis (see below), as the densities were 100x larger than anywhere else and were not comparable to the other fields. However, intake rates in this field were used to estimate plateau levels of intake rate.

We fitted the measured intake rates to Holling's functional response equation. For this purpose we used the intake rates from the field with extremely high rice densities to calculate the handling time ( $T_h$ ). The probing success rate was highest at this site, achieving 60%, and the high rice densities suggest in this field birds needed nearly no time to search, thus  $T_h$  was simply the reciprocal of the intake rate. Since we had no empirical measure of the instantaneous area of discovery ( $a$ ), we calculated the value that maximized the fit to our data, using the least squares method. Afterwards, we calculated the minimum necessary intake rate for godwits to compensate their daily energetic expenditure (DEE, calculated using the allometric equation in Kersten & Piersma, 1987), assuming only diurnal foraging at 9.5 h per day (average day length in Portugal during the study period), an energy density of 0.35 kJ/rice kernel, and a digestive efficiency of 60% (L. Zwarts pers. comm.). Finally, we extrapolated the expected rice GUD from this minimum intake rate (Piersma *et al.*, 1995).

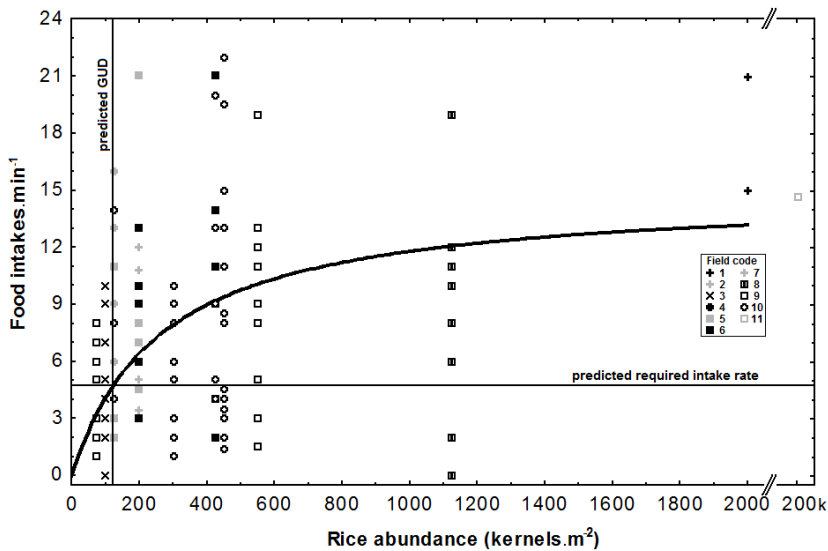
To test whether godwit foraging had an effect on rice densities, we fitted hierarchical linear models to our observations. We used a cumulative measure of godwit use of the rice fields by calculating cumulative godwit days as the average number of godwits counted on a rice field multiplied by the number of days between the first and last time godwits were detected in that particular field. On a few occasions there were isolated days when a field was found empty, but used again in the next day, so we only considered the godwits stopped using a field after two or more days of absence. These isolated days with zero godwits were also included when calculating the average number of godwits and the cumulative godwit days. Furthermore, since the presence of straw in the samples was found to positively affect the amount of rice (samples with straw,  $4468 \pm 1010$  rice kernel/m<sup>2</sup>; samples without straw,  $365 \pm 530$  rice kernels/m<sup>2</sup>;  $t = 8.4$ , d.f. = 207,  $p < 0.001$ ), this was

corrected by including a “presence of straw” factor in the analysis, as this factor may affect the distribution of rice densities within a field and influence the ability of godwits to find rice kernels. Each sample in a rice field was nested within a factor for field. To include time in the analysis, observations were assigned to weeks and a factor “week” was used. All analyses were made using the ML Win software, which uses Bayesian models by Markov Chain Monte Carlo (MCMC) method, as well as iterative bootstrapping to estimate the generalized multilevel linear models (Goldstein, 1995). To compare different models, a test based on likelihood ratios was used, which can be approached by a Chi square distribution.

To confirm that godwits move towards rice fields with higher rice abundances we analysed sightings of individually marked birds. In recent years, many black-tailed godwits have received individual colour ring combinations for individual identification in the field (e.g. Gunnarsson *et al.*, 2005b; van den Brink *et al.*, 2008). A total of 172 individuals with colour rings were detected during our work. Both European subspecies of godwits, *Limosa l. limosa* and *L. l. islandica*, occur in Portugal during the winter, the first during northward migration stop-over, the second as a winterer. Despite being mostly habitat segregated, with *limosa* in freshwater habitats and *islandica* in brackish and salt water habitats, there is some overlap in the rice fields (Alves *et al.*, in press; Chapter 4). To ensure that only staging birds were analysed, we analysed movements of birds ringed in The Netherlands during the breeding season, which can be unequivocally assigned to the nominate subspecies. This left us with 84 individuals to work with, of which we observed movement between rice fields for only 31 (only one movement per bird). The weekly re-sighting rate of marked birds was 29% (Lourenço *et al.*, in press a), so an important proportion was missed every week; however, the fact that all observed movements were one way only, gives some confidence that these reflect actual movements. For each of these 31 movements we determined whether the move occurred towards a field with higher rice density (at least 100 rice kernels/m<sup>2</sup> more), similar rice density (give or take 100 rice kernels/m<sup>2</sup>) or lower rice density (at least 100 rice kernels/m<sup>2</sup> less). The movements were compared with the proportional availability of rice fields with higher, similar or lower rice densities at the date of the movement. We used all sampled fields for this analysis, even the ones located at large distances from the origin of the movement, as we have evidence that movements often occur at both short scales and large scales (Lourenço & Alves, 2009). Since proportions of field types always sum to 1 and are not inter-independent (unit-sum constraint; see Aitchison, 1986), we used compositional analysis to examine our data (for more details see

## Results

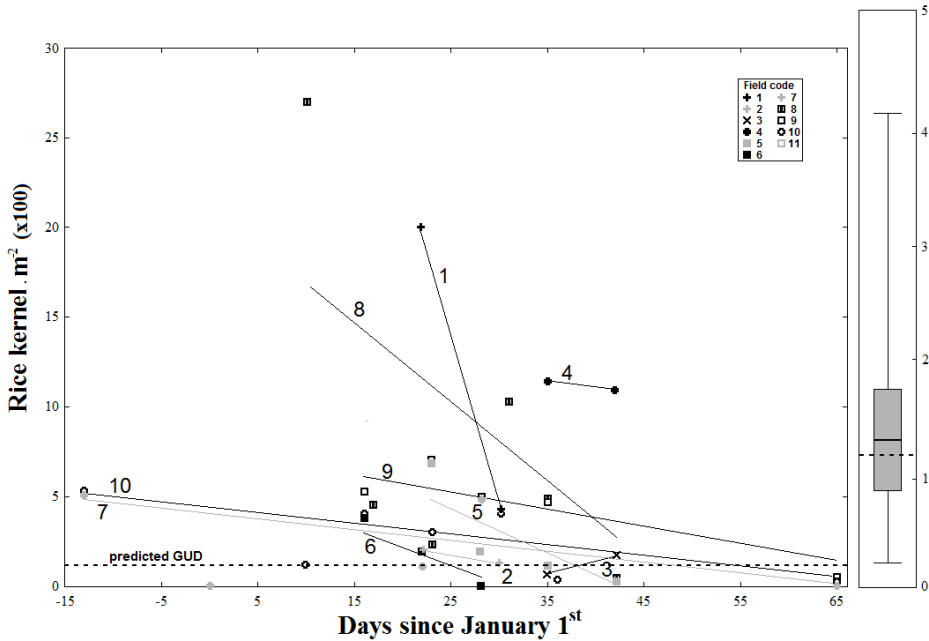
The proportion of birds foraging was estimated at  $89.4 \pm 7.2\%$  ( $n = 86$  flocks) which can be assumed to be the average portion of time spent foraging by each bird (Altmann, 1974). The remaining ones were roosting (7.1%) or preening (3.5%). Overall, the probe rate was  $15.5 \pm 1.3$  probes.min<sup>-1</sup> and the food intake rate was  $7.0 \pm 1.2$  food items.min<sup>-1</sup> (in both cases,  $n = 270$ ). Probing success varied between 37 and 60%. None of these variables varied significantly along the stop-over period, nor had any significant correlation with bird density. Probing success was significantly higher at higher rice densities ( $R^2 = 0.27$ ,  $n = 132$ ,  $p < 0.001$ ).



**Figure 5.1:** Relationship between average food intake rate and rice abundance. Each data point was coded with a symbol representing the field where the data was collected. Data were fitted to Holling's functional response equation, assuming  $T_h = 4.03s$ . The best fit was found with  $a = 9.41 \text{ cm}^2.s^{-1}$ . The horizontal line shows the minimum intake rate godwits need to achieve their DEE (4.73 kernel.min<sup>-1</sup>) and the vertical line indicates the extrapolated rice GUD (122.8 kernels.m<sup>-2</sup>).

In the unharvested field, godwits consumed  $14.9 \pm 2.7$  food items.min<sup>-1</sup>, which translates in an estimated handling time,  $T_h = 4.03s$ . We then found the value for  $a$  that

optimized the fit of our data to Holling's functional response at  $9.4 \pm 1.7 \text{ cm}^2 \cdot \text{s}^{-1}$  ( $R^2 = 0.21$ ,  $n = 132$ ,  $p < 0.01$ ) (Fig. 5.1). The minimum intake rate to sustain the calculated DEE of 567  $\text{kJ} \cdot \text{day}^{-1}$  was determined to be  $4.73 \text{ rice kernels} \cdot \text{min}^{-1}$ , which gives a GUD of 123 rice kernels  $\cdot \text{m}^{-2}$ .

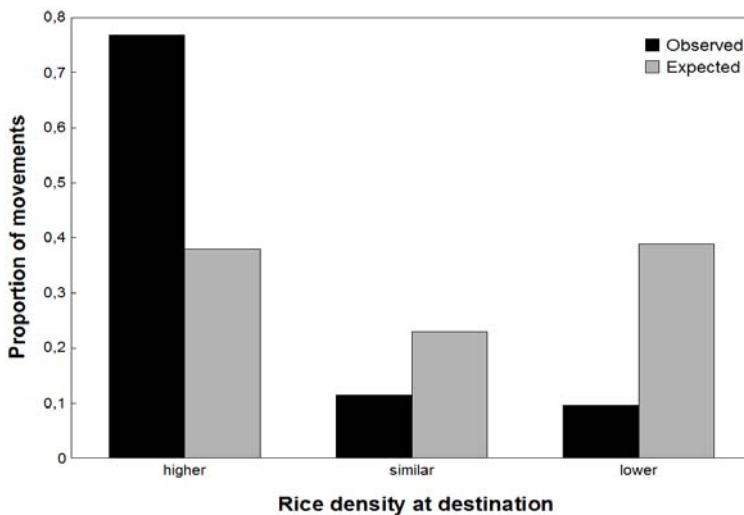


**Figure 5.2:** Variation in the food abundance in each rice field along the stop-over period. Each line represents the linear regression of rice densities on one rice field, and in almost all cases the trend is clearly negative. The dashed line represents the 123 kernels  $\cdot \text{m}^{-2}$  GUD extrapolated from the functional response. On the right side is a zoomed view of the lower part of the rice density scale showing the distribution of observed GUDs (excluding field 4). Box represents  $\pm \text{SE}$ , whiskers represent the range.

We found no significant correlation between initial rice abundance and how intensely a field was used by the godwits ( $R^2 = 0.18$ ,  $n = 10$ ,  $p > 0.1$ ), indicating a non-proportional distribution of godwits amongst fields of varying food abundance. Despite this, there was a clear negative relationship between the cumulative godwit days and rice abundance ( $\chi^2 = 70.6$ , d.f. = 1,  $p < 0.001$ ), and rice abundances in each rice field decreased along the course of the season ( $\chi^2 = 12.9$ , d.f. = 1,  $p < 0.001$ ) (Fig. 5.2). The GUDs, measured in the fields after godwits stopped using them, averaged  $231 \pm 106 \text{ kernels} \cdot \text{m}^{-2}$  ( $n = 10$ ). However, this

average is strongly influenced by a very high final rice density ( $1150 \pm 316$  kernels.m<sup>-2</sup>) found in one field (field 4). If we exclude this outlier, we find an average final rice density of  $134 \pm 49$  kernels.m<sup>-2</sup> (n = 9), very similar to the 123 kernels.m<sup>-2</sup> GUD predicted by the functional response relationship (Fig. 5.1). This can be interpreted as the rice giving up densities (GUD) for godwits foraging on our study areas.

Our results suggest that godwits move to a different field when local rice densities become too low. Indeed, 77% of the movements of 31 colour-ringed birds were towards fields with higher rice abundance, while only 10% moved into fields estimated to have less rice. Godwits moved to rice fields with higher rice abundance more than randomly expected (Compositional Analysis,  $\Lambda = 0.29$ ,  $p < 0.01$ ), considering the availability of rice fields with different rice densities at the time of each movement (Fig. 5.3).



**Figure. 5.3:** Comparison between the proportion of observed individual movements towards fields with different rice densities (black bars) and expected values based on the availability of rice fields with varying rice densities (grey bars).

Furthermore, for 14 of the moving birds we have data on the change in intake rates before and after they moved. The 11 that moved to higher rice densities had an increase in their intake rate (before:  $5.6 \pm 0.6$  food items.min<sup>-1</sup>, after:  $7.3 \pm 0.5$  food items.min<sup>-1</sup>; Wilcoxon matched pairs test:  $Z = 2.14$ ,  $n = 11$ ,  $p < 0.05$ ). The 2 birds that moved to lower rice densities had a slight decrease (before: 5.5 food items.min<sup>-1</sup>, after: 5.0 food items.min<sup>-1</sup>), as did the bird that moved to an area of similar rice density (before: 6.1 items.min<sup>-1</sup>,



after: 5.3 items.min<sup>-1</sup>).

## Discussion

The intake rates measured were affected by rice density. With increasing rice densities, the intake rate increased, which is consistent with the idea that foraging is more efficient in habitat units with higher food abundance. Black-tailed godwit food intake rates in the rice fields matched the expectations of Holling's functional response curve. The fit to Holling's equation was within the range of values reported by other studies (average  $R^2 = 0.43 \pm 0.24$ , range: 0.01-0.97, in 23 studies done on 8 different species, Goss-Custard *et al.*, 2006). The instantaneous area of discovery that best fitted our data was  $9.4 \pm 1.7 \text{ cm}^2.\text{s}^{-1}$ , which is almost three times higher than the calculated value for black-tailed godwits foraging on estuarine bivalves ( $3.3 \pm 0.7 \text{ cm}^2.\text{s}^{-1}$  in Gill *et al.*, 2001b). This suggests that rice kernels are more easily detected than bivalves, or that the sediment structure of rice fields facilitates the search for small objects (see Piersma *et al.*, 1998). One way in which godwits could increase their efficiency in the rice fields would be if they can detect the presence of straw and associate that to a higher rice density.

The average rice GUDs measured in the field closely matched the expected value assuming that godwits would leave a rice field when intake rates no longer sustain the allometrically predicted DEE. There was some variation between fields, but it was not very large, with the exception of field 4 which had considerably higher rice densities after godwits left. This value could be due to a sampling error, but could also mean that the foraging costs in that field were much higher (van Gils *et al.*, 2004). In fact, this field was adjacent to a railway bridge, and the frequent passage of trains flushed the godwits. Disturbance is known to significantly reduce habitat quality (Gill *et al.*, 2001c; van Gils & Tijssen, 2007) and could in this case be increasing the costs of foraging, leading to the observed high GUD.

Overall, 120-140 kernels/m<sup>2</sup> is likely to be the threshold below which birds react by moving to a new field. This means godwits leave a foraging patch just before the food density drops below the necessary level to maintain their energetic balance. However, in our study the birds are at a migration staging site, where they need to re-fuel for further migration. This means they need to obtain enough energy to survive, plus the necessary energy to replenish their fat stores. Our results suggest that a simple foraging rule, namely, leaving a foraging site when food intake falls below the DEE can be sufficient to guarantee

the necessary high intake rates for a staging migratory bird. Such patch-leaving decisions can allow a forager to cope with limitations in their ability to perceive food abundance and optimize habitat use despite those limitations (Griffen, 2009).

Ideal Free Distribution models predict that resource patches will be used proportionally to the abundance of food (Fretwell & Lucas, 1970). However, we did not find any correlation between rice abundance and godwit use of the different fields. These data suggest that staging black-tailed godwits do not use the rice fields proportionally to food availability. Differential metabolic costs of foraging, predation risk and/or the ability to perceive food abundance can cause foragers to use resource patches in a manner not proportional to food abundances (van Gils *et al.*, 2004; van Gils & Tijssen, 2007). Such costs might explain the variation in GUD across fields.

Another factor limiting the ability to perceive food abundance can be unequal food availability within a rice field. In fact, the samples with straw had much higher rice densities. The question is then whether godwits are able to detect these small-scale variations in food distribution. Godwits foraging in mudflats seem to use prior knowledge to increase the ability to rapidly perceive the small-scale distribution pattern of their food (Dias *et al.*, 2009). It is likely that at such small scales this can also happen in the rice fields, for instance by focusing the foraging effort on patches with straw. However, if this or other small-scale factors affecting the availability of food are not perceived by the godwits, this would cause resource depletion to have stronger effects on intake rates.

One further limitation is likely to affect how the godwits perceive food availability. The rice fields used by the godwits may be as much as 70 km apart in the meandering valleys of the Tejo and Sado tributaries. How are they able to detect the best foraging sites at this spatial scale? Previous knowledge is not likely of much help, as the quality of the rice fields varies much between years (pers. obs.). However, godwits prefer fields that have been ploughed and that are flooded (Lourenço & Piersma, 2008a; Chapter 3), and these characteristics are easy to see from the air.

Black-tailed godwits frequently use the rice fields at very high densities, with flocks of over 10,000 individuals using a single field of no more than a few hectares. Such strong flocking behaviour suggests the need to defend against predators or possibly an important role of social information to find the best foraging sites (Németh & Moore, 2007). The raptor community in our study area mostly consists of common buzzard *Buteo buteo*, marsh harrier *Circus aeruginosus* and common kestrel *Falco tinunculus* (Lourenço, 2009), all

unlikely to represent a significant threat to adult godwits. Nevertheless, they do cause an alarm reaction in godwit flocks (pers. obs.), and so might be influential in the choice of foraging sites. The raptor densities were higher around the Tejo than in the Sado estuary (Lourenço, 2009). That most rice fields used by the godwits in 2007 were in the Sado estuary is consistent with this hypothesis. On the other hand, flock sizes are on average higher in the Tejo, and rice GUDs in the Tejo ( $118 \pm 33$  kernels.m<sup>-2</sup>, n=2 fields) were similar to the ones in the Sado (excluding field 4,  $142 \pm 44$  kernels.m<sup>-2</sup>, n=7 fields), so predation costs do not seem to be of importance for deciding when to abandon a foraging patch. In migrating birds the marginal value of energy is rather high, as they need to fuel-up as fast as possible, which leads to low predation costs (Brown & Kotler, 2004). Indeed, transient bar-tailed godwits *Limosa lapponica* in the Wadden Sea do not seem to avoid dangerous places either (Duijns *et al.*, 2009).

Since in the rice fields used by godwits there are no other important rice consumers (Lourenço & Piersma, 2008a; Chapter 3), our results clearly show that godwit flocks have a strong effect on rice densities. On average, they reduced rice availability by  $50\% \pm 20\%$  (n=10). Such a decrease is comparable to recorded levels of depletion of insect larvae by passerines at a stop-over site in the Gulf of Mexico (30-65% in Moore & Yong, 1991), of mudflat invertebrates by staging shorebirds at a coastal site in Massachusetts (with one exception, 30-90% in Schneider & Harrington, 1981), and of chironomid larvae by shorebirds at an inland river mudflat in Hungary (87% in Székely & Bamberger, 1992). Despite this reduction in rice abundances in individual fields, and the observed functional response of food intake rates, the overall average intake rate did not vary along the stop-over period. Again, this seems to confirm the idea that godwits abandon fields when the local rice densities depress their intake, to search for fields with higher rice densities, similar to what is known for Brent geese *Branta bernicla* foraging on coastal habitats in the U.K. (Vickery *et al.*, 1995), red knots *Calidris canutus* foraging on mudflats in the Wadden Sea (van Gils *et al.*, 2006b) or Bewick's swans *Cygnus columbianus bewickii* feeding on harvested sugar beet fields (van Gils & Tijssen, 2007).

The presence of individually colour-marked individuals in the foraging flocks provided us with an opportunity to confirm that individual godwits do move from depleted fields to fields with higher rice abundance. Despite the relatively low sample size (n = 31 birds), the movements of colour-ringed black-tailed godwits to fields with higher rice abundances much more than expected by chance alone, are consistent with the idea that birds abandon

depleted fields to move into areas with higher rice abundance. The fact that the birds that moved to fields with higher rice density had an increase in their intake rates underpins the notion that foraging site selection is driven by food availability.

Clearly, resource depletion is an important factor in the habitat availability and site selection for black-tailed godwits staging on Iberian rice fields. The intensive foraging activity of large godwit flocks depletes the rice kernels in the soil to a point where birds need to move to a new field in order to find advantageous foraging grounds. Since rice kernels in winter are a non-renewable resource, fields that become depleted will no longer represent available habitat for the remaining staging period, thus depletion reduces the availability of good quality foraging sites during the stop-over period. This effect can be partially compensated by the phased ploughing of the rice fields (Lourenço & Piersma, 2008a; Chapter 3), which offers new feeding opportunities, but requires frequent switches between sites. Currently, farming practices do provide this favourable situation of fields becoming available along the staging period, but any changes in this *status quo* could have serious consequences for the quality of this staging habitat for godwits in Iberia.

Migratory birds are often challenged with such unpredictabilities in the spatial and temporal availability of their food (e.g. Davis & Smith, 2001). Godwits seem to have evolved the ability to quickly detect the best foraging patches, and by following a simple rule they are able to leave each foraging site before it becomes unprofitable, thus maximizing their overall food intake.

### **Acknowledgements**

We would like to thank all the landowners who kindly allowed access to their fields and often provided useful information on where to find the flocks. We would also like to thank N. Groen, N. Cidraes-Vieira and all other observers who provided re-sightings of individually colour-marked birds. We also thank J.A. van Gils for very helpful suggestions on early drafts of this chapter, and T.G. Gunnarsson and two anonymous reviewers for additional comments. This work was funded by the Portuguese “Fundação para a Ciência e Tecnologia” through grant SFRH/BD/21528/2005.





# Chapter 6

## **Phenology, stop-over dynamics and population size of migrating black-tailed godwits *Limosa limosa limosa* at a key staging area, the Tejo and Sado rice plantations**

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*Staging episodes are often critical periods in the life of migrants. Despite this, there is little published information about the staging period of the black-tailed godwit *Limosa limosa* in the rice fields of the Iberian Peninsula, which form an important staging area for this Red-listed species.*

*Between 2005-6 and 2008-9 we studied the staging period of black-tailed godwits in the rice fields surrounding the Tejo and Sado estuaries, Portugal. Godwits were counted weekly and flocks were scanned for colour-ringed individuals which were mostly from the Dutch breeding grounds. We analysed phenology, dynamics of the stop-over, and estimated the size of the Portuguese staging population as well as the total breeding population of which the staging birds are part.*

*Godwits started arriving in January. Numbers peaked in the second half of February, after which they quickly departed from the area. Data from the early 1990s suggest that numbers have decreased since then, and that they now peak later. Individual staging duration averaged 22.6 days for 2007 and 25.3 days in 2009, and increased towards the end of the staging period. We estimated that a total of 59200 birds used the area in 2007 and 53100 in 2009. Using density estimates of colour-ringed birds, we estimated the population size for the western part of the *L. l. limosa* population at 133200-140700 birds. This is higher than previous estimates based on inventories of the breeding population, but accounts for birds that do not breed in a given year.*

*Although this means that 38-44% of the NW European breeding black-tailed godwits stage in Portugal, processes in Iberia are not likely to have contributed to the population decline as the area for rice cultivation has increased. Nevertheless, now that the population is totally dependent on human-made habitats, changes in rice farming practices in Iberia could have great impact.*



## Introduction

Staging episodes are considered critical in the annual life cycle of migratory birds (Piersma & Baker, 2000; Chernetsov, 2006; Buehler & Piersma, 2008) and can have downstream consequences for their survival, breeding success and demographics (e.g. Newton, 2006). Important aspects of the staging period are its timing and duration, and knowledge of the turn-over rate of individuals at a given site is crucial to understanding the importance of staging sites for the conservation of migratory species (Chernetsov, 2006). Despite this, stop-over ecology has remained one of the least studied aspects of avian migration (Lindström, 1995).

Continental black-tailed godwits *Limosa limosa limosa* now mostly breed in the agricultural grasslands of Northern Europe. Their breeding range extends from the UK and The Netherlands in the west to near Russia in the east (Thorup, 2006; Gill *et al.*, 2007). The western part of the population is believed to be relatively isolated (Höglund *et al.*, 2008), both during the breeding season (breeding mostly in The Netherlands, but also in Germany, Belgium, France, Denmark, Sweden, Norway and the UK) and in winter (when they use coastal sites in West Africa). A significant portion of this sub-population stages on the rice fields of the Iberian Peninsula during northward migration (Kuijper *et al.*, 2006; Lourenço & Piersma, 2008b), where they forage on rice kernels to accumulate energy for the subsequent flights (Lourenço & Piersma, 2008a; Chapter 3). In Iberia, the nominate subspecies co-occurs with the Icelandic black-tailed godwit *Limosa l. islandica* (Gunnarsson *et al.*, 2005b). Although the two populations are mostly segregated by habitat, with *islandica* in coastal estuaries and *limosa* in freshwater wetlands, there is some overlap in the rice fields (Alves *et al.*, in press; Chapter 4).

The western *limosa* population has undergone serious population declines over the last decades, probably by as much as 50% since the 1980s (Piersma, 1986; SOVON, 1987; SOVON, 2002; Teunissen & Soldaat, 2005). Much of this decline has been associated with agricultural intensification in the breeding areas (Beintema *et al.*, 1995; Schekkerman & Müskens, 2000; Schekkerman *et al.*, 2008).

Although black-tailed godwits appear to find good feeding conditions at the Portuguese staging sites (Lourenço & Piersma, 2008a; Chapter 3), little is known about the timing and precise numbers using these areas. Black-tailed godwits are known to be early migrants. They start northward migration in December and are present at the Iberian staging areas until March (Kuijper *et al.*, 2006). In this study we capitalized on the large number of

black-tailed godwits that received individual colour-ring combinations at Dutch breeding sites in recent years (e.g. van den Brink *et al.*, 2008). Assuming the marked birds mix with others at the staging sites, this allows for a robust estimation of size of the source population (White, 1996; Gunnarsson *et al.*, 2005b).

In order to better understand the staging processes of this declining population and to clearly show the importance of these staging sites, we provide data on the timing of occurrence of continental black-tailed godwits in the rice fields surrounding the estuaries of the Tejo and Sado rivers, in central Portugal (see also Lourenço *et al.*, 2009). We aim to (1) describe the current phenology in comparison with the situation in the early 1990s, (2) estimate staging duration of individual godwits and the total number of godwits using this staging area, and (3) estimate the size of the source population, the western *L. l. limosa*.

## Methods

### *Phenology*

Field work took place in the winters 2005-6 through 2008-9. The main rice field areas around the Tejo and Sado river estuaries were surveyed for godwit presence in each winter, from early December to mid March. This covers the period when black-tailed godwits migrate through the area (Kuijper *et al.*, 2006). For more information on the study area see Lourenço *et al.* (2009). Each site was visited at least three times per week, and weekly counts were made for the total area. The observed phenology was compared with data for 1991-2 and 1992-3 (R. Rufino, unpub. data) to check for possible changes in the timing of stop-over since then.

### *Staging duration*

Since 2004, continental black-tailed godwits have received individual combinations of 4 colour rings and one leg-flag at breeding sites in the Netherlands (e.g. van den Brink *et al.*, 2008). Icelandic black-tailed godwits have received colour-ring combinations in different parts of their range since the 1990s (Gunnarsson *et al.*, 2005b). In Portugal, all flocks were checked for the presence of colour-marked individuals. In the different winters, we found 16 (2005-6), 66 (2006-7), 71 (2007-8) and 127 (2008-9) different Dutch individuals in each year. However, only in 2006-7 and 2008-9 did we achieved a stable re-sighting effort throughout the study period. Therefore, we only used the data sets from 2006-7 and 2008-9

for the staging duration analysis.

We used the program MARK (Cooch & White, 2006) to analyse the mark-recapture data, with week as the temporal unit; daily re-sighting rates were too low. Model selection was based on Akaike's information criterion corrected for small sample size ( $AIC_c$ ). All models used the logit link function. We assessed goodness-of-fit (GOF) for the most general model in each set by the bootstrapping method included in MARK. We calculated the deviances from 100 simulations of data that are not over-dispersed. We accepted a general model if its deviance ranked over 90 of the 100 rank-ordered deviances simulated. We also tested for overdispersion: the median  $\hat{c}$  was 0.95 for 2006-7 and 0.92 for 2008-9, which indicates a slight under-dispersion of the data. In MARK we obtained two types of models, the first to estimate the *phi* parameter (survival) and the second to estimate the *gamma* parameter (seniority). The first predicts the chance that an individual present just after time  $t$  will still be present just before time  $t+1$ , whilst the second predicts the chance that an individual present just before time  $t$  was already present just after time  $t-1$  (Pradel, 1996).

To calculate the stop-over duration, we used the most parsimonious models found in MARK for *phi* and *gamma* and applied these in software SODA (Schaub *et al.*, 2001) that provided a stop-over duration estimate ( $\pm$  SD) for each week. In the first winter we had eight staging duration estimates. In the second winter, when re-sightings of colour-ringed birds started two weeks earlier, we had 10.

#### *Number of black-tailed godwits staging in Portugal and population estimate*

The *gamma* parameter describes the probability that an individual present just before time  $t$  was already present just after time  $t-1$ . We can use it to estimate how many new birds arrive at the site just before time  $t$  as the number of birds counted each week ( $t$ ) multiplied by  $1-\textit{gamma}$  calculated for that week. Also, adding all new birds from each week we obtain an estimate of the total number of birds migrating through these staging sites. Colour-ring observations confirmed that low numbers of the subspecies *L. l. islandica* also occurred in the same rice fields, which complicates this calculation. Based on the proportion of ringed birds from each subspecies in each week of the *L. l. limosa* stop-over period, less than 10% were *L. l. islandica* (Alves *et al.*, in press; Chapter 4). On this basis, we excluded the *L. l. islandica* birds, and estimated the number of *L. l. limosa* individuals that were present each

week. This number was then used, together with the *gamma* parameter, to calculate the new birds arriving each week.

Past ring recoveries have shown that the *limosa* black-tailed godwits visiting Iberia come exclusively from North-western Europe (UK, France, Belgium, The Netherlands, Germany, Denmark, Norway and Sweden) (Haverschmidt, 1963; Beintema & Drost, 1986). During our field work we observed birds from at least four different breeding populations from this range: two from the Netherlands, one from Germany and one from the U.K. This indicates that there is significant mixing of birds from different breeding populations at the staging sites. We therefore assumed that birds seen in Iberia are a random sample of birds from the western population, and used the density of ringed birds in our samples to obtain an estimate of its size.

To estimate the density of ringed birds we sampled 81 (in 2007), 67 (in 2008) and 76 (in 2009) godwit flocks, considering a different flock per site and per sampling day. In each flock, we checked all birds for which we could see the legs, starting at one end of the flock and counting until either the end of the flock or until the flock flew up. We checked an average  $691 \pm 49$  birds per flock, counting how many birds were colour ringed and identifying from which colour ring scheme they were. Only birds ringed with the University of Groningen ringing scheme (van den Brink *et al.*, 2008) were used for the calculations, as it was only for these birds that we had a reliable estimate of how many were alive in each winter (see below). Birds from other ringing schemes were treated as though not ringed.

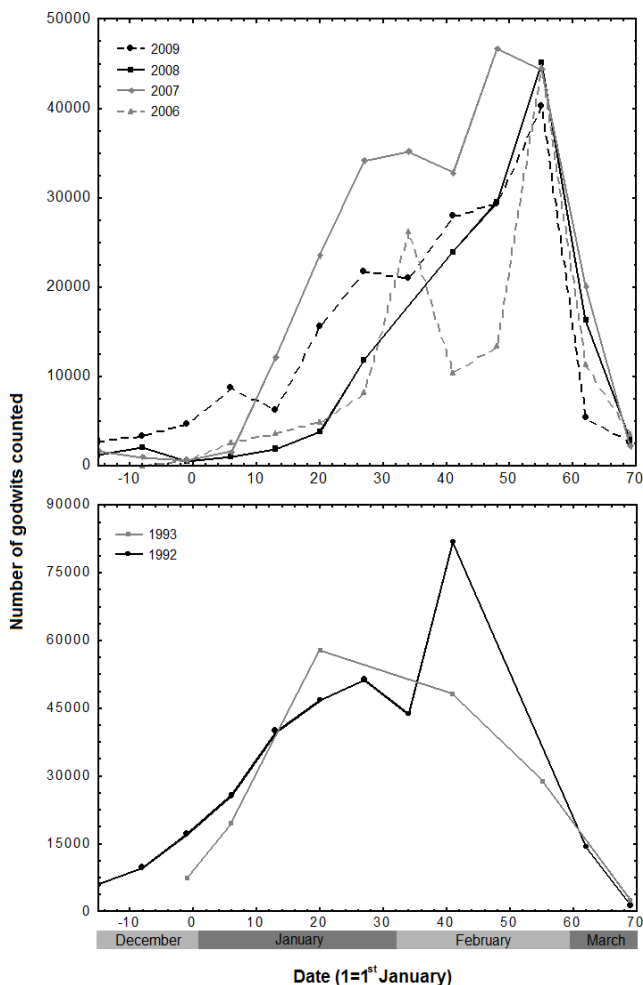
Furthermore, we used samples of the density of ringed birds collected following the same methodology in another Iberian staging site, the Extremadura rice fields located along the Guadiana river near Mérida, Spain ( $38^{\circ} 58' \text{ N}$ ,  $5^{\circ} 59' \text{ W}$ ) (Sánchez-Guzmán *et al.*, 2007). A total 75 (2007), 111 (2008) and 200 (2009) godwit flocks were sampled there, but flock sizes were considerably smaller with an average  $151 \pm 11$  birds per flock.

To know how many ringed birds from the University of Groningen ringing scheme were alive at the time of the observations in each year, we used the best available yearly survival estimates for this ringed population, 0.91 for adults and 0.53 for first calendar year birds (R. Kentie, unpub. data). These numbers are likely to underestimate the number of ringed birds alive, as these figures are for yearly survival, while the birds are ringed in the breeding areas in May and the observations were made in January and February, so not a full year had passed. However, since they already undergone a southbound migration, a whole

summer and autumn in Africa and a large part of the northbound migratory flight, the remaining mortality until the following breeding season is likely to be low. All samples of the density of ringed birds, separated by year and country were input in program NOREMARK (White, 1996; Gunnarsson *et al.*, 2005b) in which we used JHE closed population model estimation to calculate population estimates with 95% confidence intervals.

## Results

### *Phenological pattern, now and then*



**Figure 6.1.** Total counts of black-tailed godwits in the four recent winters (2006-9) and in the two winters in the 1990s (1992 and 1993).

Over the four studied winters we found a similar phenology in the Tejo and Sado rice fields. Although some birds were already present in December, godwits mostly started to arrive in early January, reaching peak numbers in the second half of February. The birds left the area in the beginning of March (Fig. 6.1). In 2006, the pattern was somewhat different, with two separate peaks and a dip in between. This was probably because between the peaks many birds were at a location that was not yet counted (see Discussion). Data available for 1992 and 1993 suggests that the migration peak occurred on average some three weeks earlier than what was found here. Peak numbers were very similar among the four recent years (mean = 44,185 birds, SD = 2768), while in the 1990s there was much more variation. The current peak numbers were 46% lower than the maximum peak from the 1990s (Fig. 6.1).

#### *Stop-over dynamics*

The most parsimonious models obtained in MARK were the ones that assumed a constant *survival* probability (*phi*) during the first weeks, and a varying *phi* in the final weeks (Tables 6.1 and 6.2). In 2007 the best models assumed that the re-sighting probability was constant during the stop-over period, being estimated at  $29 \pm 6\%$ . In 2009 the best models assumed a fully temporal re-sighting probability, which averaged  $28 \pm 3\%$ .

**Table 6.1.** Comparison between the different survival (*phi*) models constructed in MARK for the 2007 data set. *Phi* = survival probability, *P* = resighting probability, *t* = temporal variation, *c* = constant. Notations like 5c+2t mean the parameter is constant in the first five periods (weeks) and shows temporal variation in the last two. Models with lowest AICc are the most parsimonious. All other models tested were less parsimonious and are not shown here.

Model	AICc	$\Delta$ AICc	AICc Weight	N. Param.	Deviance
Phi(5c+2t). P(c)	261.51	0.00	0.41	2	56.28
Phi(4c+3t).P(c)	262.58	1.07	0.24	3	55.25
Phi(c).P(t)	263.60	2.10	0.14	8	45.21
Phi(6c+t).P(c)	263.71	2.20	0.14	2	58.48
Phi(c).P(c)	265.04	3.54	0.07	2	59.82
Phi(t).P(c)	273.67	12.17	0.00	8	55.28
Phi(t).P(t)	273.91	12.41	0.00	13	43.42

**Table 6.2:** Comparison between the different survival ( $\phi$ ) models constructed in MARK for the 2009 data set.  $\phi$  = survival probability, P = resighting probability, t = temporal variation, c = constant. Notations like 7c+2t mean the parameter is constant in the first seven periods (weeks) and shows temporal variation in the last two. Models with lowest AICc are the most parsimonious. All other models tested were less parsimonious and are not shown here.

Model	AICc	$\Delta$ AICc	AICc Weight	N. Param.	Deviance
Phi(8c+t). P(t)	521.00	0.00	0.47	10	148.72
Phi(7c+2t).P(t)	521.86	0.86	0.31	11	147.33
Phi(c).P(t)	523.77	2.77	0.12	10	151.24
Phi(6c+3t).P(t)	523.97	2.97	0.11	12	147.16
Phi(t).P(t)	534.89	13.89	0.00	17	145.90
Phi(c).P(c)	535.25	14.25	0.00	2	182.27

The best models for *gamma* assume this parameter to be fully temporal. In 2007 there was little difference between a model where the re-sighting probability was constant and another where it varied in time (Tables 6.3 and 6.4). Model averaging provided an estimate  $35 \pm 2\%$  re-sighting probability over the stop-over period. In 2009 the best models assumed a fully temporal re-sighting probability, which averaged  $32 \pm 3\%$ .

**Table 6.3.** Comparison between the different seniority ( $\gamma$ ) models constructed in MARK for the 2007 data set.  $\gamma$  = seniority parameter, P = resighting probability, t = temporal variation, c = constant. Models with lowest AICc are the most parsimonious. All other models tested were less parsimonious and are not shown here.

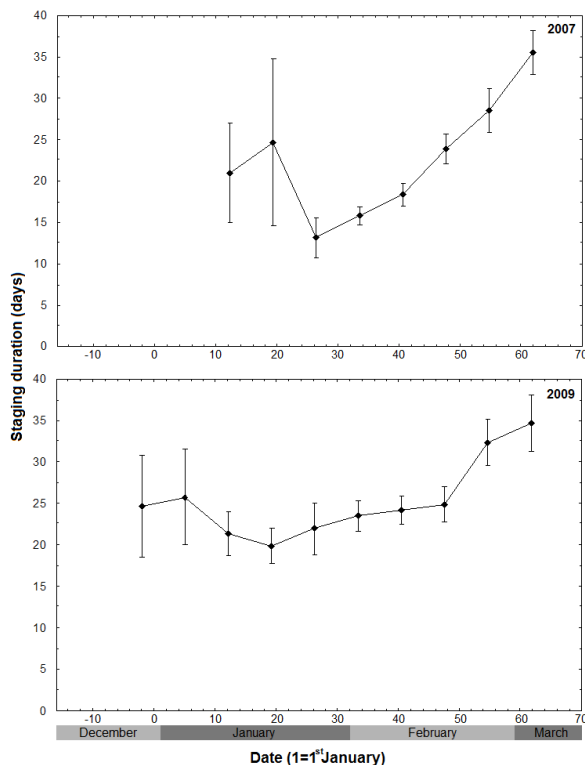
Model	AICc	$\Delta$ AICc	AICc Weight	N. Param.	Deviance
Gamma(t).P(c)	272.13	0.00	0.54	8	48.7
Gamma(t).P(t)	273.34	1.20	0.30	12	46.9
Gamma(c).P(t)	274.53	2.40	0.16	8	51.7
Gamma(c).P(c)	296.81	24.68	0.00	2	67.9

For the staging duration analysis, only the most parsimonious model for both the *phi* and *gamma* parameters were used in SODA. In both years the staging duration seemed to vary with time, becoming longer closer to the end of it (Fig. 6.2). Staging duration was

similar in the two years, averaging  $22.6 \pm 7.2$  days (range: 13.1–35.5 days) in 2007 and  $25.3 \pm 3.6$  days (range: 19.8–34.6 days) in 2009.

**Table 6.4:** Comparison between the different seniority (gamma) models constructed in MARK for the 2009 data set. Gamma = seniority parameter, P = resighting probability, t = temporal variation, c = constant. Models with lowest AICc are the most parsimonious. All other models tested were less parsimonious and are not shown here.

Model	AICc	$\Delta$ AICc	AICc Weight	N. Param.	Deviance
Gamma(t).P(t)	575.04	0.00	0.98	17	193.25
Gamma(c).P(t)	583.98	8.95	0.02	10	206.97
Gamma(t).P(c)	595.91	20.87	0.00	10	216.98
Gamma(c).P(c)	601.28	27.74	0.00	2	229.87

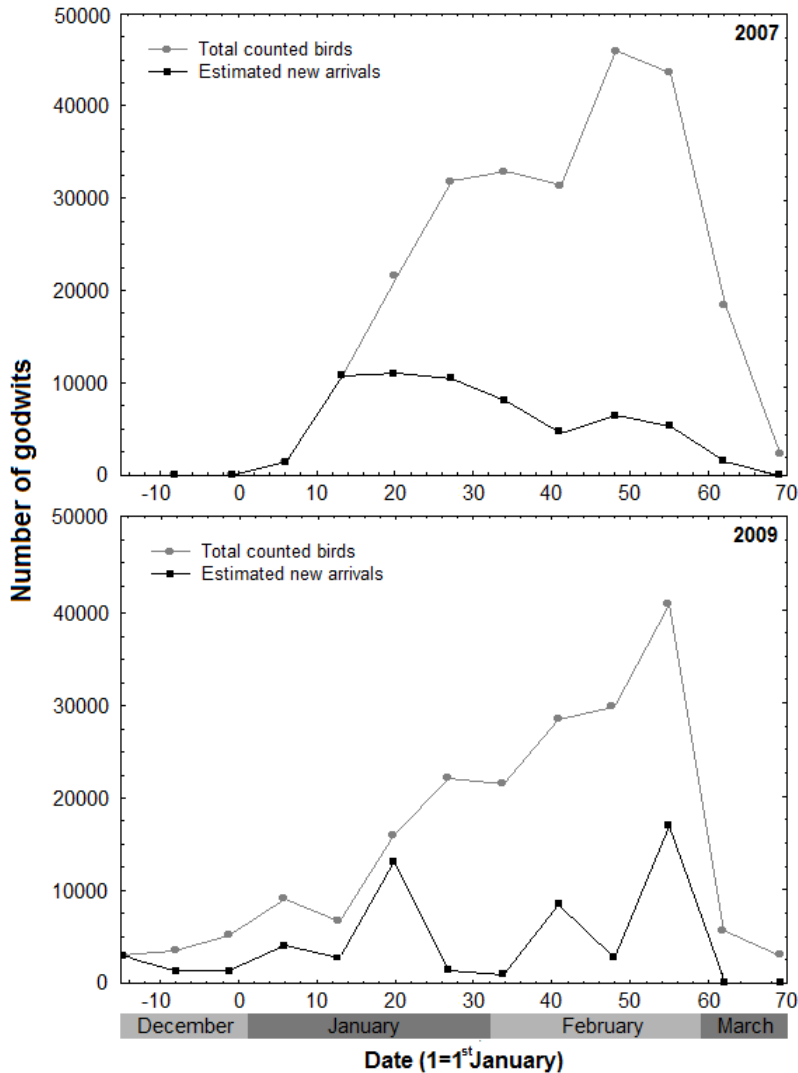


**Figure 6.2:** Average staging duration  $\pm$  SE for individual black-tailed godwits present in the study area in each week of the staging period.



### *Number of black-tailed godwits staging in Portugal and a new population estimate*

In 2007 we observed that black-tailed godwits arrived at a somewhat constant rate of about 10000 birds/ week for the first three weeks, after which the rate of new arrivals slowed down to almost zero by the end of February (Fig. 6.3). In 2009 the arrival pattern was different, with three distinct arrival peaks, one in January and two in February (Fig. 6.3). Summing all the new birds for each week, we estimated the total number of birds migrating through the area at  $59200 \pm 2900$  for 2007 and at  $53100 \pm 4600$  for 2009.



**Figure 6.3:** Comparison between the total numbers of black-tailed godwits counted (grey line) and estimated new arrivals (black line) in each week of the staging period in 2007 and 2009.

From 2007 to 2009 we observed an increasing trend in the density of ringed birds, as well as a decrease in the variation between samples, both likely to follow from the fact that the population of birds with ring combinations from the University of Groningen scheme increased during this period. Combining the samples of the density of ringed birds with the number of ringed birds, from the relevant ringing scheme, estimated to be alive in each year, we obtained consistent population estimates ranging from 133151 to 140722 birds (Table 6.5). We thus conclude that 38-44% of the western population of *Limosa l. limosa* used the rice fields in Portugal during the period of our study.

**Table 6.5.** Noremark population estimates for the western population of *L. l. limosa*. We present the number of ringed birds from the University of Groningen ringing scheme estimated to be alive each winter (ringed population), the number of flocks sampled (samples), the total number of birds checked and the population estimates with their 95% confidence intervals (C.I.).

Year	Country	Ringed population	Samples	Total birds checked	Population estimate	95% C.I.
2007	Portugal	241	81	45129	133200	113478-157694
2007	Spain	241	75	14882	140700	98176-211985
2008	Portugal	425	67	40041	139700	117697-167534
2009	Spain	425	111	15246	139900	104994-192261
2009	Portugal	552	76	39711	138700	117582-164694
2009	Spain	552	200	30945	135600	113456-163883

## Discussion

We estimated that the total number of birds migrating through the Portuguese rice fields was roughly 25% higher than the peak counts. This clearly shows the importance of taking into account the turn-over of birds at staging sites to correctly assess their importance (e.g. Frederiksen *et al.*, 2001; Schaub *et al.*, 2001). That 38-44% of the western *L. l. limosa*'s use Portugal during northward migration confirms the great importance of these sites for this near-threatened population (Kuijper *et al.*, 2006; Lourenço *et al.*, 2009). Despite this, most of these rice fields are outside the local protected areas and no management measures are currently enforced to assure that the staging conditions currently experienced by the godwits will remain in the future.

The phenology was generally similar across the four years. If we exclude the first week

of February in 2006, when we probably missed some birds which were using a rice plantation not yet surveyed at that time, the pattern is basically the same in all years. Numbers peak at 44,000-45,000 birds in the second half of February, after which the sites are quickly abandoned by the godwits, which are presumably leaving towards their breeding areas. In a nearby stop-over area in the Spanish Extremadura, the migratory peak is not quite as stable, ranging between the first and third week of February and being on average earlier (Masero *et al.*, 2007).

Peak counts in the 1990s seemed to occur on average three weeks earlier than during our study, but there was large variation between the two years for which data are available. Also, at that time counts were not performed every week, so the data might not be comparable in terms of timing. Still, a later stop-over in Iberia could be in accordance with the apparently larger reduction in the numbers stopping over in France than in Iberia (Lourenço & Piersma, 2008b). Overall, the population is known to be declining across its range, but if birds remain longer in Iberia they are likely to overfly France altogether in order to arrive early at their breeding sites. In fact, arrival dates at breeding sites in The Netherlands start in the beginning of March (J.C.E.W. Hooijmeijer *et al.*, unpub. data), shortly after the departure from Portugal.

The maximum count in the early 1990s reached nearly 82000 birds, which means peak numbers have reduced by 46% since then. Even if we assume all the birds passing through the area in that year were present on the occasion when 82000 were counted, the present data still shows a 28% decrease over the last 15 years. However, it is unlikely that all birds could be present at the same time in the staging area. If the turn-over rate was similar to today and the number of birds passing through the area in the 1990s was roughly 25% more than the average between the two known peak counts, then the decline would again be around 40%. These figures are within the scale of the decline witnessed in the breeding areas (50% since the early 1980s, Piersma, 1986; SOVON, 1987; SOVON, 2002; Teunissen & Soldaat, 2005). Although there are no reliable data on overall population changes in Spain in the last decades (Kuijper *et al.*, 2006), numbers have probably declined in the Coto Doñana area, a traditional staging site. In the Extremadura rice fields numbers have increased as this is a novel staging area that has only become available for godwits following the vast irrigation projects in the 1980s (Sánchez-Guzmán *et al.*, 2007; Lourenço & Piersma, 2008b)

On average, black-tailed godwits remained in the area for 22-25 days, although the

latest birds seemed to stay longer than early arriving birds. This means that there is a larger turn-over of birds in the beginning of the season, with birds arriving and departing. In February, the turn-over is reduced, the arrivals lead to a build up of birds, culminating in the peak counts, while departures seem to be delayed until most birds depart almost simultaneously in the beginning of March. Such an increase in staging time towards the end of the staging period, coupled with a very well timed group departure might suggest that the birds delay their departure to await favourable condition on the breeding grounds. Maybe leaving too early towards the breeding areas would imply a risk of facing bad weather and frozen soils that make food unavailable. Also, staying in Iberia longer instead of making further stop-overs in France might be the safest option, as the hunting pressure is much higher in France (Gill *et al.*, 2007)

At the Extremadura staging areas, in Spain, average staging duration was estimated at 21.7 days in 2007 (J.A. Masero *et al.*, unpub. data). This is very similar to what we observed in Portugal and suggests that turn-over rates are similar at both of these Iberian staging sites.

The lower number of godwits seen in France, during migration, in recent years (Lourenço & Piersma, 2008b) could be explained by the relatively low turn-over in Iberia. The reason for this change in France could be an increase in the available foraging habitat in Iberia, where the hunting pressure is lower. Recent work has shown that the Iberian rice fields provide a very profitable foraging habitat for godwits (Masero *et al.*, 2007; Lourenço & Piersma, 2008b). In Portugal, the extent of rice plantations actually decreased by at least 25% in the last three decades. However, in Spain the area used for rice cultivation increased by 35% over the same period, resulting in an overall 28% increase of the rice cultivated area in Iberia (FAOSTAT, 2009). Even if not all of these rice fields are usable by godwits, as they have very specific habitat requirements (Lourenço & Piersma, 2008a; Chapter 3), overall the available high quality habitat in Iberia seems to have increased. This increase in the potentially available habitat suggests that stop-over processes in Iberia are not contributing to the ongoing population decline. However, the population is now almost exclusively dependent on man-made habitats, making it very sensitive to any future changes in the extent of rice cultivation or in rice farming practices, which can easily fluctuate according to the profitability of planting rice and the economic incentives that rice planters receive from the EU (GPPAA, 2006).

The total European population of *limosa* black-tailed godwits was estimated at 86500-

120000 breeding pairs in 2000 (Thorup, 2006), but the western part of this population, migrating through Iberia, would have amounted to 53200-59600 pairs or c. 110,000 individuals (Thorup, 2006). Our estimate of roughly 135000-140000 is slightly larger, but includes adults that for some reason skip a breeding season, which can be an important proportion in some years and at some breeding sites (P.M. Lourenço *et al.*, unpub. data) and also some second calendar year birds that venture north. Covering only three years, and considering the uncertainty associated with the estimates, these data do not establish a current rate of population decline. However, a repetition of this study in the next 5 to 10 years could provide robust estimates of the current rate of population decline.

### **Acknowledgements**

We want to thank all the observers who reported sightings of colour-marked birds in Portugal and Spain, namely F. Mandema, J.A. Masero and his team, N. Cidraes-Vieira, P. Potts and several members of the Farlington Ringing Group. R. Rufino provided us with the count data from the 1990s and J.A. Masero provided information on staging duration of black-tailed godwits staging in the Spanish Extremadura. The University of Extremadura generously provided housing and access permission for us in the several visits we made to their field sites to search for our ringed birds. T.G. Gunnarsson and K. Kraaijeveld provided many useful comments to this chapter. PML was supported by a grant from the Portuguese “Fundação para a Ciência e Tecnologia”, JAA was supported by a grant from the Calouste Gulbenkian Foundation and TP received a start-up grant from the University of Groningen. BirdLife-Netherlands enabled some of us to travel south to meet up with the godwits through the Global Flyway Network.



# Chapter 7

**Repeatable timing of northward departure, arrival and breeding in black-tailed godwits *Limosa l. limosa*, but a surprising absence of domino effects**

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*Migrants are time-stressed because early breeding is often advantageous. The timing of migration and breeding are believed to be repeatable between years and the timing of sequential events is expected to be correlated because of a “domino effect” and influence breeding success. We studied a colour-marked population of black-tailed godwits *Limosa l. limosa* both on staging areas in Portugal and on breeding areas in the Dutch province of Fryslân. For each individual we measured the timing of the staging period (both median and last date), the arrival date on the breeding area and the egg laying date. Furthermore, we measured average egg volume as a surrogate of breeding success. The date of departure from the staging areas (last staging date), the arrival date on the breeding areas, and the egg laying date were repeatable among years in individual black-tailed godwits. The arrival dates of males and females were correlated, both within pairs and overall, and males arrived on average 2.5 days earlier. The timing of the staging period, the timing of arrival and the timing of egg laying were not correlated. Average egg volume per clutch was negatively correlated with laying date. Early arriving birds spent a larger portion of the available pre-laying period before laying their eggs than late arriving birds. The repeatability in the itineraries, the correlation in the arrivals of males and females and the observed protandry are consistent with observations in other migrants. Surprisingly, despite evidence for early breeding being advantageous, we found no evidence of a “domino effect”. Apparently, individuals followed a wide variety of strategies both in the duration of the migration between staging and breeding areas and in the time spent between arriving at the breeding area and egg laying.*



## Introduction

Avian migrations are often portrayed as periods of severe time constraint. This is particularly the case during the migration to the breeding grounds (Farmer & Wiens, 1998), as birds often need to arrive early at their breeding sites (Lindström & Alerstam, 1992; Kokko, 1999; Drent *et al.*, 2006). Early-arriving birds tend to have higher breeding success than birds arriving later (e.g. Hötker, 2002; Neto & Gosler, 2005; Smith & Moore, 2005), as they may have better chances to acquire the best territories and nest sites (Myers, 1981; Oring & Lank, 1982), and will have time to re-nest should the first attempt fail (Reynolds *et al.*, 1986). In income breeders, early birds will have more time to collect the necessary nutrients for egg production (Drent, 2006). Finally, early chicks often are more likely to survive (Drent *et al.*, 2006).

In a few migration systems, the timing of individuals has now been shown to be repeatable among successive years, both at departure from the non-breeding grounds (Rees, 1989; Battley, 2006), upon arrival on the breeding areas (Møller, 2001; Hötker, 2002; Bêty *et al.*, 2004), and upon arrival on the non-breeding grounds (Rees, 1989). Some studies have failed to find repeatable timing in free-living migrants and explain the lack either to changes with age (Potti, 1998) and to changes in territory quality (Forstmeier, 2002).

The annual life-cycles of migrants can be seen as a series of interconnected sequential events (Piersma, 1987; Newton, 2006; Buehler & Piersma, 2008). The stages leading to the breeding season start in the winter quarters when birds fuel-up prior to departure, followed by migration flights when the stored energy is spent, migratory staging when further fuelling takes place, arrival on the breeding grounds and, finally, the start of the breeding process. With time being of the essence, the timing of each event is likely to depend on the timing of the previous events (e.g. Marra *et al.*, 1998; Norris *et al.*, 2003; Tryjanowski *et al.*, 2004). Piersma (1987) coined the term “domino effect” for the connectedness between these sequential life-cycle stages. An individual that leaves late from the winter quarters will be expected not to be among the earliest arriving on the breeding grounds, or among the earliest breeders.

Habitat quality can affect fuelling rates and consequently the individual timing of departure from the non-breeding grounds (Marra *et al.*, 1998; Piersma *et al.*, 2005) and arrival on the breeding grounds (Gill *et al.*, 2001; Norris *et al.*, 2003). Individual differences in migratory timing can also be explained by age, as younger animals are often later to arrive (Mitrus, 2007; Vergara *et al.*, 2007; Cooper *et al.*, 2009) and to lay eggs

(Vergara *et al.*, 2007) than older ones. There also may be systematic differences between the sexes in migration timing. In most migrant species the males are earlier than females, a condition known as protandry (Morbey & Ydenberg, 2001). Protandry has been associated with competition for territories (Morbey & Ydenberg, 2001) and high levels of sperm competition (Kokko *et al.*, 2006). The pattern is the opposite in sex-role reversed species, such as in the polyandrous spotted sandpiper *Actitis macularia*, in which females are earlier in arrival (Oring & Lank, 1982). In Icelandic black-tailed godwits, paired males and females have been shown to have synchronized schedules (Gunnarsson *et al.*, 2004).

If individual schedules are consistent between years and the timing of sequential migratory events is correlated and has fitness consequences, individuals would be “trapped” in seasonal cycles that would intensify fitness inequalities; in the fullness of time natural selection would fine-tune the schedules of each population. Nevertheless, as usual even with fitness-correlated traits (Houle, 1992), there remains significant variability between individuals within the same season, even when considering adults of the same sex (e.g. Potti & Montalvo, 1991; Hötker, 2002; Oppel *et al.*, 2008; Petersen, 2009).

In this contribution we present detailed data on the timing of staging during northward migration, and on the timing of arrival and breeding 2000 km further north, of individually marked black-tailed godwits *Limosa limosa limosa*. We aim to investigate (1) whether individual schedules are repeatable between years; (2) determine if males and females arrive synchronously; (3) determine if the timing of sequential life cycle events is correlated; and we discuss (4) whether differences in timing could have fitness consequences.

## Methods

### *Study population*

The continental black-tailed godwit *Limosa limosa limosa* is long-lived, believed to be mostly monogamous and forms stable couples that can last for several years (Groen, 1993). It is a ground-nester and both parents tend the nest and the precocial chicks until fledging (Cramp & Simons, 1983). Black-tailed godwits of the *limosa* subspecies breed in the agricultural grasslands of northern Europe, having their main breeding stronghold in The Netherlands, a country that holds almost half the population (Thorup, 2006). This population winters in West Africa, using rice fields and the few remaining natural wetlands as foraging habitat (Beintema *et al.*, 1995; Zwarts *et al.*, 2009). During northward

migration, from late December to early March, these godwits stage in rice fields on the Iberian Peninsula (Lourenço *et al.*, in press a; Chapter 6), where they mostly feed on spilled rice grains (Lourenço & Piersma, 2008a; Chapter 3) until departure to the breeding areas.

### *Staging area*

The rice fields around the Tejo (38° 57'N, 8° 54'W) and Sado (38° 24'N, 8° 38'W) river estuaries, in the central coast of Portugal, are one of the key staging areas in Iberia (Lourenço *et al.*, in press a; Chapter 6). In the four winters 2005-2006 to 2008-2009, all the rice cultivations used by godwits in the area (Fig. 7.1; Lourenço *et al.*, 2009) were intensely surveyed throughout the staging period and all godwit flocks were monitored for colour-rings.

To establish the individual timing of staging we used two measures: the median date of all sightings of an individual in the staging area, and the date of the last sighting of an individual at the staging area. The intense re-sighting effort yielded a re-sightings probability of 0.3 per week (Lourenço *et al.*, in press a; Chapter 6) and in the subsequent analyses we used all available information, even if the individual was only sighted once during the whole staging period of a particular year.

### *Breeding area*

Since 2004, we have monitored birds breeding in a 415 ha area managed partially for meadow birds, called Workumerwaard (52° 59'N, 5° 24'E). While this remained the core study site, from 2006-2009 the study area was expanded to cover a total area of c. 8000 ha in the south-west of the province of Fryslân, The Netherlands (Fig. 7.1). Since 2004, adults captured on the nest late in incubation and older unfledged juveniles received individual colour-ring combinations (Schroeder *et al.*, 2008; van den Brink *et al.*, 2008).

Each year, from the beginning of March, this area was under intense and continuous surveillance to detect arriving colour-marked birds. At this time the grass is low, and the long-legged black-tailed godwits ranging in small groups are easy to find and their rings detected and read. However, from the second week of April the re-sighting effort was reduced because more time had to be placed in monitoring nests; at this stage the grass becomes so long that reading colour-rings on legs becomes more difficult. We thus excluded from our analysis all individuals that were seen less than three times before 15 April each year. Otherwise we believe individuals were sighted within a few days, and

certainly within a week, of arrival at their breeding sites within our study area in Fryslân.

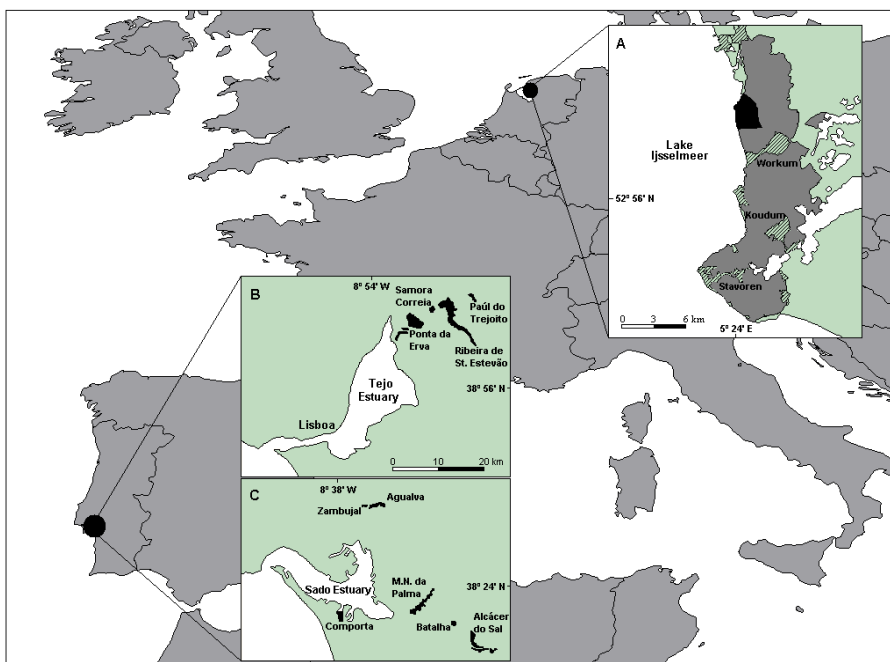


Figure 7.1: Map including the location of the staging areas in Portugal and the breeding area in Fryslân, The Netherlands. Panel A presents the study area in Fryslân, in black is the core study site (Workumerwaard) monitored between 2004-2009, in dark grey is the area monitored between 2006-2009, the dashed areas represent urban areas. Panels B and C present the study areas around the estuaries of the Tejo and Sado rivers, in black are the monitored rice field areas.

From mid-April local volunteers and our professional team thoroughly searched the area for nests of ground breeding meadow birds, and reported the approximate location of all black-tailed godwit nests. We then visited each nest, determining its precise location with a GPS. We measured the width and length of the eggs, in order to calculate their volume (Preston, 1974). The eggs were floated in water to measure their buoyancy, which was used to determine the incubation stage and thus estimate both the laying date of the first egg and the hatching date, assuming an incubation time of 25 days (van Paassen *et al.*, 1984; Liebezeit *et al.*, 2007). A small digital video camera was placed near every nest to identify whether the parents were colour-marked, and if so, to identify which individuals attended the nest (van den Brink *et al.*, 2008; McKinnon & Bêty, 2009). In the final days before

hatching, the nests were visited again, to catch the adults, which were ringed and measured, and to determine whether the nest successfully hatched. When found on the nest, the hatchlings were also marked and measured. During the following weeks, we attempted to catch nearly fledged juveniles, to mark and measure them. The rate of re-nesting is lower than 10% (J. Schroeder *et al.*, unpub. data) and the very few cases detected (n=3) were excluded from the present analysis.

Adults were sexed on the basis of plumage and body size, later verified by molecular assays using blood samples collected when birds were caught (Schroeder *et al.*, in press).

#### *Repeatability in departure, arrival and breeding in males and females*

We tested the expectation that the individual migratory timings are repeatable between years. We calculated repeatabilities following Lessells & Boag (1987) for three distinct measures of timing: the date of last sighting on the staging grounds, interpreted as the departure date; the date of first sighting on the breeding grounds, interpreted as the arrival date; and the egg laying date. In all three cases we did this separately for males and females. SE were calculated following Becker (1984).

We also compared, for each year, the average arrival date of all males and females. Also, we compared the arrival dates of individuals known to be paired. Finally, we tested whether, in both cases, male and female arrival dates were correlated. We did this by using reduced major axis (RMA) regression, to account for the variance in the arrivals of both males and females. RMA regression allows one to account for variability in both variables, and is a better method than ordinary least squares (OLS) when, as it is the case in our dataset, both variables have the same scale and expected error distribution (Fig. 7.2).

#### *Correlation between timing of sequential events and egg volume*

We tested possible correlations between the timing of the staging period, the timing of arrival at the breeding area, and the timing of breeding. We only used individuals for which we had data on the timing of different events in the same year. To avoid pseudo-replication, in individuals for which we had data over two or more years, we randomly selected only one year by attributing pseudo-random numbers to all years and choosing the one with the lowest figure. We used GLMs to test for an effect of the timing of an event on the timing of each subsequent event. In all cases we used year as a factor to account for differences between years due to uncontrolled factors, like weather. All individuals used for these

analyses were ringed as adults.

To compare the length of the pre-nesting period in birds that arrived either earlier or later in the season we needed to account for the fact that a late arriving bird necessarily has less time to breed until the end of the season. As an unbiased measure we used the proportion of the available pre-nesting time, i.e. the time between arrival and the egg laying date of the last nest in each year, used by each bird. We compared this measure between the first and last quartile of arrivals (i.e. the first 25% birds to arrive and the last 25 % birds to arrive).

Breeding success is difficult to determine in this species, so we used average egg volume per clutch as a surrogate measure of the likelihood of breeding success as it is correlated with both the chance of hatching and the survival of fledglings (Schroeder *et al.*, 2006; Schroeder, 2010). We tested whether the timing of each event during and after migration correlated with egg volume. This again was achieved by using GLMs for the timing of each event and using year as a factor.

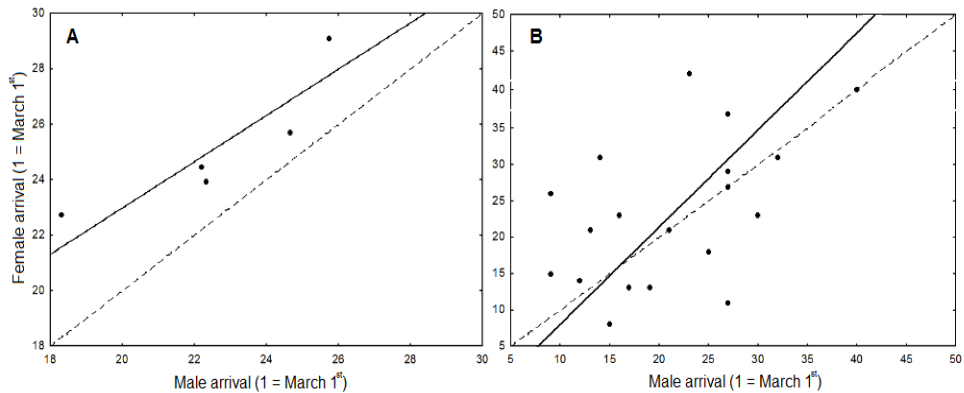
We determined the statistical power of these analysis using post-hoc statistical power analysis for multiple regression, that take into account the sample size and the observed  $R^2$ , assuming  $\alpha=0.05$  (Cohen, 1988; Cohen *et al.*, 2003).

## Results

We found that both the timings of departure from staging grounds, arrival on breeding grounds and egg laying were significantly repeatable in both individual males and females (Table 7.1). The individual between-year repeatability in departure date and in arrival date was higher for females than for males. Overall, males arrived on average 2.5 days earlier than females ( $t = 2.71$ ,  $p < 0.01$ ,  $n = 151$ ) and the average arrival dates of males and females in each year were correlated ( $F_{(1,3)} = 10.19$ ,  $p < 0.05$ ) (Fig. 7.2). The arrival dates of male and females known to be paired were correlated ( $F_{(1,19)} = 6.68$ ,  $p < 0.05$ ) (Fig. 7.2), with males arriving on average 2.5 days earlier than females; this difference achieved statistical significance at the 10% confidence level (paired  $t = 1.79$ ,  $p < 0.10$ ,  $n = 21$ ). By definition the repeatability in egg laying was similar in both sexes, but repeatability was higher for departure dates than for arrival on the breeding grounds and egg laying.

**Table 7.1:** Repeatability in the timing of departure from the Portuguese staging areas, arrival on the Dutch breeding area and egg laying in male and female black-tailed godwits. We present the repeatability  $\pm$  SE, the  $n_0$ , the F-statistic and the P value associated with each test.

Stage	Sex	Repeatability	$n_0$	Statistic	P value
Departure	females	0.42 $\pm$ 0.09	2.28	$F_{(30,53)} = 2.17$	< 0.01
	males	0.30 $\pm$ 0.07	2.62	$F_{(19,36)} = 2.07$	< 0.05
Arrival	females	0.29 $\pm$ 0.03	3.08	$F_{(80,154)} = 2.28$	< 0.001
	males	0.18 $\pm$ 0.02	4.06	$F_{(69,158)} = 1.99$	< 0.001
Egg laying	females	0.18 $\pm$ 0.04	2.34	$F_{(70,163)} = 1.86$	< 0.01
	males	0.16 $\pm$ 0.05	2.40	$F_{(48,111)} = 1.57$	< 0.05

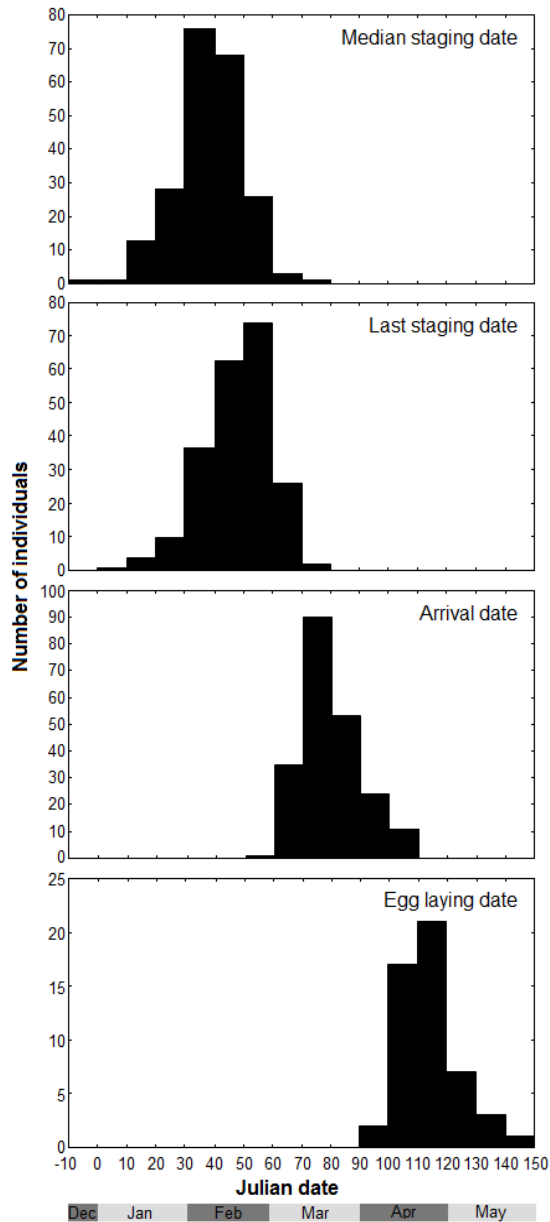


**Figure 7.2:** Correlation between male and female arrival dates. In panel A we present the average arrival date of all males and females in each study year, in panel B we present the arrival dates of paired birds. The full lines are the Reduced Major Axis (A: explained variance = 76.2%,  $p < 0.05$ ; B: explained variance = 26.8%,  $p < 0.05$ ), the dashed lines represent simultaneous arrivals ( $x = y$ ).

There was considerable variation in the timing of individual itineraries (Fig. 7.3). We found no evidence for correlation between the timing of staging in Portugal and the timing of arrival on the Dutch breeding grounds or the timing of egg laying (Fig. 7.4). In none of the cases was year significantly correlated with the response variable. The statistical power of these analyses was high (0.72-0.97; Table 2).

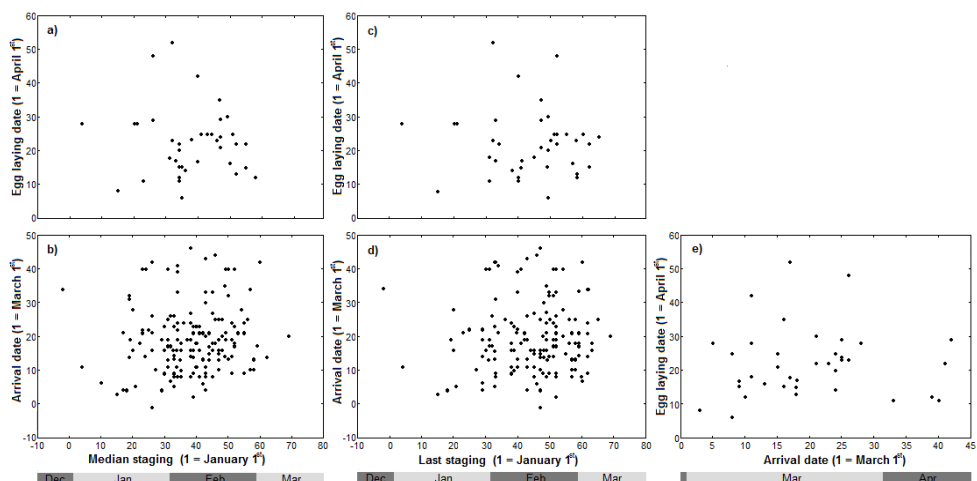
The first arrivals used a larger proportion of the available pre-laying intervals for the respective years before laying the first egg than the last arrivals (Mann-Whitney test:

$Z=2.19$ ,  $p<0.05$ ,  $n=20$ ), suggesting that the first birds waited longer to start breeding than the late birds (Fig. 7.5).



**Figure 7.3:** Variation between individuals in the different measures of timing: median staging date and last staging date in Portugal, and arrival date and egg laying on the Dutch breeding area. The months are detailed in the x axis.





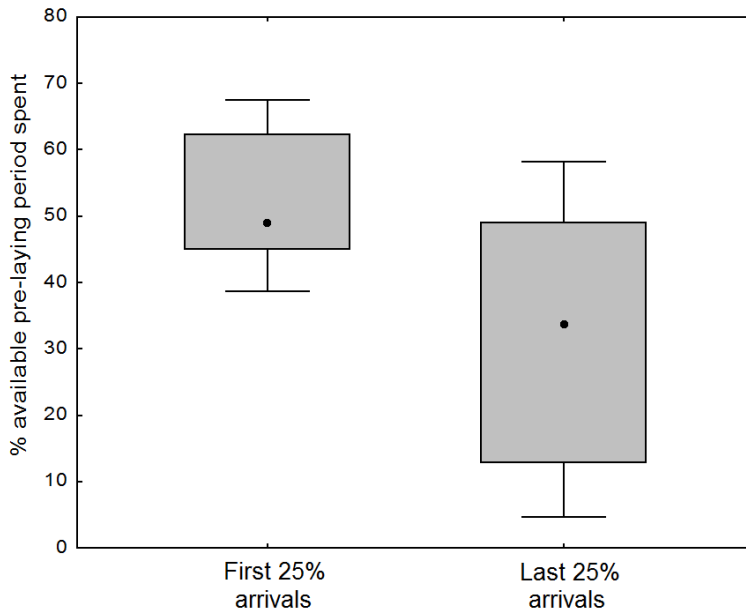
**Figure 7.4:** Lack of correlation between the timing of different life cycle events in individual birds. The panel represent the relation between a) median staging day and egg laying date; b) median staging day and arrival date; c) last staging day and egg laying date; d) last staging day and arrival date; and e) arrival date and egg laying date. The months are detailed in the x axis.

**Table 7.2:** Results of GLMs testing the correlation between timing of an event (predictor) and the timing of subsequent events (response). We present the value of the F statistic, the p value, the  $R^2$  and the statistical power of each analysis.

Predictor	Response	Statistic	P value	$R^2$	Power
Median SO	Arrival	$F_{(1,149)} = 2.19$	$> 0.10$	0.06	0.79
Last SO	Arrival	$F_{(1,149)} = 0.35$	$> 0.50$	0.07	0.74
Median SO	Egg laying	$F_{(1,38)} = 0.01$	$> 0.50$	0.18	0.72
Last SO	Egg laying	$F_{(1,38)} = 0.12$	$> 0.50$	0.22	0.81
Arrival	Egg laying	$F_{(1,38)} = 0.15$	$> 0.50$	0.34	0.97

Neither median staging day ( $F_{(1,36)} = 1.38$ ,  $p > 0.10$ , Power: 0.77) nor last staging day in Portugal ( $F_{(1,36)} = 0.04$ ,  $p > 0.50$ , Power: 0.68) were correlated with average egg volume. Arrival date also had no significant correlation with average egg volume ( $F_{(1,36)} = 0.06$ ,  $p > 0.50$ ) but the power of this analysis was rather lower (0.51). As we expected from previous work on this godwit population (Schroeder, 2010), average egg volume was negatively

correlated with egg laying date ( $F_{(1,36)}=11.06$ ,  $p<0.01$ ).



**Figure 7.5:** Median proportion of the available pre-laying period, calculated as the proportion of the time between the arrival of each individual and the date when the last nest was layed in the respective year, used by the first 25% black-tailed godwits to arrive and by the last 25% to arrive before the first egg was layed in their nest. The boxes represent interquartile range and the whiskers indicate the range.

## Discussion

Individual schedules were significantly repeatable among years, both in male and female black-tailed godwits. Repeatable arrival dates have been shown in other migratory systems, namely in barn swallows *Hirundo rustica* (Møller, 2001), garden warblers *Sylvia borin* (Pulido & Berthold, 2003), snow geese *Anser caerulescens* (Bêty *et al.*, 2004) and in the Icelandic subspecies of black-tailed godwit *Limosa l. islandica* (Gunnarsson *et al.*, 2006). The only study on departure timing from staging grounds (in snow geese) found no repeatability (Bêty *et al.*, 2004), but other studies focusing on the date of departure from the wintering areas found repeatable individual schedules in both Bewick's swans *Cygnus columbianus bewickii* (Rees, 1989) and bar-tailed godwits (Battley, 2006). The egg laying dates have also been shown to be repeatable in several species including barn swallows

(Bańbura & Zieliński, 2000) and common murre *Uria aalge* (Sydeman & Eddy, 1995).

Arrival dates of males and females were correlated and we observed the expected protandry, with males arriving on average 2.5 days earlier, similar to what has been described for another black-tailed godwit population (Gunnarsson *et al.*, 2006). Such repeatability in individual schedules, together with the considerable level of pair synchrony observed, suggests that each individual has well defined migratory schedules.

There is evidence that in our study population early breeding is advantageous (Schroeder *et al.*, 2006; Schroeder, 2010). Black-tailed godwits, like most Charadriiformes, have a fixed clutch size (Cramp & Simons, 1983; Beintema *et al.*, 1995), so the level of parental care and egg volume are the only ways in which these birds can adjust their investment in a clutch (Székely & Cuthill, 2000; Adamou *et al.*, 2009). Since, in our study population, early laying females invest in larger eggs (Schroeder *et al.*, 2006), the benefit for early breeding seems to be perceived by the birds. Despite this, there is considerable variation between individual schedules. Birds would actually be predicted to lay their eggs earlier than when they do (Schroeder, 2010). To some extent, age differences influence the timing of breeding with more experienced birds breeding earlier (Potti, 1998). However, in our study we only analysed birds ringed as adults.

Although some cases are known of mismatches in the timing of sequential events (e.g. Both *et al.*, 2005a), the majority of studies that looked into this issue found that, as expected, the timings of sequential events are correlated and have an effect on breeding success (e.g. Tryjanowski *et al.*, 2004; Neto & Gosler, 2005; Vergara *et al.*, 2007). Our results show no correlation between the timing of the staging period and the timing of neither arrival or breeding. As migrants, due to the time constraints (Lindström & Alerstam, 1992; Marra *et al.*, 1998; Drent *et al.*, 2006) should show “domino effects” (Piersma, 1987), the absence of a correlation between the timings of staging in Portugal and arrival in The Netherlands is surprising.

We found no studies that correlated individual timing in non-breeding areas with the timing at the breeding sites. Instead, processes in non-breeding and breeding areas were linked with respect to conditions at final wintering areas rather than staging areas (Marra *et al.*, 1998; Gill *et al.*, 2001; Norris *et al.*, 2003), and showed that the quality of wintering habitat (rather than measures of individual timing there; because such measures were unavailable), correlated with the timing of events in the breeding areas. A lack of correlation between staging timing and arrival indicates considerable inter-individual

variation in the time spent travelling. Some birds left the staging areas weeks before the first arrivals in Fryslân and others arrived several weeks after all birds left the staging areas (Hooijmeijer *et al.*, 2007; Lourenço *et al.* in press a; Chapter 6); indeed, some birds were observed on their breeding territory less than a week after the last sighting in Iberia (pers. obs.). The variation probably reflects the relative use of further stop-overs at wetlands between Portugal and The Netherlands (Hooijmeijer *et al.*, 2007). Stopping in France can reduce the risk of facing adverse weather conditions upon arrival on the breeding grounds, as these conditions will be easier to predict from a nearby staging area (Piersma *et al.*, 1990; Newton, 2008) but, until recently, could imply a higher mortality risk due to hunting pressure in France (Gill *et al.*, 2007).

The lack of correlation between arrival dates and the timing of egg laying deviates from observations in other migratory species. This correlation has been shown in a wide range of species from passerines (e.g. Potti, 1998; Neto & Gosler, 2005), to storks (e.g. Tryjanowski *et al.*, 2004; Vergara *et al.*, 2007), waders (e.g. Hötter, 2002), and wildfowl (e.g. Bêty *et al.*, 2003). A non-correlation between arrival and egg laying could originate from a lack of benefit in early breeding, which is not the case here (Schroeder *et al.*, 2006; Schroeder, 2010), or from an inability to start breeding early.

Early arriving birds waited longer before starting to breed than late arriving birds. Such a result could be an artefact if many of the earlier birds made second nesting attempts and we observed them only in their second nest, artificially extending the period between arrival and breeding. However, the observed rate of re-nesting was very low and we excluded the few cases from the analysis. That early arrival does not necessarily lead to early breeding (this chapter) and that the timing of breeding is rather too late than in time in this population (Schroeder, 2010), suggest that some factor constrains the onset of egg-laying. Limited availability of food for adults, or limited availability of good quality nesting sites could contribute to this discrepancy.

In principle frozen soils could explain limited food availability, as it limits access to soil invertebrates (Rolstad & Rolstad, 1995), but frost was uncommon even in early March. Farming activities, especially the lowering of water tables have also been associated with decreased food availability for adults (Schekkerman, 1997; Kahlert *et al.*, 2007), but the extent to which this affects godwits in our study area is unclear and in most sites farming activities were minimal during the breeding season. In the core study site, the Workumerwaard, there is another possible cause for delayed egg-laying. The numbers of

barnacle geese *Branta leucopsis* wintering and staging in the area are fast increasing (e.g. van Roomen *et al.*, 2002; van Roomen *et al.*, 2007). They form flocks of many thousands and intensively graze the meadows, keeping the grass very short which seems to limit the availability of cover and thus of good nesting sites for godwits and other ground nesting birds during March and April (Kleijn & Bos, 2010). In fact, an exclusion experiment within our study area showed that only areas that were kept unavailable for geese had vegetation heights within the values observed in the vicinity of godwit nests (P.M. Lourenço *et al.* unpub. data). This suggests that godwits prefer to nest in the few patches where the grass was locally higher than in the overall grazed meadows. Still, the delay in egg-laying is also true in other parts of our study area, where the geese are not present during the breeding season. Also, across The Netherlands, the black-tailed godwit seems to be the only meadow bird failing to advance egg laying dates in response to climate change (Both *et al.*, 2005b; Schroeder, 2010; Kleijn *et al.*, in press). This suggests that some other overlaying factor, not yet described, may be forcing this species to delay, or at least fail to advance, egg laying.

Black-tailed godwits follow consistent migratory and breeding schedules year after year which would seem to reflect a genetic basis (Pulido & Berthold, 2003), but could also be explained by individual specific developmental trajectories (Gienapp *et al.*, 2008; Hendry *et al.*, 2008; Teplitsky *et al.*, 2008). In fact, phenotypic plasticity can lead to adaptations to the environment without genetic variation (Teplitsky *et al.*, 2008). Differences between individuals are not due to “domino effects” of issues starting at or before the staging grounds in Portugal. Instead, birds differ in both the duration of their migration between the staging sites and the breeding areas, and in the duration of the time spent between arrival at the breeding sites and egg laying. One possible source of these different strategies could be social behaviour (Helm *et al.*, 2006). At the staging sites godwits often time their departures so that large groups depart in the same day (Lourenço *et al.*, in press a; Chapter 6). On the breeding grounds the timing of nesting may depend on competition for good nesting locations, which may be in short supply early in the season.

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**Box 2: The different names of a migratory species**

The black-tailed godwit is a migratory species, and like so many other migrants, it often crosses human borders. In that way, animal migration reminds us of how random, and irrelevant these human made geographic lines are, and highlights the interconnection between different geographical areas, regardless of the culture, the ethnicity, the personal beliefs or the political views of those who live in these far ranging countries. Different languages are one of the many cultural aspects that characterize different countries, and they are often something that separates people. However, like life itself, the languages all have a common origin and are, in fact, something that shows how similar we all are, even when we fail to notice so. A migratory species, like the black-tailed godwit, can be called by many different names, at least as many as the number of different human cultures that it visits in the course of its migration. They have a different name in each different language, but these names have something in common, they all describe the same organism, and it is very interesting to see how different cultures highlight different aspects of the same animal in its name, but, on the other hand, how very different cultures use similar aspects of the animal, when naming it.

The Latin name, *Limosa limosa* means silty, referring to the soft mud habitats used by these birds during parts of the year. Likewise, in languages like German and Turkish the name refers to the habitat where the birds is found. In most languages, the names refer to morphological features of the animal, mostly its black tail (in languages ranging from English, French and Spanish to Indonesian), but also its larger size compared to similar species (e.g. Hungarian, Russian), its straight bill (Portuguese and Vietnamese), and the rich colours of its breeding plumage (e.g. Danish, Polish). In some languages, the black-tailed godwit is even seen as royal (Italian and Arabic), probably referring again to its size. Finally, there are languages that seem to ask the bird what it would like to be called, naming it after the onomatopoeia of its calls (Dutch and Icelandic), or describing it as a screamer (Frisian). In the next page is a necessarily incomplete list of names used in different languages. This list was made with the help of: Siegbert de Jong, Tomas Gunnarsson, Hassen Mohamed, Mateusz Siedlinski and Valentijn van den Brink.

Language	Name	Meaning
Afrikaans	Swartstertgriet	black tail
Arabic	بقويقة سلطانية	black tail
Arabic (alternative)	بقويقة سوداء الذيل	royal
Catalan	Tètol cuanegre	black tail
Czech	Břehouš černoocasý	black tail
Croatian	Crnorepa muljača	black tail
Danish	Stor kobbersneppe	large, copper coloured
Dutch	Grutto	onomatopoeia
Estonian	Mustsaba-vigle	black tail
Finnish	Mustapyrstökuiri	black tail
French	Barge à queue noire	black tail
Frisian	Skries	that screams, screamer
German	Uferschnepfe	shore, river bank
Greek	Λιμόζα	from Latin <i>limosa</i> (silty)
Hungarian	Nagy goda	large, great
Icelandic	Jadrakan	onomatopoeia
Indonesian	Biru-laut ekor-hitam	black tail
Italian	Pittima reale	royal
Latvian	Melnā puskuitala	black tail
Malay	Kedidi ekor hitam	black tail
Norwegian	Svarthalespove	black tail
Polish	Rycyk	rust coloured
Portuguese	Maçarico-de-bico-direito	straight bill
Russian	Большой веретенник	large, great
Slovak	Brehár čiernochvostý	black tail
Slovenian	Čmorepi kljunač	black tail
Spanish	Aguja colinegra	black tail
Swedish	Rödspov	red coloured
Turkish	Batak çulluğu	swamp, bog, marsh
Vietnamese	Choắt mỏ thẳng đuôi đen	straight bill and black tail







# Chapter 8

## General Discussion

Pedro M. Lourenço

This thesis focused on the ecology of continental black-tailed godwits *Limosa l. limosa* in Portuguese rice fields in January-February, an important phase during their migration from the West African wintering areas to the northwest European breeding sites. The studied population has suffered a serious population decline, decreasing by as much as 50% since the 1980s (Piersma, 1986; SOVON, 1987; SOVON, 2002; Teunissen & Soldaat, 2005), and is now red-listed (IUCN, 2009). Several studies have associated the decline with the intensification of farming methods in the breeding grounds in northern Europe (Beintema *et al.*, 1995; Schekkerman & Müskens, 2000; Schekkerman *et al.*, 2008). However, little was known about the ecology of these birds outside the breeding season, both on wintering and staging areas, information that is necessary to underpin long-term conservation efforts to maintain these spectacular long-distance migrants (Schekkerman *et al.*, 2003).

Part of the work presented here was aimed at establishing baseline information about the staging period in Portugal. As proposed by Beintema *et al.* (1995), the diet of black-tailed godwits in the rice fields appears to mostly comprise rice seeds (Lourenço & Piersma, 2008a; Chapter 3). Moreover, the habitat use of the two subspecies of black-tailed godwit that co-occur in Iberia in late winter (Gunnarsson *et al.*, 2005b; Gill *et al.*, 2007) was unravelled on the basis of the availability of individually marked birds of known breeding origin. In fact the two subspecies are mostly habitat-segregated, with *islandica* using estuarine habitats and *limosa* the rice fields, but with a small degree of overlap (Alves *et al.*, in press; Chapter 4).

Godwits are very selective in terms of habitat preferences in the rice fields: only fields that are flooded and ploughed hold sufficient rice to attract the godwits (Lourenço & Piersma, 2008a; Chapter 3). Still, the availability of such fields seems to be sufficient, and farming activities during the staging period provide new foraging options through ploughing, allowing the godwits to sustain high levels of food intake despite the depletion of previously used rice fields (Lourenço *et al.*, in press b; Chapter 5). Godwits maintain high intake rates by moving towards new fields when the local food density falls below a certain threshold. This threshold rice density was measured to be approximately the necessary amount to maintain their daily energetic requirements (Lourenço *et al.*, in press b; Chapter 5), suggesting that simple patch-leaving decisions can allow a forager to cope

with food depletion and optimize habitat use despite the limitations in the ability to perceive food abundance (Griffen, 2009).

Our ability, quite unique for the present study system, to follow individual birds during both the their staging in Portugal and after arrival and during the breeding season in The Netherlands, enabled us to analyse whether the timing of the staging period is correlated with the timing of events in the breeding season. In migratory populations, each step of the yearly cycle may have downstream consequences for the following steps, in what has been named a “domino effect” (Piersma, 1987). Conditions found outside the breeding range can influence the timing of departure from the non-breeding grounds (Marra *et al.*, 1998; Piersma *et al.*, 2005) and arrival on the breeding grounds (Gill *et al.*, 2001a; Norris *et al.*, 2003), which can then have consequences in terms of breeding success (Hötter, 2002; Smith & Moore, 2005) as early breeders tend to be more successful (Tryjanowski *et al.*, 2004; Neto & Gosler, 2005; Drent *et al.*, 2006). To some surprise, we found no evidence of such a domino effect in black-tailed godwits. Despite evidence that breeding early is advantageous for black-tailed godwits (Schroeder *et al.*, 2006; Schroeder, 2010), and that individuals have well set schedules that are repeatable year after year (Chapter 7), the timing of staging in Iberia, and in particular the timing of departure from the staging area, are not correlated with the timing of reproductive events (Chapter 7).

Clearly the rice fields around the estuaries of the Tejo and Sado rivers are a critical staging area for black-tailed godwits. For a period of a few months, roughly 40% of the western *limosa* population migrates through this area (Lourenço *et al.*, in press a; Chapter 6). The current farming practices provide sufficient profitable foraging habitat for godwits, and at the moment this staging period does not seem to limit their ability to arrive early at the breeding grounds, nor have any clear consequences in terms of breeding success. With the data presently available, we can only conclude that the staging processes in Portugal are not contributing to the ongoing population decline of the continental black-tailed godwits. Still, the current trends for a reduction in the rice-farmed area (FAOSTAT, 2009), modernized farming methods with drainage of the fields in winter (Lourenço & Piersma, 2008a; Chapter 3), and predictions for a decrease in rainfall in Iberia due to climate change (Goodess & Jones 2002) may change the conditions in the long-term.

## **Interactions between rice field management and bird abundance**

Much like in other geographic areas (Elphick, 2000; Maeda, 2001; Richardson & Taylor, 2003), the rice fields in Portugal harbour important numbers of several waterbird species in winter, even presenting similar densities when compared with local natural wetlands (Granadeiro *et al.*, 2007; Lourenço & Piersma, 2009; Chapter 2).

The density of waterbirds wintering in the rice fields is influenced by farming practices. The two main farming variables are the presence of water and the timing of ploughing. During the growing period, when the crop is in the fields, the water levels must be carefully kept at the ideal levels to maximize yield. In southern Europe, the harvest takes place in October and November, while sowing only occurs in spring, so in winter, the period when rice fields use by birds is highest (Sánchez-Guzmán *et al.*, 2007), water levels can vary. In some cases the rice fields are artificially drained in order to dry the stubble, that can then be burned. In other situations the rice fields are kept flooded artificially so that water helps the decomposition of plant material (Stafford *et al.*, 2006). Finally, there are cases where the water level is not controlled and depends only on the amount of rainfall. The ploughing of the fields can occur at any time in winter, so birds may find both ploughed and unploughed rice fields while wintering in these areas. Rice fields that are flooded and rice fields that have already been ploughed attract the most birds (Lourenço & Piersma, 2009; Chapter 2).

Flooding rice fields has been shown to be favourable for aquatic birds in California (Elphick & Oring, 1998, 2003) and the presence of open water increased the density of waterbirds in rice fields in Taiwan (Chan *et al.*, 2007). The presence of more birds in flooded areas is probably linked with higher food availability. Within our study area storks, herons and egrets mostly prey on the introduced Louisiana crayfish *Procambarus clarkii* (Correia, 2001) which is mostly found in inundated areas (Marques & Vicente, 1999). Other species like flamingo *Phoenicopterus roseus* and avocet *Recurvirostra avosetta* prey on small invertebrates from the water or the upper layers of sediment (Moreira, 1995b; Arengo & Baldassarre, 2002) and thus require at least some water to forage. Flooded fields also held the highest densities of waste rice, that is spilled during harvest (Lourenço & Piersma, 2008a; Chapter 3). The presence of water can cause loss of rice seeds due to decomposition (Stafford *et al.* 2006), but the presence of granivorous passerines in dry fields quickly depletes the rice (Elphick, 2004). This depletion appears so severe that in our study area only flooded fields hold this important food source and can sustain black-tailed godwits. Accordingly, godwits showed a clear preference for flooded fields Lourenço &

Piersma, 2008a; Chapter 3).

The effect of ploughing on birds is less straightforward. In Japan bird abundance in the rice fields is negatively affected by ploughing (Maeda, 2001), possibly due to a reduction in seed availability (Shimada, 1999), while in Portugal the availability of rice seeds is higher in ploughed fields (Lourenço & Piersma, 2008a; Chapter 3). In California small waders were more common in ploughed fields, but overall bird densities were lower (Elphick & Oring, 1998; 2003). Our results suggest indeed that waders prefer ploughed fields, maybe because ploughed fields become levelled, reducing the presence of obstacles and allowing for an early detection of predators, conditions favoured by waders (Cresswell, 1994). Black-tailed godwit preference for ploughed fields seems to be explained by higher rice seed abundance (Lourenço & Piersma, 2008a; Chapter 3). Unlike waders, storks, herons and egrets are more abundant in fields yet to be ploughed, a pattern that fits with the observation that invertebrate abundance and biomass are lower after human intervention in the fields (Marques & Vicente, 1999).

Clearly, the way rice fields are managed in winter can have important consequences for the conservation of waterbirds. This is of particular importance as in many parts of the world the fast-paced loss of natural wetlands due to drainage and other human developments forces birds away from their original habitats and into human made alternatives, namely rice plantations (Elphick, 2000; Lawler, 2001; Tourenq *et al.*, 2001b). Maintaining part of the rice fields flooded throughout the winter seems to be the most advantageous measure for the bird community. Unfortunately, this seems to go against the trend of modern rice cultivation, where most fields are drained in order to burn the stubble. Still, burning rice fields has serious consequences in terms of atmospheric pollution (Badarinath *et al.* 2006) and some countries deemed this practice illegal (Elphick & Oring, 1998). Also, the activity of foraging birds in flooded fields accelerates straw decomposition and reduces weed biomass, thus substituting for the effect of controlled burning (Bird *et al.*, 2000, van Groenigen *et al.*, 2003, Manley *et al.*, 2005). Instead of draining fields, blocking field drainage to help retain rainwater, a management method suggested for rice fields in North America (e.g. Elphick & Oring 2003, Manley *et al.* 2005), is likely to be beneficial both for farmers and bird conservation.

In terms of ploughing, different species have different preferences. Since ploughing must take place in winter, but not necessarily at a specific time, we suggest that phasing the ploughing activities throughout the season will generate a mosaic of ploughed and

unploughed fields, ideal to guarantee that all species can find their ideal habitat. The presence of some set-aside fields can also be advantageous for northern lapwing *Vanellus vanellus*, common redshank *Tringa totanus* and white stork *Ciconia ciconia* (Lourenço & Piersma, 2009; Chapter 2). In the case of black-tailed godwits, the large size of their flocks, and the limited availability of the rice seeds they forage on leads to a fast depletion of the available rice fields (Lourenço *et al.*, in press b; Chapter 5). Since the ploughing of the rice fields increases the availability of rice seeds, phased ploughing will guarantee that new foraging options will become available along the staging period, assuring that the high levels of food consumptions necessary to fuel-up for migration can be maintained.

### **Foraging site selection in a constantly changing food-landscape**

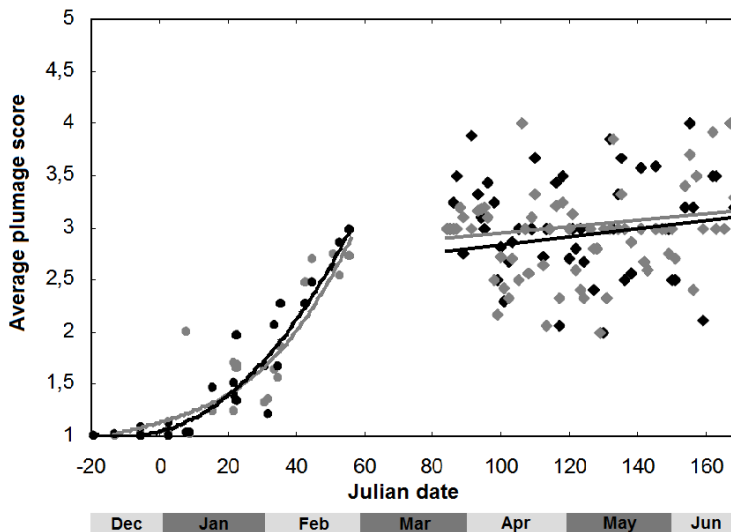
During the staging period, in Portugal, godwits are faced with a constantly changing distribution of the rice seeds that form the bulk of their diet (Lourenço *et al.*, in press b; Chapter 5). During staging episodes, migrants often gather in large numbers in small areas, which leads to a fast depletion of the food resources (Schneider & Harrington 1981; Moore & Yong 1991; Székely & Bamberger 1992). This was the case in our study area, where food densities decreased by an average 50% due to godwit feeding activity. On the other hand, due to farming activities, new fields become available along the staging period.

Black-tailed godwit food intake rates in the rice fields matched the expectations of Holling's functional response curve, increasing logistically with increasing food densities (Holling 1959; Piersma *et al.* 1995). This fit allowed us to estimate the rice density that would correspond to the necessary rice intake rates to sustain the allometrically predicted daily energetic requirement. The final rice densities measured after the godwits stopped using a field were closely matched to this value estimated from the model, suggesting that indeed this was the food density threshold below which birds react by moving to a new field (Lourenço *et al.*, in press b; Chapter 5).

This result suggested that, in order to maximize food intake during their staging period, godwits follow a simple patch-leaving decision (Griffen, 2009). In fact, individually marked birds sighted in the area moved towards fields of higher rice density much more than expected by chance alone, and these birds increased their intake rates after making such a move (Lourenço *et al.*, in press b; Chapter 5). By following this patch-leaving rule black-tailed godwits were able to cope with food depletion and capitalize on the new foraging opportunities provided by farming activities, maintaining a constant average



intake rate over the entire duration of the staging period. This average intake rate was roughly 40% higher than their daily energetic requirements which is certainly necessary to sustain the extraordinary energetic requirements faced by a staging migrant (Zwarts *et al.*, 1990; Wikelski *et al.*, 2003; Bowlin *et al.*, 2005). Throughout the staging period we scored the plumage of random sets of 100 birds, and later scored in the same manner colour-marked individuals spotted in the breeding area, which clearly showed that body moult takes place while staging in the rice fields (Fig. 8.1). Moult can be costly, especially for migrants that are time-stressed and need to quickly accumulate energy. In a closely related species, the bar-tailed godwit *Limosa lapponica*, moult was estimated to represent only 7% of the costs of the simultaneous energy storage at a staging site, still only the individuals in a good nutritional conditions were able to afford it (Piersma & Jukema, 1993). Black-tailed gowits staging in Portuguese rice fields are clearly able to moult (Fig. 8.1), which seems to confirm they are in a good nutritional condition.



**Figure 8.1:** Average plumage scores (1-winter plumage to 5-bright breeding plumage) for the back (in black) and breast (in grey) of birds scored in the staging areas (circles) and in the breeding area (diamonds). Godwits arrive in the staging area with their winter plumage and undergo the full body moult there as no further increase seems to occur in the breeding area. Staging area: n=100 birds each day; Breeding area: n=1-12 birds each day. All individuals scored by the same observer.

Also, from a sample of 39 birds captured in the rice fields close to the end of the staging period, all but two were estimated to have sufficient body stores to perform direct flights to breeding areas in The Netherlands (Alves *et al.*, unpub. data) according to a flight simulation model (Pennycuik, 2008).

Both the moulting and the accumulation of energy stores are evidence that these birds are ingesting energy well above the daily requirement for maintenance, and underline the importance of maintaining the high intake rates that are allowed by frequently moving towards new foraging locations as soon as intake rates fall below the critical threshold.

### **Staging duration, population size and the international importance of Portuguese rice fields**

The counts in Portugal give evidence of an ongoing decline in this population. Despite the large number of godwits currently staging in the studied rice fields, the current peak counts of roughly 45000 are over 40% lower than numbers counted in the early 1990s (Lourenço *et al.*, in press a; Chapter 6). This tallies well with declines observed in the breeding areas (Piersma, 1986; Teunissen & Soldaat, 2005; Schroeder *et al.*, 2009b). The staging period lasts between late-December and early March, with peak numbers occurring in the second half of February. Individual godwits remain in the area for an average of 22-25 days, which is similar to observations in other staging sites in Spain (J.A. Masero *et al.* unpub. data). However, individual staging duration is not constant throughout the whole period, instead it increases towards the end possibly because birds delay departures in order to leave simultaneously.

An important aspect of the dynamics of the staging period is the turn-over of birds, which often masks the real numbers migrating through a staging site (e.g. Frederiksen *et al.* 2001, Schaub *et al.* 2001). When this was taken into account, the number of black-tailed godwits migrating through Portuguese rice fields was considerably higher than the peak counts, reaching 53100-59200 birds. Since the western *limosa* population has now been estimated at 135,000-140,000, this staging site as a whole harbours roughly 38-44% of the population (Lourenço *et al.*, in press a; Chapter 6). The rice fields around the Tejo and Sado estuaries are not a continuous area, the rice fields are scattered around the valleys of the main rivers and their tributaries, which expand far beyond the limits of the estuaries. This poses a problem for the conservation of this population because even though the estuaries are recognized for their importance for biodiversity, many of the rice fields are outside the

local protected areas (Lourenço *et al.*, 2009).

### **Repeatable migration schedules and lack of evidence for domino effects**

Migrants often show repeatable individual schedules year after year. This has been reported for the timing of departure from the non-breeding grounds (Rees, 1989; Battley, 2006; Chapter 7), for the timing of arrival at the breeding grounds (Møller, 2001; Bêty *et al.*, 2004; Gunnarsson *et al.*, 2006; Chapter 7) and for the timing of egg laying (Sydeman & Eddy, 1995; Bańbura & Zieliński, 2000; Chapter 7). Such a consistency in migratory and breeding schedules may reflect a strong genetic component to these behaviours (Pulido & Berthold, 2003), but could also be explained by individual specific developmental trajectories (Gienapp *et al.*, 2008; Hendry *et al.*, 2008; Teplitsky *et al.*, 2008), as phenotypic plasticity can lead to adaptations to the environment without genetic variation (Teplitsky *et al.*, 2008).

In black-tailed godwits, the arrival dates of males and females are correlated (Gunnarsson *et al.*, 2006b; Chapter 7), both when considering the average arrival date of all males and females in each year and when considering birds known to be paired. Males arrive on average 2.5 days earlier than females which is consistent with the expected protandry of non-polyandrous species (Oring & Lank, 1982; Morbey & Ydenberg, 2001).

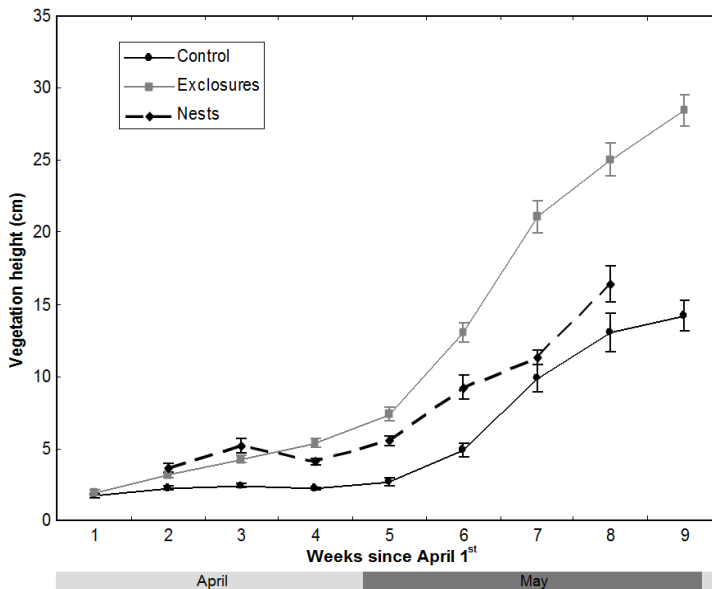
Individual schedules seem to be tightly set and well matched to that of their partners. Also, there is evidence that early breeding is advantageous in black-tailed godwits and that this benefit for early breeding is perceived by the birds (Schroeder *et al.*, 2006; Schroeder, 2010). Such constraints would be expected to cause a domino effect during migration (Piersma, 1987), with birds that are early leaving the winter grounds or in the staging areas being the first to arrive in the breeding areas and breed (e.g. Tryjanowski *et al.*, 2004; Neto & Gosler, 2005; Vergara *et al.*, 2007).

Surprisingly, no evidence for such domino effects was found. The timing of the staging period is not correlated with the timing of arrival in the breeding area, and neither of these events is correlated with the timing of egg laying (Chapter 7). Also, there is evidence that these birds fail to breed as early as they would be expected to (Schroeder, 2010).

Apparently, different individuals follow different strategies. The duration of the migration between the staging areas and the breeding areas can vary from less than a week to over four weeks. This variation is likely to reflect whether these individuals fly directly to the breeding areas, or either make further stop-overs along the French coast. Stopping in

France can reduce the risk of facing adverse weather conditions upon arrival on the breeding grounds, as these conditions will be easier to predict from a closer staging area (Newton, 2008) but imply a higher mortality risk due to hunting pressure in France as long as the spring hunt is allowed (Gill *et al.*, 2007).

Also the time spent between arriving at the breeding area and actually laying the eggs varies considerably. This variation does not seem to be random. In fact, early arriving birds tend to wait longer before breeding than late arriving birds (Chapter 7). Although the exact cause behind this unexpected result is not yet clear, we have speculated that the current presence of very large concentrations of barnacle geese *Branta leucopsis* in one part of the Dutch study area, the Workumerwaard, where most of the present work was carried out, during the first half of the godwit breeding season limits the availability of good-quality nesting locations, because the grass in the meadows is kept short by grazing geese. There is some evidence supporting this hypothesis. An exclusion experiment made in the area showed that vegetation height was on average twice as high in areas where the geese were not allowed to graze than in random locations in the same meadows (Fig. 8.2).



**Figure 8.2:** Variation in vegetation heights along the breeding season in goose exclosures (n=8; 4 measurements in each exclosures of 3x3m), in random location in the same meadows (n=8; 4 measurements in each location within an area of 3x3m) and in recently initiated godwit nests (n=2-19; 4 measurements within 1m of the nest).

Also, measurements within 1m of recently initiated godwit nests indicated that the vegetation height there was higher than that measured in random location, but not as high as in the goose exclosures (Fig. 8.2). This seems to confirm that godwits nest in the few available patches where the vegetation height is higher than average, but cannot find sites where the vegetation is as high as would be possible without the impact of the geese. This could force godwits to postpone egg laying until more nesting locations with higher vegetation become available. Still, this possible effect of geese grazing is only limited to the Workumerwaard and thus cannot explain delayed egg laying in other areas. There is evidence that meadow birds are advancing egg laying dates across The Netherlands, possibly because of increased use of fertilizers and climate change (Beintema *et al.*, 1985; Both *et al.*, 2005b), but this is not the case in black-tailed godwits, at least since the 1970s (Schoeder, 2010; Kleijn *et al.*, in press) which suggests that some further overlaying factors deter these birds from laying earlier.

### **Godwit conservation and the future of rice farming in Portugal**

We have established that the rice fields around the Tejo and Sado estuaries are a critical staging area for black-tailed godwits migrating from West Africa to The Netherlands. Moreover, only rice fields that are flooded and that are ploughed early enough will provide profitable feeding conditions.

Modernization of rice farming and a lack of economic incentives for farming rice are likely to peril the current conditions found by godwits in Portugal. We believe that the implementation of “godwit-friendly” management guidelines for rice farmers in the lower valleys of the Tejo and Sado rivers, namely ensuring that part of the rice fields are kept flooded in winter and phasing ploughing activities to ensure the availability of newly-ploughed fields throughout the winter, are the key to protect this staging site.

One of the problems with this is that a large part of the rice plantations used by godwits are not under any legal protection. In fact, of the 12 surveyed rice field sites that on some occasion held over 1% of the overall population (1400), only 4 are completely inside the local Special Protection Areas, 3 are partially inside, and the other 5 are outside. This means that overall only 27% of the total rice field area used by godwits is under some legal protection (Table 8.1). In many of these sites hunting is allowed. Although godwit hunting is prohibited, the rice fields are visited by many hunters looking for snipes, frequently causing significant disturbance to the foraging godwit flocks (European Communities,

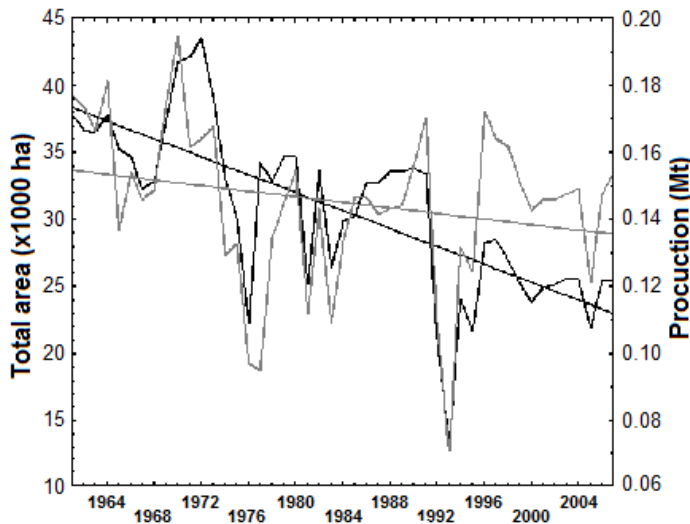
2007). It is also possible that some poaching takes place when hunters are presented with large flocks of godwits while searching for other birds. Also, for most of the area there is no management plan, and no guarantees that the current farming scheme, which is favourable for the birds by maintaining flooded fields and with ploughing starting early in the winter, will remain unchanged in the future. Finally, the two most important sites, Paúl de Belmonte and Samora Correia are respectively within 7 and 13 km of the chosen location for the new international airport of Lisboa, which is under planning at the moment. Not only are the sites close to the possible future airport, but the flight route of the birds when moving between these locations and their nocturnal roost in the salt marshes bordering the Tejo estuary are likely to come even closer to the airport site with potentially dire consequences for both godwits and air traffic (Lourenço & Alves, 2009).

**Table 8.1:** Summary of the 12 rice field sites where over 1% of the population was counted, including site area (ha) and proportion included in the local Special Protection Area, the maximum count, the % of the population included in that count (assuming the maximum estimate of 140000 birds), and the winter in which the maximum count occurred.

Site	Area (%SPA)	Max. Count	% Population	Winter
Paúl do Trejoito	202 (0%)	18000	12.9%	2006/07
Paúl de Belmonte	496 (0%)	38000	27.1%	2006/07
Samora Correia	532 (0%)	35600	25.4%	2008/09
Giganta	246 (100%)	4000	2.9%	2008/09
Zambujal	50 (100%)	7500	5.4%	2007/08
Agualva	44 (13%)	3850	2.8%	2008/09
Marateca	8 (0%)	3250	2.3%	2006/07
Palma	216 (0%)	11000	7.9%	2006/07
Alcácer do Sal	145 (59%)	2790	2.0%	2006/07
Montevil	98 (100%)	19000	13.6%	2007/08
Monte Novo	60 (100%)	2300	1.6%	2008/09
Comporta	117 (39%)	10000	7.1%	2005/06
All rice fields	2214 (27%)	46700	33.4%	2006/07

It is also critical that these rice cultivations continue to exist. In the last five decades the area covered by rice crop in Portugal decreased by almost 40% (Fig. 8.3). This negative

trend is due to both abandonment of previously explored plantations and because of substitution by other crops, namely maize (GPP, 2008), which is of considerably lower value for biodiversity (Kirk *et al.*, 2001; Laiolo, 2005; Kopij, 2008). These changes are caused by a decrease in the profitability of rice production. Since most of these farmers are subsidized by the EU (GPP, 2008), the continuity of rice farming around the estuaries of the Tejo and Sado rivers and the implementation of farming practices that are compatible with biodiversity conservation depend on the European Common Agricultural Policy (CAP) and its enforcement by the Portuguese state.



**Figure 8.3:** Evolution of rice production in Portugal between 1961 and 2007 (FAOSTAT, 2009). The grey lines represent the total production (Mt) and the black lines represent the total area (x 1000 ha) occupied by this crop.

To guarantee that godwits will continue to find favourable condition in the long term during their staging period in Portugal, it is critical that rice farming is not substituted by other crops and that management guidelines are implemented by the local farmers and farming cooperatives. Ideally, the rice plantations used by godwits should be included in the local protected areas, to facilitate the enforcement of the suggested guidelines, and hunting in these areas should be banned for the duration of the black-tailed godwit staging period. Continued monitoring of this staging area should establish whether any of the resulting policies are successful.





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# Summaries

## Summary

Staging episodes are critical in the life-cycle of migratory species. The conditions found in the staging areas can affect the speed of the migration, the survival of individuals and ultimately their breeding success upon arrival in the breeding grounds. The continental black-tailed godwit *Limosa l. limosa* is a long-lived migratory bird. This population breeds in the agricultural grasslands of northern Europe and winters in fresh water habitats in West Africa. During the pre-nuptial migration these birds stage in the Iberian Peninsula, where they gather in large numbers to forage in rice plantations. These rice plantations are not only important for godwits, but also hold a rich bird community, which is dependent on the agricultural management of this agro-ecosystem.

In this thesis we studied the staging ecology of black-tailed godwits in Portuguese rice fields, analysed the dynamics of this staging period and explored possible correlations between the staging period and breeding season events. In chapter 1 we reviewed the significance of staging ecology in the framework of bird migration and presented the study population and the study area. In chapter 2 we analysed the correlations between rice farming practices and waterbird abundance, concluding that most species have higher abundances in flooded fields, while ploughing the rice fields is mostly favourable for waders, but not for storks, egrets and herons. Chapter 3 starts by describing the diet of black-tailed godwits in the rice fields, which mostly comprises rice seeds. Based on this dietary preference, we analysed the habitat selection of black-tailed godwits, which show a preference for fields that are flooded and ploughed, and explained this pattern in terms of the abundance of rice seeds in the soil. The results of the first two chapters lead us to propose that flooding the rice fields in winter and phasing the ploughing activities throughout the season guarantee ideal conditions for the bird community in the rice fields while maintaining the profitability for the farmers.

In chapter 4 we explore the habitat segregation between the two subspecies of black-tailed godwit present in Portugal in winter, the continental *L. l. limosa* and the Icelandic *L. l. islandica*. Using re-sightings of individually marked birds of known breeding origin we showed that *limosa* godwits are mostly present in rice field areas, which are mostly fresh water environments, while *islandica* individuals mostly use salt water estuarine habitats. Still, there is a small degree of overlap between the two subspecies in winter.

In Chapter 5 we explore the foraging ecology of black-tailed godwits in rice fields in more detail. We show that the foraging activity of godwit flocks causes significant

depletion of the rice seeds in the fields. We show that the intake rates are influenced by food density according to the expectations of Holling's functional response. Based on this fit we estimated the rice density that would correspond to the necessary rice intake rates to sustain the allometric energy requirements and showed that this rice density closely matches the observed rice density in the fields after being depleted by godwits. Individual godwits seem to abandon a field when rice densities fall below this critical threshold, and move towards fields of higher rice density more than expected by chance alone. In this way, godwits maintain a stable intake rate throughout the staging period, and are able to ingest energy well above the daily requirement for maintenance.

Chapter 6 explores the phenology and dynamics of the staging period. We show that godwits are present in Portuguese rice fields between late December and early March, with numbers peaking around 45000 birds in the second half of February. These peak counts suggest that numbers declined by at least 40% since the early 1990s. We also showed that the migratory peak now occurs some three week later than in that period. Individuals stay in the area for an average 22-25 days, but the staging duration increases towards the end of the staging period. When turn-over is taken into account, we estimated that a total 53100-59200 birds use the area at present. Using the densities of ringed birds present in the flocks in staging areas in both Portugal and Spain, we estimated that the western portion of the *limosa* population, which migrates through the area, currently totals 135000-140000, meaning that 38-44% of this population currently uses the rice plantations around the Tejo and Sado estuaries.

In Chapter 7 we expand the study to the breeding areas, in The Netherlands, exploring possible correlations between the timing of the staging period and the timing of breeding events. We showed that individual birds follow repeatable schedules year after year, both in terms of the departure date from the staging area, the arrival date in the breeding area and the egg-laying date. Despite evidence that early breeding is advantageous in black-tailed godwits and that this benefit for early breeding is perceived by the birds we found no evidence for domino effects during migration. The timing of the staging period is not correlated with the timing of arrival in the breeding area, and neither of these events is correlated with the timing of egg laying. Also, there is evidence that these birds fail to breed as early as they would be expected to. Individuals seem to follow different strategies in both the time spent migrating from the rice fields in Portugal to the breeding area in The Netherlands, and in the time spent between arriving in the breeding areas and starting to

breed. Some possible causes behind these differences are debated in this thesis, but the exact reasons for the observed pattern are not yet clear.

The work presented in this thesis lead us to conclude that the conditions currently found by black-tailed godwits during their staging period in Portugal are not contributing to the ongoing decline of this population. Still, current trends for the modernization of rice farming and for the reduction of the area devoted to rice cultivation, together with future changes in the weather patterns may pose threats in the long-term. We propose the implementation of some management guidelines for rice farming: maintaining the fields flooded in winter and phasing the ploughing of the fields throughout the winter. Also, we propose that some of the rice plantations should be included in the local protected areas, as a means of enforcing the management guidelines and ensuring the long-term conservation of this critical staging area for black-tailed godwits.

## Resumo

Os episódios de passagem, durante a migração, são críticos no ciclo de vida das espécies migradoras. As condições encontradas pelas aves nestas zonas de passagem podem afectar a velocidade da migração, a sobrevivência e, eventualmente, o sucesso reprodutor após chegarem às áreas de reprodução. O maçarico-de-bico-direito *Limosa limosa* é uma ave migratória de vida longa. A subespécie continental *L. l. Limosa* reproduz-se nos prados agrícolas do norte da Europa, invernando em habitats de água doce na África Ocidental. Durante a migração pré-nupcial estas aves fazem uma passagem migratória na Península Ibérica, onde se juntam em grandes bandos para se alimentarem nos arrozais. Estes arrozais são importantes não apenas para os maçaricos, mas suportam também uma rica comunidade de aves, as quais dependem da gestão agrícola deste agro-ecossistema.

Nesta tese, estudámos a ecologia de passagem migratória dos maçaricos-de-bico-direito nos arrozais em redor dos estuários do Tejo e do Sado, em Portugal. Analisámos a dinâmica do período de passagem migratória e explorámos possíveis correlações entre o período de passagem migratória e eventos na época de reprodução. No capítulo 1 fizemos uma revisão da importância da ecologia de passagem migratória no contexto da migração das aves e apresentámos a área de estudo e a população estudada. No capítulo 2 analisámos as correlações entre as práticas agrícolas nos arrozais e a abundância de aves aquáticas nestas zonas, tendo concluído que a maioria das espécies estudadas apresentam densidades mais elevadas em arrozais alagados. Os arrozais lavrados são mais favoráveis para as limícolas enquanto que as cegonhas e as garças preferem arrozais que ainda mantêm o restolho. O capítulo 3 começa por descrever a dieta dos maçaricos nos arrozais, que se baseia nas sementes de arroz. Analisámos também a sua selecção de habitat, sendo que estas aves preferem arrozais alagados que já foram lavrados. Estes padrões de selecção de habitat são explicados pela abundância de sementes de arroz no solo. Os resultados destes dois capítulos levaram-nos a propôr que manter os arrozais alagados no Inverno e fasear a lavra ao longo de toda a estação pode garantir condições ideais para a avifauna dos arrozais, ao mesmo tempo que mantém a produtividade agrícola.

No capítulo 4 explorámos a segregação de habitat entre as duas subespécies de maçarico-de-bico-direito presentes em Portugal no Inverno: a subespécie continental *L. l. Limosa* e a subespécie islandesa *L. l. Islandica*. Usando avistamentos de indivíduos, marcados com combinações individuais de anilhas coloridas nas áreas de reprodução, mostrámos que os maçaricos da subespécie *L. l. limosa* utilizam sobretudo arrozais, que são

essencialmente habitats de água doce, enquanto que a subespécie *L. l. islandica* utiliza sobretudo habitats estuarinos salinos. Contudo, existe uma pequena fracção de indivíduos de cada subespécie que utiliza o outro habitat.

No capítulo 5 explorámos em maior detalhe a ecologia alimentar dos maçaricos-de-bico-direito nos arrozais. Mostrámos que a actividade alimentar dos maçaricos causa depleção significativa do arroz disponível nos arrozais. As taxas de ingestão de arroz são influenciadas pela densidade de alimento no solo, de acordo com a relação funcional de Holling. Através desta equação, estimámos a densidade de arroz que corresponde à taxa de ingestão necessária para assegurar os requisitos energéticos estimados alometricamente. Essa densidade, estimada através da equação de Holling, correspondeu com exactidão à densidade de arroz observada nos arrozais depois de abandonados pelos maçaricos. Os maçaricos parecem abandonar um arrozal quando a densidade de arroz atinge esse nível crítico, movendo-se para novos arrozais, onde a densidade de arroz é mais elevada, mais do que seria esperado aleatoriamente. Desta forma, os maçaricos mantêm taxas de ingestão de arroz constantes ao longo do período que passam na zona, sendo estas bem superiores aos níveis exigidos para a sua sobrevivência, como é de esperar numa zona de passagem migratória.

No capítulo 6 explorámos a fenologia e a dinâmica do período de passagem migratória. Mostrámos que os maçaricos estão presentes nos arrozais portugueses desde meados de Dezembro até ao início de Março, com as contagens a atingirem um pico de cerca de 45000 indivíduos na segunda metade de Fevereiro. Estas contagens máximas sugerem que o efectivo diminuiu em pelo menos 40% desde o início dos anos 90. Os dados sugerem também que o pico da passagem migratória ocorre agora cerca de três semanas mais tarde do que nessa época. Cada indivíduo permanece cerca de 22-25 dias na região, mas a duração da permanência aumenta no final do período de passagem. Tendo em conta o turn-over de aves ao longo do período de passagem, estimámos que um total de 53100-59200 indivíduos utiliza actualmente a zona. Utilizando a densidade de indivíduos marcados, em bandos tanto em Portugal como em Espanha, estimámos a dimensão da população ocidental da subespécie *L. l. limosa*, que migra através desta região, sendo esta composta no presente por cerca de 135000-140000 aves. Isto significa que 38-44% desta população utiliza actualmente os arrozais em redor dos estuários do Tejo e do Sado.

No capítulo 7 levámos o estudo até às áreas de reprodução, na Holanda, explorando as possíveis correlações entre o timing do período de passagem migratória e o timing dos

eventos na época de reprodução. Mostrámos que cada indivíduo segue calendários repetíveis ano após ano, tanto na data de partida da zona de passagem migratória, como na data de chegada à área de reprodução e na data da postura. Apesar de se ter provado que reproduzir-se cedo é vantajoso para os maçaricos-de-bico-direito e que esta vantagem é percebida pela aves, não encontrámos qualquer prova de que ocorram efeitos de dominó durante a migração. A data de partida da zona de passagem migratória não está correlacionada com a data de chegada à área de reprodução, e nenhum destes eventos está correlacionado com a data da postura. Diferentes indivíduos parecem seguir estratégias diferentes no que respeita à duração da migração entre os arrozais portugueses e as áreas de reprodução na Holanda, e à duração do período entre a chegada à área de reprodução e a postura. São discutidas algumas causas possíveis para estas diferenças, mas as causas exactas para o padrão observado não estão ainda bem clarificadas.

O trabalho apresentado nesta tese levou-nos a concluir que as condições actualmente encontradas pelos maçaricos-de-bico-direito, durante o seu período de passagem migratória em Portugal, não estão a contribuir para o declínio populacional em curso. No entanto, as tendências actuais para uma maior modernização do cultivo do arroz e para uma redução da área plantada com arroz em Portugal, juntamente com alterações futuras nos padrões meteorológicos da região, podem colocar ameaças a longo prazo. Proposemos a implementação de algumas medidas de gestão agrícola: manter os arrozais alagados no Inverno e fasear a lavra ao longo de toda a estação. Proposemos também que algumas das áreas de arrozal sejam integradas nas áreas protegidas do Tejo e do Sado, como forma de facilitar a implementação das medidas propostas e assegurar a conservação a longo prazo desta zona de passagem migratória crítica para o maçarico-de-bico-direito.

## Samenvatting

Doortrekplaatsen zijn kritisch in de levenscyclus van migrerende soorten. De condities in deze gebieden kunnen de snelheid van de migratie, de overleving van individuen en uiteindelijk het broedsucces bij aankomst in de broedgebieden beïnvloeden. De continentale grutto *Limosa l. limosa* is een trekvogel met een lange levensduur. Deze populatie broedt in de weilanden van Noord-Europa en overwintert in zoetwater-gebieden in West-Afrika. Gedurende de trek voorafgaand aan de paarvorming verblijven deze vogels op het Iberisch schiereiland, waar zij verzamelen in grote aantallen om te foerageren op rijstplantages. Deze rijstplantages zijn niet alleen belangrijk voor de grutto's, maar onderhouden ook een rijke vogelgemeenschap, die afhankelijk is van het landbouwkundig beheer van dit agro-ecosysteem.

In dit proefschrift hebben we de doortrekecologie van grutto's in de Portugese rijstvelden bestudeerd, de dynamiek van deze verblijfsperiode geanalyseerd en mogelijke samenhang tussen de doortrekperiode en gebeurtenissen in het broedseizoen verkend. In hoofdstuk 1 hebben we het belang van doortrekecologie in het raamwerk van vogeltrek overzien en beschrijven we de onderzoekspopulatie en het onderzoeksgebied. In hoofdstuk 2 hebben we de samenhang tussen rijstverbouw-praktijken en overvloed aan watervogels geanalyseerd, concluderend dat de meeste soorten in grotere aantallen aanwezig zijn in overstroomde velden, terwijl het ploegen van de rijstvelden gunstig is voor waadvogels, maar niet voor ooievaars en reigers. Hoofdstuk 3 start met een beschrijving van het dieet van de grutto in de rijstvelden, dat voornamelijk bestaat uit rijstzaden. Gebaseerd op deze voedselvoorkeuren hebben we de habitatselectie van de grutto geanalyseerd, waaruit een voorkeur blijkt voor velden die overstroomd en omgeploegd zijn, en verklaren we dit patroon door middel van de hoeveelheden rijstzaden in de grond. De resultaten van de eerste twee hoofdstukken laten ons aannemen dat overstroming van de rijstvelden in de winter en fasering van de ploegactiviteiten gedurende het seizoen de ideale condities voor de vogelgemeenschap in de rijstvelden creëren terwijl het gebied winstgevend blijft voor de boeren.

In hoofdstuk 4 verkennen we het verschil in leefgebied tussen twee ondersoorten van de grutto die aanwezig zijn in Portugal in de winter; de continentale *L. l. limosa* en de IJslandse *L. l. islandica*. Door herhaalde waarnemingen van individueel gemerkte vogels met een bekende broedafkomst te gebruiken tonen we aan dat *limosa* grutto's vooral aanwezig zijn in rijstveld-gebieden, die veelal zoetwatermilieus zijn, terwijl *islandica*



individueen vooral de zoute riviermonding-gebieden gebruiken. Hoewel er in de winter enige overlap tussen de twee ondersoorten is.

In hoofdstuk 5 verkennen we de foerageerecologie van grutto's in de rijstvelden gedetailleerder. We tonen aan dat de foerageeractiviteit van grutto-zwermen zorgt voor uitputting van de rijstzaden in de velden. We laten zien dat de inname-ratios beïnvloed worden door de voedseldichtheid volgens de verwachtingen van Holling's functionele response. Gebaseerd op deze reactie beramen we de rijstdichtheid, die correspondeert met de benodigde rijstinname om de allometrische energie-eisen te onderhouden, en tonen we aan dat deze rijstdichtheid nauw overeenkomt met de geobserveerde rijstdichtheden na uitputting van de velden door grutto's. Individuele grutto's lijken velden te verlaten wanneer de rijstdichtheden onder deze kritieke drempel vallen, en verplaatsen zich naar velden met een hogere rijstdichtheid zonder dat er alleen sprake is van toeval. Op deze manier handhaven de grutto's een stabiele inname-ratio gedurende de doortrekperiode, en zijn zij in staat om energiehoeveelheden tot zich te nemen die ruim boven de dagelijkse behoefte liggen.

Hoofdstuk 6 verkent de fenologie en dynamieken van de doortrekperiode. We laten zien dat grutto's aanwezig zijn in de Portugese rijstvelden tussen eind december en begin maart, met de grootste aantallen (ongeveer 45000 vogels) in de tweede helft van februari. Deze piektellingen geven aan dat de aantallen met minstens 40% zijn afgenomen sinds begin jaren negentig. We tonen ook aan dat de migratiepiek nu ongeveer drie weken later plaats vindt in vergelijking met die periode. Individueen verblijven gemiddeld 22 tot 25 dagen in het gebied, maar de verblijfsduur neemt toe aan het eind van de doortrekperiode. We schatten dat 53100 tot 59200 vogels momenteel van het gebied gebruik maken wanneer turn-over in beschouwing wordt genomen. Gebruikmakend van de dichtheden van geringde vogels in zwermen in doortrekgebieden in zowel Portugal als Spanje schatten we dat het westerse gedeelte van de *limosa* populatie, dat door dit gebied trekt, momenteel uit 135000 tot 140000 individuen bestaat. Dit betekent dat 38 tot 44% van de huidige populatie gebruik maakt van de rijst plantages rond de Tejo en Sado riviermondingen.

In hoofdstuk 7 breiden we het onderzoek uit tot de broedgebieden, in Nederland, waar we mogelijke samenhang tussen het tijdstip van de doortrekperiode en het tijdstip van broeden verkennen. We laten zien dat individuele vogels jaar op jaar herhaalde schema's volgen, zowel aangaande de datum van vertrek uit het doortrekgebied, als de aankomstdatum in het broedgebied en de startdatum van het eileggen. Ondanks bewijs dat vroeg broeden gunstig

is voor grutto's en dat dit voordeel door de vogels wordt waargenomen, vonden we geen aanwijzingen voor domino effecten gedurende de trek. Het tijdstip van de doortrekperiode hangt niet samen met het tijdstip van aankomst in het broedgebied, en geen van beide hangt samen met de tijdstip van eileg. Tevens is er bewijs dat deze vogels er niet in slagen om zo vroeg te broeden als van ze verwacht wordt. Individuen lijken verschillende strategieën te volgen, zowel wat betreft de duur van de trek van de rijstvelden in Portugal naar het broedgebied in Nederland, als de periode tussen aankomst in het broedgebied en de start van het eileggen. Mogelijke oorzaken van deze verschillen worden besproken in dit proefschrift, maar de exacte redenen voor dit geobserveerde patroon zijn nog niet duidelijk.

Met het werk gepresenteerd in dit proefschrift concluderen we dat de omstandigheden die grutto's thans ondervinden gedurende hun doortrekperiode in Portugal niet bijdragen aan de aanhoudende achteruitgang van deze populatie. Toch kunnen trends in de modernisatie van rijstverbouwing en vermindering van het gebied bestemd voor rijstbouw, gecombineerd met toekomstige veranderingen in weerpatronen, bedreigingen vormen op de lange termijn. We stellen de invoering van bepaalde beleids richtlijnen voor rijstverbouwing voor: het onder water blijven zetten van de velden in de winter en de fasering van het ploegen van de velden gedurende de winter. Verder stellen we voor dat een aantal rijstplantages in lokaal beschermde gebieden kan opgenomen worden, als een methode om de beleidsrichtlijnen af te dwingen en hiermee op de lange termijn bescherming te garanderen voor deze kritieke doortrekgebieden voor de grutto.





# Other Publications

### **List of other papers published during the time of this thesis (2006-2010)**

Lourenço, P.M. 2006. Seasonal abundance of aquatic birds at Óbidos lagoon. *Airo*, 16: 23-29.

*Despite being one of the largest coastal lagoons in Portugal, the Óbidos Lagoon and its bird community has received little attention and there is almost no published information on the aquatic birds that occur in this area. Monthly bird counts were performed (September 2004 to July 2005) directed at all the aquatic bird species present in the lagoon. Throughout the year, I evaluated the seasonal abundance of each species and the relative importance of waders (Charadrii), gulls (Laridae), wildfowl (Anatidae), egrets and herons (Ardeidae) and others (including Phalacrocoracidae, Threskiornithidae, Phoenicopteridae, Rallidae and Sternidae). There was a mean of 1660 aquatic birds per count. During autumn and winter, waders were the most abundant group (41-40%), followed by gulls (29-22 %) and wildfowl (22-28%). In spring, these three groups had similar abundances (26-34 %), while in the summer, gulls (64%) were clearly the most abundant, followed by waders (23%), and wildfowl (9%). Amongst the most abundant species were the mallard *Anas platyrhynchos* (352 individuals/count); the waders, dunlin *Calidris alpina* (268 ind./count), grey plover *Pluvialis squatarola* (67 ind./count), ringed plover *Charadrius hiaticula* (63 ind./count); the gulls, lesser black-backed gull *Larus fuscus* (198 ind./count), yellow-legged gull *L. cachinnans* (181 ind./count) and black-headed-gull *L. ridibundus* (171 ind./count). During the winter, some species achieved nationally important numbers, showing that this coastal lagoon is one of the top five sites in Portugal, for those species. Also worthy of notice was the presence of greater flamingo *Phoenicopterus roseus* and oystercatcher *Haematopus ostralegus*, throughout the year (with the exception of July), and the observation of species that are uncommon in Portuguese wetlands, namely Brent goose *Branta bernicla* and Arctic tern *Sterna paradisaea*.*

Lourenço, P.M. 2007. Analysing the faecal samples of ragworm predators: not just a matter of counting mandibles. *Ardea*, 95: 151-155.

*Ragworms Hediste diversicolor are an important prey item in the diet of many estuary birds. The standard method for estimating the number of ragworms in faeces or pellets is*

*simply dividing the counted number of ragworm mandibles by two, which can easily lead to an underestimation of the real number of ragworms present. Here, I present two alternative methods, which avoid bias in estimates of the number of ragworms in samples. I compared the three methods by applying them to faecal samples of grey plover *Pluvialis squatarola* and redshank *Tringa totanus* from the Tagus estuary, Portugal. The alternative methods yielded significantly higher estimates of the number of ragworms present in each sample, a difference that can have repercussions on the outcome of dietary studies of ragworm predators. The pros and cons of each method are discussed with regard to the use of faeces and pellets for ecological research, and the situation in which each method could be applied is discussed.*

Lourenço, P.M. & Piersma, T. 2008. Changes in the non-breeding distribution of continental black-tailed godwits *Limosa limosa limosa* over 50 years: a synthesis of surveys. Wader Study Group Bulletin, 115: 91-97.

*Over the years a large body of information has been gathered regarding the migratory and wintering distribution of black-tailed godwits *Limosa limosa*. Much of this information is only available in the so-called "grey" literature. Here we present a summary of non-breeding count data for the continental race *L. l. limosa* covering the last fifty years. We suggest that there have been important changes in the winter and spring-staging distribution and numbers of this now threatened population. The winter distribution covers a wide area from Senegal and Guinea-Bissau in the west, through Mali and Chad and extends into the Middle East as far as Iran. During spring, the most important staging sites are around the Mediterranean basin, with key areas in Iberia and France. Throughout the range, numbers have changed over time. Today, areas in West Africa, like Senegal, Morocco and, to some extent, Guinea-Bissau have much lower numbers of godwits than 20 years ago, whereas in Mali, Chad and north Cameroon numbers have remained more or less stable. Larger numbers of godwits now occur in southern Europe, Portugal and Spain; but the French wetlands have lost some of their past importance.*

Lourenço, P.M.; Silva, A.; Santos, C.D.; Miranda, A.C.; Granadeiro, J.P. & Palmeirim, J.M. 2008. The energetic importance of night foraging for waders wintering in a temperate estuary. *Acta Oecologica*, 34: 122-129.

*Many species of waders forage extensively at night, but there is very little information on the relevance of this behaviour for the energy budget of waders wintering in estuarine wetlands. Quantitative data on diurnal and nocturnal intake rates can indicate the extent to which birds need to forage at night to supplement their diurnal energetic intake, or rather show a preference for nocturnal foraging. We compared day and night foraging behaviour, diet, and energy consumption of several wader species in the Tejo estuary, Portugal. There were significant differences between diurnal and nocturnal foraging behaviour. In general, birds moved less at night and scolopacid waders tended to use more tactile foraging methods. Although birds consumed the same type of prey in the two periods, the relative importance of each type changed. Overall, energy consumption was higher during the day except in grey plover, which achieved higher crude intake rates at night. Our results support the assertion that night foraging is an important part of the energy balance of waders during late winter, but that in most species it is less profitable than diurnal foraging.*

Lourenço, P.M. & Alves, J.A. 2009. Bird movements in the vicinity of the Campo de Tiro de Alcochete: are bird collisions an important risk in the proposed area of the New Airport of Lisboa? *Wader Study Group Bulletin*, 116: 175-180.

*Knowledge about the local bird community is key information when planning the construction of a new airport. Aircraft can cause serious impact on the local avifauna, but the birds can also pose a serious threat to aircraft. A new international airport is currently being planned for the Lisbon metropolitan area. The location that has been selected is Campo de Tiro de Alcochete, near the internationally important Tejo estuary wetland, and in the vicinity of areas under rice cultivation known to be important for the local bird community. We use available data on the movements of individually marked black-tailed godwits *Limosa limosa*, Eurasian spoonbills *Platalea leucorodia* and one lesser black-backed gull *Larus fuscus*, to examine whether these bird species are likely to cross the paths of aircraft approaching and departing from the future airport. We also use*



information on the phenology and abundance of these species to better understand the threat that these birds might pose to aircraft. All three species cross the planned approach and departure routes of the runways of the new airport. Black-tailed godwits in particular cross these routes at all planned aircraft flight altitudes and even overfly the airport site itself. The large number of birds potentially involved in these movements increases the threat to air traffic. There are several limitations to our study, especially a lack of information on bird flight altitudes. We therefore highlight the need for further and more detailed studies on the movements of these and other bird species around the airport site. However, by overlapping known individual movements of the three species with aircraft flight routes, we present sufficient data to demonstrate that bird collisions are a real hazard if the airport is built at Campo de Tiro de Alcochete. These findings call into question the wisdom of the proposed airport location and highlight the necessity for thorough research on the impacts of the birds on aircraft safety as well as the impact of aircraft on the local avifauna.

Lourenço, P.M. 2009. Rice field use by raptors in two Portuguese wetlands. *Airo*, 19: 13-18.

Rice plantations are internationally recognized for their importance as an agricultural habitat for birds. Despite being mostly used by aquatic birds, raptors also use this habitat. Portugal is one of the main rice producers in Europe. Despite this, little information is available regarding the bird community in these areas. The present study aims to describe the abundance of wintering birds of prey in the rice plantations around the estuaries of the Tejo and Sado rivers. In the winter 2005-2006 transects were performed by car in several rice plantations, and comparatively high raptor densities were found. A total of nine species were identified, the most abundant being the buzzard *Buteo buteo* ( $3.51 \pm 0.40$  indivíduos/10 km), the common kestrel *Falco tinnunculus* ( $1.88 \pm 0.32$  ind./10 km), the marsh harrier *Circus aeruginosus* ( $1.86 \pm 0.31$  ind./10 km) and the black-shouldered kite *Elanus caeruleus* ( $1.07 \pm 0.21$  ind./10 km). Some of these species were significantly more abundant in the Tejo than in the Sado. The buzzard had a temporal trend, with densities decreasing throughout the winter. This study underlines the importance of rice plantations as a wintering habitat for birds of prey, so the maintenance and management of these areas should be considered when planning the conservation of raptors in Portugal.

Lourenço, P.M., Groen N., Hooijmeijer J.C.E.W. & Piersma T. 2009. The rice fields around the estuaries of the Tejo and Sado are a critical stop-over area for the globally near-threatened black-tailed godwit *Limosa l. limosa*: Site description, international importance and conservation proposals. *Airo*, 19: 19-26.

*Rice fields are a globally important habitat for waterbirds. Portugal is one of the main rice producers in Europe, but little is known about how these rice fields are used by the avifauna. The continental black-tailed godwit Limosa l. limosa is likely the most important avian population using Portuguese rice fields during the winter and here we describe the main rice plantation areas used by these birds, report their international importance and propose some conservation measures for these areas. The plantations around the Tejo, Sado and Mondego lower basins were surveyed for three winters and peak counts reach roughly 45 000 birds each year. We define eleven areas, all around the Tejo and Sado estuaries as most important for this population, almost all holding over 1% of the population at some point during the surveys. Three areas, Paúl do Trejoito, Paúl de Belmonte and Samora Correia harboured, at least once, over 15% of the population during peak counts, and overall the eleven areas harboured over one third of the population each year. Despite this, most of these rice plantations are outside the local Special Protection Areas, and some of the most important ones lay at close distance from the proposed site for the new international airport of Lisboa. We propose some management guidelines for this area, in terms of banning hunting during key periods, and of ideal farming practices to maximize black-tailed godwit habitat availability. We also believe the international importance of these areas for this near-threatened species, as well as the potential risk of collisions, should be taken into serious consideration when deciding the location of the new airport.*





# Acknowledgements

A PhD is a long, and sometimes lonely journey. It is also an opportunity to meet a large number of interesting and unforgettable persons. A great many people were a part of my journey over the last four years, without their help, support and friendship my work would have been impossible. Therefore I would like to thank them all:

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I don't think field work in Fryslân would have been possible without the organizing skills of Jos Hooijmeijer and his never ending diplomacy towards the local landowners. I lost track of the many countless times I had to call him asking for information or advice during each field season. In the day when I first arrived in The Netherlands to start the field work, in 2006, Jos invited me for dinner at his house, with his family. Coming from a Latin country I didn't realize how special this was until later, when I learned that Dutch people close to never invite people to their houses unless they are already close friends. Jos also came to Portugal and helped with the field work there. Both he and Niko Groen helped collecting important data and managed to keep the field work running in 2008 during a time when I was seriously ill.

The two secretaries that “took care” of the Animal Ecology Group during my time there, Suus Baker and Joyce Rietveld, made all the bureaucracies surrounding the PhD a much easier task. I have to say those bureaucratic aspects of the work seem a whole lot harder to me than any concealable amount of field work, analytical work or even staying calm while reading destructive referee commentaries, so I am really, really grateful to both Suus and Joyce for their help.

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In 2006 I had to quickly learn all about field work with breeding birds in a place where the farmers feel the birds are their own and don't particularly like foreigners (with this I mean non-Frisians). My teacher was, more than anyone else, Julia Schroeder. She managed to pass on to me all that she had learned by herself in the two previous years. More than that, we shared countless days in Gaast discussing godwits, field work, student projects, cooking, Dutch food, Dutch weather, and many other things. Finally, I also have to thank Julia for the opportunity to hold in my hands a museum specimen of a godwit captured in 1859, about the time when Darwin was publishing his ground breaking book that changed biology forever.

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hold the record for the most ruff rings read by a “godwit person”. It was really nice meeting Claudia, Angela, Katie, Scott, Emily, Robbie, Katharine, Marianne, Tamas, and of course Lucie, who is now responsible for the ruff project.

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When I started planning this work I only had a map of all the rice fields in Portugal (all 25000 ha of them) and no good ideas on how to get around this huge area searching for godwits. Two persons were extremely helpful at this stage, helping me narrow down the search (and sometimes expand it as well) and becoming a rice field expert. My thanks go to Carlos Pereira and Nuno Cidraes-Vieira

The field work in Portugal was often very hard work, driving countless kilometres every day and spending a great many hours counting flocks and scanning the flocks for rings. I am very grateful for everyone who joined me in the field there and made the work so much more fun. The list is long, but I would like to thank Alexandre, Ana F., Andreia, Ana R., Cláudia, David, Filipa, Israel, João, Zé, and probably a few others I don't remember, for their help and company. Two persons deserve special mention because they also helped me collecting soil samples in almost 150 different fields, in different occasions: Freek and Catarina.

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*Animals have this in common with each other; unlike humans they appear to spend every minute of every hour of every day of their lives being themselves. A tree-frog (as far as we can ascertain) doesn't wake up in the morning feeling guilty that it was a bad tree-frog, nor does it spend any time wishing it were a wallaby or a crane-fly. It just gets on with the business of being a tree-frog, a job that it does supremely well. We humans, well... we are never content, always guilty, and rarely that good at being what nature asked us to be - Homo sapiens.*

**Stephen Fry in “The Book of Animal Ignorance”**

